

Ecological versatility and its importance for the distribution and abundance of coral reef wrasses

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ABSTRACT: Ecological versatility, the degree to which organisms fully exploit the available resources, is an important component of ecological and evolutionary theory. However, patterns and consequences of versatility in coral reef fish have received little attention. Using a comparative approach, this study tested the consequences of ecological versatility on the distribution and abundance of juvenile wrasses (family: Labridae) in Kimbe Bay, Papua New Guinea. Resource use was examined along 4 different resource axes (horizontal distribution or reef zone, vertical distribution or depth, microhabitat and diet). Stepwise multiple regressions were used to test for relationships between niche breadth and patterns of abundance and distribution. Most exhibited a degree of apparent specialisation on at least one resource, but none were specialised along all resource axes. In terms of juvenile diet, the majority of species exhibited a high reliance on harpacticoid copepods. Microhabitat specialisation was associated with low local abundance and narrow distribution among depth zones. However, diet and macrohabitat specialisation were poor predictors of local abundance, and no relationships between local abundance, and local and regional distribution were observed. We conclude that the relationship between versatility and abundance/distribution is dependent on the resource in question. A greater understanding of the degree of ecological versatility in relation to different resources is necessary to predict how reef fishes will respond to escalating human impacts on coral reefs.

KEY WORDS: Coral reef fish · Depth distribution · Diet · Habitat use · Harpacticoid copepods · Specialisation · Labridae

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INTRODUCTION

The range of resources used by organisms has important implications for ecological patterns at both population and community levels (Ross 1986). The different abilities of species to exploit resources and perform in various environments are often important in limiting their abundance and distribution (Schoener 1974, Brown 1984, Hanski et al. 1993, McPeck 1996, Hughes 2000). Knowledge of species resource requirements can provide insights into how populations are regulated and how ecological communities are structured. Ecological versatility has been defined as

‘the degree to which organisms can fully exploit the available resources in their local environment’ (MacNally 1995, p. 19). Versatile species are those that exploit a large number of resources and are usually referred to as generalists (Pianka 1974, Futuyama & Moreno 1988, MacNally 1995), while specialists exploit only a narrow range of resources (Futuyama & Moreno 1988, MacNally 1995, Timms & Read 1999). As extreme specialists and generalists are likely to represent opposite ends of a resource-use continuum (Rachlin et al. 1989, Morris 1996), the term versatility was coined to encompass the whole spectrum (MacNally 1995). The consequences of ecological versatility

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are receiving increasing attention due to the high extinction risk associated with ecological specialisation in a changing environment (Hawkins et al. 2000, Harcourt et al. 2002, Davies et al. 2004, Hobbs et al. 2011).

Ecological versatility has been suggested to play a major role in determining local patterns of distribution and abundance. This was formalised by Brown (1984), who proposed that species with broad environmental tolerances and resource generalists will have the capacity to achieve high local densities and be able to survive in more places and hence over larger areas. In contrast, species that have narrow environmental tolerances, which are able to use only a narrow range of resources (specialists), will be unable to attain either high local densities or extensive distributions (Brown 1984). In a similar vein, there may be a relationship between ecological versatility, and regional and geographic abundance and distribution. Species with wide geographic ranges have been shown to be more abundant than species with narrow distributions (Hanski 1982, Bock & Ricklefs 1983, Gaston 1990, Gaston 1994, Hanski & Gyllenberg 1997). These general ecological patterns have been documented over a broad diversity of taxa, in different biogeographic regions and in a variety of habitats (Gaston & Blackburn 1996).

While many studies provide support for Brown's ecological specialisation hypothesis (e.g. Gaston 1988, Inkinen 1994, Pyron 1999, Hughes 2000, Bean et al. 2002), support is not universal (Fowler & Lawton 1982, e.g. Hanski et al. 1993, Gregory & Gaston 2000, Gaston & Spicer 2001). Few explicit tests have been carried out and the vast majority have focused on terrestrial organisms (Gaston et al. 1997, Gaston & Spicer 2001). In addition, as animals use a range of resources, it is critical to know the level of specialisation on different resources. Resource utilisation in animals can be viewed in a hierarchical framework, from the use of 'macrohabitats' in which an individual spends most of its time, to the use of 'microhabitats' within an individual's home range, to the selection of particular elements (food items) from different microhabitats (Manly et al. 1993). A full evaluation of the effects of specialisation on distribution and abundance requires niche breadth to be quantified along different resource axes.

For coral reef fishes, patterns of ecological versatility and their consequences for distribution and abundance have received relatively little attention (but see Munday & Jones 1998, Bean et al. 2002, Jones et al. 2002, Pratchett et al. 2008, Hobbs et al. 2010). According to Ross (1986), many fishes seem to be highly versatile and opportunistic, displaying high overlap

in resource use. They have an extraordinary potential for trophic niche expansion, exploitation of highly fluctuating and diverse trophic resources, and for being facultative rather than obligate specialists (Liem 1984, 1990). However, a large number of coral reef fishes show high degrees of apparent specialisation, being associated with either 1 biotic microhabitat, 1 prey group or 1 symbiotic partner (Fautin & Allen 1992, Munday 2004, Pratchett 2005). This suggests that for coral reef fishes, specialisation might be more pronounced and important for abundance and distribution than previously thought. Furthermore, studies have shown that specialised coral reef fish species display low local abundances, in accordance with Brown's theory (Munday 2000, Bean et al. 2002, Gardiner & Jones 2005). However, recent evidence suggests that coral reef fish species with small geographic ranges around isolated islands can have high local abundances (De Martini & Friedlander 2004, Hobbs et al. 2011).

Recent studies have shown declines in fish communities associated with degrading coral reef habitats (Jones et al. 2004, Wilson et al. 2006, Wilson et al. 2009), especially species specialised on live coral (Pratchett et al. 2006, Graham 2007). The community-wide response to degradation and variation in resource availability will fundamentally depend on the versatility of the constituent species. Gardiner & Jones (2005) suggested that communities composed of a high proportion of resource specialists that are specialised on a particular habitat type that is undergoing degradation will be particularly vulnerable. However, species are not necessarily specialised on all resources, and not all resources are necessarily in decline. Determination of the degree of versatility of reef fishes in relation to different resources is needed to understand the effect of coral reef degradation on their abundance and distribution.

The overall aim of this study was to examine the effects of ecological versatility on the abundance and distribution of a group of coral reef wrasses from the family Labridae. The family Labridae encompasses species that range from those with highly specialised diets to highly opportunistic carnivores. They utilise a number of different habitats and are found at a variety of different depths (Green 1996, Myers 1999, Allen et al. 2003). They are also an important component of the ichthyofauna on coral reefs throughout the world, being the second most species-rich family on the Great Barrier Reef, Australia (Thresher 1991, Randall et al. 1997). To avoid the complication of ontogenetic shifts in ecology, the present study focuses on the juvenile life stage.

The specific goals were to (1) examine patterns of apparent specialisation or niche breadth along 4 different resource axes (horizontal distribution or reef zone, vertical distribution or depth, microhabitat and diet); (2) test the hypotheses derived from Brown's (1984) theory that greater niche breadth for any one resource is associated with (i) a greater local abundance, (ii) a greater local distribution among habitats and (iii) a greater geographic range; and (3) test if there is a relationship between local abundance and geographic range, i.e. species with wide geographic ranges have high local abundances.

MATERIALS AND METHODS

Study site and species

The study was carried out at Kimbe Bay, West New Britain Province, Papua New Guinea (5° 30' S, 150° 05' E). Kimbe Bay has a dense network of platform reefs ranging in size from tens to hundreds of metres in diameter, and several small continental islands surrounded by well-developed fringing reefs (Munday 2002). The reefs used in this study are

located close to shore, extending down to depths of >200 m and breaking the surface at low tide. The reefs can be clearly split into several reef zones: the reef flat, the windward reef crest and slope/wall, and the leeward reef slope. Eleven species from the family Labridae were chosen for this study: *Diproctacanthus xanthurus*, *Halichoeres argus*, *H. chloropterus*, *H. hortulanus*, *H. melanurus*, *H. purpurascens*, *Labrichthys unilineatus*, *Labroides dimidiatus*, *Oxycheilinus celebicus*, *Paracheilinus filamentosus* and *Thalassoma lunare*. These species were chosen because they were expected to encompass a wide range of patterns in resource use and to differ in their local abundances. Niche breadth data for these species were collected during March and April 2002 on 9 reefs (Lady Di, Limuka, Rakaru Diri, Hanging Gardens, Garbuna, Reef 1, Reef 2, Donna's and Vanessa's, Fig. 1). As part of another study examining seasonal patterns of recruitment and densities of new recruits of the same species, juvenile fish were surveyed every 4 to 8 wk between December 1998 and April 2001 at different depths on 6 reefs (Gava Gava, Limuka, Luba Luba, Madaro, Mahonia Front and Walindi Front; Srinivasan & Jones 2006).

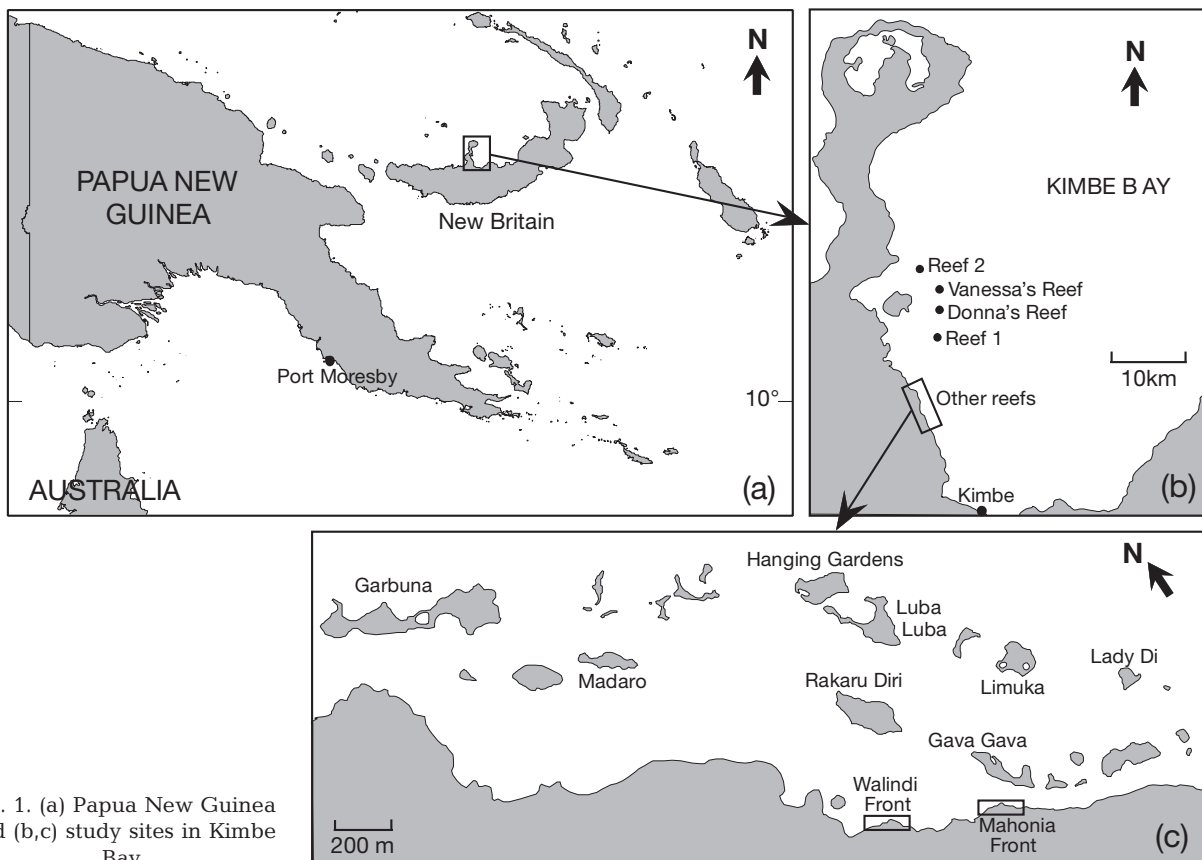


Fig. 1. (a) Papua New Guinea and (b,c) study sites in Kimbe Bay

Local distribution among depth zones, reef zones and microhabitats

Niche breadth can be measured by observing the distribution of individual organisms within a set of resource states or resource categories (Krebs 1999). The specialist's resource range should be included in that of the generalist's as this makes the judgment of the relative degree of specialisation more reliable (McNaughton & Wolf 1970, Futuyma & Moreno 1988). To observe the distribution of individual wrasses within large- and small-scale habitat categories, transects were randomly placed on the windward (2 transects) and leeward (2 transects) sides of 9 different reefs in Kimbe Bay, a total of 36 transects. Depth, reef zone and microhabitat were recorded for each juvenile found within the 20 m wide transect. To cover a large depth and habitat range, transects were placed at 20 m depth and run up the slope or wall, over the crest and across the reef flat of each reef sampled. Transects ended where the reef broke the surface and varied in length, from 18 to 48.5 m long. Transects were simply a way of making sure that similar amounts of effort were allocated to the whole depth range available for the study. Each transect

was divided into 8 depth categories and 8 reef zone categories (Table 1). The local distribution of a species was described as the distribution across reef and depth zones on a single reef. Occurrence in a large number of reef zones denotes a broad horizontal distribution, while occurrence in a large number of depth zones denotes a broad vertical distribution. Microhabitats were divided into 19 microhabitat categories (Table 1), based on major non-living and living substrates. Live coral was divided according to growth form, as reef fishes are known to exhibit preferences for particular growth forms of coral (Gardiner & Jones 2005, Bonin et al. 2011).

Diet

In order to estimate selectivity of food resources, 20 or more random juveniles of each species were collected from reefs around Kimbe Bay for gut content analyses. Juveniles were caught with a hand net after being anaesthetised with a 1:10 clove oil/ alcohol solution administered from a hand-held spray bottle. Following capture, fish were held on ice to stop any breakdown of tissue until placed in separate vials of 10% buffered seawater/ formalin solution. In the laboratory, guts were removed from the specimens under a stereomicroscope and their contents were sorted. Prey items were temporarily mounted on a slide with Grey and Wess mountant and were taxonomically identified to class and, if possible, order under high magnification. Prey items were divided into 23 categories, based on major prey groups from similar environments (e.g. pelagic, benthic or parasitic, Table 1). The number of different prey categories per gut and the percentage each prey category constituted per gut was recorded. Two coefficients (mean volumetric percentage, MVP, and percentage frequency of occurrence, PFO) were calculated to determine the relative importance of prey items in the diet. The MVP of a prey is the sum of individual volumetric percentages for the food items divided by the number of specimens examined. The PFO is the number of stomachs containing a particular prey item as a percentage of the total num-

Table 1. Depth and reef zones, microhabitats and food items used for studying resource use in juveniles (juv.) from 11 wrasse species in Kimbe Bay, Papua New Guinea. All corals are hard corals except 'black coral' and 'soft coral'. par.: parasitic

Depth zones (m)	Reef zones	Microhabitats	Food items
0.0–2.5	Back patch	Bare rock	Harpacticoid copepods
2.5–5.0	Back wall	Dead coral	Calanoid copepods
5.0–7.5	Back slope	Rubble	Cyclopoid copepods
7.5–10.0	Back crest	Sand	Parasitic copepods
10.0–12.5	Reef flat	Turf	Cirripedi (barnacle) larvae
12.5–15.0	Front crest	Macroalgae	Amphipods
15.0–17.5	Front slope	Sponge	Gnathid amphipod larvae (par.)
17.5–20.0	Front wall	Soft coral	Isopods
		Fire coral	Ostracods
		Black coral	Tanaeids
		Branching coral	Crabs (megalopa-stage)
		Bushy coral	Nauplii
		Corymbose coral	Bivalves (juv.)
		Digitate coral	Gastropods (juv.)
		Columnar coral	Polychaetes
		Tabular coral	Insects
		Encrusting coral	Diatoms (<i>Coscinodiscus</i>)
		Massive coral	Dinoflagellates (<i>Paradinium</i>)
		Solitary coral	Forams (<i>Globigerinida</i>)
			Protozoans
			Coral polyps
			Eggs/egg mass
			Fish scales

rate vials of 10% buffered seawater/ formalin solution. In the laboratory, guts were removed from the specimens under a stereomicroscope and their contents were sorted. Prey items were temporarily mounted on a slide with Grey and Wess mountant and were taxonomically identified to class and, if possible, order under high magnification. Prey items were divided into 23 categories, based on major prey groups from similar environments (e.g. pelagic, benthic or parasitic, Table 1). The number of different prey categories per gut and the percentage each prey category constituted per gut was recorded. Two coefficients (mean volumetric percentage, MVP, and percentage frequency of occurrence, PFO) were calculated to determine the relative importance of prey items in the diet. The MVP of a prey is the sum of individual volumetric percentages for the food items divided by the number of specimens examined. The PFO is the number of stomachs containing a particular prey item as a percentage of the total num-

ber of stomachs containing food. Unidentifiable prey items were not included as a prey category in the calculations of food selectivity coefficients, as most of the fish guts contained a high percentage of these items (often >50%). Including this category would have resulted in all labrid species having high niche overlap, i.e. all specialised on unidentifiable prey. We acknowledge, however, that actual niche overlap between species may vary from that estimated in this study, depending on whether unidentified items were the same or different between species.

Niche breadth

Niche breadths for depth, reef zone, microhabitat and diet of 11 species of wrasses were calculated using Levins' (1968) niche breadth formula. This measures the uniformity of distribution of individuals among the resource categories as:

$$B = 1/(\sum p_j^2) \quad (1)$$

where B is Levins' measure of niche breadth and p_j is the proportion of individuals found in or using resource state j . The range of B is from 1 to n , where n is the total number of resource categories. B is minimal when all individuals occur in only 1 resource state (minimum niche breadth, maximum specialisation). To facilitate comparisons among species, Levins' niche breadth was standardised in accordance with Hurlbert (1978) using the formula:

$$B_A = (B-1)/(n-1) \quad (2)$$

where B_A is Levins' standardised niche breadth, B is Levins' measure of niche breadth and n is the number of possible resource categories. The standardised niche breadth (B_A) is expressed on a scale from 0 to 1, where a value close to 0 represents a narrow niche breadth and high specialisation.

Local abundance

Local abundances for the 11 study species were estimated using depth-stratified visual transects. Four 50 × 2 m transects were randomly placed at each of 4 depths (0, 2, 6 and 10 m) on the windward sides and at 2 m on the leeward sides of 4 platform reefs (Gava Gava, Limuka, Luba Luba and Madaro) and at each of 3 depths (0, 2 and 6 m) on 2 areas of fringing reef (Mahonia Front and Walindi Front). All newly settled individuals within 1 m on each side of the 50 m transect tape were recorded. Juveniles were

of a similar size range to those surveyed for niche breadth. Depths deeper than 2 m were not surveyed on the leeward sides of the reefs as the cover of hard substrata generally did not extend beyond 3 to 4 m depth on this side of the reef. This was also the case for depths beyond 6 m on the fringing reefs. As these surveys were part of a study examining seasonal patterns (Srinivasan & Jones 2006), they were carried out a total of 20 times, every 4 to 8 wk, from December 1998 to April 2001, with a total of 108 transects surveyed each time.

Although niche breadth data and local abundance data were collected at different time periods, niche breadth data were collected less than 1 yr after the last of the abundance surveys, and it was assumed that the relative abundances of juveniles of the 11 wrasse species would not have changed significantly over this time. In addition, although there has been a gradual decline in coral cover on these reefs (Jones et al. 2004), patterns of microhabitat use of juvenile wrasses were assumed to have not changed significantly between the 2 time periods.

Geographic range

The geographic range of each species was assessed from the literature (Myers 1999, Froese & Pauly 2002, Allen et al. 2003). Range size was calculated as the relative size of the biogeographic region in which each species is found, i.e. the area between the outermost limits of a species occurrence. A contour map for each species was constructed in a similar fashion to Allen et al. (1998) using occurrence data from Myers (1999), Froese & Pauly (2002) and Allen et al. (2003). The size of each species' geographic range was estimated by digitising maps using Sigma Scan computer software.

Data analyses

Multiple stepwise regression was used to test for relationships between niche breadth and local abundance, local distribution (vertical and horizontal distribution) and geographic range, respectively. For local abundance and geographic range, all 4 niche dimensions (depth, reef zone, microhabitat and diet) were used as predictor variables. However, depth was omitted from the analysis involving local vertical distribution, and reef zone was omitted from the analysis involving local horizontal distribution, as these 2 sets of variables were not independent.

RESULTS

Local distribution among depth zones, reef zones and microhabitats

Halichoeres argus displayed the narrowest depth range (0 to 2.5 m), followed by *H. hortulanus* (0 to 5 m, Fig. 2). *H. chloropterus*, *Labrichthys unilineatus* and *Thalassoma lunare* were found between 0 and 15 m, but were most abundant between 0 and 5 m. *Labroides dimidiatus* and *H. melanurus* were found throughout the 20 m depth range, but were most frequently observed between 0 and 10 m. *Diproctacanthus xanthurus*, *H. purpurascens* and *Oxycheilinus celebicus* were evenly spread throughout most depth zones. However, *O. celebicus* was rarely found in depths less than 5 m. *Paracheilinus filamentosus* was found between 5 and 20 m, displaying highest percent occurrence between 15 and 20 m (Fig. 2).

Substantial differences among species were found in the number of broad reef zones occupied. Two species (*Halichoeres argus* and *H. hortulanus*) were predominantly found on the reef flat (Fig. 3). *H. chloropterus* and *Labrichthys unilineatus* were found on reef flats and crests or shallow parts of the reef slope on both sides of the reef. *Diproctacanthus xanthurus*, *H. purpurascens*, *Oxycheilinus celebicus* and *Paracheilinus filamentosus* were only found on reef slopes and walls, both on the front and back of reefs. The remaining 3 species (*H. melanurus*, *Labroides dimidiatus* and *Thalassoma lunare*) were apparent reef zone generalists, occupying most of the available reef zones (Fig. 3).

Halichoeres melanurus, *H. purpurascens* and *Oxycheilinus celebicus* were very general in their use of microhabitats, utilising most of the microhabitat categories in this study (Table 2). *Thalassoma lunare* and *Labroides dimidiatus* were found in most micro-

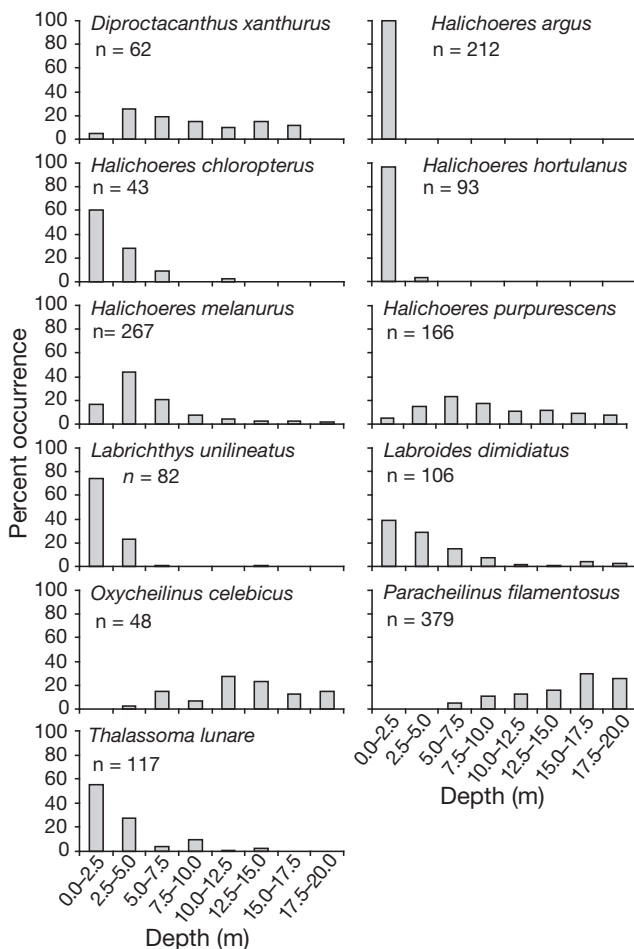


Fig. 2. Local vertical distributions of 11 species of juvenile wrasses on coral reefs in Kimbe Bay, Papua New Guinea, shown as the percent occurrence of individuals in each of the 8 depth zones

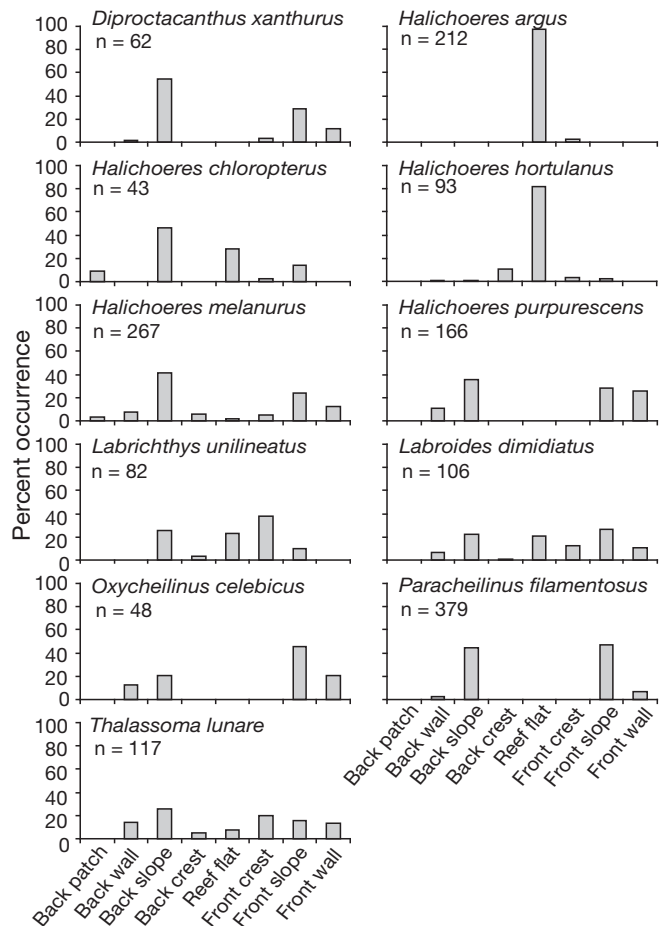


Fig. 3. Local horizontal distributions of 11 species of juvenile wrasses on coral reefs in Kimbe Bay, Papua New Guinea, shown as the percent occurrence of individuals in each of the 8 reef zones

habitats but more than 70% of the individuals were associated with live hard corals. *Diproctacanthus xanthurus* and *Labrichthys unilineatus* were found almost exclusively on live hard coral (over 95%). *Paracheilinus filamentosus* was most commonly found associated with rubble on reef slopes and walls. *H. chloropterus* was mainly found on dead substrata, mostly rubble (and turf). *H. argus* was associated with turf-covered dead coral/rubble, while *H. hortulanus* was found in sand, rubble gutters along the reef crest, shallow slope or reef flat (Table 2). For 7 species (*O. celebicus*, *D. xanthurus*, *H. melanurus*, *H. purpurescens*, *Labroides dimidiatus*, *Labrichthys unilineatus*, *T. lunare*), over 55% of the individuals occupied live coral. All of these species, except *Labrichthys unilineatus*, were very general in their use of live corals. *Labrichthys unilineatus* was mostly associated with bushy or branching corals from the families Acroporidae and Pocilloporidae (Table 2).

Diet

Most juvenile wrasses showed a high selectivity for harpacticoid copepods; however, the importance of harpacticoids in the diet differed among species. Calanoid copepods were the dominant prey items of *Halichoeres purpurescens* and *Paracheilinus filamentosus*, constituting 32 and 23% of their diet content, respectively (Table 3). *Labrichthys unilineatus* fed exclusively on live coral. *Labroides dimidiatus* showed high selectivity for parasitic gnathid isopod larvae, which constituted over 90% of their diet. *Diproctacanthus xanthurus* was also highly selective on parasites, gnathid isopod larvae as well as copepods, which constituted 59 and 24% of the diet content, respectively (Table 3).

Niche breadths

In general, niche values covered the whole spectrum from highly specialised diets and microhabitat use to quite gener-

Table 2. Relative proportions (%) of juveniles from 11 wrasse species associated with different microhabitats, including living and non-living substrata in Kimbe Bay, Papua New Guinea. The highest value for each species is in bold. n = number of individuals sampled per species; (-) species not recorded in this macrohabitat

Micro-habitat	<i>Diproctacanthus xanthurus</i>	<i>Halichoeres argus</i>	<i>Halichoeres chloropterus</i>	<i>Halichoeres hortulanus</i>	<i>Halichoeres melanurus</i>	<i>Halichoeres purpurescens</i>	<i>Labroides dimidiatus</i>	<i>Labrichthys unilineatus</i>	<i>Oxycheilinus celebicus</i>	<i>Paracheilinus filamentosus</i>	<i>Thalassoma lunare</i>
Bare rock	-	0.9	-	-	0.7	0.6	4.7	-	-	-	5.1
Dead coral	-	0.5	11.6	-	0.4	4.8	-	10.4	0.3	-	-
Rubble	-	6.1	37.2	19.4	12.7	5.4	8.5	8.3	84.2	-	-
Sand	-	9.4	9.3	75.3	3.0	0.6	0.9	-	-	-	-
Turf	-	61.8	32.6	5.4	21.3	10.2	11.3	8.3	1.1	6.0	-
Macroalgae	-	-	2.3	-	1.5	-	-	2.1	-	-	-
Sponge	1.6	-	-	-	4.9	7.2	1.9	8.3	2.4	-	2.6
Live coral											
Soft coral	-	0.5	-	-	12.4	16.9	7.5	-	18.8	6.3	15.4
Fire coral	4.8	-	-	-	1.1	2.4	-	-	-	-	1.7
Black coral	-	-	-	-	-	-	-	2.1	-	-	-
Branching coral	50.0	2.4	7.0	-	15.7	12.7	34.9	41.5	29.2	1.6	9.4
Bushy coral	8.1	2.8	-	-	8.2	1.8	6.6	42.7	-	-	21.4
Corymbose coral	9.7	1.4	-	-	2.2	2.4	3.8	9.8	-	1.8	17.9
Digitate coral	16.1	13.2	-	-	1.5	9.0	6.6	1.2	2.1	-	2.6
Columnar coral	-	-	-	-	1.9	-	1.9	-	-	-	-
Tabular coral	8.1	-	-	-	2.2	3.6	4.7	-	2.1	2.4	6.0
Encrusting coral	-	0.5	-	-	3.4	6.0	0.9	-	4.2	-	-
Massive coral	1.6	0.5	-	-	6.0	16.3	5.7	4.2	-	-	12.0
Solitary coral	-	-	-	-	0.7	-	-	-	-	-	-
n	62	212	43	93	267	166	106	82	48	379	117

Table 3. Mean volumetric percentage (MVP) and percentage frequency of occurrence (PFO) for food items in the diets of 11 wrasse species in Kimbe Bay, Papua New Guinea. Values for the prey category most commonly selected by each species are in bold. n = total number of individuals studied for each species. For full species names see Table 2

Food items	D. xanthurus		H. argus		H. chloropterus		H. hortulanus		H. melanurus		H. purpur-escens		L. dimidiatus		L. unilineatus		O. celebicus		P. filamentosus		T. lunare			
	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO	MVP	PFO		
n	18	21	21	17	17	21	21	21	28	28	19	19	18	30	20	37	21							
Crustaceans																								
Harpacticoid copepods	–	–	66.5	42.2	82.4	57.8	100.0	68.3	82.1	17.6	42.1	–	–	–	37.3	65	14.1	54.1	53.6	95.2	–	–		
Calanoid copepods	0.5	5.6	1	14.3	11	23.5	0.3	9.5	8.9	42.9	32.1	57.9	–	–	–	–	28.5	70	23.2	59.5	4.8	23.8		
Cyclopoid copepods	0.5	5.6	3.1	9.5	1.4	11.8	0.6	14.3	2.3	10.7	17.4	47.4	–	–	–	–	12.5	35	19.7	59.5	6.4	23.8		
Parasitic copepods	24.2	50.0	–	–	–	–	–	–	–	–	4.3	5.3	6.4	16.7	–	–	–	–	–	–	–	–		
Cirripedi (barnacle) larvae	–	–	0.6	9.5	–	–	4.2	23.8	4.5	14.3	11.8	10.5	–	–	–	–	–	–	–	–	–	–		
Amphipods	11.3	16.7	1.4	4.8	13.9	29.4	3.3	19	2.5	14.3	0.3	5.3	–	–	–	–	0.5	5	0.9	2.7	7.6	28.6		
Gnathid amphipod larvae (parasitic)	59.5	72.2	1.8	19	4.1	11.8	4.3	28.6	–	–	0.7	10.5	90.8	94.4	–	–	–	–	3.8	13.5	1.0	4.8		
Isopods	–	–	–	–	–	–	6.6	19	0.2	3.6	–	–	–	–	–	–	–	–	0.2	2.7	0.6	4.8		
Ostracods	–	–	6.1	19	–	–	7.1	19	–	–	2.3	15.8	–	0.2	3.3	8.1	30	–	–	–	–	–		
Tanaids	–	–	–	–	–	–	–	–	0.5	10.7	–	–	–	–	–	–	–	–	0.8	2.7	0.2	4.8		
Crabs (megalopa-stage)	–	–	1.9	4.8	–	–	1.4	4.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
Nauplii	–	–	–	–	–	–	0.1	4.8	–	–	–	–	–	–	–	–	–	–	9.4	43.2	–	23.8		
Other																								
Bivalves (juv)	–	–	–	–	2.1	5.9	–	–	–	–	5.9	5.3	–	–	–	–	–	–	3.4	21.6	–	–		
Gastropods (juv)	0.2	5.6	3.9	23.8	7.5	35.3	3.5	23.8	–	–	0.3	5.3	–	–	–	–	–	0.3	5	1.8	18.9	–		
Polychaetes	–	–	0.3	4.8	–	–	2.2	4.8	2.8	7.1	2.0	5.3	–	–	–	–	–	7.3	15	–	–	4.1	9.5	
Insects	–	–	3.5	28.6	0.3	5.9	5.5	14.3	2.4	7.1	–	–	–	–	–	–	–	–	–	–	–	5.5	23.8	
Diatoms (Coscinodiscus)	–	–	0.3	4.8	–	–	–	–	7.3	21.4	–	–	–	–	–	–	–	–	–	–	–	–		
Dinoflagellates (Paradinium)	–	–	–	–	0.4	5.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
Forams (Globigerinida)	–	–	8.8	42.9	14.2	41.2	2.1	19	0.2	3.6	5.5	31.6	–	–	–	–	–	2.2	5	3.7	18.9	0.4	9.5	
Protozoans	–	–	–	–	3	5.9	–	–	–	–	–	–	–	–	–	–	–	–	–	2.7	13.5	–	33.3	
Coral polyps	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Eggs/egg mass	–	–	0.6	4.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Fish scales	4.0	16.7	–	–	–	–	–	–	0.1	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	
													2.8	27.8	–	–	–	–	1.9	10	0.6	2.7	1.4	9.5

alised with regard to macrohabitat use (depth ranges and reef zones occupied). No species was either a specialist or a generalist in its use of all resources. In terms of both microhabitat use and diet, species displayed niche values at the lower end of the spectrum, indicating a general trend of specialisation in these resources by juvenile wrasses. *Halichoeres purpureus*, *H. melanurus* and *Thalassoma lunare* were the most general of all species in the use of microhabitats, but the highest niche breadth value among these species was only 0.5 (Table 4). The narrowest niche breadths with regard to diet were displayed by *Labrichthys unilineatus*, *Labroides dimidiatus* and *H. melanurus*, while *Paracheilinus filamentosus* had the highest niche breadth value of 0.3 (Table 4).

Local abundance and niche breadth

Halichoeres melanurus was the most abundant species, followed by *Thalassoma lunare* and *H. purpureus* (Fig. 4). The remaining species were all relatively rare, i.e. ≤ 1 individual per 100 m² (Fig. 4). There was a significant positive relationship between niche breadth for microhabitat and local abundance ($r^2 = 0.606$, $p = 0.005$). The most abundant species were among those with the greatest niche breadths for microhabitat (i.e. *H. melanurus*, *T. lunare* and *H. purpureus*). There were no relationships between the other 3 niche dimensions (depth, reef zone or diet) and abundance.

Local distribution and niche breadth

Halichoeres melanurus had the broadest distribution across reef

Table 4. Niche values for different niche dimensions (depth, reef zone, microhabitat and diet) of 11 species of juvenile wrasses in Kimbe Bay, Papua New Guinea. A low niche value represents a narrow niche breadth and high specialisation. Likewise, a high value represents a wide niche breadth and low specialisation. n = number of categories within each niche dimension

Species	Depth (n = 8)	Reef zone (n = 8)	Microhabitat (n = 19)	Diet (n = 23)
<i>Diproctacanthus xanthurus</i>	0.69	0.22	0.13	0.06
<i>Halichoeres argus</i>	0.00	0.01	0.08	0.05
<i>Halichoeres chloropterus</i>	0.17	0.30	0.15	0.15
<i>Halichoeres hortulanus</i>	0.01	0.07	0.04	0.08
<i>Halichoeres melanurus</i>	0.38	0.42	0.41	0.05
<i>Halichoeres purpurescens</i>	0.81	0.36	0.47	0.20
<i>Labroides dimidiatus</i>	0.39	0.59	0.28	0.01
<i>Labrichthys unilineatus</i>	0.09	0.38	0.10	0.00
<i>Oxycheilinus celebicus</i>	0.62	0.31	0.30	0.14
<i>Paracheilinus filamentosus</i>	0.54	0.20	0.02	0.28
<i>Thalassoma lunare</i>	0.22	0.69	0.35	0.10

zones, occupying all 8 reef zones, while *H. argus* displayed the narrowest distribution, occupying just 2 reef zones (Fig. 5). No relationships were found between any of the 3 niche values (depth, microhabitat or diet) and local horizontal distribution, i.e. across reef zones. However, there was a significant positive relationship between microhabitat niche breadth and local vertical distribution, i.e. among depth zones ($r^2 = 0.433$, $p = 0.028$). The species with the highest microhabitat niche value had the broadest local vertical distribution (*H. purpurescens*), and the species with the lowest microhabitat niche values had the narrowest vertical distributions (*H. argus*, *H. hortulanus*, *H. chloropterus* and *Labrichthys unilineatus*).

Geographic range and niche breadth

Thalassoma lunare had the largest geographic range, closely followed by *Halichoeres hortulanus* (Fig. 5). *H. purpurescens* and *Paracheilinus filamentosus* had the smallest ranges of the 11 species, with range sizes roughly a third of that of *Thalassoma lunare* (Fig. 5). There were no relationships between niche values (depth, reef zones, microhabitats or diet) and geographic range. *H. purpurescens* was the most generalised species in all 4 niche dimensions, but it had the most restricted geographic range. In contrast, *H. hortulanus*, which is an apparent depth specialist, had the second widest geographic range.

Local abundance and geographic range

There was no relationship found between local abundance and geographic range in the 11 labrid species examined ($r^2 = 0.045$, $p = 0.533$). Species with wide geographic ranges did not seem to have high local abundances in this study.

DISCUSSION

The results from this study suggest that ecological versatility in fishes from the family Labridae in Kimbe Bay, Papua New Guinea, plays an important role in the distribution and abundance of species on a local scale. A broad use of microhabitats was associated with high local abundances and broad local depth distributions, suggesting that the degree

of specialisation on a microhabitat-level may well restrict the abundance and distribution of juvenile wrasses. However, no relationship was found between local abundance and distribution. In addition, on a larger (geographic) scale, ecological versatility does not appear to be important for limiting the distribution of species.

The results of this study provide limited support for Brown's (1984) hypothesis linking specialisation and abundance. We found that use of a broad range of microhabitats was associated with high local abundances and broad depth distributions. On the other hand, no other relationship between niche breadth and local distribution and abundance was found for the remaining resources. On a larger scale, no associations between either niche breadth or local abun-

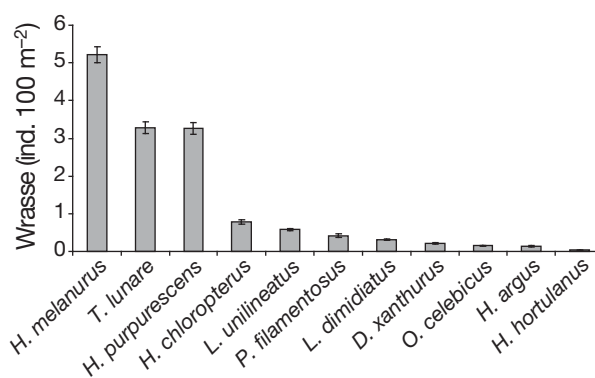


Fig. 4. Mean densities of 11 species of juvenile wrasses on coral reefs in Kimbe Bay, Papua New Guinea. Error bars are ± 1 SE. For full species names see Fig. 2

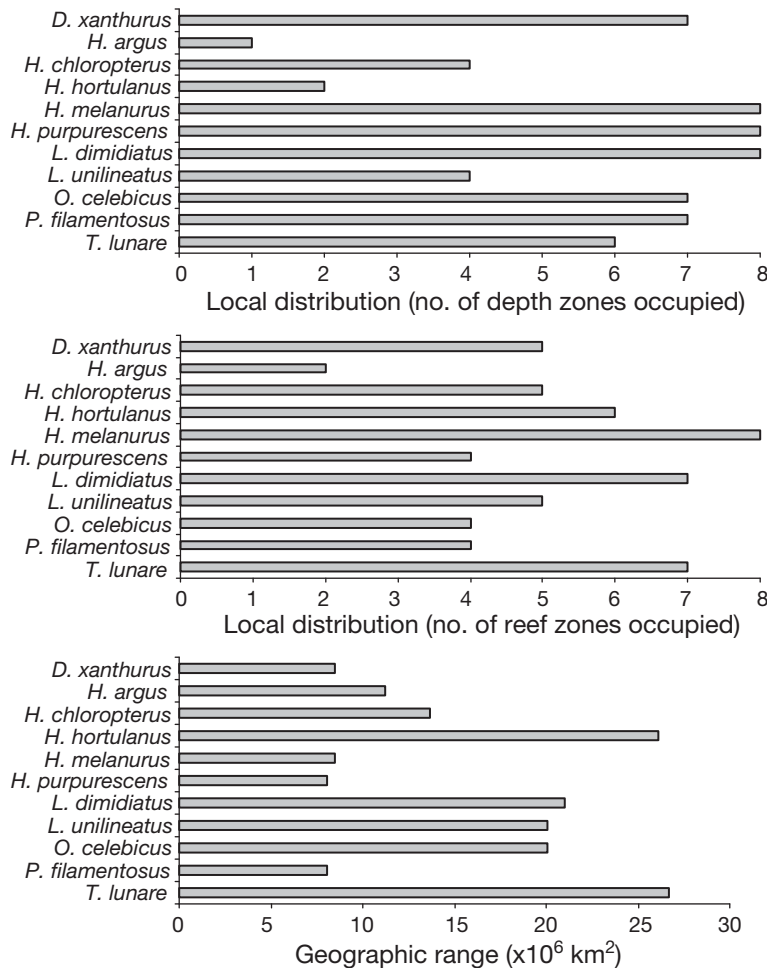


Fig. 5. Local and geographic distributions for 11 species of juvenile wrasses in Kimbe Bay, Papua New Guinea. Local distribution expressed as vertical (no. of depth zones) and horizontal (no. of reef zones) distribution. Geographic distribution expressed as geographic range (km²). For full species names see Fig. 2

dance and geographic range were detected. The local patterns are consistent with previous studies in Kimbe Bay, Papua New Guinea, on coral dwelling gobies (Munday 2000), triggerfish (Bean et al. 2002) and cardinalfish (Gardiner & Jones 2005), all of which found that the most specialised species had the lowest local abundances. Microhabitat specialisation was also found to restrict the depth distribution among a group of triggerfish (Bean et al. 2002).

Many of the niche parameters measured, including habitat zone, depth and microhabitat, are likely to co-vary. Hence, further work is required to identify the specific resources limiting abundance. Given that microhabitat availability is known to change with depth, experimental studies are required to distinguish the roles of microhabitat and depth per se on local abundance (e.g. Srinivasan 2003). Also, this

study focused on juveniles, and given that versatility may change with ontogeny, the applicability of our results to adult fishes requires further investigation.

According to Brown's (1984) hypothesis, the low local abundance and narrow distribution displayed by many taxa can be explained by high resource specialisation. Specialists are expected to have lower local abundances and limited distributions because the extent of suitable resources is likely to be more restricted for specialised species than for species that can use a variety of resources. *Halichoeres hortulanus* appeared to be the most specialised species in terms of microhabitat and was also found to be the least abundant species with a restricted depth range in our study, suggesting that this species' local abundance and distribution might be limited by the restricted number of microhabitats available on the reef. *H. hortulanus* was always found in sand or rubble gutters in shallow water, and its abundance and distribution are likely to be restricted by the availability of its preferred microhabitat. The 3 most abundant species in our study (*H. melanurus*, *Thalassoma lunare* and *H. purpurescens*) were the most generalised in terms of microhabitat usage. They also displayed the broadest depth distributions. Being a microhabitat generalist most likely allows a species to access and move among a broader range of resources in other niche dimensions than a microhabitat specialist would,

hence enabling it to achieve higher local abundance. However, if a species specialises on the most abundant resources, then specialisation and low abundance need not be associated (Jones et al. 2002). For example, the anemonefish *Premnas biaculeatus* on the Great Barrier Reef, Australia, and on coral reefs of Papua New Guinea is a habitat specialist but is still the most abundant species of anemonefish in these regions (Fautin & Allen 1992).

According to Brown (1984), species-abundance distributions and species-range distributions should have the same mechanistic basis, i.e. both should be dependent on the versatility displayed by a particular species. Gaston (1996) suggested that species-range-size distributions are simply species-abundance distributions on a larger scale. Species with narrow habitat requirements might have difficulty in colonis-

ing new areas and hence have a limited range. Geographic range was correlated with niche breadth in a number of terrestrial studies (Gaston 1988, e.g. Inkinen 1994, Pyron 1999, Hughes 2000), but not in the present study. Instead, contrary to predictions, there was no relationship between niche breadth and geographic range for any of the resources, i.e. resource specialisation does not limit the geographic range of these species. Similar results were found by Jones et al. (2002) for 2 groups of coral reef fishes, anemonefishes and butterflyfishes. There is, however, some support for the specialisation/geographic range relationship in coral reef fishes from a study by Hawkins et al. (2000), where depth, habitat and distribution data on coral reef fish were compiled from a number of sources. Hawkins et al. (2000) showed that there was a trend for restricted-range species to have narrower depth ranges; however, only 57% of restricted-range species had high levels of microhabitat selectivity.

The results from the present study suggest that the geographic ranges of coral reef fishes are not limited by the level of ecological versatility. Although specialised coral reef fish are most often locally rare, high levels of specificity do not necessarily result in narrow geographic ranges. Factors other than niche specialisation appear to be of greater importance in restricting geographic distributions. For example, the dispersal and establishment abilities of a species can strongly influence its geographic range. It has been suggested that factors such as dispersal characteristics may be more influential as spatial scale increases (Palmer et al. 1996). The time larvae spend in the plankton stage varies between species (Victor 1986, Cowen 1991, Leis 1991) and may have a profound effect on species geographic range. However, other factors including competition, predation, climatic/environmental tolerances and historical events have also been suggested to limit the distribution of species (Gaston 1996), and should not be ignored in models predicting patterns of distribution in coral reef fish.

It has been suggested that resource specialists may be more prone to rapid decline and extinction than generalists, due to their inability to switch resources when preferred resources become scarce (Jones et al. 2002). Several studies have found that the abundance of coral dwelling fishes rapidly declined when corals they inhabited declined in numbers (Bouchon-Navaro et al. 1985, e.g. Munday et al. 1997, Munday 2004). Munday (2004) also found that specialists suffered proportionately greater losses in abundance than generalists when coral habitat declined. Most

juvenile wrasses in our study displayed some level of microhabitat specialisation. Furthermore, we found a positive relationship between microhabitat specialisation and abundance, suggesting that the most specialised species are likely to be at risk if their preferred habitats decline.

More than half of the species were predominantly associated with live coral, particularly branching and bushy hard corals. Juvenile fish are often found associated with live branching corals, as these provide shelter and protection from predators (Öhman & Rajasuriya 1998, Öhman et al. 1998). Branching corals are more sensitive to disturbances such as storms and coral bleaching than corals of other growth forms (Woodley et al. 1981, Hughes & Connell 1999) and hence many of the labrid species in this study may be at risk if such disturbances increase as predicted. Major changes are occurring on coral reefs around the world, and 50% of the remaining coral reefs are in decline (Wilkinson 2004). On several inshore reefs in Kimbe Bay, there was a gradual decline in branching coral cover from 1997 to 2001 (Jones et al. 2004). Recent studies have highlighted the effect of degraded coral reefs on fish communities, and particularly fish species that are dependent on live coral for food or habitat are negatively affected (Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008, Wilson et al. 2009).

Many of the juvenile wrasses in this study also displayed high dependency on a single food item (haracticoid copepods). Clearly, these species are potentially at risk should degradation of reefs extend to this resource. While loss of coral may have little impact on planktonic food, the effects of coastal runoff and ocean warming on the food-base requires further investigation.

In conclusion, this study provides support for the hypothesis that ecological versatility in juvenile wrasses can have implications for the abundance and distribution on a local scale. However, contrary to Brown's hypothesis, we found no relationship between ecological versatility and geographic range or between species abundance and distribution. Species are not versatile in all resources at once, and hence a relationship between versatility and abundance/distribution is dependent on which resource is being investigated. For many reef fishes, high levels of habitat specialisation may well restrict local abundances, but levels of specialisation are unlikely to limit geographic distributions. Other factors that are likely to be important for limiting geographic distributions in these communities, such as relative dispersal ability, require further investigation.

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