

Microhabitat use of juvenile coral reef fish in Palau

Victor S. Ticzon · Peter J. Mumby ·
Badi R. Samaniego · Sonia Bejarano-Chavarro ·
Laura T. David

Received: 12 March 2011 / Accepted: 29 March 2012 / Published online: 4 May 2012
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Abstract While relationships between adult fish density and structural habitat features are well established, relatively little is known about the habitat associations of juvenile reef fish. In a reserve system in Palau, we quantified microhabitat association with juvenile reef fish community structure, and determined the influence of foraging space, predator size and confamilial attraction on juvenile and adult pomacentrid abundance. Habitat structure and juvenile reef fish communities differed significantly among microhabitats with one exception: no difference was found between foliose and consolidated rubble microhabitats. Overall, pomacentrids characterised the juvenile community structure of each microhabitat. The abundance of early juvenile pomacentrids is simultaneously determined by microhabitat structure and predator size, with little

evidence for settlement selection near adults. The results also suggest that the influence of habitat structure become weaker with ontogeny which in part, drives large predators to negatively influence the abundance of adult pomacentrids. The results have important implications on management, specifically in prioritizing areas for protection, and in modeling the impacts of habitat loss on reef fish communities.

Keywords Microhabitat complexity · Juvenile reef fish · Foraging space · Predation

Introduction

The early settlement and post-settlement success of organisms is a fundamental aspect of population dynamics for marine organisms (Caley et al. 1996). Events occurring before, during or after settlement on the benthos contribute to the variability and unpredictability of recruitment in coral reef fishes (Hixon and Carr 1997; Caselle 1999; Schmitt and Holbrook 1999; Lecchini 2005; Cowen et al. 2006). It is clear that dynamic interactions exist between habitat structure (i.e., the physical and biological nature of the substratum) and post-recruitment processes such as predation (Jones 1991; Hixon and Beets 1993; Almany 2004a, b; Bonin et al. 2009), social facilitation (Karplus et al. 2006), and antagonistic interactions (Öhman et al. 1998; Letourneour 2000; Buston 2003a). The importance of habitat utilization in

V. S. Ticzon (✉) · L. T. David
Ocean Color and Coastal Oceanography Lab, Marine
Science Institute, University of the Philippines,
Velasquez St., Diliman,
Quezon City 1101, Philippines
e-mail: ticzonvs@yahoo.com

P. J. Mumby · S. Bejarano-Chavarro
Marine Spatial Ecology Lab, School of Biological Sciences,
University of Queensland,
Goddard Building, St. Lucia Campus,
Brisbane QLD4072, Australia

B. R. Samaniego
School of Environmental Science and Management,
University of the Philippines-Los Banos College,
Laguna 4030, Philippines

juvenile fish is shown by the drop in mortality rate from the pelagic settlement stage to recruitment stage (Doherty and Sale 1985; Kaufman et al. 1992; Gutierrez 1998; Almany and Webster 2006). In fact, reef fish recruitment patterns are strongly dependent on the interaction between the physical and biological attributes of a particular habitat, and both adults and juveniles respond to habitat complexity (Sale et al. 1984; Risk 1997; Gutierrez 1998; Nemeth 1998; Lirman 1999; Booth 2002; Holbrook et al. 2002; La Mesa et al. 2002; Almany 2004a, b; Andrews and Anderson 2004; Gratwicke and Speight 2005; Brooks et al. 2007; Cabaitan et al. 2008; Graham et al. 2008; Wilson et al. 2008a, b; Bonin et al. 2009; Wilson et al. 2010).

The structural complexity of coral reefs results, in part, from the size distribution of particular morphotypes of coral. The resulting microhabitats are characterised by complex micro-scale topography and variable shelter (i.e., holes, crevices, overhangs), and create a heterogenous substrate that influences the diversity (Gratwicke and Speight 2005) and density (Andrews and Anderson 2004) of reef fish recruits by dictating shelter characteristics and the availability of other resources, primarily food (Hixon 1991; Risk 1997; Friedlander and Parrish 1998; Almany 2004a, b; Andrews and Anderson 2004; McCormick and Hoey 2004; Gratwicke and Speight 2005). Features of physical complexity mediate the level of competition for food and other resources among recruits (Levin 1994; Bonin et al. 2009), and influence the foraging success of predators (Beukers and Jones 1997; Anderson 2001; Holbrook and Schmitt 2002; Almany 2004a, b) by restricting predator movement or excluding them from shelters with small refuge holes (Gratwicke and Speight 2005). Studies have shown that microhabitats characterised by numerous small shelter holes were least preferred by resident predators (Gratwicke and Speight 2005) and were shown to have higher survivorship of early juvenile reef fish (Beukers and Jones 1997; Almany 2004b). Hence, predator foraging space, or the degree of penetrability or impenetrability of a refuge area to hunting predators, is a critical factor that influenced post-settlement success of juvenile reef fishes.

While there has been extensive literature on the relationship between habitat complexity and adult reef fish, a paucity of information exists on the relationships between microhabitat type and juvenile fish

communities. Possible explanations for this gap include limited attempts to categorize microhabitat types, use of a limited number of metrics to characterize microhabitats, difficulty in field survey, and the consequences of fishing which often affect either the abundance of predators or, in extreme cases, even the abundance of juveniles. Here, we provide an empirical assessment of the microhabitat associations of juvenile reef fish in a high-diversity system of the tropical Pacific, in which there has been minimal human intervention. The study used multiple complexity measures to differentiate microhabitats and compared microhabitat associations of juvenile reef fishes across seven microhabitat types identified in the study area. The study also provides evidence on the importance of predator foraging space and predator size in driving early juvenile abundance of pomacentrids at the microhabitat scale. Limiting this part of the analysis to include only the dominant reef fish family in the study site (i.e., Pomacentrids) better elucidates juvenile reef fish and microhabitat relationships since pomacentrids exhibit strong habitat attachment (Holbrook et al. 2000; Schmitt and Holbrook 2000; Buston 2003a) and a diverse array of habitat association (Allen et al. 2000).

This study aim specifically to (a) differentiate microhabitats in terms of rugosity, shelter opening, and refuge abundance; (b) establish an association (if any) between microhabitat type and juvenile reef fish community structure; and, (c) identify important post-settlement processes at the microhabitat scale. Three hypotheses were tested in the study:

H₁: Microhabitats vary in terms of structural complexity and juvenile reef fish assemblage. The synergistic interaction of coral growth forms, colony arrangement, CaCO₃ deposition, and reef erosion, result in a highly heterogeneous substratum, characterised by complex micro-scale topography and variable shelter (i.e., holes, crevices, overhangs) size and abundance. These features of the microhabitat are important factors considered by reef fish recruits (Öhman et al. 1998; Brooks et al. 2007).

H₂: Resident predators are less likely to be associated with microhabitats that have small foraging space (Gratwicke and Speight 2005) since this will curtail their movement and exclude them from shelter with small refuge holes. Predator

foraging space reflects on the degree of penetrability or impenetrability of a refuge area to hunting predators. In the study, foraging space is the remaining margin in the refuge gap when hunting predators enter the structure.

H₃: Habitat complexity drives early juvenile abundance by mediating predation. Highly complex microhabitats characterised by numerous small shelter holes were shown to have reduced mortality of early juvenile reef fish (Beukers and Jones 1997; Almany 2004b).

Materials and methods

Study area

The study was conducted at Ngederrak Reef in the Republic of Palau, located at 7°16'49.87" N, 134°27'59.51" E to 7°17'40.87" N 134°29'04.45" E. The reef is 2.6 km long, and forms the inner barrier reef of the double barrier reef system in the south-eastern side of Koror (Fig. 1). No fishing is allowed on the reef and the reserve regulations are actively enforced and respected. The reef slopes gently from the reef crest to a sand bottom at a depth of 18 m or deeper. The cemented reef crest is dominated by filamentous algae and low relief tabulate acroporids (diameters 10–20 cm). The rest of the reef area is characterised by spurs of large coral mounds and grooves. The sides of the fossilized mounds are dominated by foliose corals (e.g., *Echinopora* and *Montipora*) growing alongside patches of branching corals (primarily *Acropora*) and, in some areas, with consolidated rubble. Aggregations of branching *Millepora* and *Acropora* cover a significant (35 %) portion of the reef slope surveyed. In 2006, consolidated rubble also covered a significant (40 %) portion of the outer reef slope though the cover of this habitat had declined to 9 % by 2008 and were mostly replaced by branching *Acropora*. Surveys were conducted on the forereef in April 2006 and May 2008. In both survey periods, pomacentrids were the most abundant group of reef fish. Of the 32 fish families recorded, pomacentrids comprised close to 50 % of all fishes observed in the study area.

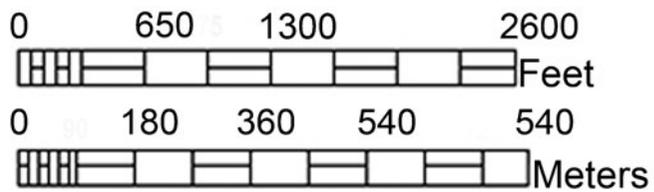
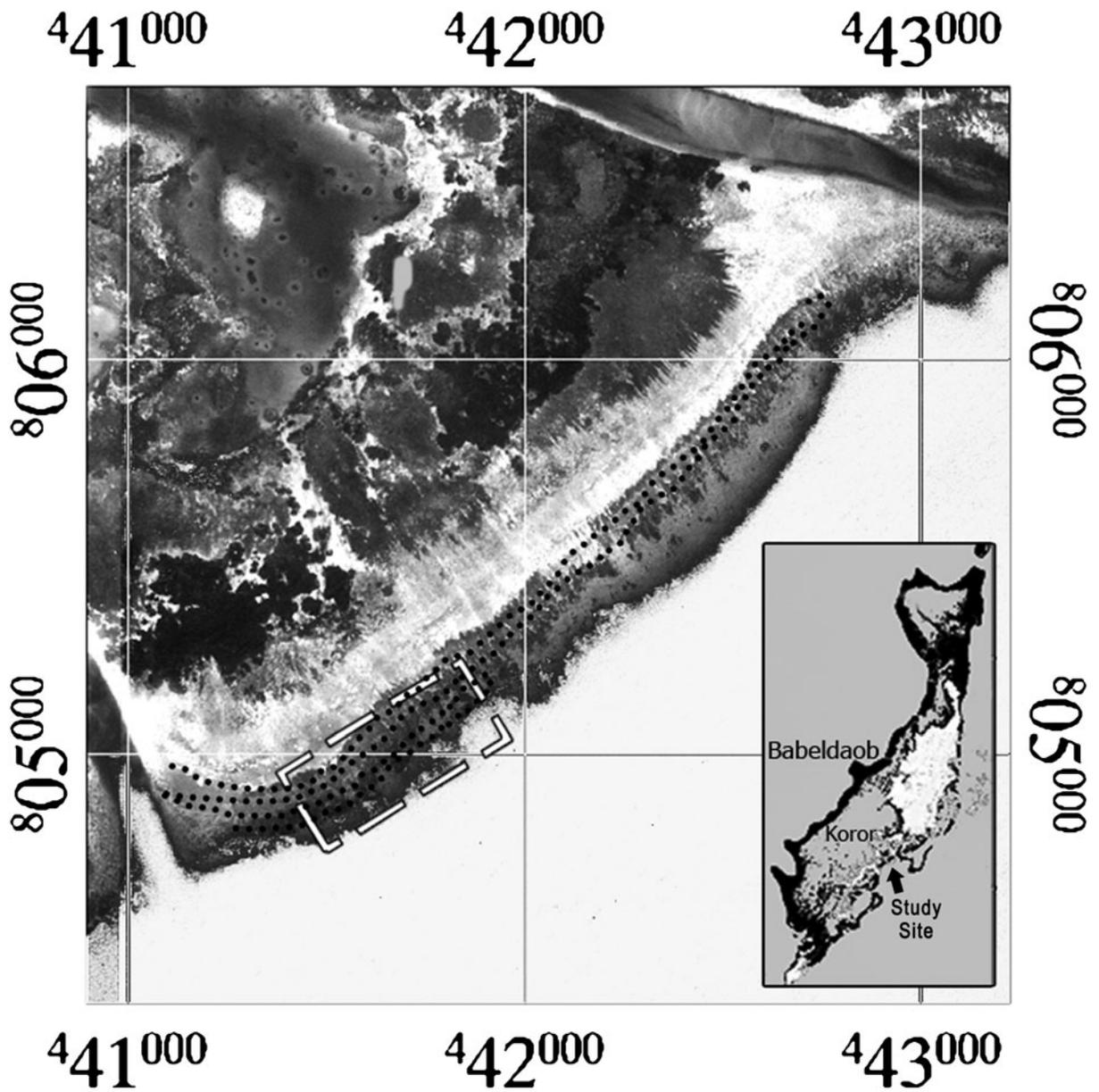
Identification of microhabitat types

Microhabitat types were identified from a reef-wide videotranssect survey and in situ habitat assessment of

Ngederrak reef conducted in the initial stage of the study. The goal was to identify different habitat types that were structurally distinct and with extensive coverage so as not to limit replication. A total of seven microhabitat types were identified on the forereef of Ngederrak (Table 1). A “microhabitat” is defined here as the dominant structural feature within a 5 × 5 m plot. Although previous studies have used “microhabitat” to represent part of the benthos characterised by a single substrate type at much smaller spatial dimensions (Sale et al. 1984; Holbrook and Schmitt 2002), the relative homogeneity of the majority of the sampled plots in the study made it possible to increase the spatial coverage of each microhabitat type. However, in several sampling plots where other structural features were present and could not be excluded (e.g., Sand and Foliose), it was ensured that these other growth forms do not predominate the plots. The spatial dimension used in the study was deemed best for 3 reasons. First, the spatial dimension allows for better characterisation of the physical feature of each microhabitat. Second, the community structure of juvenile reef fish for each microhabitat will be better represented. Lastly, overlaps in resident predator foraging area will be minimized or totally avoided. Foraging area of resident predators is hard to define. However, the absence of predator movement between adjacent microhabitats eliminates possible compounding effect of multiple predation in a particular microhabitat. In the study, the microhabitat was considered as the basic sampling unit and each microhabitat plot served as individual replicate for the analyses.

Field surveys

To elucidate microhabitat association of juvenile reef fish and determine the influence of microhabitat structure and predation on early juvenile abundance, a nested, robust set of microhabitat and reef fish data were analysed. In 2006, microhabitats were delineated from 14 randomly placed 50 m transects. Ten microhabitat plots were placed adjacent to each other in continuous rows along each transect. In 2008, 17 plots were added but sampling for this period was more purposive. Only microhabitats with few replicates for structural characterisation in 2006 (i.e., mostly Foliose and Coarse branching) were surveyed during this sampling period. A minimum 20 m distance was maintained between microhabitats sampled. A total of 157 ($n=140$ in 2006, and $n=17$ in 2008) plots



Map Scale: 1:50,000

Table 1 Microhabitats of Ngederrak reef and the structural features under each category

General microhabitat	Characteristic substrate feature
Fine branching dominated (Fine Branching, Fbr)	60 % to 100 % of the quadrat is covered by fine branching corals mostly <i>Millepora</i>
Coarse branching dominated (Coarse branching, Cbr)	60 % to 100 % of the quadrat is covered by coarse branching <i>Acropora</i> ; some quadrats mixed with corals of different life forms
Foliose dominated (Foliose, CF)	Greater than 50 % foliose cover; some quadrats mixed with massive and/or branching life forms; some mixed with rubble
Consolidated rubble (ConR)	Consolidated rubble covered with sponges and algae; some consolidated rubble area is mixed with 10 % branching forms
Hard Bottom (Hard Bottom, HB)	Coralline pavement interspersed with massive, encrusting and tabulate corals; located in the reef crest and coralline mounds
Rubble (Rubble, Rub)	Loose rubble; some areas mixed with less than 20 % massive and branching forms
Sand (Sand, S)	Predominantly sand with sparse rubble; some areas also mixed with massive and branching forms

classified under seven microhabitats were surveyed for reef fish. However, only 153 were analysed for microhabitat association since four plots were devoid of juvenile reef fish. Benthic parameters of interest were measured in 70 of these plots. It was ensured that sufficient replicates ($n \geq 8$) with rugosity, refuge size measurements and abundance were provided for each microhabitat class (entire plots for rugosity and 1×1 m quadrats for refuge size and abundance). To minimize fish disturbance, fish census was conducted before measurements of benthic complexity were taken.

The presence of resident predators was then determined for the 70 microhabitat plots with measured structural complexities. Resident predators were found in only 43 of these 70 plots. To increase the robustness of the dataset, 11 plots with resident predators and refuge opening measurements were added increasing the total number of samples to 54. However, these additional plots were not included in structural ordination of microhabitats since no rugosity measurements were taken for these samples. Table 2 presents a summary of the total number of 25 m² plots surveyed sampled for each microhabitat type under different tasks.

Except for the Hard Bottom microhabitat which was mostly located on the reef crest, the remaining microhabitats were relatively spread in the study area, within a narrow depth range of 6–10 m of the reef slope. Microhabitat distance from the reef crest

(Shulman 1985) was not considered because of the contiguity of the reef and the relative proximity of the surveyed microhabitats. This eliminates reef fish recruit isolation and possible differences in larval supply as factors affecting recruit abundance in different microhabitats.

Fish census

Fish visual census was conducted in each plot using a technique modified from English et al. (1994). The entire suite of reef fishes was surveyed in each microhabitat plot. Fish were identified to the lowest possible taxon and their abundance quantified by actual counts. The total length of individual fish was estimated and each was categorized as juveniles (approximately 1 to 5 cm) and adults (greater than 5 cm). Juvenile reef fishes were identified based on their color patterns and size. Greater attention was given to juveniles and resident predators during the survey.

The limited movement of resident predators made it easier to associate them to a particular microhabitat and was therefore entered reliably in the analysis. In addition, resident predators have strong negative influence on abundance, at least for sedentary, newly settled reef fishes such as pomacentrids (Holbrook and Schmitt 2002; Almany 2004b). This makes it an important post-settlement factor to consider in the overall picture. In contrast, roving predators were excluded from the analysis primarily because they could not be clearly associated with a particular microhabitat and essentially

◀ **Fig. 1** Location of study area, Ngederrak Reef, Koror State, Republic of Palau. The *white box* shows the approximate extent of the area surveyed. The *black broken lines* represent the videotransect tracks

Table 2 Breakdown of the number of sampled plots per microhabitat type per task

Study tasks	Microhabitat							Total replicates
	Fbr	Cbr	CF	ConR	HB	Rub	S	
Reef fish community assessment	32	20	13	19	20	31	18	153
Microhabitat complexity survey	8	12	10	10	12	9	9	70
Predator foraging space determination	13	9	7	3	5	15	2	54

would constitute a source of variability which could obscure the results. It was assumed that predation pressure by transient piscivores was equally distributed across microhabitats since the plots were all situated in the same reef area. To eliminate inconsistencies, particularly in estimating size of juvenile reef fishes, all fish census was conducted by the same observer for both sampling periods. In each 25 m² plots, the microhabitat type was identified and recorded.

Data on resident predators were examined for possible occurrence of the same individuals on different microhabitats. It is critical that predator movement across habitat types is determined since we are dealing with actual counts of resident predators in the analysis. Body depth of each resident predator was then computed by multiplying the total length estimate of the species with its reported percent body depth (%BD) (Froese and Pauly 2009) divided by 100. Substitute values from other similarly shaped fish were used for species with no published %BD values. For *Paracirrhites forsteri*, and *Cirrhichthys falco*, the %BD of *Cephalopholis urodeta* was used while the %BD of *Thalassoma lunare* was used for *Cheilodipterus artus*, *Cheilodipterus macrodon*, and *Synodus variegatus*.

Microhabitat assessment

Microhabitat complexity was characterised by rugosity, refuge opening dimensions (i.e., length and width of opening), and refuge abundance. These metrics were used as sample factors in differentiating structural complexities among microhabitats.

Rugosity measurement

Rugosity is a common measure of the degree of architectural complexity of an area (Alvarez-Filip et al. 2009). Strictly avoiding overlaps, two to four rugosity measures were derived from randomly selected

sections of the microhabitat. Rugosity was measured using a 2 m metal chain with 0.2 cm link size draped as close as possible over the substrate. A small link chain was used because fine-scale surface heterogeneity has been found to be an important structuring factor in reef fish communities (Nanola et al. 1990). A 2 m metal ruler was then laid proximal to the chain to measure horizontal distance, from which a rugosity index, RI, was calculated as:

$$RI = \frac{\text{Total chain length}}{\text{Total length covered by the chain in a straight distance}}$$

A *Rugosity Index* of 1 indicates that the substrate is flat.

Shelter characteristics

Shelter or refuge areas in the reef are cavities, holes, and spaces between branch networks that are sufficiently deep for juvenile reef fish to utilise as shelters. The dimensions of refuge openings were measured and counted within a randomly selected 1 m² area inside the plots. On site, the 25 m² plots was divided into nine smaller subplots labeled 1 to 9 in zigzag format, starting from the plot in the upper left most corner. The 1 m² quadrat for refuge assessment was placed inside the subplot that corresponds to the randomly generated number obtained before each dive. The longest opening length and width were measured using a flexible metal ruler. Refuge areas with a cross-sectional diameter of less than 1 cm were not considered in the analysis because most juveniles could not access refuge areas that small. Refuge abundance was determined as the total number of holes with a minimum diameter of 1 cm, within the 1 m² area. For branching-dominated microhabitats, a 25 cm × 25 cm plastic plots was laid on top of coral branches and photographed. The gaps between

the branches were measured using the image analysis software, ImageJ.

Data analysis

The use of adjacent 5 m plots along 50 m transects in 2006 required testing for possible autocorrelation between adjacent plots. This was carried out using PRIMER (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley 2006) and a *T*-test (Quinn and Keough 2002). A similarity matrix was generated using the Bray-Curtis similarity coefficient for the fish community structure in each 5 m plot surveyed. For each microhabitat type, the null hypothesis was that the similarity among adjacent plots of the same microhabitat is not systematically different to the similarity among non-adjacent plots of the same microhabitat (i.e., if the null hypothesis was rejected and adjacent plots were more similar to one another than non-adjacent plots then spatial autocorrelation was significant). For each microhabitat type, the comparison of similarity coefficients between adjacent and non-adjacent plots was found to be insignificant, implying that significant spatial autocorrelation was absent at a scale of adjacent 25 m² plots.

Analysis of Similarity (ANOSIM; Clarke 1993) was used to quantify specific differences in habitat structural complexity and reef fish community structure of the different microhabitats. Non-metric multidimensional scaling (nMDS) was performed to show graphically the differences in complexity among microhabitats, while Similarity Percentage (SIMPER) was used to determine juvenile reef fish species responsible for differences in community structure among microhabitats (Clarke and Warwick 2001; Wilson et al. 2008b). ANOSIM and nMDS were also used to establish resident predator and microhabitat associations.

To calculate the foraging space of resident predators, mean microhabitat gap size and mean body depth for each predator species was determined. Foraging space was calculated by subtracting the mean body depth of the resident predator from the mean habitat gap size per microhabitat plots sampled. The foraging space was categorized as being either impenetrable (−8 to 0 cm) or penetrable to predators (Almany 2004a). The *T*-test was used to determine significant differences in mean predator abundance between plots categorised as impenetrable (i.e., where foraging is limited to ambush on the outside or surface of the

habitat) and those that are penetrable. One way analysis of variance (ANOVA) was conducted to determine significant differences in mean predator abundance and to test for variability in resident predator size across microhabitats (Holbrook et al. 2002; La Mesa et al. 2002). In the latter, biomass was used as the response variable, and Box-Cox transformation was performed to normalize the response variable and meet the assumptions of the test. A test for independence using Fisher's exact test (Frederick 1997; Nemeth 1998) was also conducted to determine if there was independence between a predator's ambush habit (i.e., waiting in holes or perched on substrate) and foraging space.

To explain early juvenile abundance of pomacentrids, stepwise multiple regression analyses were conducted using resident predator size, foraging space, and adult pomacentrid abundance as test variables (Friedlander and Parrish 1998; Brooks et al. 2007). Variables were transformed to normalize the data and meet the assumptions of the model. Early juvenile and adult pomacentrid abundance were square root transformed while predator body depth was log transformed. No data transformations were performed on foraging space. Early juveniles are limited to pomacentrids with 1 to 3 cm total length (Van Woessik et al. 2009). Late juveniles (4 to 5 cm total length) were not included in the analysis to obtain a more focused response from early settling pomacentrids. Furthermore, by dropping these intermediate sizes, possible errors from visual estimates between early juveniles and adults were reduced. The degree of influence of foraging space and predator size on adult abundance was also investigated using the same analysis.

Results

Correspondence between microhabitat types and juvenile reef fish assemblage

The overall physical complexity of microhabitats varied strongly and significantly (Global $R=0.66$, $p<0.0001$, $n=70$; Fig. 2). Although seven microhabitat classes were defined on the basis of the dominant physical structure, not all exhibited significant differences in terms of the complexity measures used. Ordination of the complexity metrics led to five

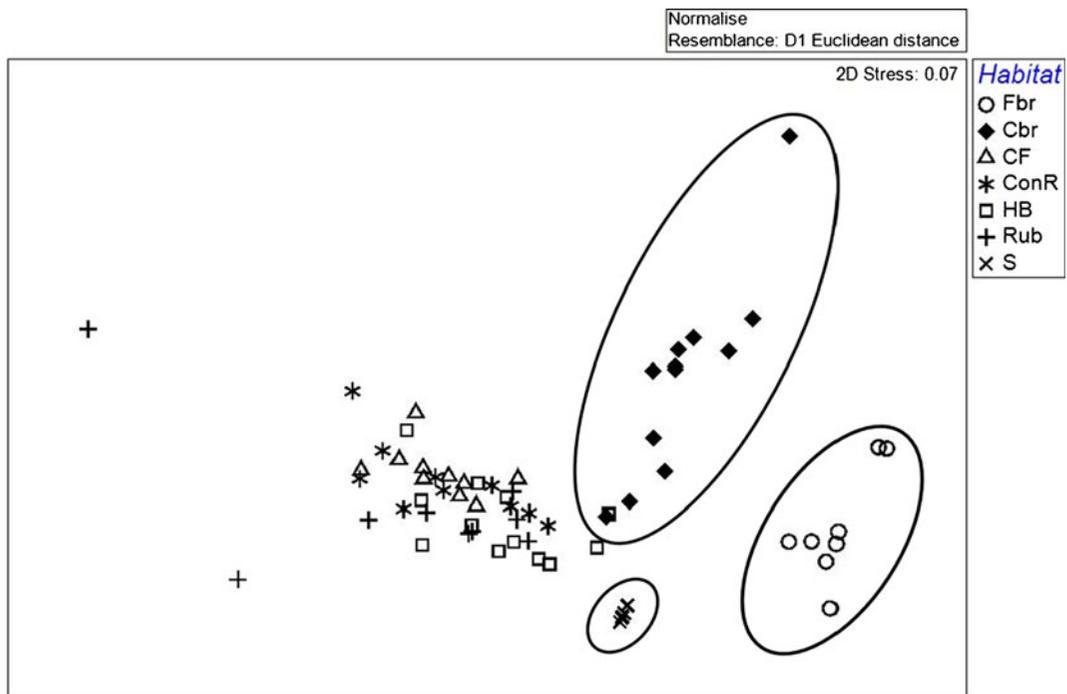


Fig. 2 MDS ordination of microhabitats based on square root transformed habitat complexity measures and Bray-Curtis similarities (Fbr-Fine branching, Cbr-Coarse branching, CF-Foliose,

ConR-Consolidated Rubble, HB-Hard Bottom, Rub-Rubble, and S-Sand). The distance in space reflects the level of dissimilarity between samples. Global $R=0.66$, $p<0.001$, $n=70$

groupings of microhabitats; (1) Fine branching, (2) Coarse branching, (3) Foliose dominated, (4) Sand dominated, and (5) Dead Coralline habitats, which subsumed Hard Bottom, Consolidated Rubble and Rubble. Except for the Foliose microhabitat, which is structurally similar to Consolidated Rubble, live coral-dominated microhabitats remained distinct from Dead Coralline and Sandy microhabitat types.

With the exception of the Foliose and Consolidated Rubble microhabitats, juvenile fish community showed weak to moderate overlaps in species composition among microhabitat types (Global $R=0.26$, $p<0.001$, $n=153$; Table 3). Differences in community structure occurred despite the noted similarities in complexity among the Dead Coralline habitats. Juvenile reef fish community assemblage was most distinct between the two most structurally different microhabitats investigated: the Fine Branching and Sand microhabitats.

The Bray-Curtis dissimilarities among microhabitats were largely attributed to differences in the juvenile composition and abundance of pomacentrids (Table 3). *Pomacentrus moluccensis* (Pom molu),

Chromis ternatensis (Chr tern), and *Chromis viridis* (Chr viri) abound in live coral microhabitats, while *Pomacentrus emarginatus* (Pom emar), *Plectroglyphidodon lacrymatus* (Ple lacr), and *Chromis margaritifer* (Chr marg) distinguished dead coralline microhabitat types. Interestingly, the *Acropora*-associated *Amblyglyphidodon curacao* (Amb cura) (Allen et al. 2000) was found to be strongly associated with the Foliose-dominated and Consolidated Rubble habitat types. Sand microhabitats were characterised primarily by *Pomacentrus amboinensis* (Pom ambo). Although *Dascylus aruanus* (Das arua) was also found to contribute highly in differentiating Sand with Fine Branching and Dead Coralline microhabitats, its association with Sand microhabitat is artificial. *D. aruanus* was strongly associated with branching coral heads of *Acropora* and/or *Pocillopora* enclosed inside several plots sampled for Sand. Although these branching colonies comprise less than 5 % of the predominantly sandy substrate, juvenile *D. aruanus* were found to aggregate on these isolated coral heads. It is important to note that the low abundance, or even absence, of other

high-relief, coral-associated juveniles in the Rubble and Sand habitats also contributed strongly to their significant dissimilarities to live coral habitats.

Resident predators and foraging space

A total of 13 species of resident predators classified under four families were identified in the study (Table 4). The majority of these predators were strongly associated with coral thickets and fossilized structures, utilising branches, structural relief, and crevices for concealment, refuge, and launching areas for ambush. *Cephalopolis urodeta* was the most common resident predator, followed by *Paracirrhites forsteri*, which was found in five of the seven microhabitat types. Close examination of the resident predator data showed the absence of similar sized individuals of the same species in the observed

microhabitats. This supports the notion that resident predators did not move across adjacent microhabitats and that predator movement was restricted within the 25 m² area.

Resident predators had no clear microhabitat association as shown by low Global R (Global $R=0.02$, $p<0.04$; Fig. 3). Surprisingly, the penetrability or impenetrability of the microhabitat foraging space did not influence predator abundance (Fig. 4). It was also hypothesized that perched or hovering predators would be more abundant in microhabitats with zero foraging space, while predators concealed in holes would be more abundant in microhabitats with positive foraging spaces. However, Fisher’s exact test for independence found no difference in the distribution of perched and concealed predators in microhabitats with zero and positive foraging space ($p=0.47$, $n=53$).

Table 3 Matrix showing differences in reef fish juvenile composition and abundance, between the different microhabitats assessed in Ngederrak forereef. R-statistic marked with an asterisk (*) indicate significant variations in refuge features between the microhabitat pair. Included in each cell are the top contributors to recruit community dissimilarity (%) between microhabitats compared. Black highlights indicate higher average abundance of the species in the column microhabitats. Shades of gray indicate higher average abundance of the species

in the row microhabitats. The abundance of the following pomacentrids dictate the difference in community structure of juvenile reef fish across microhabitat types: *Amb cura-Amblyglyphidodon curacao*, *Chr marg-Chromis margaritifera*, *Chr tern-Chromis ternatensis*, *Chr viri-Chromis viridis*, *Das arua-Dascyllus aruanus*, *Ple lacr-Plectroglyphidodon lacrymatus*, *Pom ambo-Pomacentrus amboinensis*, *Pom emar-Pomacentrus emarginatus*, and *Pom molu-Pomacentrus moluccensis*

Habitat	Coarse Branching	Fine Branching	Foliose	Consolidated Rubble	Hard Bottom	Rubble	Impt. Species in Grp. Species % similarity
Coarse Branching							Pom molu 48.54%
Fine Branching	0.101* Chr viri 16.95% Pom molu 14.20% Chr tern 10.01% Amb cura 7.87%	-	-	-	-	-	Pom molu 62.08%
Foliose	0.085 Chr tern 13.69% Chr viri 14.37% Pom molu 13.18% Amb cura 9.69%	0.255* Chr tern 19.14% Pom molu 14.20% Amb cura 9.10% Chr viri 6.64%	-	-	-	-	Amb cura 25.79%
Consolidated Rubble	0.218* Pom molu 16.54% Chr viri 16.42% Amb cura 11.51% Chr tern 8.14%	0.351* Pom molu 18.62% Amb cura 10.87% Chr tern 9.75% Ple lacr 6.49%	0.091 Chr tern 18.51% Amb cura 13.73% Pom molu 10.68% Ple lacr 7.04%	-	-	-	Ple lacr 51.61%
Hard Bottom	0.323* Pom molu 17.34% Chr viri 14.50% Amb cura 7.88% Chr tern 5.96%	0.496* Pom molu 20.07% Chr tern 7.42% Amb cura 6.55% Chr marg 5.75%	0.11* Chr tern 16.40% Amb cura 10.93% Pom molu 10.63% Chr marg 7.59%	0.163* Amb cura 12.55% Ple lacr 9.52% Pom molu 9.48% Chr marg 8.13%	-	-	Chr marg 23.80%
Rubble	0.149* Pom molu 17.40% Chr viri 17.39% Amb cura 7.34% Ple lacr 6.50%	0.234* Pom molu 19.47% Chr tern 8.64% Ple lacr 6.24% Chr viri 6.24%	0.167* Chr tern 17.65% Pom molu 11.27% Amb cura 9.14% Ple lacr 7.05%	0.109* Amb cura 11.97% Pom molu 11.38% Ple lacr 9.14% Pom emar 7.93%	0.230* Pom molu 11.29% Chr marg 9.51% Pom emar 8.38% Ple lacr 8.02%	-	Ple lacr 30.06%
Sand	0.386* Pom molu 18.35% Chr viri 16.76% Pom ambo 7.58% Amb cura 6.94%	0.510* Pom molu 21.24% Pom ambo 8.76% Das arua 6.81% Chr tern 6.41%	0.443* Chr tern 15.25% Amb cura 10.35% Pom molu 9.98% Pom ambo 7.72%	0.436* Pom ambo 11.71% Amb cura 10.80% Ple lacr 9.86% Das arua 8.77%	0.312* Pom ambo 11.65% Das arua 9.08% Chr marg 8.65% Pom emar 7.14%	0.154* Pom ambo 11.54% Pom molu 10.48% Das arua 10.06% Ple lacr 8.65%	Pom ambo 53.06%

Table 4 Mean density of resident predators identified in the different microhabitats of Ngederrak foreereef. Enclosed in parenthesis are standard deviations

Predator		Number of predators/100 m ² of microhabitat						
Family	Species	Coarse branching	Fine branching	Foliose	ConR	Hard bottom	Rubble	Sand
Apogonidae	<i>Cheilodipterus artus</i> ^b	0.20 (0.87)	–	–	–	–	–	–
	<i>Cheilodipterus macrodon</i> ^b	0.20 (0.87)	0.12 (0.69)	–	–	–	–	–
Cirrhitidae	<i>Cirrhitichthys falco</i> ^a	–	–	–	–	–	0.26 (1.42)	–
	<i>Paracirrhites forsterii</i> ^a	–	0.24 (0.96)	0.57 (1.40)	0.21 (0.89)	0.19 (0.85)	0.13 (0.71)	–
Serranidae	<i>Aethaloperca rogae</i> ^b	–	0.12 (0.69)	–	–	–	–	–
	<i>Anyperodon leucogrammicus</i> ^b	–	–	–	–	–	0.13 (0.71)	–
	<i>Cephalopolis argus</i> ^a	–	–	0.29 (1.03)	–	0.19 (0.85)	0.52 (1.36)	–
	<i>Cephalopolis leopardus</i> ^b	–	0.36 (1.15)	0.29 (1.03)	–	–	–	–
	<i>Cephalopolis urodeta</i> ^a	1.20 (3.41)	0.49 (1.31)	0.29 (1.03)	0.21 (0.89)	0.57 (1.41)	1.16 (0.39)	0.24 (0.94)
	<i>Epinephelus merra</i> ^a	–	0.12 (0.69)	0.57 (1.40)	–	–	0.13 (0.71)	–
	<i>Plectropomus maculatus</i> ^a	–	–	–	–	0.19 (0.85)	–	–
	<i>Variola louti</i> ^a	0.20 (0.87)	0.24 (0.96)	–	–	–	0.39 (1.19)	0.24 (0.94)
Synodontidae	<i>Synodus variegates</i> ^a	–	0.12 (0.69)	–	–	–	0.13 (0.71)	–
Total Resident Predator	1.80	1.81	2.01	0.42	1.14	2.85	0.48	

^a Ambush prey from perched or hovering position

^b Ambush prey from holes/crevices

Factors influencing early juvenile and adult pomacentrid abundance

Resident predators were observed in 53 of the 153 plots surveyed in the study. In general, predator density did not vary among microhabitats ($p=0.13$). In all but eight of these microhabitats, only one resident predator was observed. Two resident piscivores were noted in each of the eight remaining microhabitats. This overall homogeneity in the distribution of resident predators is the primary reason why we looked at the influence of predator size on early juvenile abundance instead. Predator size significantly varied among microhabitat types ($p=0.01$).

The results provide correlative evidence that the abundance of pomacentrids is simultaneously determined by the outcome of predator size and habitat complexity, and that there is little evidence for a settlement selection near adult members of the family (Fig. 5, Table 5). The results show that presence of

larger predators significantly reduce both early juvenile and adult damselfish abundance (Fig. 5, Table 5) while foraging space only influences the abundance of small, newly settled pomacentrids. Smaller foraging space harbors significantly higher juvenile pomacentrids but has no clear influence on adult abundance.

Discussion

Differences in the structural complexity of microhabitats in Ngederrak reef is viewed as an important driver in determining the community structure of juvenile reef fish. Juvenile reef fish showed clear habitat associations even when the measured structural differences among microhabitats are subtle (i.e., dead coralline microhabitats). Separation in juvenile reef fish community among microhabitats could be traced primarily to the relative abundance of species highly associated with high relief branching forms

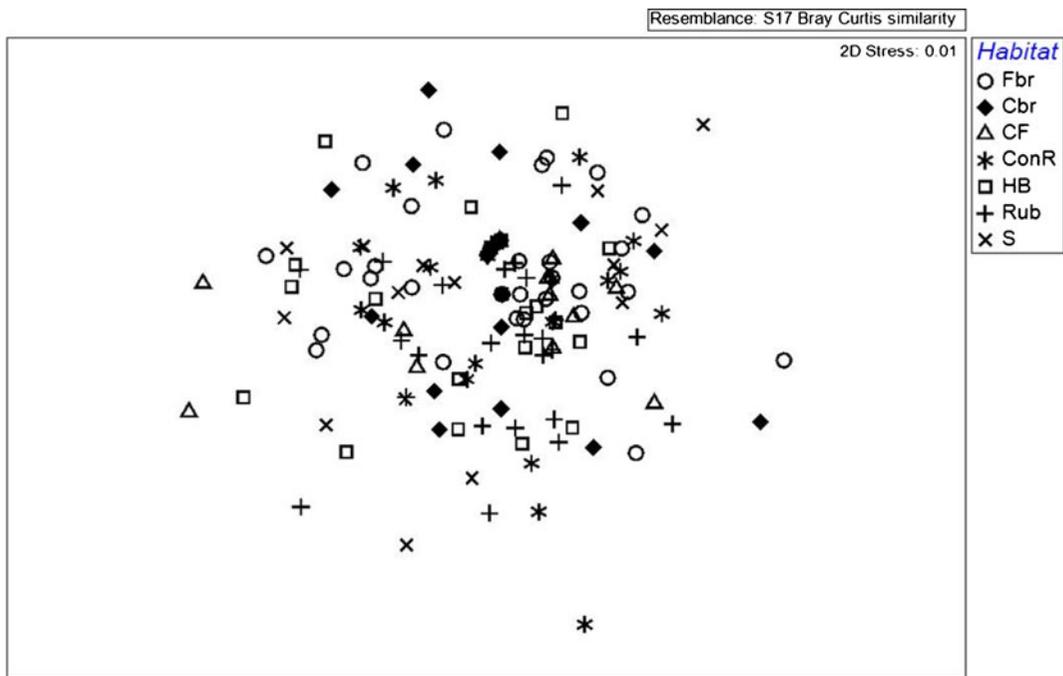


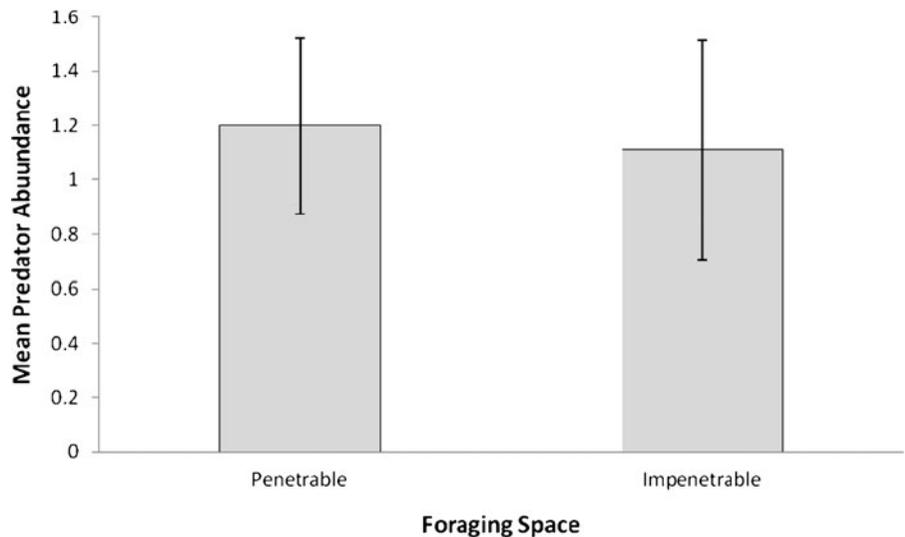
Fig. 3 MDS ordination of predators and microhabitats showing the absence of microhabitat preference of resident predators (Global $R=0.02$, $p<0.04$, $n=154$)

(*P. moluccensis*, *C. viridis*, and *C. ternatensis*), sand (*P. amboinensis*), and algal dominated coralline habitats (*P. emarginatus*, *P. lacrymatus*). The abundance of these damselfishes in these microhabitat types indicates early juvenile settlement preferences for these microhabitats and could be a product of post-settlement migration (Frederick 1997), or if recruits settle randomly on the reefs, their higher survival

rates in these more complex microhabitats (Beukers and Jones 1997). In both scenarios, the role of habitat mediation and predation are important drivers that influenced early juvenile abundance.

In the study area, resident predators, regardless of their size and ambush behaviors, hunted across microhabitats, irrespective of foraging space. Resident predators appeared to be loosely associated with multiple

Fig. 4 Predator abundance on microhabitats with penetrable and impenetrable foraging space. *T*-Test show no significant differences in predator abundance between penetrable and impenetrable habitat types ($p<0.49$, $n=54$). Fisher’s Exact Test also showed no significant differences in abundance of perched and concealed resident predators between the two habitat types ($p<0.47$, $n=54$)



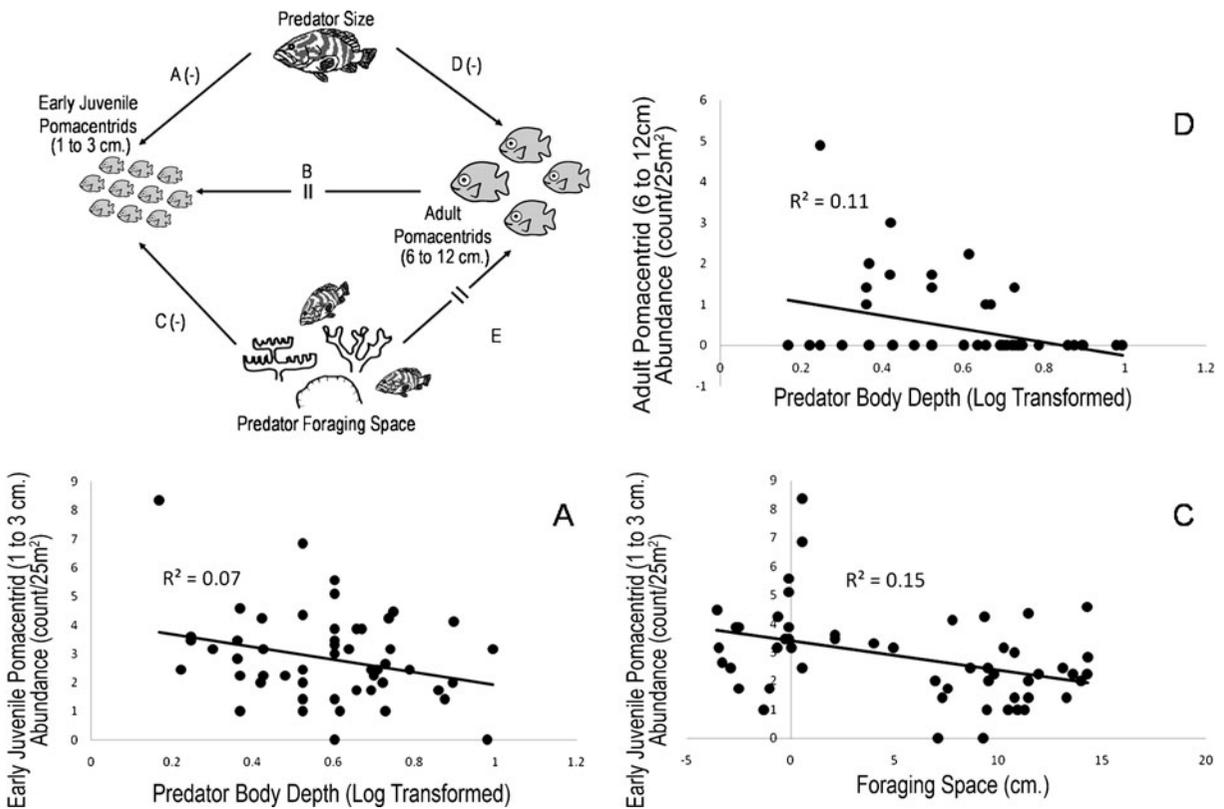


Fig. 5 An illustrated representation of microhabitat interactions affecting damselfish abundance. Significant interactions between parameters are represented by a continuous arrow. The

positive and negative signs reflect the relationship between parameters. The scatter plots show the distribution of data points for significant relationships

microhabitats and not strongly influenced by their ability to penetrate the reef structure to chase prey or by their ambush habits. Nonetheless, it is important to bear in mind that the structural complexity of the respective microhabitats may still deter the darting

hunting behavior commonly observed in most ambush predators.

The lack of microhabitat association among resident predators might occur for several, non-exclusive reasons. First, the resident predators may not be

Table 5 Summary statistics for the multiple regression analyses showing strength of relationships between damselfish abundance (dependant variable) foraging space, confamilial density,

and predator size (independent variables). The fourth column links the numerical values to Fig. 5

Regression model	Dependent variable (damselfish abundance/25 m ²)	Independent variable	Diagram flow	Regression coefficient	SE coefficient	P value
Model 1	Early Juvenile	Predator size	A	-2.81	1.06	0.01
		Adult Count	B	-0.04	0.06	0.47
		Predator foraging space	C	-0.11	0.03	0.001
Model 2	Adult	Predator size	D	-0.15	0.07	0.03
		Predator foraging space	E	0.01	0.02	0.69

utilising the reef framework as a means of avoiding larger predators (e.g., if they adopted a flight response to predation). Second, resident predators may seek shelter in the reef but the overall patchiness of microhabitats across the reef means that safe (penetrable) habitat can be reached rapidly if predators are observed (thereby allowing the residents to forage widely in a variety of habitats). Third, resident predators may attack prey when they are at a distance from their refuge areas, and seldom chase prey inside the reef structure. Lastly, it is also possible that competitive or antagonistic relations with conspecifics or other predators drive this loose association with microhabitats. However, such predatory behaviour needs to be documented further.

Habitat structure exerts a strong influence on early juvenile pomacentrid abundance because it is at this most vulnerable stage that the role of habitat complexity in regulating predation is most important. In this stage of early settlement, juvenile reef fish require suitable refuge areas that would decrease the foraging success of predators (Beukers and Jones 1997; Almany 2004a, b; Gratwicke and Speight 2005; Cabaitan et al. 2008). The aggregation of small juveniles on microhabitats with small foraging space hints at the importance of predation as a structuring force, influencing newly settled damselfishes. Indeed, predator size, used here as a proxy for predation (which increases with predator size), was correlated with a significant decline in early juvenile abundance.

Detecting confamilial attraction is not always straightforward (Jones 1988) and obtaining strong correlative evidence is difficult, especially at this geographically limited spatial scale in the wild (Stone and Roberts 1992). To test confamilial effects, it may be expected that these relationships between adults and early juveniles will be found in spite of post-settlement processes and ontogenetic shifts. This is difficult to establish for three reasons. First, the decision of early juveniles to settle with adult pomacentrids or not is not a response to social facilitation only, but is also influenced by the combined effects of food availability, predation, and antagonistic interactions. It is likely that in the presence of adult pomacentrids, forcible evictions and recruitment prevention by resident adults cause early juvenile mortality (Buston 2003a, b), or their migration to less suitable habitats (Öhman et al. 1998). Such hierarchy-driven antagonistic behavior is believed to be a widespread phenomenon that influences group dynamics of reef fishes (Buston 2003a). As

a selection strategy for site-attached reef fish like the pomacentrids, it maintains the dominance of larger (i.e., older) size class by favoring their survivorship through: (1) rapid growth and eventual escape from predation by gape-limited predators; and (2) access to better shelter, particularly in patchy habitats or in dangerous terrain (Sogard 1997; Buston 2003a, b). Second, provided there is considerable amount of time between the early juvenile and adult stage, it is possible that random post-settlement events such as predation and migration took place, thereby weakening the relationship. Lastly, elevating the analysis at the family level took into consideration the differential response of individual species with adults (Jones 1988; Öhman et al. 1998; Booth 2002; Buston, 2003a; Karplus et al. 2006). Simultaneous occurrence of species-specific attraction and antagonistic interactions in the different microhabitats could have obscured correlative relationship between early juvenile and adult pomacentrids. For adult damselfishes, the influence of foraging space becomes weak. Their insignificant role at this stage could be attributed to processes relating primarily to ontogenetic shifts. It is logical to posit that as fish grow larger, they move out of microhabitats with small foraging space and utilize other habitats better suited to their needs. Movement at this stage is better afforded since the increase in their body size makes them less vulnerable to predation (Sogard 1997). This stage-structured use of habitats observed in coral reef fishes is advantageous because it alleviates predatory bottlenecks in early demersal ontogeny (Mumby et al. 2004), satisfies changes in feeding requirement (Cocheret de la Moriniere et al. 2003), and allows for greater reproductive success (Morgan and Vincent 2007). This weak correlative evidence between adults and microhabitat structure could explain in part the significant negative effect of predator size on adult abundance.

The study's results coincide with previous reports that demonstrate species specific habitat preference of juvenile reef fishes to particular microhabitat types (Wilson et al. 2008a, b; Wilson et al. 2010), and the importance of refuge space in the survival of early juvenile pomacentrids (Öhman et al. 1998; Booth 2002; Holbrook and Schmitt 2002; Buston 2003a, b; Wilson et al. 2010) and other small bodied reef fishes (Graham et al. 2008; Pratchett et al. 2008). The abundance of these small bodied reef fishes in turn, influence predator abundance (Wilson et al. 2008a, b),

further establishing the importance of maintaining an intact benthic refugia.

In the light of the predicted impact and irreversibility of climate change (Solomon et al. 2009) compounded by the lack of new and integrated management approaches to sustain coral reef function in exploited areas (Graham et al. 2008; Mumby and Steneck 2008), the physical structure of coral reefs remain highly vulnerable to erosion and so are the community structure of its associated reef fishes (see the works of Graham et al. 2008; Pratchett et al. 2008; Wilson et al. 2010). It is therefore critical at this stage to acquire information that would contribute to the understanding of community associations and predict potential ecosystem response to the increasing stress brought about by climate change. The presence of strong microhabitat-juvenile relationship suggests the potential use of microhabitat types in identifying areas of high reef fish diversity. This has important implications in conservation and management, particularly in delineating the spatial extent of protected areas based on the spatial distribution of different habitat types that are deemed important in the stage structured development of reef fishes (Wilson et al. 2010). In addition, the results of the study have important implication in modeling for the impacts of habitat loss on reef fish. By identifying the relative susceptibility of the microhabitats to the warming ocean temperature, it is possible to determine the relative vulnerability of reef fishes, at least the small bodied group. Lastly, the results of the study generally support the implementation of targeted management strategies that recognize the critical components of habitat structure.

Acknowledgments We thank David Idip, Yannek Meunier, Anders Knudby, Alan Lim, the staff of the Palau International Coral Reef Center for their support in the conduct of the study, and to the reviewers who generously shared their insights on the study. The study was funded by the World Bank/Global Environment Facility Coral Reef Targeted Research Project. Additional funding was provided by Natural Environment Research Council and an Australian Research Council fellowship. The study was conducted in accordance to the existing laws of the Republic of Palau.

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