RESEARCH ARTICLE

Context is more important than habitat type in determining use by juvenile fish

Michael Bradley · Ronald Baker · Ivan Nagelkerken · Marcus Sheaves

Abstract

Context Habitat characteristics are often equated with habitat function for animals. However, in heterogeneous landscapes, similar habitat types occur in different environmental contexts. In the marine realm, landscape studies have been confined to particular environments, rather than encompassing entire seascapes, due to incompatible sampling methods required in different situations.

Objectives We examined the interactive structuring effects of local habitat characteristics and environmental context on assemblage composition.

Methods We used a single technique—remote underwater video census—to explore the importance of habitat type (biotic structural components, substrate, and depth) and environmental context (marine vs estuarine) in structuring juvenile fish assemblages throughout an entire coastal region. In this model system, a range of structural habitat types were present in both estuarine and marine contexts.

Results The 1315 video surveys collected show a clear hierarchy in the organisation of juvenile fish communities, with assemblages first distinguished by environmental context, then by habitat type. Marine and estuarine mangroves contained entirely different assemblages, and likewise for rocky reefs and submerged aquatic vegetation. Our results suggest that two functionally different 'seascape nursery' types exist at local scales within a single region, defined by their context.

Conclusions The context of a location can be of greater significance in determining potential habitat function than what habitat-forming biota and substrates are present, and apparently similar habitat types in different contexts may be functionally distinct. These findings have important implications for local-scale management and conservation of juvenile fish habitats, particularly in regard to offsetting and restoration.

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Introduction

Habitat characteristics (such as vegetation type) have long been recognised as the key determinant of animal communities throughout land and seascapes (Southwood 1977). Accordingly, the habitat characteristics of a location have long been equated with the functional role of that habitat for animals. However, ecologists have recently started to examine how context can influence the assemblage of animals found in certain habitats. Physical context (e.g. Bellwood et al. 2002), ecological context (e.g. Laundré et al. 2010), spatial context (e.g. Turner 1989), and temporal context (e.g. Law and Dickman 1998), all modify the way habitats are used by animals. Thus, together, habitat characteristics and contextual factors interact to determine the distribution of animals (Sisk et al. 1997). Local habitat characteristics tend to be consistently important predictors of animal presence, while contextual factors are usually only important when considered in combination with local habitat characteristics, and their importance tends to vary according to the taxa and system under investigation (Atauri and de Lucio 2001; Mazerolle and Villard 1999). Understanding both the relative importance of these factors, and how they interact, is essential for understanding how animals are causally linked to their environment, and how they might respond to change.

For some systems and taxa, we still do not have a systematic understanding of how contextual and local habitat factors interact to determine the distribution of animals. On many coasts, a suite of similar habitat types are present across a patchwork of marine and estuarine contexts, often in quite close proximity. Seagrass meadows, for example, can occur anywhere from enclosed low-salinity swamps to the seabed of the continental shelf, including bays and reefs in between (Carruthers et al. 2007). Studies have rarely explicitly tried to encompass the full breadth of variation present in these contextually heterogeneous regions, despite the fact that many fauna have the potential to use both marine and estuarine environments (Able 2005). This raises the question: do

animals relate to these habitats across their full range, or are their habitat relationships context dependent? And, if so, how do habitat characteristics and contextual factors interact to determine assemblages in these regions? This remains a large and critical gap in our understanding (Faunce and Layman 2009; Sheaves 2017).

For juvenile fish, developing a detailed understanding of habitat relationships in these regions is particularly important. The juvenile phase in the life cycle can be a critical population bottleneck (Chambers and Trippel 2012) and during this period, growth and mortality can be mediated by habitat (Tupper and Boutilier 1997). This can lead to complex habitat requirements. A common Caribbean reef fish, *Haemulon flavolineatum,* shifts between rubble, seagrass, mangroves and boulders to optimise survival and growth during its juvenile phase (Grol et al. 2014). Accordingly, the availability of appropriate juvenile habitats can have strong impacts on populations of adults (Nagelkerken et al. 2017). Knowledge of habitat use by juvenile fish is used to assign functional nursery roles to particular habitat types, such as mangroves or saltmarsh (Whitfield 2017). Thus, knowledge of habitat use by juvenile fish underpins efforts to conserve species and sustain fishery production (Crowder et al. 2000; Nagelkerken et al. 2012).

Until now, our ability to understand fish habitat use along many coastlines has been hindered by a lack of comparable methods. On coastlines with significant terrestrial run-off, fish communities are typically investigated using a range of non-comparable techniques. Traditionally, marine habitats have been surveyed using visual census by divers (Barnes et al. 2012). The disturbance associated with divers often triggers a flight response in fish, so in more turbid areas, visual census by divers is inviable because the flight distance can often be greater than the range of visibility. In addition, in many estuarine areas diver surveys are not possible because of large predators (e.g. crocodiles). Instead, soft bottom estuarine habitats have been surveyed with trawling methods (Rozas and Minello 1997), and structured estuarine habitats, such as mangroves, have been surveyed indirectly with netting techniques (Sheaves et al. 2012). Consequently, it has been difficult to compare habitat use and assemblage structure both between different habitats types in estuarine environments, and between

estuarine and marine habitats. In these regions, the influence of terrestrial run-off and the different contexts its presence or absence creates, are a considerable source of potential variability in habitat use (Kimirei et al. 2015; Whitfield and Pattrick 2015).

In this study, we use a single technique, low disturbance remote underwater video census, to characterise juvenile habitat use throughout the full range of shallow habitats available in a region, in both marine and estuarine contexts. The development of affordable, high quality underwater video units has been a major break-through in overcoming the problem of fish flight response in limited visibility situations (Sheaves et al. 2016), enabling ecologists to accurately define fish-habitat relationships in a range of inaccessible and challenging environments (Cappo et al. 2003; Bradley et al. 2017). This technology allowed us to directly compare juvenile fish habitat use across different habitats and contexts for the first time. Our study area provided natural experimental conditions with a diversity of structural habitat types present in both estuarine and marine areas. We used machine-learning analysis to observe non-linear relationships and complex interactive effects between factors. Here, we examine how local habitat characteristics and context contribute to the organisation of assemblages throughout an entire region, to understand the interplay of these two factors in heterogeneous coastal environments.

Materials and methods

Study site

Sampling was carried out between 2012 and 2015 in the Hinchinbrook region (18°S, 146°E), off north-eastern Australia (Fig. 1), which encompasses areas of the mainland, as well as Hinchinbrook Island and the Palm Islands. Hinchinbrook Island lies adjacent to the mainland separated by a channel which contains a diverse mosaic of habitats. Terrestrial run-off from two rivers and many small creeks produce seasonal and daily variations in salinity (Wolanski et al. 1990). This large estuarine channel consists of mangrove forest, intertidal sand and mud flats, and sub-tidal rocky boulder fields, biogenic soft bottom and vegetated habitats (Alongi et al. 1998; Bradley et al. 2017). By contrast, the eastern coast of Hinchinbrook island

(i.e. ocean-facing side) is composed of extensive sandy flats, smaller creeks, as well as non-estuarine bays and fringing coral reefs. The Palm Islands lie 15 km offshore, and do not experience significant variations in salinity. This near-shore complex of 10 continental islands, contains a diverse mix of intertidal mangrove forest, reef flat with areas of live coral, rubble, seagrass, macro-algae and unvegetated sand, subtidal boulder fields, and extensive fringing coral reefs.

The study region contains almost the entire breadth of coastal and nearshore benthic habitats commonly available to fish species in north-eastern Australia (Sheaves 2009), allowing the diversity of habitat variation to be encompassed without confounding among-habitat differences with faunal differences among regions. Accordingly, any differences in species-specific juvenile presence between habitat types can be more reliably attributed to physical, geomorphic and biological factors at the habitat patch scale, rather than at the oceanographic scale, and are not due to latitudinal or climatic differences in species distributions.

Video sampling

We sampled juvenile fish assemblages with unbaited video point census surveys, which provided 1315 samples for analysis. This study builds directly on Bradley et al. (2017), and the methods described therein. The high replication technique used is particularly suitable for defining fish-habitat relationships, as predictor and response variables are captured at the same spatio-temporal scale (Hannah and Blume 2012). Each sample consisted of 15 min of continuous undisturbed video recording; periods of disturbed sediment and boat presence immediately following deployment were discarded, and > 100 m between camera and vessel was maintained during recording. The camera was orientated horizontally at an angle of 0° and a field of view of 130°, positioned at a height of 10 cm relative to the substratum. A patterned plastic strip was fixed 0.5 m from the lens in the camera's field of view to provide a standard measure of water clarity. Potential biases due to water clarity were reduced by only including videos above a minimum threshold of 0.5 m (i.e. when the patterns on the strip were visible). As baited cameras would attract fish from surrounding areas, our deployments were
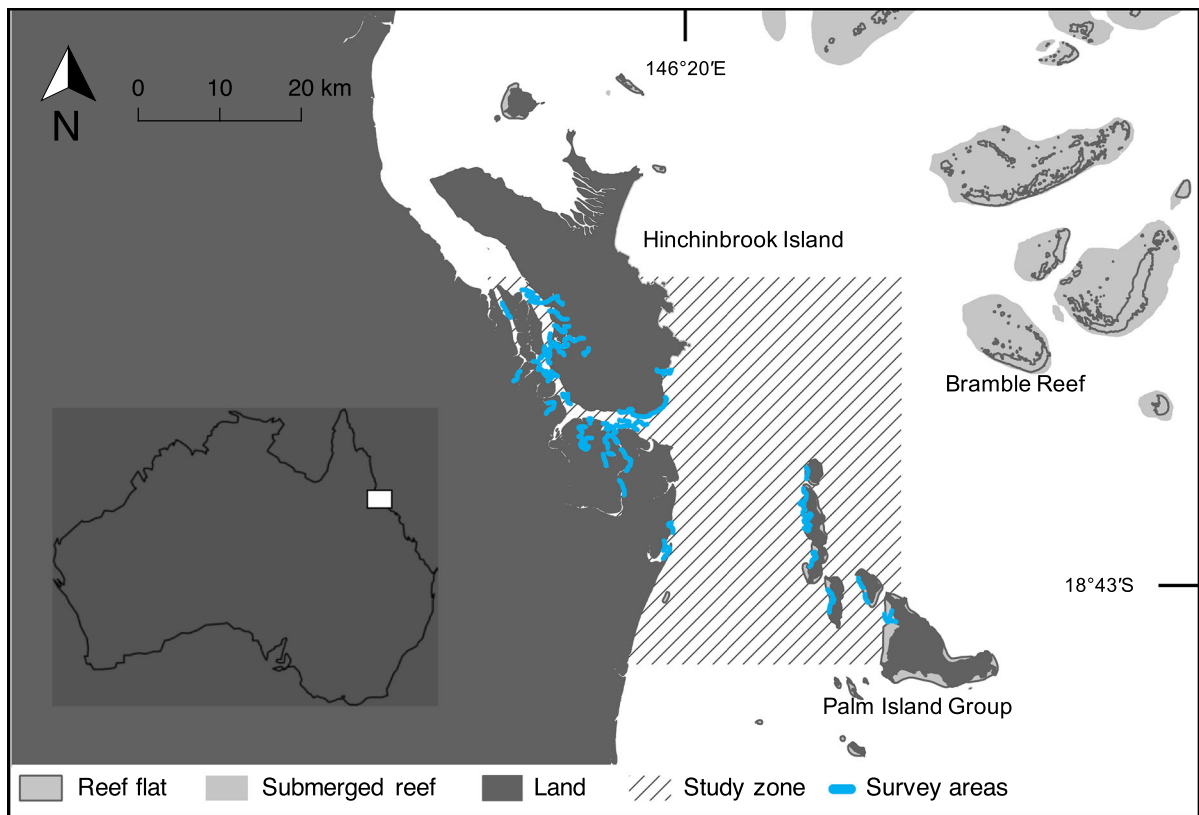
Fig. 1 Location of the Hinchinbrook/Palm Islands region in North Eastern Australia, and the areas covered by video point census surveys

unbaited. This provided a point census of fish taxa present, as well as biological and structural habitat characteristics. We recorded fish species presence, and measured species abundance using the maximum number of individuals seen within the field of view in any single video recording frame (30 frames per second) over the 15 min sample (MaxN), to avoid multiple counts of the same individuals (sensu Harvey et al. 2007).

We determined substrate texture and dominant biotic habitat for each video sample, based on a visual estimate of what occupied the greatest percentage area visible in the field of view. Our classification scheme (Table 1) is a simplification of Ball et al. (2006), and resulted in 20 different combinations of substrate and biota found throughout the region—giving us 20 putative habitat types, of which some were commonly found, and others only rarely encountered (Supplementary material Appendix 1, Table A1). By partitioning habitat characteristics

finely, we could observe the combination of characteristics that juvenile fish actually responded to in our subsequent analyses. The water depth of every video deployment was determined by acoustic depth sounder. We distinguished estuarine from marine areas based on regular periodic fluctuations in salinity established by previously published research (Wolanski et al. 1990), ground-truthed at the time of video sampling by measuring salinity.

We identified all juvenile fish present in the video sample to the lowest taxonomic level possible. Classification as juveniles was based on juvenile markings, body shape and patterns of shading (Allen 1985; Wilson 1998; Allen et al. 2012; Froese and Pauly 2016), rather than size. For taxa where there were clearly defined visual differences in these characteristics between recently settled individuals (e.g. weeks or months post-settlement) and older juveniles (e.g. years post-settlement), we divided juveniles into 'early' and 'late' phases. Identifications were reviewed by at least two

Table 1 Classification scheme used for determining habitat attributes

Variable	Category	Definition
Substrate texture	Pavement	Consolidated/unbroken rock pavement
	Boulder	Grainsize > 200 mm
	Cobble	Grainsize > 63–200 mm
	Gravel	Grainsize > 2–63 mm
	Sand	Grainsize 0.002–2 mm, composed primarily of sand
	Mud	Grainsize 0.002–2 mm, composed primarily of silt
Dominant biota	Bare	No visually obvious biota
	Seagrass	Members of the following seagrasses genera: *Cymodocea, Halophila, Halodule, Thalassia* and *Zostera*
	Macroalgae	Members of the phyla Ochrophyta and Chlorophyta
	Mangrove	Emergent marine vegetation. In this region, the seaward edges of forests are dominated by the genera *Rhizophora*
	SI	Sessile Invertebrates, including: cnidarian structures, barnacles, soft coral, sponges of the family Tetillidae as well as other unidentified sponges
	Coral	Extensive hard coral cover
	Woody debris	Fallen trees with structurally complex form

Each video sample was classified according to both their substrate texture and dominant biota, resulting in a compound habitat category (e.g. 'mud-mangrove' or 'boulder-macroalgae', see Supplementary material Appendix 1, Table A1)

additional experts to ensure consistent identification. Identifications where consensus could not be reached were assigned to the level of taxonomic grouping (e.g. genus) where consensus was achieved. Several taxa could only be identified to higher taxonomic levels because the characteristics that distinguish some closely related species (e.g. fin ray counts or morphological measurements) could not be distinguished. In assemblage analysis, species were grouped to higher taxonomic levels when less than 80% of individuals could be positively identified to species level. When more than 80% were positively identified, we still only included positively identified individuals in analyses for that species. It was often impossible to identify early juvenile stage individuals in the genera *Siganus* and *Lethrinus* to species level. On the occasions where individuals of these genera swam within close range of the camera, positive identification to species level was possible, based on differences in juvenile markings. It was not possible to identify juveniles for the families Mugillidae, Clupeidae and Gobiidae.

Survey design

Surveys were conducted during daylight hours and periods of relatively low turbidity to ensure conditions appropriate for video sampling. Accordingly, sampling occurred between June and December, outside the North Australian monsoon. The minimum water depth surveyed was 0.5 m, and the maximum water depth surveyed was 10 m. Sampling was carried out during the full breadth of variation in tidal inundation (max. tidal amplitude 3.9 m) both in terms of the tidal cycle (high-low) and tidal periods (springs and neaps). Independence of video samples was maintained by leaving > 20 m between deployments, with cameras usually spaced 50–100 m apart. Efforts were made to sample the entire breadth of habitat variation present in the region. Initially, the study area (Fig. 1) was sampled randomly, with cameras placed at random intervals from the shore, to achieve broad spatial replication. After reviewing the metadata, targeted sampling was performed to boost replication in substrate/biota combinations with low representation, though for some rare combinations of biota and substrate, this could not be achieved (Supplementary material Appendix 1, supplementary methods—survey design). The resulting data set was not completely orthogonal, but it did capture the major variation in habitat across the depth range (0–10 m) throughout the study zone (Supplementary material Appendix 1, Table A1). While the resulting data set is not strictly

stratified, differences in replication between habitat types are representative, and are accounted for by the analytical pathway detailed below.

Statistical analysis

Rather than using our own preconceived classification of nursery habitat types and analysing for differences in assemblage composition between them, we 'let the species tell their own story' (Field et al. 1982). We avoided a priori habitat categories by partitioning habitat characteristics finely, pooling all samples and employing a series of Classification and Regression Tree (CART) analyses. Juvenile presence and assemblage composition is used to identify habitat qualities that juveniles relate to, which is then used to define juvenile habitat types in an empirical way.

While all available habitats were surveyed extensively, samples from coral habitats were not pooled with the other data in our tree analyses, as coral habitat is known juvenile habitat for many reef fish species that do not utilise other potential coastal nursery habitats surveyed in this study (Dorenbosch et al. 2005; Honda et al. 2013). Following the classification used by Kimirei et al. (2011), we pooled shallow coral habitat from the crest, flat, and back-reef, and deeper coral habitat from the reef slope. As we were only interested in seeing if coral was an important juvenile habitat for those species using other juvenile habitats, for simplicity only species that had been encountered in other habitats as well are presented. The results of these reef surveys are presented alongside the results from the non-coral nursery habitats identified in the following analyses for comparison.

Firstly, to broadly examine the use of different habitats by juvenile fish, each video sample was given a binary classification according to whether any juveniles of any species were present (1) or not (0). Univariate classification tree analysis was performed using the 'party' package in R (Hothorn et al. 2010), with habitat characteristics (a single identifier combining dominant biota and substrate texture—see Table 1.) as the predictor variable. The resulting tree presents the significant differences in the data set based solely on habitat, and the p-values associated with each split. This allowed us to distinguish the habitat types where juveniles were usually present (juveniles found in > 70% of samples) from the habitat types where juveniles were usually absent

(juveniles found in < 30% of samples), regardless of their estuarine or marine context.

Secondly, of the habitats where juveniles were usually present, we sought to determine which predictor variables were linked to differences in juvenile fish species composition by using multivariate regression tree analysis. The univariate tree had identified several habitat categories where, throughout the region, regardless of estuarine or marine context, juveniles were usually absent (juveniles found in < 30% of samples). Multivariate distance measures tend to behave erratically when many sparse samples are included in analysis (Clarke et al. 2006). Habitat types where less than 30% of samples contained juveniles were excluded, to allow the multivariate analysis to identify patterns of juvenile presence rather than being overwhelmed by zeros due to species absences. The data for these excluded habitat types is presented along with the juvenile habitat types for comparison (Supplementary material Appendix 1, Table A2). For the same reasons, we removed all videos where no juveniles were present, and we ran the tree analysis using three different arbitrary decision rules to eliminate rare taxa: excluding taxa that occurred in < 3%, < 5% and < 10% of samples. The same tree structure was returned for all three decision rules, indicating the structure was robust to all species that occur in > 3% of samples. This is the final tree presented (Fig. 3a). The multivariate regression tree analysis was performed with Bray–Curtis dissimilarity as the distance measure, using the mvpart package in R (De'ath 2007; Ouellette and Legendre 2012).

Based on the predictors that best explained both juvenile presence and species composition, we defined six functionally different juvenile habitat categories (each of which combine several of the original finely partitioned habitat categories): shallow estuarine rocky reef, deep estuarine rocky reef, estuarine mangroves and woody debris, marine rocky reef, marine seagrass and macroalgae, and marine mangroves. Each category is defined by a distinct juvenile fish assemblage (Fig. 3b). For each juvenile habitat defined we present presence/absence information for all species and life stages identified (Supplementary material Appendix 1, Table A2). To examine differences in habitat use for common fish species, we calculated the individual probability of encountering each of the 16 most frequently encountered juvenile

species in our data set (determined by presence, summed and ranked across all samples), in each juvenile habitat based on all data. We used approximate Bayesian computation in R to estimate the probability of encounter for each fish species life stage and estimate the uncertainty around that probability. For those common taxa where both early and late juvenile stages could be confidently distinguished, relative density was estimated for each juvenile stage in each juvenile habitat type. To estimate relative density, CPUE (MaxN per 15 min video sample) was calculated for each habitat.

Results

Juvenile presence

Juveniles were observed primarily in structurally complex habitat rather than unstructured habitats. The 1254 non-coral fish-habitat video samples were classified into 20 different combinations of substrate texture and dominant biota during video analysis. Of these putative habitat types, four were identified in univariate tree analysis (based on presence/absence of any juveniles) as having consistently low occurrences of juveniles (< 30% of samples) regardless of depth and marine or estuarine context (Fig. 2). In three open bottom habitats (bare gravel, mud and sand) juvenile encounter was extremely rare (5.0%). In seagrass beds with muddy substrate, juvenile encounter was also low (28.6% presence). Assemblage analysis was then
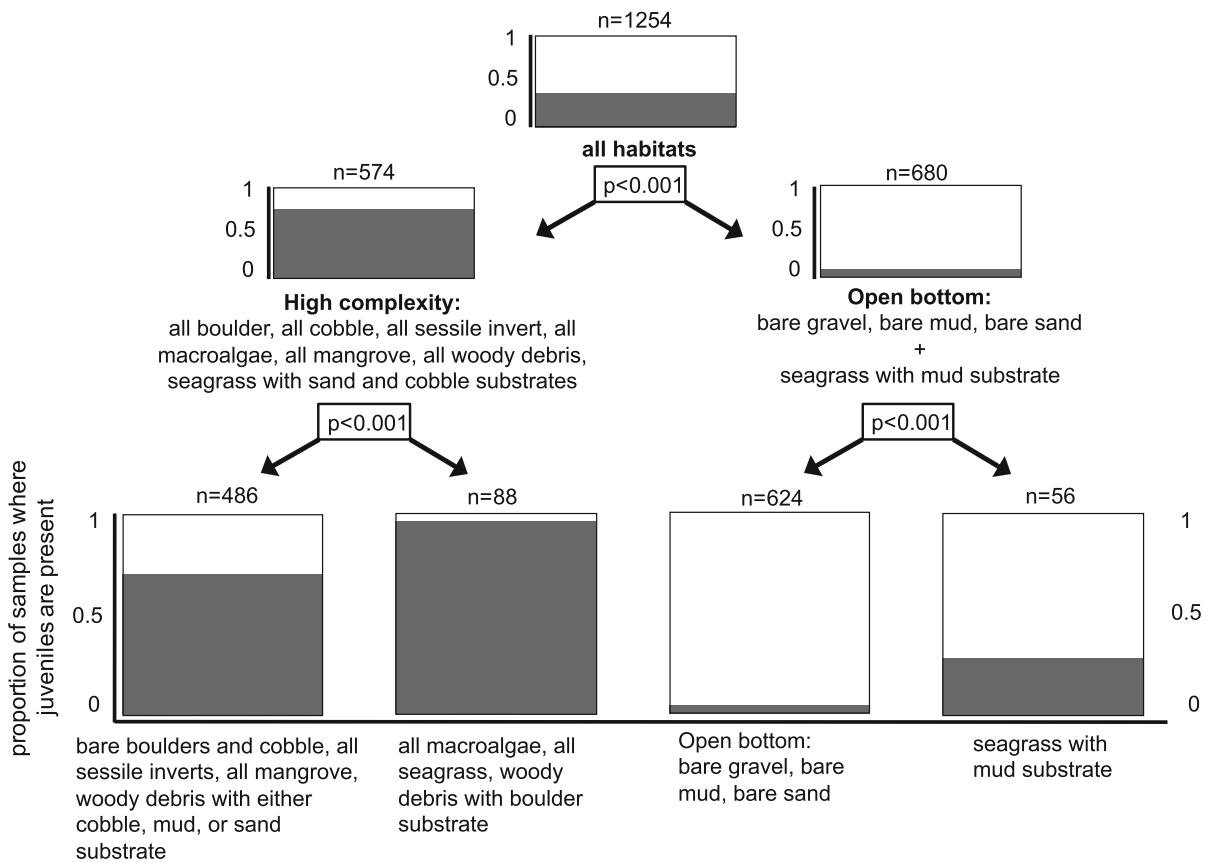

Fig. 2 Univariate classification tree of the presence or absence of juvenile fish, performed on all non-coral samples (n = 1254). Each division is labelled with the variable used in the split, the result of the significance test of the difference between the two groups separated by the split, and on either side of this label, the categories separated by the split. Black bars indicate the proportion of samples where juveniles were present in each terminal node. See Table 1 for explanation of habitat categories

performed on the remaining samples containing juveniles (n = 417 video samples) from the 16 other putative habitat types where juvenile encounters were more common (> 70%).

Juvenile assemblage composition

Multivariate analysis of fish assemblage composition showed a clear hierarchy in the organisation of juvenile fish communities, with assemblages being first distinguished by environmental context, and then by habitat type, lumping the 16 different combinations of habitat characteristics into six functionally dissimilar juvenile habitats (Fig. 3a): shallow estuarine rocky reef, deep estuarine rocky reef, estuarine mangroves and woody debris, marine seagrass and macroalgae, marine rocky reef, and marine mangroves.

Multivariate regression tree analysis of video samples separated those from marine environments and those from estuarine environments (Fig. 3a). Within these two environmental contexts, samples were split based on habitat attributes; however, the particular habitat attributes that made up important juvenile habitat differed between the two contexts (Fig. 3a). Within estuarine contexts, the fish assemblage varied most between rocky habitats and mangrove or woody debris habitats, and the assemblage in rocky habitats also varied according to depth. Rocky habitats included samples that were bare, as well as those from rocky substrates with seagrass, macroalgae, and encrusting sessile invertebrates as their dominant biota. Within marine environments, the assemblage varied most between sandy mangroves and all other structured habitat, which then differed based on either the presence of submerged aquatic vegetation (seagrass and macroalgae), or rocky substrate. This last node included both bare rocky substrates, and rocky substrates with mangroves. The major difference in assemblage structure between the two salinity contexts is clearly illustrated by the probability of encounter of individual species among habitats across the seascape (Fig. 3b). A set of taxa were only found as juveniles within estuarine contexts, including species from the families Lutjanidae, Labridae and Sparidae. Another set of juveniles were found across both estuarine and marine contexts, but were more frequently encountered in marine habitats. This included species from the families Carrangidae,

Fig. 3 a Multivariate regression tree showing the major ▶ divisions in juvenile assemblage composition throughout the region. Analysis was performed on all samples from the 16 putative habitat types where juvenile encounters were > 70%, excluding those samples where no juveniles were present (n = 417). Each division is labelled with the factor used in the split and the set of categories or values that are separated by the split. The distance of descending branches in the dendrogram is proportional to the difference between groups. b Approximate Bayesian computation was used to estimate both the probability of encounter for each fish species life stage and the uncertainty around that probability. Histograms below each terminal node show probability of encounter with 95% confidence intervals for the 16 most commonly encountered juvenile taxa in shallow habitats of the Hinchinbrook/Palm Islands region. As histograms show modelled presences, error bars are sometimes visible even when there were no recorded occurrences—an encounter rate of zero in the data set does not necessarily mean a zero probability of encounter. Back and fore reef habitats are also displayed in this figure for comparison, though they were not included in the CART analysis. Taxa are ordered according to their presence in the six habitats (grey shading): species in the first 6 rows are only present in the three estuarine habitats, the second group (rows 7-13) are present in both the estuarine habitats and the marine habitats, and the third group (rows 14-21) are only present in the marine habitats. *JP* (entire) Juvenile Phase, *EJP* Early Juvenile Phase, *LJP* Late Juvenile Phase

Lethrinidae, Lutjanidae, Nemipteridae and Siganidae. A third set of taxa were only found in marine contexts, and included species from the families/sub-families Labridae, Lutjanidae, Mullidae, Pomacentridae, Scarinae and Terapontidae.

Locations with the same habitat characteristics harboured a completely different set of species depending on the marine or estuarine context in which they were found. Estuarine mangroves contained an entirely different assemblage to marine mangroves, and likewise for rocky reefs, and submerged aquatic vegetation.

Habitat use patterns of early vs. late juveniles

Of taxa that were encountered in > 3% of total samples, where both early and late juvenile phases could be identified, habitat use patterns were often different according to juvenile phase, but remained within either an estuarine or marine context (Fig. 4). In general, early juvenile stages mostly occupied a single habitat type, and were found infrequently in other habitat types. By contrast, late juvenile stages were frequently encountered in 2-4 habitat types. In
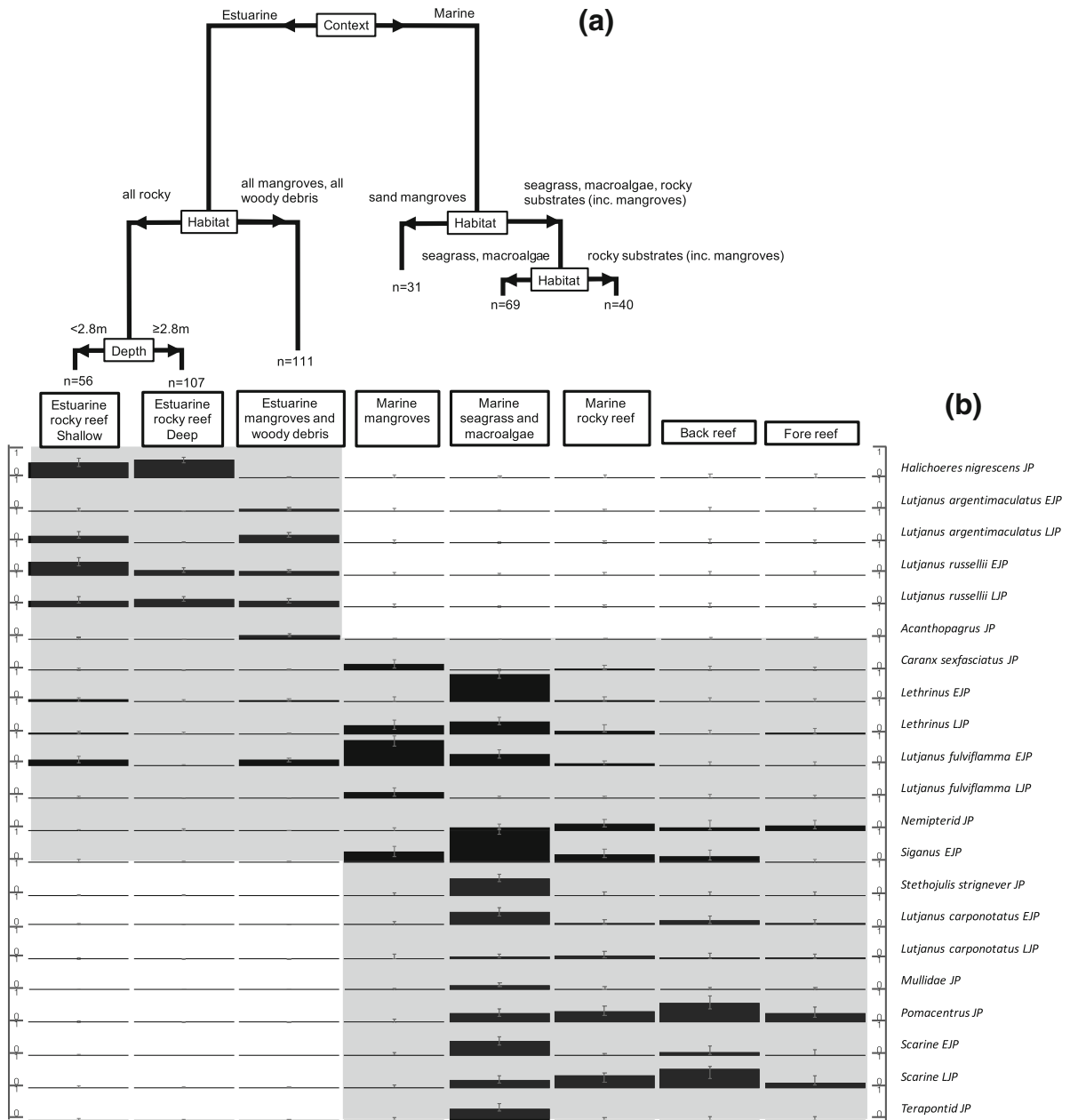
the marine environment, there was a trend of early juveniles in macroalgae and seagrass vegetated habitat, and late juveniles in the mangroves, rocky reef and back reef habitats. One exception to both these patterns is *Lutjanus fulviflamma*, which is found as an early juvenile in areas of both estuarine and marine salinities, and is found as a late juvenile almost exclusively in a single habitat type—marine mangroves.

Discussion

For juvenile fish in our study, the context of a structured habitat—in this case, whether it was in an
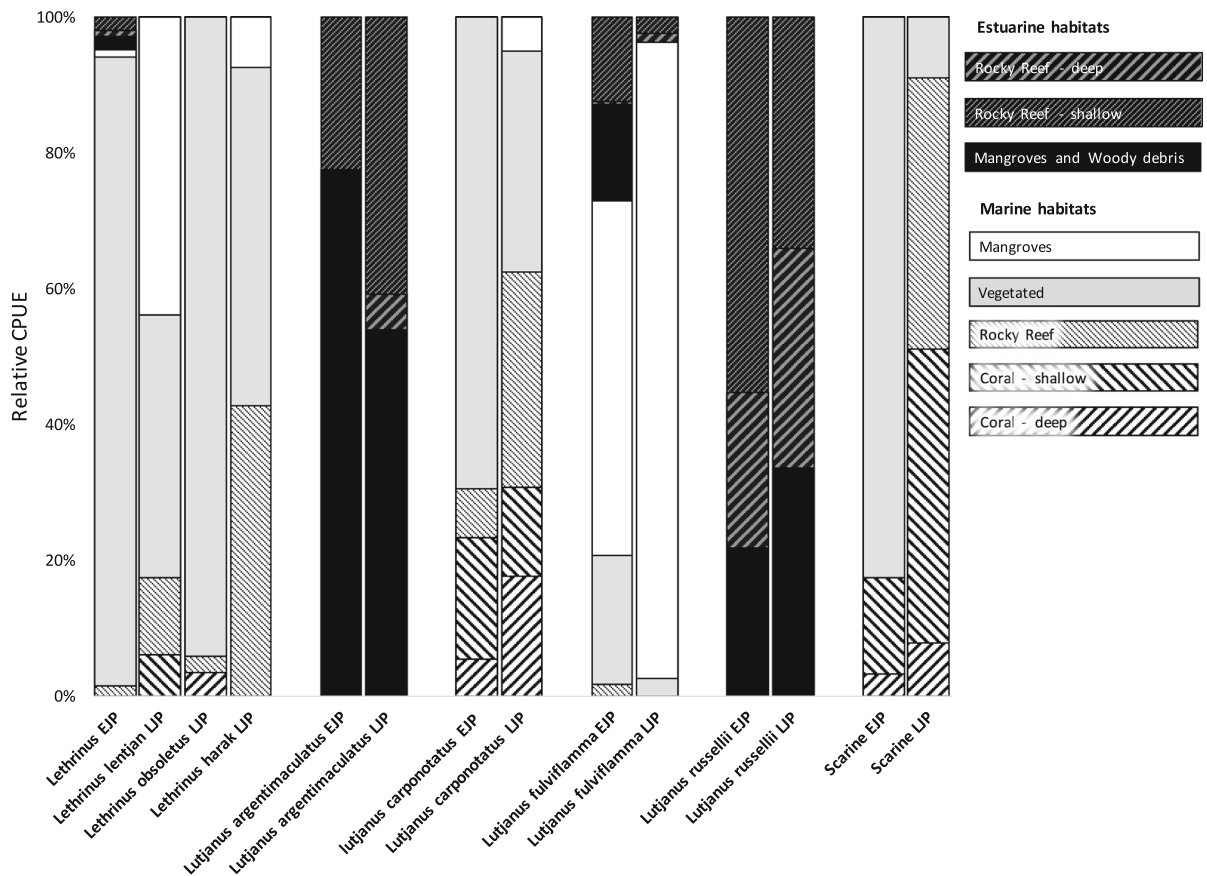
Fig. 4 Overall habitat use patterns for different juvenile life-stages (*EJP* Early Juvenile Phase, *LJP* Late Juvenile Phase) of Lethrinids, Scarines, *Lutjanus carponotatus, Lutjanus fulviflamma, Lutjanus argentimaculatus,* and *Lutjanus russellii.* For the Lethrinids, 'Lethrinus EJP' includes all Lethrinus early juveniles—both those individuals that could be identified to species level and those that could not-including but therefore not limited to *Lethrinus atkinsoni, Lethrinus genivittatus, Lethrinus nebulosus, Lethrinus obsoletus, Lethrinus harak,* and *Lethrinus virgatus.* For the Scarines, early juveniles could not be distinguished to species level aside from individuals of the species *Leptoscarus vaigiensis,* and late juveniles could not be distinguished to species level aside from individuals of the species *Scarus rivulatus*

estuarine or marine area—was more important than the characteristics of that structured habitat—for instance, whether it was a mangrove forest or a rocky reef. Apparently similar habitat types appear to function as a juvenile habitat for a completely different set of species depending on the marine or estuarine context in which they are found. This provides clear evidence of the over-riding importance of context-dependency in animal-habitat relationships of the coastal zone. Our study demonstrates that habitat types should not be treated as homogenous units, and need to be defined by their environmental context before their habitat functions can be evaluated and predicted.

Mangroves

The *Rhizophora*-dominated mangrove forests of our study area may have a very similar intertidal structural appearance in estuarine and marine waters, but are used by a different set of juvenile fauna. In estuarine environments, mangroves and woody debris appear to function as similar habitat. As far as juvenile fish are concerned, long after a tree has perished, its structural qualities can provide valuable subtidal habitat (Nagelkerken and Faunce 2008). This complex of living and dead trees serve as the predominant juvenile habitat for a range of coastal and reef species. These include important fisheries species such as *Acanthopagrus pacificus, A. australis, Lutjanus*

argentimaculatus, *L. russellii, Epinephelus coioides* and *E. malabaricus*. By contrast, sandy mangroves in marine environments appear to function mainly as habitat for juvenile trevally, reef snapper and emperors. While juvenile fish were frequently encountered there, marine mangroves were the predominant juvenile habitat for only two species, *Lutjanus fulviflamma* and *Caranx sexfasciatus*. Marine mangroves on rocky substrates appear to function as an extension of other rocky reef habitat (discussed below). The habitat value of mangroves elsewhere also appears to be defined by estuarine or marine context (Igulu et al. 2014). In Florida, distinct fish assemblages are associated with mangrove prop-root habitat according to estuarine influence, with juvenile Lutjanids and Haemulids occurring in near-marine salinity mangroves, and more estuarine taxa predominating upstream (Ley et al. 1999). In the case of the goliath grouper *Epinephelus itajara*, large differences in density, home ranges size and growth were found between estuarine and marine contexts (Koenig et al. 2007), indicating serious fitness differences between contexts. Apparently, context greatly modifies the habitat function of mangroves for juveniles.

Submerged aquatic vegetation

Vegetated soft substrates in marine environments were found to be juvenile habitat for coral reef fish, supporting the most diverse assemblage of juveniles of any habitat surveyed. Importantly, this included both seagrass and macro-algal habitats, which were found in multivariate analysis to be indistinguishable in terms of juvenile assemblage. While seagrass beds are well known juvenile nurseries (Nagelkerken et al. 2000b; Heck et al. 2003), macro-algal beds can also serve a very similar function (Evans et al. 2014; Tano et al. 2017). Very little macroalgae were found in estuarine contexts in our study. Areas of seagrass in estuarine contexts were not commonly used as juvenile habitat. Most juveniles that did use these areas (early juvenile lethrinids, siganids and terapontids) also used marine seagrass and macro-algal beds with much higher rates of encounter. However, a much wider range of terapontid species were found in estuarine seagrass beds, indicating that these beds may serve distinct juvenile habitat functions from marine beds. For seagrass beds, their estuarine or marine context appears to determine both the tendency to

provide a juvenile habitat function and the species of juveniles that utilise them.

Rocky reef

Rocky reef seems to perform completely different juvenile habitat functions depending on the context in which it is found. In marine environments, it was found to be important juvenile habitat for a range of coral reef fishes, with many of the juvenile species found here also present in shallow coral habitat or marine seagrass. Few species were present at higher densities in rocky reef than these alternative habitats. The exceptions being late juvenile *Lutjanus carponotatus*, and early juvenile *Scolopsis lineata*. In estuarine environments, rocky reef appears to provide important habitat for snappers, particularly early-juvenile *Lutjanus russellii*, and late-juvenile *Lutjanus argentimaculatus*, *L. johnii* and *L. russellii*. Here, shallow rocky reef harbours a greater diversity of juveniles at a greater density than deep rocky reef, which appears to harbour a depauperate assemblage aside from the wrasse *Halichoeres nigrescens* and late juvenile *L. russellii*. Our results show that rocky reef provides juvenile habitat for different species in estuarine and marine contexts.

Habitat linkages—seascape nurseries

Internal consistencies in juvenile habitat use within estuarine and marine areas suggest that two functionally different 'seascape nursery' types exist at local scales within a region. Our study identified two sets of habitat types inhabited by two sets of juvenile fauna; one defined by estuarine conditions and the other by marine conditions. We found almost no cross-over in the species of juveniles using each seascape type; i.e. each had its own characteristic juvenile assemblage. This indicates that these two seascape types function somewhat independently. Within each, juveniles of most taxa used more than one habitat type. This finding suggests that individuals are likely to use multiple habitat types within a seascape. Indeed, most nursery species use multiple habitat types (Nagelkerken et al. 2000a; Nagelkerken 2007) to optimise foraging and refuge throughout diel and tidal cycles (Dorenbosch et al. 2004; Hammerschlag et al. 2010). Furthermore, we found evidence that supported the presence of habitat shifts for some species between

different juvenile stages (in the species where we could confidently identify different juvenile stages). Shifts in habitat use are common during juvenile development (Kimirei et al. 2011) and appear to be driven by trade-offs between food availability and predation risk (Grol et al. 2014). Together, our results suggest that in both estuarine and marine contexts, juveniles use a mosaic of habitats within seascapes (Sheaves et al. 2014). Seascape nurseries like this have been identified around the world—in the Caribbean, many juveniles settle in coral rubble, move to seagrass beds, then switch to the diurnal occupation of mangroves with nocturnal feeding forays in adjacent seagrass beds (Nagelkerken et al. 2015). However, the presence of distinct types of seascape nurseries operating side by side has not been reported. The presence of multiple nursery seascape types may be common in coastal and nearshore environments globally. In South Africa (Whitfield and Pattrick 2015) and Portugal (Prista et al. 2003), different suites of juvenile fish were found to use estuary systems and adjacent coastal areas. In contrast, in the Middle Atlantic Bight, inner continental shelf habitats function interchangeably with estuarine habitats as nursery grounds for common marine fishes (Woodland et al. 2012). Perhaps only particular coastal settings harbor multiple seascape nurseries, where tidal range, rainfall and geomorphology interact to produce the conditions for segregated juvenile communities. At the very least, we can predict that in low rainfall settings this segregation does not tend to occur (e.g. Nagelkerken et al. 2000a), whereas in high rainfall settings it is at least possible (e.g. this study). We have found that multiple kinds of independent seascape nurseries can potentially operate in close proximity, which has strong implications for local-scale management and conservation of juvenile fish habitats.

Key differences between estuarine and marine seascapes

The differences in juvenile habitat use between estuarine and marine contexts are likely due to a range of factors. A myriad of co-varying contextual factors can be encompassed in the contrast between estuarine and marine areas. The factors that determine nursery function, and the thresholds where this function switches from one type to another, is not definable from this study. Terrestrial runoff simultaneously determines a range of factors that can impact fish distribution, such as salinity (Martino and Able 2003), temperature (Attrill and Power 2004), sediment and nutrient loads (Cyrus 1992; DeMartini et al. 2013), and dissolved oxygen (Eby and Crowder 2002). This is necessarily going to affect how fish use habitats in their aquatic landscape (Marshall and Elliott 1998; Zhang et al. 2009). These factors can in turn define the kinds of biotic habitats present in a location, their spatial configuration, and their micro and macro faunal assemblages (Fabricius et al. 2005), determining food availability and predation risk–elements of context that are intrinsically important in nursery value (Kimirei et al. 2015). This illustrates that habitat value can be a dynamic rather than static property. Changes in rainfall and run-off could alter the assemblages of juveniles using particular habitats in a particular location (Valesini et al. 1997). This has implications for future change. Significant changes in terrestrial runoff due to anthropogenic drivers such as climate change or upstream development could alter the habitat function of coastal and nearshore habitats (Santos et al. 2018).

Habitat complexity

For the juveniles identifiable in this study, a prerequisite for a high probability of encounter in surveys appears to be habitat complexity. Areas with complex structure have long been recognised as important nursery habitat (Beck et al. 2001; Laegdsgaard and Johnson 2001; Heck et al. 2003; Gratwicke and Speight 2005). Structure provides interstitial spaces that can be utilised as refuge by small juvenile fishes (Dahlgren and Eggleston 2000), and the size of interstitial space has been effectively linked to the body size of fish that use it (Hixon and Beets 1989, 1993). Our results corroborate studies that have convincingly demonstrated the relative importance of complex habitat through directly comparable sampling between structured and adjacent unstructured areas (Minello and Rozas 2002) and experimental manipulation (Verweij et al. 2006). However, above a minimum threshold, structural complexity is unlikely to be the only factor that distinguishes valuable juvenile habitat (Grol et al. 2011).

Limitations

We measured probability of encounter and relative abundance (MaxN) in different habitats, both of which indicate frequency or commonality of use, and provide a relative measure of density. Although frequency or abundance of juveniles do not necessarily directly relate to nursery value, in a general sense, high densities of juveniles in a habitat are strongly indicative of nursery function (Prista et al. 2003; Whitfield and Pattrick 2015). As habitat use is a necessary precondition of nursery function, this is a logical starting point upon which further research can build. While we have not investigated the range of other measures put forward by authors for determining nursery function, such as contribution to adult populations (Beck et al. 2001; Dahlgren et al. 2006), we see this is a necessary trade off made in order to take a broad look at the factors structuring juvenile habitat use. It is on this basis that the range of Hinchinbrook region coastal habitats have been discussed above.

Our study did not account for temporal variation in a strictly orthogonal way due to constraints on optimal sampling conditions and sampling effort. Seasonal peaks in juvenile recruitment, which may either be over or under represented in our dataset, mean that our rates of encounter for early juvenile stages are unlikely to be truly representative of the entire year. Therefore, we have focused our interpretation on differences in species composition, rather than absolute rates of encounter, and have included even low encounter habitats in our interpretation of juvenile habitat use (Supplementary material Appendix 1, Table A2).

Conclusion

Estuarine and marine areas were used by different juvenile fish, and the habitats found within each area were used in very different ways. Because of this, the habitats occurring in either area should be considered different, even when dominated by the same habitat-forming plants or animals. It is often tacitly assumed that patches of the same habitat type have equivalent ecological roles. These assumptions of equivalence are often employed in ecosystem based species management, the practise of environmental offsetting, and restoration activities. Wherever they are employed, these assumptions can have serious environmental and social consequences if incorrect. The primacy of context dependence in the habitat relationships of juvenile fish in our study complicates these assumptions, implying that a robust understanding of context must be considered before equivalence can be assumed with confidence.

Compliance with ethical standards

Conflicts of interest   The authors declare that they have no conflict of interest.

Ethical approval   This work was conducted with the approval of the JCU Animal Ethics Committee (protocol A2258), and conducted in accordance with DAFF general fisheries permit #168652 and GBRMP permit #CMES63.

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