Specialization within a shifting habitat mosaic underpins the seasonal abundance of a tropical fish

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**Abstract.** Habitat availability can be a key driver for the distribution and abundance of animals occupying heterogeneous landscapes. How species respond to regular changes in patch habitat structure, however, remains poorly understood, especially within seasonal seascapes. We explored the importance of patch habitat quality for the seasonal population dynamics of a widespread reef fish, *Leptoscarus vaigiensis*, within a shifting mosaic of seaweed patch habitats. Following dietary and behavioral assessments of *L. vaigiensis* microhabitat preferences, we used best subsets model selection to explore the relative importance of seaweed canopy attributes (cover, height, density) and the abundance of putative competitors and predators for explaining regional variations in *L. vaigiensis* density across summer and winter. Dietary analysis (*n* = 53 individuals) and behavioral observations (*n* = 1014) indicated that *L. vaigiensis* are habitat specialists that primarily consume brown seaweeds and prefer areas within patches that have tall (>30 cm height) canopy-forming seaweeds (*Sargassum*, *Sargassopsis*) at low to intermediate densities (1–5 holdfasts per m²). Accordingly, we found seaweed percent cover and canopy height were two of the most powerful predictors for *L. vaigiensis* abundance, with major seasonal shifts in *L. vaigiensis* abundance from summer to winter strongly related to patch-level changes in canopy cover and height. We conclude that patch habitat quality, based upon microhabitat preferences, can be a powerful predictor for the response of species to a seasonally shifting habitat mosaic, and that high-quality patches that provide seasonal refuges should be a focus for spatial conservation and management.

**Key words:** canopy complexity; microhabitat; patch quality; *Sargassum*; seascape; seasonality.

**INTRODUCTION**

Complex linkages exist between the distribution and abundance of a species and the availability of their preferred habitats (Levin 1992, Brown et al. 1995, Hanski 1998). In species occupying heterogeneous landscapes, both theory and empirical evidence suggests their abundance can be a function of patch area and/or isolation (e.g., Moilanen and Hanski 1998, Hensgen et al. 2014, Stier et al. 2014). While landscape ecology predicts that habitat quality can also exert an overriding influence upon patch-level abundances (Morris and Brown 1992, Pickett and Cadenasso 1995), few studies have found empirical support for this prediction in marine ecosystems (e.g., Carr 1994, Wilson et al. 2012, 2014). A key challenge has been determining the indicators...

Fishes play diverse and important roles in marine ecosystems, where they show marked variations in their habitat requirements and specialization (Chittaro 2004, Wilson et al. 2008, Pratchett et al. 2014). For example, some coral reef fishes exclusively depend upon a single coral species for food and shelter, whereas other fishes access a much wider range of resources (Munday 2004, Graham 2007, Wilson et al. 2008). Such differences in resource specialization at the microhabitat scale can translate to population-level responses to changes in habitat quality and quantity (Morris and Brown 1992, Mayor et al. 2009). For instance, disturbances that result in coral loss have led to the local extinction of specialized coral-dwellers and corallivores (Bellwood et al. 2006a, Wilson et al. 2008, Pratchett et al. 2014). While the impacts of such acute habitat loss from stochastic events have been relatively well documented, much less is known about how fishes respond to more predictable habitat changes, such as the seasonal cycles within seaweed patches (Lefèvre and Bellwood 2010, Afeworki et al. 2013, Fulton et al. 2014).

Seaweed meadows are prominent components of coastal seascapes that can support a unique and diverse assemblage of fishes (Chaves et al. 2013, Kobryn et al. 2013, Wilson et al. 2014). Notably, tropical seaweed meadows around the world exhibit dramatic changes in canopy structure across summer and winter seasons (Lefèvre and Bellwood 2010, Afeworki et al. 2013, Fulton et al. 2014). While some evidence suggests these shifts in canopy structure may drive differences in the diversity and abundance of seaweed-associated fishes (e.g., Afeworki et al. 2013, Chaves et al. 2013, Wilson et al. 2014), species-specific responses to seasonal changes in seaweed habitat quality remain poorly understood (Aburto-Oropeza et al. 2007).

We adopt a multiscale approach to assess how seasonal changes in patch quality, defined here as the availability of preferred microhabitats, may influence the distribution and abundance of a widespread tropical reef fish, *Leptoscarus vaigiensis* (Quoy and Gaimard 1824). Focusing upon seaweed patch habitats at Ningaloo, which display complex variations in canopy structure over space and time (Fulton et al. 2014), we aimed to (1) establish the diet and microhabitat preferences of *L. vaigiensis* within seaweed patches, and (2) determine the extent to which these microhabitat preferences explain the regional and seasonal abundance of *L. vaigiensis*. In doing so, we explore key predictions that microhabitat specialization will interact with shifts in patch quality to explain rapid seasonal fluctuations in the abundance of a tropical fish.

**METHODS**

**Study species and location**

*Leptoscarus vaigiensis* is distributed throughout the Indo-Pacific, where they are thought to exclusively occupy seagrass and seaweed habitats (Choat and Randall 1986, Wilson et al. 2010, Gullström et al. 2011) and support subsistence fisheries (Davies et al. 2009, Chong-Seng et al. 2014). *Leptoscarus vaigiensis* is nominally considered a macrophyte browser (Choat and Randall 1986, Hoey et al. 2011, Chong-Seng et al. 2014) within the herbivorous parrotfishes tribe (Scarini) of the family Labridae (Westneat et al. 2014) within the herbivorous parrotfishes tribe (Scarini) of the family Labridae (Westneat and Alfaro 2005). Published estimates (Choat and Randall 1986, Gullström et al. 2011) and our observations (Appendix A) indicate a transition from juvenile to adult in *L. vaigiensis* at around 8 cm total length (TL).

Subtidal regions of Ningaloo lagoon are dominated by patches of stony corals or fleshy seaweeds embedded in a matrix of sand-covered limestone pavement, with very little seagrass habitat (Kobryn et al. 2013). Seaweed-dominated patches are composed of the canopy-forming macroalgae genera *Sargassum* and *Sargassopsis*, with an understory of macroalgae (primarily *Lobophora, Padina*, and *Dictyota*) that becomes apparent when the seasonal growth-decay cycle of *Sargassum* and *Sargassopsis* causes major canopy reductions in winter (Fulton et al. 2014). Our study was conducted within the Coral Bay region, where we surveyed fish and habitat structure within nine seaweed-dominated patches (Sites 1–9) spread across a 10 km length of the Ningaloo lagoon, along with a sand-dominated (i.e., 0% seaweed cover) and four coral-dominated sites (Fig. 1). Seaweed sites were haphazardly selected as discrete patches of similar area (4500–5500 m²)
that spanned a range of seaweed coverage (10–70% of benthic area) within each patch during summer. All sites were of similar depth (2–5 m) and at least 900 m apart. Surveys were conducted during Austral summer (February 2014) and repeated at the same sites during Austral winter (July 2014) to correspond with seasonal peaks and troughs in the seaweed canopy, respectively (Fulton et al. 2014). Sea surface temperatures during our study were typical of the seasonal range for the Coral Bay region (19–29 °C, Fulton et al. 2014).

**Data collection**

Microhabitat preferences of *L. vaigiensis* were assessed through both gut content analysis, and *in situ* visual observations of foraging and sheltering behavior within seaweed patches at Ningaloo. Diet was explored through gut contents analysis of individuals collected during summer (February 2014) at a separate collection site (>600 m away from the other survey sites) with average levels of habitat coverage (39% *Sargassum*/*Sargassopsis*, 27% bare pavement, 14% sand, 10% *Lobophora*, and 10% other macroalgae) similar to our seaweed survey sites. Individual fish were collected in the afternoon, to maximize gut fullness, using barrier nets and hand spears, then euthanized and preserved in an ice-water slurry within an hour and later frozen to preserve diet colors. In the laboratory, gut contents were extracted from the anterior half of the gut and assessed using the random grid method of Bellwood et al. (2006b). This involved spreading gut contents evenly over a Petri dish and overlaying a grid of 100 squares, of which 40 random squares were open to view. Presence (number of open squares where a dietary type present) and relative dominance (number of open squares where a dietary item was most abundant) were quantified for each gut content sample under a dissecting microscope (10–40× magnification). Labroid gut contents tend to be highly processed by pharyngeal jaws, making genus-level dietary identification impracticable, so diet was categorized as: seaweed, calcareous sediment, amorphous organic matter (AOM), and animal matter, with seaweeds further classified according to color (brown, green, red) and structure (foliose or filamentous if apparent, otherwise “thallus”), following Choat et al. (2002).

Behavioral use of seaweed microhabitats by *L. vaigiensis* during foraging were assessed via instantaneous census (Fulton and Bellwood 2002) at two seaweed patch sites (Sites 1 and 2), which

![Figure 1. Location of study at (a) Ningaloo, Western Australia, with (b) sites within the lagoon of the Coral Bay region dominated by either canopy-forming seaweeds, corals or sand.](image)
involved two divers swimming non-overlapping paths through each site and recording for each *L. vaigiensis* individual (or a randomly selected individual within each group) total length (TL), activity (feeding, traveling, or resting), substratum type (pavement, sand, or seaweed genus) immediately below the fish or being fed upon, seaweed canopy height (floating *in situ*) nearest to the individual, and the density of canopy-forming seaweed within a 0.5 × 0.5 m quadrat centered on the point of observation. All observations were made in the morning to minimize time-of-day effects. On arriving to the seaweed patch, the observers waited an initial 5 min before starting microhabitat observations, and then moved slowly through the patches and maintained a minimum distance of 5 m from the target fish to minimize observer effects (Fulton and Bellwood 2002). A total of 1014 independent behavioral observations were collected (~250 per site, per season) and compared against microhabitat availability at the same sites (see below).

Patch-level assessments of fish abundance were made at each site using underwater visual census along six 30 m belt transects to record all *L. vaigiensis*, and other fish that may be putative competitors (macroalgae browsers from the genera *Siganus* and *Naso*; Choat et al. 2002, Vergès et al. 2012) or predators (piscivores from the genera *Cheilinus*, *Cheilodipterus*, *Epinephelus*, *Hologymnosus*, *Labracinus*, *Lutjanus*, *Synodus*, and *Thalassoma*; Connell 1998, Bellwood et al. 2006b, Holmes et al. 2012, Ashworth et al. 2014) of *L. vaigiensis*. Each transect comprised two passes: (1) all fishes greater than and equal to 10 cm TL within a 1 m wide band were recorded first, followed by a (2) return pass to record all fishes less than 10 cm TL within a 1 m wide band. This two-part design has been found to be most effective for estimating fish density within complex habitats (Bellwood and Alcala 1988, Horinouchi et al. 2005). Adjacent transects were at least 5 m apart and run in serial to minimize fish recounts.

Patch-level assessments of habitat availability were made at each site for a range of possible habitat quality measures, including benthic composition, seaweed canopy height, and density of canopy-forming seaweeds (Anderson 1994, Levin and Hay 1996, Wilson et al. 2014). Benthic composition was measured as the distance to nearest 5 cm) occupied along a 10 m line transect by different substratum types (sand, rubble, pavement), coral, and/or seaweed genera. Where canopy-forming seaweed (*Sargassum*, *Sargassopsis*) occurred, canopy height was measured as the vertical distance from the substratum to the top of the floating seaweed canopy (to nearest centimeter) at 2 m intervals along the line transects (n = 6 per transect). The density of canopy-forming seaweeds (number of holdfasts within 0.5 × 0.5 m quadrat) was also measured at the same 2 m intervals along the 10 m line transects.

**Data analysis**

We explored *L. vaigiensis* dietary patterns (across 12 categories) using permutational multivariate analysis of variance (PERMANOVA), performed on square root transformed data compiled into a Bray–Curtis resemblance matrix, with life history stage (juvenile/adult around 8 cm TL) as a fixed factor, followed by graphical presentation of mean proportions of dietary categories consumed. We used the relativized electivity index of Vanderploeg and Scavia (1979) to examine whether *L. vaigiensis* microhabitat use was non-random relative to microhabitat availability. Using our behavioral observations of *L. vaigiensis* and habitat assessments at the same two seaweed sites, we explored microhabitat use in terms of within-patch variations in benthic composition (percent cover of benthos), seaweed canopy height, and density of canopy-forming seaweed. Three categories of benthic composition (canopy-forming seaweed of genera *Sargassum* and *Sargassopsis*, other seaweeds, sand/pavement), four categories of seaweed canopy height (0–10, 11–20, 21–30, >30 cm), and three categories of canopy-forming seaweed holdfast density (0–3, 4–5, >5 holdfasts per 0.25 m²) were used, to ensure there were no zero records in any category for either microhabitat availability or *Leptoscarus* microhabitat use. Electivity indices (Eᵢ) were calculated for each season (summer, winter) and site (Sites 1, 2) using $E_i = \frac{W_i - (1/n)}{W_i + (1/n)}$, where $n$ is the number of microhabitat categories; $W_i$ is the selectivity coefficient for microhabitat category $i$, calculated as $W_i = \frac{r_i/p_i}{\Sigma r_j/p_j}$, where $r_j$ is the proportional use and $p_j$ the proportional availability of the microhabitat category $i$ at each seaweed site during each season. Electivity values of zero indicate random.
use, while above and below zero indicate preference and avoidance, respectively (Lechowicz 1982).

Patch-level differences in fish abundance, seaweed composition, and canopy structure were examined using PERMANOVA with the two factors of site (random) and season (fixed). Fish abundances were converted to the same density for each replicate (individuals 150/m$^2$) by combining counts from the 1 and 5 m transect widths using density conversion factors (Chenal and Thompson 1997, Appendix B). Separate PERMANOVAs were then conducted on resemblance matrices for: (1) $L. vaigiensis$ density, (2) seaweed composition (percent cover of seaweed genera), (3) canopy-forming seaweed structure (cover, height, and density), (4) density of other macroherbivore fish genera, and (5) density of piscivorous fish predator genera. Resemblance matrices were constructed using the modified Gower (base 10) measure for fish densities, and the Bray–Curtis measure on square root transformed data for seaweed composition. Substratum types such as sand, pavement, and coral were omitted from these analyses as they were strongly inversely correlated ($r = -0.9$) with seaweed cover. Three seaweeds ($Actinotricha$, $Asparagopsis$, blue-green algae) were combined in an “other” category due to being recorded only four or less times across all the replicates. Seaweed canopy structure data were normalized to account for the vastly different measurement scales of each variable (cm, percentage of cover, density), and then constructed into a resemblance matrix using Euclidean distances (Anderson et al. 2008). All PERMANOVAS were conducted with permutation of residuals under a reduced model and a maximum of 9999 permutations. To determine which predictor variables were most related to variations in $L. vaigiensis$ density, we used multivariate distance-based linear models and the Akaike information criterion corrected for finite samples (AICc) to conduct a best subsets model selection that considered all possible combinations of predictor variables. The most parsimonious model was chosen as that with the fewest variables within two AICc of the top model, and the relative importance of variables was assessed via the sum of weighted AICc scores (Burnham and Anderson 2002). Variations in $L. vaigiensis$ abundances were visualized for the most parsimonious model using a distance-based redundancy analysis ordination. These analyses were conducted in Primer (version 6.1.12) with Permanova+ (version 1.0.2).

**Results**

$Leptoscarus vaigiensis$ were entirely restricted to seaweed-dominated patches over summer and winter, with nil individuals surveyed in the sand and coral-dominated sites. $Leptoscarus vaigiensis$ gut contents consisted mostly of brown seaweed (predominantly foliose and thallus fragments), followed by AOM and sediment (Fig. 2a), with no significant difference between juveniles and adults (pseudo-$F_{1.53} = 1.15$, $P = 0.33$). However, some subtle differences were apparent in the presence of certain dietary

Fig. 2. Mean composition of juvenile and adult $Leptoscarus vaigiensis$ gut contents in terms of the (a) dominance and (b) presence of amorphous organic matter (AOM), calcareous sediment, animal matter, and seaweed fragments of different color and structure (foliose, filamentous, thallus).
categories (pseudo-\(F_{1,53} = 9.49, P < 0.01\)), such as more animal matter and green filamentous seaweed in juvenile \(L. \ vaigiensis\) gut contents (Fig. 2b). Microhabitat use observations revealed that both adult and juvenile \(L. \ vaigiensis\) not only fed upon brown macroalgae, mostly \(Sargassum\) and \(Sargassopsis\), but also \(Dictyota\), \(Lobophora\), and \(Padina\). Indeed, \(L. \ vaigiensis\) displayed a positive preference for brown canopy-forming seaweeds (\(Sargassum/Sargassopsis\)) during all types of foraging activity over both summer and winter (Fig. 3a). Moreover, \(L. \ vaigiensis\) tended to use areas of a seaweed patch that had taller canopy heights (Fig. 3b), and low to intermediate seaweed canopy densities (Fig. 3c).

Significant differences in \(L. \ vaigiensis\) density and habitat structure were apparent among seaweed sites, which varied in complex ways across summer and winter (Table 1, Fig. 4). While \(L. \ vaigiensis\) mean density (±SE) generally halved from summer (16.6 ± 2.8 ind. 150/m\(^2\)) to winter (8.6 ± 1.6 ind. 150/m\(^2\)), this was not consistent across all seaweed patches, with increases at some sites (Sites 5 and 9) and no change at others (Site 6) from summer to winter (Fig. 4a). Overall means for seaweed canopy cover and canopy heights also tended to drop from summer to winter (36.7% ± 6.6% to 21.5% ± 1.9% and 21.2 ± 2.4 to 15.7 ± 0.5 cm, respectively), but there was little change in mean density of canopy-forming seaweeds (3.8 ± 0.3 to 4.0 ± 0.5 ind. 150/m\(^2\)), and the direction and extent of seasonal changes were highly site-specific (Fig. 4b–d). While there were also significant variations in the density of other macroherbivore and piscivorous fishes among sites, no consistent seasonal effect was evident (Table 1b, c). Accordingly, best subsets model selection indicated that a combination of \(Sargassum\) percent cover, seaweed canopy height, and \(Lobophora\) percent cover provided the best explanation for \(L. \ vaigiensis\) density variation across sites and seasons (Table 2, Fig. 5). In particular, higher densities of \(L. \ vaigiensis\) were associated with the percent cover of \(Sargassum\) and seaweed canopy height (Fig. 5b). Moreover, the magnitude of change in seaweed canopy cover (Fig. 6a) and seaweed canopy height (Fig. 6b) from summer to winter was strongly related to seasonal changes in \(L. \ vaigiensis\) density across the study region.

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**Fig. 3.** Microhabitat elecitivity of *Leptoscarus vaigiensis* toward: (a) substratum composition of canopy-forming seaweeds (*Sargassum, Sargassopsis*), non-canopy seaweeds (e.g., *Lobophora, Dictyota, Padina*), and sand/pavement, (b) seaweed canopy heights (in 10 cm categories), and (c) seaweed canopy densities (in no. holdfasts per m\(^2\) categories), at two sites within the Ningaloo lagoon, during summer and winter seasons. Positive values indicate preference for a microhabitat category (i.e., high use relative to availability), while negative values indicate avoidance.
**Discussion**

Seasonally dynamic patch habitats, such as the seaweed meadows examined here, can create a shifting habitat mosaic to which species can respond according to their habitat preferences and level of specialization (Bormann and Likens 1979, Johnson et al. 1992, Morris and Brown 1992). In *L. vaigiensis*, we find a habitat specialist that occurs exclusively in seaweed meadows at Ningaloo throughout their life history, where they largely consume canopy-forming seaweeds and strongly associate with areas of high seaweed cover and tall canopy heights. Accordingly, these strong microhabitat preferences provided key indicators of habitat quality for *L. vaigiensis* that helped explain pronounced spatial and temporal variations in their patch-level abundance. Our findings reflect the tight links that have been found between habitat availability and fish abundance in seaweed habitats (e.g., Carr 1994, Aburto-Oropeza et al. 2007, Nash et al. 2014, Wilson et al. 2014), and extend this to reveal the profound consequences for a fish population inhabiting a seasonally dynamic seascape. Underpinning these strong relationships was resource specialization, with *L. vaigiensis* both consuming and sheltering within specific seaweed microhabitats. Comparatively, shifts in habitat structure appeared to play a larger role than abundance of potential herbivorous fish competitors, or fish predators.

**Table 1.** Summary of PERMANOVAs comparing the density of (a) *Leptoscarus vaigiensis* juveniles and adults, (b) other macroherbivore fishes, and (c) piscivorous fishes, along with seaweed (d) community composition (percent cover of genera) and (e) canopy structure (percent cover, height and density of canopy-forming seaweeds), during summer and winter at nine seaweed meadows within Ningaloo lagoon. Significant terms (*P* < 0.05) are highlighted in bold font.

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</table>
Such specialization means that *L. vaigiensis*, and the many other species that associate with habitat-forming seaweeds, can be sensitive to seasonal fluctuations in their preferred seaweed canopy structure (Carr 1994, Levin and Hay 1996, Wilson et al. 2014). Consequently, high-quality patches that maintain a high seaweed canopy year-round can provide key winter habitats for these fish, and may be of similar importance as the seasonal patch habitats used by breeding butterflies (Fleishman et al. 2002, Dennis et al. 2003, Flockhart et al. 2015). Only through understanding these consequences of habitat heterogeneity can we develop effective approaches for the spatial management and conservation of patch-dependent species (Turner 1989, Hanski and Thomas 1994, Moilanen and Hanski 1998).

Meadows of canopy-forming seaweeds, which are highly sensitive to both seasonal and stochastic environmental change (Lefèvre and Bellwood 2010, Fulton et al. 2014), are increasingly being recognized as key marine habitats. Seaweed meadows can provide hotspots for new fish recruits, as well as support a range of adult fishes that play important ecosystem functions (Terazono et al. 2012, Chaves et al. 2013, Evans et al. 2014, Wilson et al. 2014). However, as illustrated here and in studies of fish occupying other canopy-forming habitats such as seagrasses (Horinouchi 2007, Gullström et al. 2011, Hensgen et al. 2014), not all patches support similar levels of fish abundance and diversity. In deciphering which patches are high- and low-quality fish habitat, we find that canopy complexity is highly informative at both local and regional scales. Studies spanning seaweed, seagrass, and coral reef habitats have also found canopy complexity to be a key metric to explain differences in fish diversity and abundance at various life history stages (Carr 1994, Almany 2004, Hensgen et al. 2014, Wilson et al. 2014). However, anthropogenic or natural disturbances have illustrated that species can respond in different ways to complex changes in habitat structure (e.g., Carr 1994, Graham 2007, Nash et al. 2014).

Understanding species-specific responses to habitat change requires an appreciation of their multiscale preferences and extent of specialization (Levin 1992, Wilson et al. 2008, Devictor et al. 2010). Species–habitat relationships are inherently scale-dependent according to the different processes that underpin patterns of resource use within a population (Brown et al. 1995, Moilanen and Hanski 1998, Mayor et al. 2009). Accordingly, broad-scale patterns of distribution and abundance can arise from local-scale patterns of microhabitat selection, particularly in habitat specialists (Morris and Brown 1992, Brown et al. 1995, Mayor et al. 2009). Indeed, we found *L. vaigiensis* preferring areas of high seaweed canopy cover and height, and in turn, these two measures of canopy complexity provided some of the strongest translations for their spatial and seasonal abundance. In comparison,
abundances of potential predator and competitor fishes were poor predictors for patch-level variations in *L. vaigiensis*. This aligns with studies of fishes occupying seagrass beds, where predation risk has been found to be relatively unimportant for patch-level variations in fish distribution and abundance (Horinouchi 2007, Horinouchi et al. 2013, Hensgen et al. 2014). In these cases, fish habitat preferences for certain types of canopy structure may override potential predation risk because canopy complexity does not affect the foraging efficiency of piscivorous fishes (Horinouchi et al. 2009). Notably, the response of *L. vaigiensis* to seaweed density was varied among seasons, which is likely due to canopy cover being de-coupled from canopy density throughout the seasonal growth–decay cycle of *Sargassum* (i.e., areas of high percent cover can consist of either a low density of large macroalgae, or a high density of small macroalgae; Fulton et al. 2014).

In identifying which microhabitats underpin the abundance of *L. vaigiensis*, these multiscale measures of habitat quality provide powerful predictors for how these habitat specialists respond to a changing seascape.

Complex variations in seaweed canopy structure over the study period created a “shifting mosaic” of patch habitats at Ningaloo, similar to that seen in other terrestrial and aquatic biomes (Pickett and Cadenasso 1995, Boström et al. 2011, Nash et al. 2014). While changes in *Sargassum* canopy habitat are driven primarily by seasonal fluctuations in sea temperature (Fulton et al. 2014), site-specific responses can arise from fine-scale environmental variation, seaweed recruitment, and competition (Kendrick and Walker 1995, Ferrari et al. 2012). Consequently, we found site-specific variations in seaweed habitat among accounts of high percent cover can consist of either a low density of large macroalgae, or a high density of small macroalgae; Fulton et al. 2014).
and within patches, which provided a shifting mosaic of canopy structures to which fishes may respond (Lefèvre and Bellwood 2010, Afeworki et al. 2013, Wilson et al. 2014). Within this setting, our findings aligned with the predictions of metapopulation theory, in that the changing abundance of *L. vaigiensis* was profoundly linked to the patch-level maintenance or loss of canopy quality (Turner 1989, Pickett and Cadenasso 1995, Moilanen and Hanski 1998). Regardless of whether it is purely habitat selection, asymmetrical recruitment and dispersal, and/or differential mortality that creates seasonal hotspots in abundance (Turner 1989, Johnson et al. 1992, Aburto-Oropeza et al. 2007, Mayor et al. 2009), patches that maintain high-quality canopy structure over summer to winter appeared to be critical for the sustainability of *L. vaigiensis* populations. We
suggest that these patches should be a focal point for the conservation and spatial management of such habitat specialists. Further work exploring inter-annual consistency in this habitat mosaic (i.e., do the same patches maintain high winter canopies each year?), and the concordant response of these habitat-specialist fishes, would be particularly useful (Aburto-Oropeza et al. 2007). Moreover, we see spatially explicit metapopulation modeling as a priority, to unravel the relative importance of dispersal, recruitment and mortality in driving these patch-level variations (Aburto-Oropeza et al. 2007, Berkström et al. 2013, Stier et al. 2014, Flockhart et al. 2015) and assist the adaptive management of species occupying dynamic and complex habitat mosaics.

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