

E. Vytopil · B.L. Willis

Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity

Received: 24 November 1998 / Accepted: 21 June 2001 / Published online: 11 October 2001
© Springer-Verlag 2001

Abstract The role of microhabitat in structuring epifaunal communities on four corals of varying morphology in the genus *Acropora* (*A. millepora*, *A. hyacinthus*, *A. pulchra*, *A. formosa*) was determined on two fringing reefs in the central Great Barrier Reef. Greater abundance and species richness of epifauna on tightly branched coral species in comparison to their rarity or absence on open-branched species suggests that protection afforded by complex habitats is important in structuring coral epifaunal communities. Within species, neither total colony space nor live surface area of corals was correlated with either the abundance or species richness of associated epifauna. However, space between branches significantly affected the size of *Tetralia* crabs associated with different coral species. Patterns in the size distribution of *Tetralia* on two species of *Acropora* suggest that crabs select coral hosts according to branch spacing, changing host species as they grow larger.

Keywords *Acropora* · Epifauna · Coral morphology · Microhabitat · *Tetralia*

Introduction

The role of habitat structure in determining the distribution and abundance of organisms and their ecological relationships has been shown to be important in terrestrial communities (Wiens and Rottenberry 1981; Scheibe 1987), but has received comparatively little attention in the marine environment (reviewed in McCoy and Bell 1991; Boulton et al. 1992; Caley 1993; Holbrook and Schmitt 1995; Clarke 1996; Lewis 1997). The few marine

studies that have investigated the influence of habitat structure have focused primarily on coral reef fishes, organisms that typically forage and move throughout a range of habitats (Gladfelter et al. 1980; Sale and Douglas 1984; Sale 1991; Sebens 1991; Chabanet et al. 1997). In contrast, marine invertebrates may be tightly associated with sessile hosts, and therefore the shape and complexity of habitats are more likely to affect their distribution and abundance (Williams 1984; Stoner and Lewis 1985; reviewed in McCoy and Bell 1991). Consequently, studies of closely associated organisms may contribute new insights into the role of habitat complexity in structuring marine communities.

Branching hermatypic corals typically contain assemblages of invertebrate and fish epifauna and represent discrete microhabitats that vary in complexity according to species and branching pattern. Coral form creates variations in the physical environment that may have potentially important implications for associated epifaunal organisms, including: (1) increased refuge from predation (Edwards and Emberton 1980; Bell and Woodin 1984; Sebens 1984; Witman 1985; Caley and St John 1996); (2) increased potential for niche separation (Hendrix 1980; August 1983; Giller 1984; Begon et al. 1990; Schluter and Ricklefs 1993); and (3) increased modification to the local hydrodynamic environment (Chamberlain and Graus 1975; Helmuth et al. 1997). For example, retarded water flow associated with tightly branched coral morphologies may create microhabitats characterised by relative hypoxia, increased thickness of the boundary layer, and reduced delivery of organic matter from the surrounding environment. Alternatively, reduced water flow may enhance the nutritive environment by increasing concentrations of nitrate, nitrite, and bacterial and flagellate biomass (Schiller and Herndl 1989). Thus variations in the physical environment created by coral form also may have important implications for the nutritional resources available to associated epifauna.

Studies of coral epifaunal communities have been largely restricted to the Pocilloporidae, a family exhib-

E. Vytopil · B.L. Willis (✉)
Marine Biology Department,
James Cook University,
Queensland 4811, Australia
E-mail: bette.willis@jcu.edu.au
Fax: +61-7-67251570

iting limited variation in form. A variety of investigations have suggested that patterns in epifaunal abundance, size, and species richness are related to the physical dimensions of pocilloporid coral microhabitats (Barry 1965; Patton 1974; Abele and Patton 1976; Castro 1978; Coles 1980; Tsuchiya and Yonaha 1992). Corals of the family Acroporidae exhibit a greater range of morphologies, exhibit higher species richness, and are numerically more abundant on mid- and outer-shelf reefs of the Great Barrier Reef (GBR); however, knowledge of their epifaunal communities and the relationship of these communities to the physical attributes of the coral habitat is comparatively scarce. Patton (1994) provided a qualitative comparison of epifaunal communities among *Acropora* species, but it is difficult to determine whether observed patterns should be attributed to differences among coral colonies, species, morphologies, or reef location. Glynn (1983b) suggested that crabs of the genus *Tetralia* are not found in acroporid species with widely spaced branches, but details of coral species and sample sizes are unclear. Finally, Sin (1999) determined that species of *Tetralia* crabs discriminate between corymbose (bushy) acroporid species, although no comparisons were made with host species having other morphologies. Thus our current understanding of the role of coral microhabitat in structuring *Acropora* epifaunal communities is poor.

In the present study we document epifaunal communities in four species of the coral genus *Acropora* to determine the consistency of coral–epifaunal associations among host species and morphologies. We quantify gradients in physical characteristics of coral species to identify physical attributes of the coral microhabitat that influence the structure of epifaunal communities. Our results provide the first quantitative insights into the role of coral morphology in structuring epifaunal communities.

Methods

Study site

The composition of epifaunal communities present in acroporid corals was determined at reefs adjacent to Orpheus and Pelorus Islands in the Palm Island group (18°35'S, 146°29'E). The two reefs are located approximately 12 km off the coast of mainland Australia in the central section of the GBR and both are exposed to the prevailing southeasterly trade winds. Sampling was conducted between October and November 1996.

Sampling coral host species and epifauna

Epifaunal communities were examined in four species of *Acropora* (*A. millepora* [Crossland 1952], *A. hyacinthus* [Dana 1846], *A. pulchra* [Brook 1891], and *A. formosa* [Dana 1846]) which encompass a range of branching patterns. Colonies of *A. hyacinthus* form flat plates with short, densely packed branches. *A. millepora* forms bushy colonies with longer, less densely spaced branches. *A. pulchra* and *A. formosa* colonies are typically arborescent with widely

spaced branches. *A. millepora*, *A. hyacinthus*, and *A. pulchra* were collected from shallow habitats (1–3 m, reef flat and crest), and *A. formosa* was collected from deeper reef slope habitats. Being found on the reef slope, *A. formosa* typically experiences less wave energy, emersion, and variability in physical parameters, especially temperature and salinity, than the other three species.

Two sites were sampled at each of the two reefs. Three colonies of each *Acropora* species were sampled from each site ($n=12$ colonies per species). All colonies collected were within the diameter range 150–350 mm. Corals were chiselled from the substratum, enclosed in plastic bags to prevent loss of epifauna, and transported back to Orpheus Island Research Station where they were maintained in aquaria. All corals were returned to the field following defaunation and collection of a series of colony measurements.

Macroscopic epifauna (>1 mm length) were removed from coral colonies by gentle prodding with thin rods and identified at least to family. Xanthid crabs were identified to species. Their size (i.e. carapace length measured as the distance from the median point of the frontal border to the posterior margin of the carapace), sex, and reproductive status (bearing or not bearing eggs) were also recorded. Species and numbers of associated epifauna were compared between the two arborescent species, *A. formosa* (reef slope) and *A. pulchra* (reef flat), to distinguish whether patterns in their epifaunal assemblages are attributable to host morphology or environmental regime.

Physical attributes of the coral microhabitat

To identify the physical attributes of coral hosts that affect epifaunal community structure, we compared three parameters that had the most potential to characterize the physical nature of the microhabitat provided by the plate (*A. hyacinthus*), bushy (*A. millepora*), and arborescent (*A. pulchra*) forms. *A. formosa* was not included in this comparison since its morphology is represented by *A. pulchra*. The parameters measured included total interbranch volume (i.e. total space among branches within the confines of the coral head periphery); cross-sectional area of interbranch space (i.e. area between adjacent branches); and live surface area. Total interbranch space limits the epifaunal biomass able to fit within the colony. Interbranch cross-sectional area limits the maximum size an individual may reach. Live surface area both limits the amount of habitable substrata and determines the quantity of nutritional resource available to mucus-feeding epifauna such as *Tetralia*.

Total interbranch space was measured on the corals from which epifauna had been removed. Measurements were made by determining the difference between the volume of water displaced by colonies that were wrapped tightly in a plastic bag and the same colonies immersed without a wrapping ($n=12$ measurements per growth form). Values were normalized as a percentage of the total colony volume.

Interbranch cross-sectional area was calculated for five areas (located approximately 10 mm from the base of coral branches) on nine random colonies for each of the three species of *Acropora*. Cross-sectional area was calculated as the product of two interbranch distances (the first arbitrarily selected and the second perpendicular to the first). This rectangular shape best describes the space available for habitation. Measurements were made on skeletons from James Cook University's Palm Island Coral Collection to avoid stressing live corals used in the study. Mean measures of cross-sectional space were correlated with size of crabs that were randomly selected from the appropriate coral species.

The surface area of coral colonies was determined indirectly from two calibration relationships. To determine the surface area typical of each morphological type and to avoid sacrificing large numbers of live corals, we applied a wax coating technique (modified from Stimson and Kinzie 1991; R. Jones, personal communication) to a subset of 16 colonies for each species from the Palm Island Collection. Colonies were briefly dipped in melted paraffin

wax at a temperature of 70 °C and lightly shaken to remove drips. This sealed the surface area of the coral skeletons and ensured that each had a surface of identical adhesion quality while maintaining surface topography. Once the primary surface had been coated and the initial mass determined, colonies were re-dipped and the increase in mass due to a second surface coat was determined.

Calibration relationship for determining surface area

To relate the increase in mass between wax coatings to surface area, a calibration relationship was determined using seven nylon cylinders of a known surface area ranging from 1,403.95 to 60,528.12 mm². The regression relationship between increases in mass and surface area for the cylinders ($y = 1,927.40x + 8,351.67$, $r^2 = 0.880$, $P = 0.0002$) was then used to calculate the skeletal surface area of each coral colony. Three surface area determinations were made on each colony and the mean mass increase was calculated (wax was removed between coatings by dipping in hot water). To relate surface area to projected planar surface area, the same subset of coral skeletons was photographed from directly above. Using an image analysis program (Mocha 1.2, Jandel Scientific), the exterior edges of each colony were traced from the photographs and the projected planar surface area was calculated (in square millimeters). Mean skeletal surface areas from the wax method were plotted against the planar surface area and a regression equation was calculated for each species (*A. millepora* $y = 0.002x - 0.022$, $r^2 = 0.97$; *A. hyacinthus*, $y = 0.002x - 3.482$, $r^2 = 0.95$; *A. pulchra* $y = 0.001x + 2.065$, $r^2 = 0.85$).

Estimation of surface area of experimental corals

Photographs were taken of each coral used in the epifaunal study before it was returned to the field. From these images, the planar surface area of each colony was calculated using a metric scale included in the photographs. The appropriate equation describing the relationship between planar surface area and skeletal surface area for each colony was then used to estimate the expected increase in mass due to waxing. From this predicted mass increment, the live surface area was estimated using the regression equation for the relationship between increase in mass due to waxing and surface area.

Data analysis

Three-factor hierarchical ANOVA was used to test for differences in the mean abundance and species richness of epifauna per coral head, as well as for differences in the mean size of *Tetralia*. The factors 'coral species' and 'reef' were fixed and orthogonal, and 'site' was random and nested within species. A Shannon-Weiner index of diversity was used to describe species richness and evenness of epifauna on different coral host species.

One-way ANOVA was used to test for significant differences in mean interbranch volume and cross-sectional interbranch space between *Acropora* species. Interbranch volume was quantified as a percentage of total colony volume; thus, data were arcsin transformed so that the underlying distribution would conform to the ANOVA assumption of normality. In cases where the null hypothesis was rejected, a Tukey's test was used to analyse differences between growth forms a posteriori. Surface area data were not appropriate for ANOVA since each estimate of colony surface area was calculated as a range that incorporated the 95% confidence intervals for both the conversion of planar surface area to predicted mass increase due to waxing and the conversion of predicted mass increase to colony surface area. Given that differences in surface area for each morphological type were clearly different, estimates of mean (\pm second order SE) surface areas were compared graphically. Regression analysis was used to determine if epifaunal abundance, species richness, and *Tetralia* size varied as a function of absolute interbranch volume, cross-

sectional area of interbranch space, or live surface area within a colony morphology.

Discussion and results

Epifaunal communities differed among the four *Acropora* species in terms of both abundance of individuals ($F = 32.35$; $P < 0.001$) and species richness ($F = 30.81$; $P < 0.001$; Fig. 1). Epifaunal abundance was greatest for the two more tightly branched corals, *A. millepora* and *A. hyacinthus*, and least for the two open branched corals, *A. pulchra* and *A. formosa*. This pattern was consistent across all reefs and sites.

Very few macroscopic free-living epifauna were found within colonies of *A. pulchra* and *A. formosa*, while fauna in the tightly branched corals were dominated by a variety of crabs in the genus *Tetralia* (*T. fulva*, *T. rubridactyla*, *T. nigrolineata*, *T. cinctipes*) and pontiniine shrimps in the family Palaemonidae (*Coralliocaris graminea*, *C. venusta*, and *C. nudirostris*) (Fig. 2). *Periclimenes* species of shrimps and *Gobiodon* fishes were largely restricted to colonies of *A. millepora*. *Tetralia* and *Gobiodon* species occurred most commonly as a single pair per colony, with *Tetralia* occurring as a heterosexual crab pair in 90% of occurrences in colonies of *A. millepora* and *A. hyacinthus*. Other decapod epifauna typically occurred in greater numbers. These patterns were again consistent at both reefs and at all sites. In particular, *Tetralia* crabs were never found on *A. pulchra* or *A. formosa* (Fig. 2). Thus the distribution and abundance of *Tetralia* are highly predictable for these four species of *Acropora*. The limited occurrence of *Tetralia* on only two of the four species of *Acropora* that factors other than genus of the host contribute to distribution patterns of epifauna.

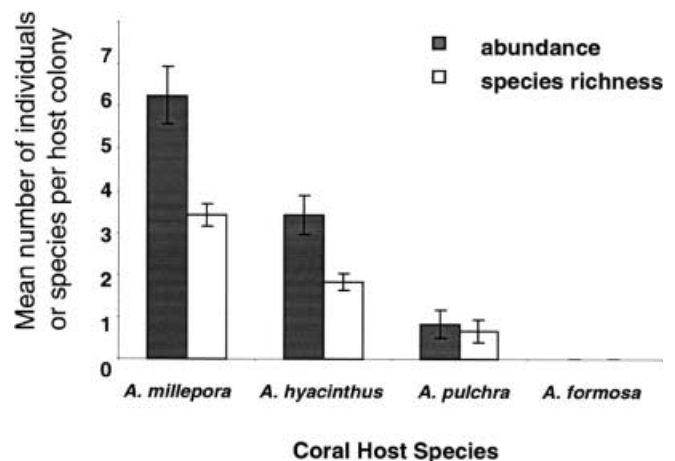


Fig. 1 Mean total abundance and species richness of epifauna per host colony associated with the corals *Acropora millepora*, *A. hyacinthus*, *A. pulchra*, and *A. formosa* ($n = 12$ colonies per coral species)

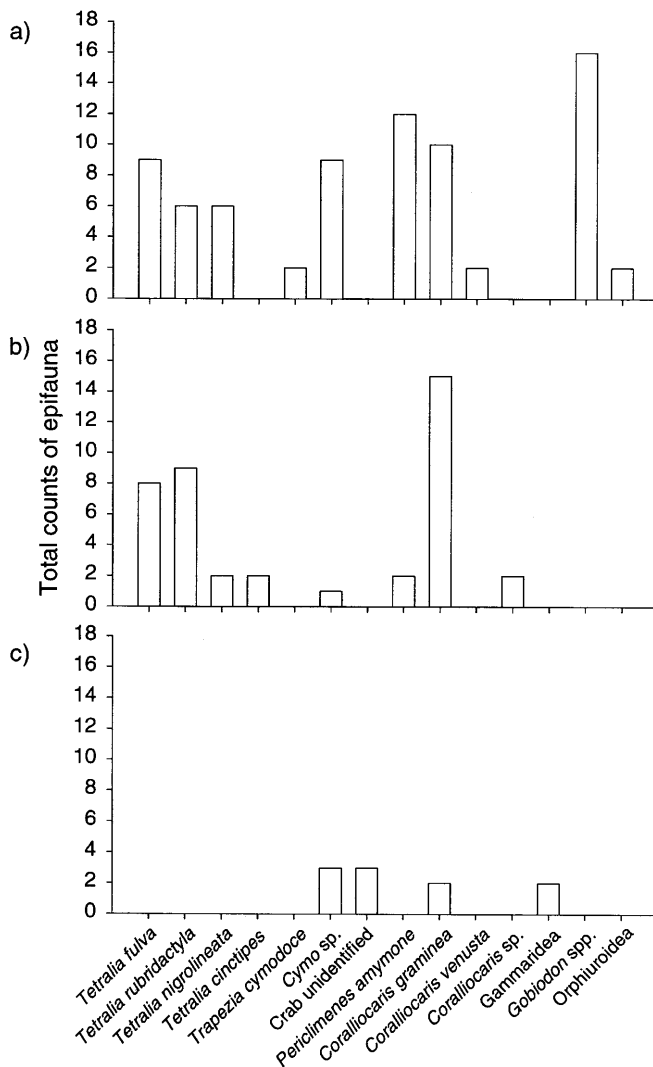


Fig. 2 Distribution and abundance of epifauna in branching corals differing in spacing and height of branching: **a** bushy form (*A. millepora*); **b** plate form (*A. hyacinthus*); **c** arborescent form (*A. pulchra*). No free-living epifauna were found in colonies of *A. formosa* (arborescent). Colony samples are pooled for all reefs and sites ($n = 12$ colonies per coral species)

T. fulva was the most commonly occurring crab (present on 40% of colonies) within the genus, followed by *T. rubridactyla* (36%), *T. nigrolineata* (18%), and *T. cincitipes* (9%) (Fig. 2). The rarity of *Trapezia* crabs in our study supports suggestions that *Trapezia* are host specific to pocilloporid corals (Patton 1966; Knudsen 1967; Glynn 1983a, 1983b; Galil 1987; Glynn 1987). In addition to the species observed in this study, Patton (1994) observed shrimps of the genus *Jocaste* and *Philarius* and fishes of the genus *Caracanthus*. The lack of these fauna in our sampling may be attributable to differences in location since they were observed in greatest abundance at Lizard Island and Tjouw Reef in the northern GBR. Despite the geographic separation of the corals sampled by Patton, overall animal frequencies and species lists are remarkably similar to the present

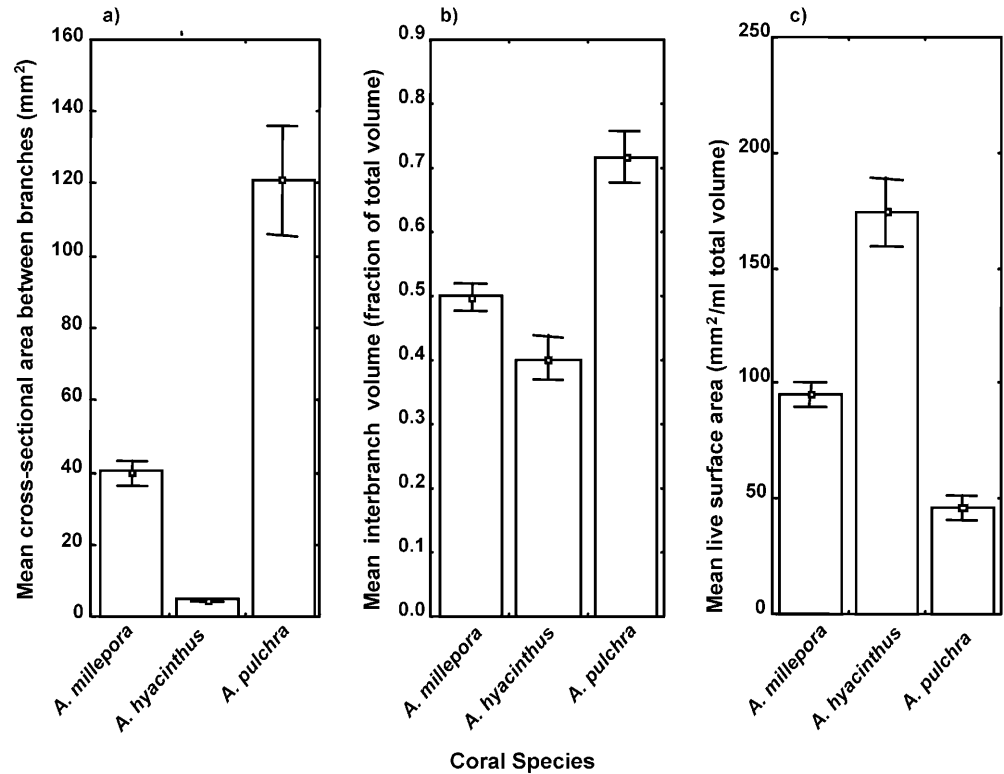
study, suggesting a consistent epifaunal assemblage associated with *Acropora* corals that is minimally affected by differences in locality.

Measurements of the physical characteristics used to describe coral microhabitat differed significantly between the three morphologies. For a given colony volume, *A. pulchra* (arborescent) had significantly more total interbranch space than *A. millepora* (bushy) and *A. hyacinthus* (plate) (Fig. 3b; $F = 24.33$; $P < 0.001$ Tukey's test). For a given colony volume, *A. hyacinthus* (plate) had the greatest surface area and *A. pulchra* (arborescent) the least (Fig. 3c). Finally, *A. pulchra* provides the greatest cross-sectional interbranch areas and *A. hyacinthus* the smallest (Fig. 3a; $F = 15.57$; $P < 0.001$, Tukey's test).

Differences in the physical characteristics of the coral microhabitat are reflected in the epifaunal communities they support. Abundance and species richness of epifauna were least on *A. pulchra* and *A. formosa*, species that provide reduced surface area for habitation despite providing a greater total volume of living space within colonies (i.e. openness of branching). Similarly, Edwards and Emberton (1980) determined that increased branching openness was correlated with decreased numbers of decapod epifauna in colonies of *Stylophora pistillata*. Although the present study is limited by lack of replication for the bushy and plate coral morphologies, the low abundance and species richness found on the two arborescent species, despite their occurrence in different habitats, suggest that morphology is more important than environmental regime or host species in determining patterns in epifaunal communities.

The almost complete absence of epifauna on arborescent morphologies suggests that it is not necessarily total habitable substratum and associated nutritional resources that determine their distributions. Since the greater epifaunal species richness in *A. hyacinthus* and *A. millepora* is associated with increased surface area per unit colony volume and this equates to increased branching complexity, we suggest that morphology is important because it determines habitat complexity. In particular, increased habitat complexity of the plate and bushy forms is associated with increased potential for niche separation and resource partitioning by epifauna. Also, the decreased habitat complexity of arborescent morphologies reduces habitat suitability as a refuge from predation or wave action. *Cymo* crabs were one of the few free-living epifauna living on *A. pulchra*, possibly because of their inconspicuous coloration and their ability to maintain a strong hold on coral branches (Fig. 2). We suggest that branch tightness is most important for the protection of associated epifauna, a suggestion corroborated by observations that vulnerable juvenile stages of *Tetralia* recruit exclusively onto colonies of *A. hyacinthus*, the coral with the tightest branching pattern (Vytopil, unpublished data). Alternatively, it is possible that more frequent disruption of the boundary layer of

Fig. 3 Mean colony dimensions of the coral species *A. millepora*, *A. hyacinthus*, and *A. pulchra*: **a** cross-sectional interbranch area; **b** interbranch volume; and **c** skeletal surface area ($n = 12$ colonies per species). Both interbranch volume and live surface area are presented as a fraction of total colony volume



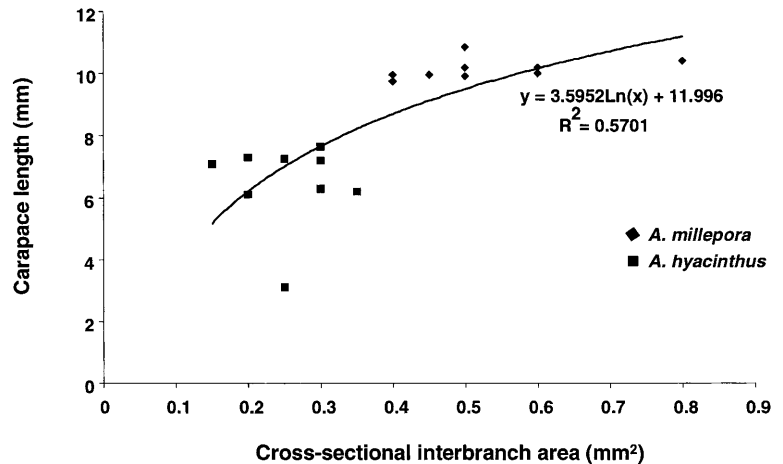
arborescent corals, and thus dispersal of associated nutritional resources (e.g. bacterial), makes this morphology less attractive to epifauna. However, the similarity in epifauna between the two arborescent corals, despite differences in hydrodynamic regime associated with their habitats, suggests that boundary layer characters are not as important as refuge from predation in determining community structure of coral epifauna.

Furthermore, we suggest that surface area per unit volume (i.e. habitat complexity) rather than surface area per se is the key to determining epifaunal distributions. Within species, there was no correlation between estimated live surface area of corals and either abundance or species richness of epifauna (r^2 ranged from 0.000 to 0.203 for six tests and corresponding P values ranged from 0.940 to 0.280). There was also no obvious relationship between total interbranch volume and either the abundance or species richness of epifauna on the four *Acropora* species (abundance: $r^2 = 0.10$, $P = 0.14$; species richness: $r^2 = 0.11$, $P = 0.14$). These findings imply that the total habitable space provided by a coral (ranging from 150 to 350 mm diameter in this study) and the amount of nutritional resource (proportional to the live surface of corals) available to mucus-feeding epifauna such as *Tetralia* (Barry 1965; Gotelli and Abele 1983; Galil 1987; Stimson 1990; Patton 1994) are not important determinants of epifaunal community composition for a given coral morphology. These results differ with those of studies that compared variation in pocilloporid decapod epifaunal communities with coral

size. For example, Tsuchiya and Yonaha (1992) determined that the abundance and species richness of epifauna on *Pocillopora damicornis* are proportional to coral head dimensions, and no epifauna were found in colonies with a total interbranch volume of less than 1.5 cm³. Similarly, other studies have found positive correlations between species richness and/or abundance of decapods with either coral size or interbranch volume within a species (Barry 1965; Patton 1974; Coles 1980). In none of these studies, however, was an attempt made to experimentally measure the live surface area of the coral. Barry (1965) and Abele and Patton (1976), in their multispecies studies, calculated surface area relative to volume using the relationship $A = V^{2/3}$. However, the relationship between area and volume will differ between corals with varying branching densities both within and between species, and such a simple characterisation of habitat does not take into account the structural complexity likely to affect the occurrence of epifauna. This study is the first to relate precise measures of coral surface area to patterns in epifaunal communities.

The almost exclusive occurrence of *Tetralia* crabs as a single heterosexual pair per coral head, despite a two-fold range in coral volume, indicates that colony size does not determine their distribution. Territorial defense has been shown to influence the structure of epifaunal communities in pocilloporid corals independent of colony size (Barry 1965; Huber and Coles 1986; Glynn 1983b; Huber 1987; Tsuchiya and Yonaha 1992). It has been argued that *Trapezia* crabs defend

Fig. 4 Relationship between *Tetralia* carapace length and cross-sectional interbranch area in colonies of *A. millepora* and *A. hyacinthus*. Line represents a log-linear regression. Crabs were pooled for all *Tetralia* species ($n=18$ crabs)



much larger territories than is needed for their resource requirements in order to increase reproductive output relative to excluded crabs that must locate a vacant colony or aggressively remove other crabs before they can reproduce (M. Huber, personal communication). Thus coral size appears to be inconsequential to patterns of occurrence of territorial symbiotic crabs.

The size of *Tetralia* crabs did not differ as a function of total interbranch volume or live surface area (measures of colony size) but was significantly correlated with cross-sectional area of interbranch space ($r^2=0.5706$, $P=0.0003$, Fig. 4). Thus, the mean size of *Tetralia* crabs was significantly greater on *A. millepora* (mean = $9.75 \text{ mm} \pm 0.14$) than on *A. hyacinthus* (mean = $6.19 \text{ mm} \pm 0.22$) ($F=240.36$, $P<0.001$; Fig. 4) and this pattern was consistent at all reefs and sites. Differences in the mean size of crabs associated with these two corals suggest that crabs either reach different maximum sizes in each species or are migrating between coral species as they grow. We conclude that the latter explanation is more likely to be correct. Patterns in recruitment of crabs onto defaunated corals show that crabs migrate into cleared habitat space, and smaller crabs prefer the tighter habitat space provided by *A. hyacinthus*, but as they grow, they must find habitats with greater living space (e.g. colonies of *A. millepora*) (Vytopil, unpublished data).

The lack of correlation between crab size and total coral surface area or volume suggests that colony size is inconsequential in determining crab size. Rather, it is the size of habitat spaces that physically restricts the maximum size of crabs, and this parameter remains constant as colony size increases. Barry's (1965) observation that animals reach a much larger size in coral species that are less compartmentalised supports our results. However, in other studies of pocilloporid corals, sizes of *Trapezia* crabs and *Pocillopora* heads were found to be significantly correlated (Castro 1978; Adams et al. 1985; Huber and Coles 1986), although it was suggested that this only applies to smaller colonies

where resources are limiting (Huber 1983; Huber and Coles 1986).

In summary, this study indicates that interspecific differences in coral morphology strongly influence the symbiotic epifaunal communities they host, with tightly branching species providing the best habitat structure. This is most likely related to the higher protection afforded by their more complex habitat structure. The cross-sectional area between branch clusters limits the maximum size of sheltering epifauna, but no other dimension of coral colonies appears to influence the abundance or species richness of epifaunal communities at the within-species level. The consistent occurrence of one heterosexual pair of *Tetralia* crabs per coral suggests that territorial behaviour, rather than coral size, primarily determines their patterns of abundance and distribution. These patterns were consistent between reefs and sites on a local geographic scale in the central GBR. Given that epifaunal communities may play an important role in maintaining the health of their coral hosts (Glynn 1983a, 1983b; Glynn 1987; Stimson 1990; Rinkevich et al. 1991; Pratchett et al. 2000; Pratchett 2001; Vytopil, unpublished data), a much greater understanding of the rich, albeit inconspicuous, biodiversity residing in corals is warranted.

Acknowledgements We wish to thank M. Huber for his intellectual guidance and practical support, P. Castro and S. Bruce for assistance with crustacean identifications, and P. Munday for *Gobiodon* identifications. K. Anthony, A. Baird, J. True, and N. Moltshaniwskyj assisted greatly with statistical advice. This is contribution number 187 of the Coral Group at James Cook University.

References

- Abele LG, Patton WK (1976) The size of coral heads and the community biology of associated decapod crustaceans. *J Biogeogr* 3:35–47
- Adams J, Edwards AJ, Emberton H (1985) Sexual size dimorphism and assortive mating in the obligate coral commensal *Trapezia*

- ferruginea* Latreille (Decapoda, Xanthidae). Crustaceana 48(2):188–194
- August PV (1983) The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64(6):1495–1507
- Barry K (1965) Ecological study of the decapod crustaceans commensal with the branching coral *Pocillopora damicornis* var. *nobilis* Verrill. Thesis, University of Hawaii
- Begon M, Harper JL, Townsend CR (1990) *Ecology*, 2nd edn. Blackwell, Boston
- Bell SS, Woodin SA (1984) Community unity: experimental evidence for meiofauna and macrofauna. *J Mar Res* 42:605–632
- Boulton AJ, Peterson CG, Grimm NB, Fisher SG (1992) Stability of an aquatic macro-invertebrate community in a multi-year hydrologic disturbance regime. *Ecology* 73(6):2192–2207
- Caley MJ (1993) Predation, recruitment and the dynamics of communities of coral-reef fishes. *Mar Biol* 117:33–43
- Caley MJ, St John J (1996) Refuge availability structures assemblages of tropical reef fishes. *J Anim Ecol* 65:414–428
- Castro P (1978) Movements between coral colonies in *Trapezia ferruginea* (Crustacea: Brachyura), an obligate symbiont of scleractinian corals. *Mar Biol* 46:237–245
- Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. *Coral Reefs* 16:93–102
- Chamberlain JA, Graus RR (1975) Water flow and hydrochemical adaptations of branched reef corals. *Bull Mar Sci* 25(1):112–125
- Clarke RD (1996) Population shifts in two competing fish species on a degrading coral reef. *Mar Ecol Prog Ser* 137:51–58
- Coles SL (1980) Species diversity of decapods associated with living and dead reef coral *Pocillopora meandrina*. *Mar Ecol Prog Ser* 2:281–291
- Edwards A, Emberton H (1980) Crustacea associated with the scleractinian coral, *Stylophora pistillata* (Esper), in the Sudanese Red Sea. *J Exp Mar Biol Ecol* 42:225–240
- Galil B (1987) The adaptive functional structure of mucus-gathering setae in trapezid crabs symbiotic with corals. *Symbiosis* 4:75–86
- Giller PS (1984) Species diversity trends – theories and hypotheses. In: Dunnet GM, Gimingham CH (eds) *Community structure and the niche*. Chapman and Hall, London, pp 93–111
- Gladfelter WB, Ogden JC, Gladfelter EH (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. *Ecology* 61:1156–1168
- Glynn PW (1983a) Increased survivorship in corals harbouring crustacean symbionts. *Mar Biol Lett* 4:105–111
- Glynn PW (1983b) Crustacean symbionts and the defence of corals: coevolution on the reef? In: Nitecki MH (ed) *Coevolution*. University Chicago Press, Chicago, pp 111–178
- Glynn PW (1987) Some ecological consequences of coral–crustacean guard mutualism in the Indian and Pacific Oceans. *Symbiosis* 4:303–324
- Gotelli NJ, Abele LG (1983) Community patterns of coral-associated decapods. *Mar Ecol Prog Ser* 13:131–139
- Helmuth BST, Timmerman BEH, Sebens KP (1997) Interplay of host morphology and symbiont microhabitat in coral aggregations. *Mar Biol* 130:1–10
- Hendrix SD (1980) An evolutionary and ecological perspective of insect fauna of ferns. *Am Nat* 115:171–196
- Holbrook SJ, Schmitt RJ (1995) Compensation in resource use by foragers released from interspecific competition. *J Exp Mar Biol Ecol* 185:219–233
- Huber ME (1983) *Ethology and population biology of Trapezia*, a xanthid crab symbiotic with reef corals, with special reference to territoriality and speciation. PhD Thesis, Scripps Institute of Oceanography, University of California, San Diego
- Huber ME (1987) Aggressive behaviour of *Trapezia intremedia* Miers and *T. digitalis* Latreille (Brachyura: Xanthidae). *J Crust Biol* 7(2):238–248
- Huber ME, Coles SL (1986) Resource utilisation and competition among the five Hawaiian species of *Trapezia* (Crustacea, Brachyura). *Mar Ecol Prog Ser* 30:21–31
- Knudsen JW (1967) *Trapezia* and *Tetralia* (Decapod, Brachyura, Xanthidae) as obligate ectoparasites of pocilloporid and acroporid corals. *Pac Sci* 21:51–57
- Lewis AR (1997) Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Mar Ecol Prog Ser* 161:37–50
- McCoy ED, Bell SS (1991) Habitat structure: the evolution and diversification of a complex topic. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure, the physical arrangement of objects in space*. Chapman and Hall, London
- Patton WK (1966) Decapod *Crustacea commensal* with Queensland branching coral. *Crustaceana* 10:271–295
- Patton WK (1974) Community structure aiming animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In: Vernberg WB (ed) *Symbiosis in the sea*. The Belle W. Baruch Library in Marine Science no. 2. University of South Carolina Press, Columbia, pp 219–243
- Patton WK (1994) Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef, Australia. *Bull Mar Sci* 55(1):193–211
- Pratchett M (2001) Influence of coral symbionts on feeding preferences of crown-of-thorn starfish. *Mar Ecol Prog Ser* 214:111–119
- Pratchett M, Vytopil E, Parks P (2000) Coral crabs influence the feeding patterns of crown-of-thorn starfish. *Coral Reefs* 19:36
- Rinkevich B, Wolodarsky Z, Loya Y (1991) Coral–crab association: a compact domain of a multilevel trophic system. *Hydrobiologia* 216/217:279–284
- Sale PF (1991) Habitat structure and recruitment in coral reef fishes. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure, the physical arrangement of objects in space*. Chapman and Hall, London, pp 197–210
- Sale PF, Douglas WA (1984) Temporal variability in the community structure of fish on coral reef patches and the relation of community structure to reef structure. *Ecology* 65:409–422
- Scheibe JS (1987) Climate, competition, and the structure of temperate zone lizard communities. *Ecology* 68(5):1424–1436
- Schiller C, Herndl GJ (1989) Evidence of enhanced microbial activity in the interstitial space of branched corals: possible implications for coral metabolism. *Coral Reefs* 7:179–184
- Schluter D, Ricklefs RE (1993) Species diversity, an introduction to the problem. In: Ricklefs RE, Schluter D (eds) *Species diversity in ecological communities*. University of Chicago Press, Chicago
- Sebens KP (1984) Water flow and coral colony size: interhabitat comparisons of the octocoral *Acyonium siderium*. *Proc Natl Acad Sci USA* 81:5473–5477
- Sebens KP (1991) Habitat structure and the community dynamics in marine benthic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure, the physical arrangement of objects in space*. Chapman and Hall, London, pp 211–234
- Sin T (1999) Distribution and host specialization in *Tetralia* crabs (Crustacea: Brachyura) symbiotic with corals in the Great Barrier Reef, Australia. *Bull Mar Sci* 65(3):839–850
- Stimson JS (1990) Stimulation of fat body production in the polyps of the coral *Pocillopora damicornis* by the presence of mutualistic crabs of the genus *Trapezia*. *Mar Biol* 106:211–218
- Stimson JS, Kinzie RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J Exp Mar Biol Ecol* 153:63–74
- Stoner AW, Lewis III FG (1985) The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *J Exp Mar Biol Ecol* 94:19–40
- Tsuchiya M, Yonaha C (1992) Community organisation of associates of the scleractinian coral *Pocillopora damicornis*: effects of colony size and interactions among the obligate symbionts. *Galaxea* 11:29–56

- Wiens JA, Rottenberry JT (1981) Habitat associations and community structure of birds in shrub steppe environments. *Ecol Monogr* 51(1):21-41
- Williams AH (1984) The effects of Hurricane Allen on back reef populations of Discovery Bay, Jamaica. *J Exp Mar Biol Ecol* 75:233-243
- Witman JD (1985) Refuges, biological disturbance and rocky subtidal community structure in New England. *Ecol Monogr* 55(4):421-445