DISTRIBUTION AND ECOLOGY OF ANIMALS ASSOCIATED WITH BRANCHING CORALS (*ACROPORA* SPP.) FROM THE GREAT BARRIER REEF, AUSTRALIA

Wendell K. Patton

ABSTRACT

Head-forming branching corals of the genus *Acropora* provide discrete live coral habitats which contain a distinct fauna of small shrimp, crabs, and fishes. Associates were collected from 141 colonies of five *Acropora* species at four localities in eastern Australia. These corals had a mean volume of 4.9 1, and contained an average of 4.5 associate species and 9.1 individuals. Almost all animals collected were obligatory associates of *Acropora,* that could be placed in six groups of related species. Crabs of the genus *Tetralia* were present on all 141 corals, *Gobiodon* fish on 89%, *Coralliocaris* shrimp on 55%, *Cymo* crabs on 38%, shrimp of the *Philarius/Periclimenes lutescens* group on 34%, and *Jocaste* shrimp on 33% of the corals examined. Twenty species of obligate associate were collected at least five times. The most common species, *T. fulva,* was found on 76% of the corals, followed by *C. superba* on 46%, and *G. quinquestrigatis* on 33%. Examination of stomach contents and feeding behavior showed that the shrimp and crabs feed on coral mucus and, to lesser and varying degrees, zooplankton, other suspended material, and coral tissue. The fish feed on zooplankton and coral tissue. Most associate species generally occurred as single male-female pairs. Distribution data indicate that established pairs exclude conspecifics, obligate associates of their own group, and facultative associates. Discrimination between *Acropora* species is likely for several species of *Gobiodon. Tetralia* pairs seem to break up and reform, while pairs of *Gobiodon* may be stable for long periods. Associate abundance declines with coral depth, seems quite similar over large areas of the Great Barrier Reef, and in one case changed over time. The evolution of coral association and the factors influencing community composition are discussed.

Branching stony corals of the genus *Acropora* (Family Acroporidae) and the genera *Pocillopora, Seriatopora* and *Stylophora* (Family Pocilloporidae) are common in the Indo-Pacific. The spaces between their branches typically contain various decapod crustaceans and fish, most of which are specialized obligatory associates of living coral. The obligate associates of the two coral families show resemblances and in some cases are closely related, but are specifically distinct (Garth, 1964; Patton, 1966; Tyler, 1971). Pocilloporid associates have been much more intensively investigated than those found within *Acropora* spp. Previous studies dealing with the taxonomy, biology and distribution of *Acropora* associates include those of Bruce (1976a, 1977), Eldredge and Kropp (1982), Galil (1986a, 1986b, 1988), Garth (1974, 1984), Glynn (1983), Lassig (1981) and Tyler (1971).

Since *Acropora* is abundant on many reefs, the species that it shelters are clearly common, albeit inconspicuous, components of the reef community. The goals of this investigation were to characterize the *Acropora* associates of eastern Australia, study the effects of host species, location and depth on community composition, and to begin an understanding of the biology and ecology of these interesting animals.

METHODS

Collecting Methods.—The basic method of this study was the careful collection of associates from individual, living heads of branching *Acropora*. Most corals were obtained at low tide from reef flats,
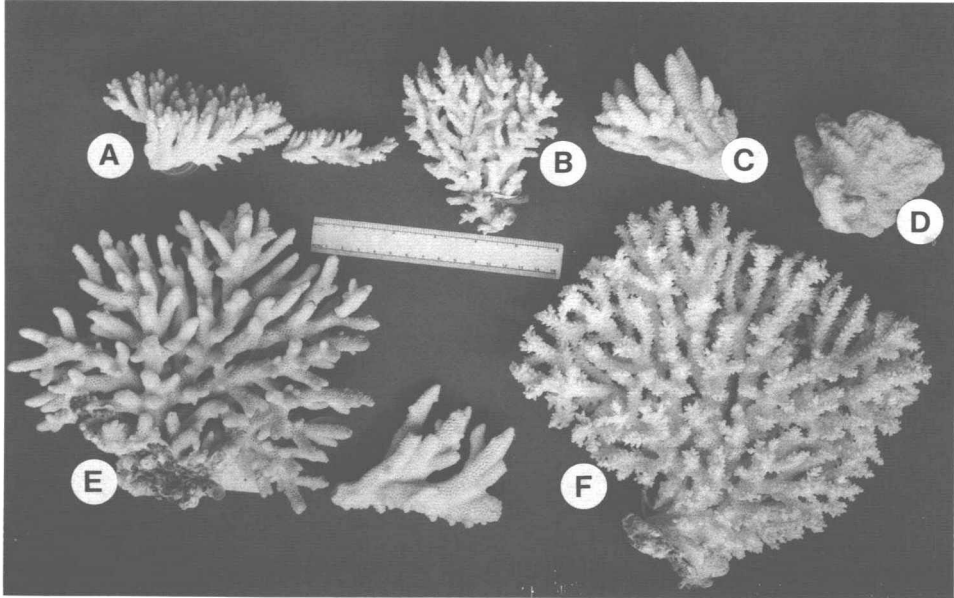
Figure 1.   Examples of *Acropora* spp. from which associates were collected. (A) Samples from two
A. hyacinthus plates with differing branch lengths. (B) *A. elseyi,* volume—0.5 l. (C) Fragment of *A.
humilis* showing consolidated base. (D) Piece of an *A. cuneata* colony. (E) *A. millepora,* a 1.6 l coral
and a fragment of a larger colony. (F) *A. nasuta,* volume—2.2 l.

back reefs or reef slopes. The coral to be collected was pried from the substrate into a screen (1 mm
mesh) and quickly lifted from the water onto a portable table. (The collections from 6 m depth were
made with SCUBA, and the coral enclosed in a cloth or plastic bag, broken loose and brought to the
surface). Each colony was measured, then broken apart. Branches were examined individually, and
animals on the coral or screen were preserved in 70% ethanol.

Coral volume was estimated by multiplying the coral's length, width and height. Associated animals
were identified in the laboratory. Carapace width was measured for crabs and total length for fish.
Crabs were sexed by the obvious difference in the shape of the abdomen. Male shrimp were recognized
by dissecting off a second pleopod and noting the presence of an appendix masculina or, in a few
cases, simply by the shape of the abdominal pleura. I was not able to distinguish the sex of fish by
external features and so the designation of a "pair" merely indicates the presence of two individuals
of the same species and same general size. Parametric statistics were employed for analysis as the
data sets that were examined did not depart significantly from normalcy.

Host Species and Collection Sites.—Currently 73 *Acropora* species, representing a wide variety of
growth forms, are recognized from the Great Barrier Reef (Veron and Wallace, 1984). Head-forming
corals provide the most shelter and contain the most associates. I thus concentrated collection efforts
on larger colonies of three common head-forming species: *A. millepora, A. humilis* (including, in all
likelihood, specimens of the closely related *A. digitifera*), and *A. nasuta* (probably also including some
A. cerialis). These species have a flattened colony form, grow from a living attachment plate, and,
almost regardless of size, tend to be composed entirely of living coral. The three species can be readily
distinguished despite their similarity in growth form (Fig. 1). Associates were collected from five other
Acropora species with differing patterns of growth. *A. elseyi* and *A. valida* have thinner branches than
the previous species and form upright, bushy clumps. The principle branches of *A. elseyi* have well
developed side branches and, in larger colonies, are often dead at their base. *A. hyacinthus* produces
flat, thin-branched plates of varying branch lengths. Reef flat colonies of *A. cuneata* are large and
open, with blunt, widely spaced branches. Lastly, associates were obtained from coralla of *A. divar-
icata* that grew outward as side-attached open frameworks of anastamosing branches. Photographs and
detailed discussion of Australian *Acropora* species can be found in Wallace (1978), Veron and Wallace
(1984), and Veron (1986).

The collections discussed here were made from four well-separated localities. 1) Heron Island reef
and the adjacent Wistari Reef (23°26'S, 151°55'E) near the southern end of the Great Barrier Reef

province. April 1971 for data in Table 1. 2) Keeper Reef, a mid-shelf platform reef of the Great Barrier Reefs (18°45'S, 147°16'E). September and October 1979. 3) The fringing reef between Palfrey and South Islands, adjacent to Lizard Island (14°42'S, 145°27'E). August and October 1979. 4) Behind Tijou Reef, a northern, outer shelf reef (13°10'S, 143°58'E). October 1979.

Field Experiments.—Data on the persistence of associates on given corals and on the recolonization of emptied colonies were obtained from marked coral heads on the reef flat at Heron Island. Each coral was separated from the substrate and tied to a piece of plastic hose. After examination or collection of the associates present, the hose was placed over an iron stake driven into the reef, holding the coral firmly in place until the next examination. Short term permanence and recolonization experiments were done in July and August 1982, a long-term permanence study from May 1992 to July 1993, and a 2 month recolonization study from July to September 1993.

Feeding Habits.—I observed the behavior of animals in the laboratory when placed with possible foods. Since the decapods are more active nocturnally, most observations were done at night and under reduced light. Carmine particles were added to coral to facilitate the observation of mucus collection and its subsequent identification within stomachs. Gut contents were analyzed for preserved field collected specimens, and for animals that had been placed with various potential food sources in the laboratory. Quantitative experiments on *Artemia* capture involved placing individual associates overnight in 800 ml beakers containing 100 ml sea water and 25 *Artemia* nauplii. After 16 h I counted the nauplii remaining.

CORAL ASSOCIATE GROUPS

The great majority of animals collected, could be placed in six groups of related species of obligate associate (i.e., species found only on living *Acropora,* Fig. 2). These groups (three of shrimp, two of xanthoid crabs, and one of fish), their most frequently collected species, and two additional obligate associate species, are briefly discussed below.

CORALLIOCARIS GROUP. In this genus of shrimp the body is somewhat flattened dorso-ventrally and the chelae of the second legs are modified as snapping structures and can produce loud clicks. The walking legs extend laterally and have a blunt, hoof-like structure at the base of the dactyl, allowing a firm grip on the coral surface. Two quite different species were commonly collected. *C. superba* (Dana, 1852) has a brilliant white body and typically occurs in male-female pairs. The less conspicuous *C. graminea* (Dana, 1852), is green with thin, longitudinal gold stripes. It is usually found in groups, with adult females outnumbering males (Bruce, 1976b; present study). Grasping behavior is strongly developed as individuals in a dish of water will readily attach to fingers placed next to them. The dactyls of the second legs are curved and contain a socket that fits over a plunger in the fixed finger. Snapping of the claw produces a loud sound, and, deduced by the vibrations set up in glass containers, exerts considerable force against an object it touches. One cheliped is always somewhat larger than the other and both are relatively larger in males than in females. *C. graminea* is normally found on a vertical *Acropora* branch with chelae hanging down and the tail pointing upwards.

JOCASTE GROUP. This shrimp genus is similar to *Coralliocaris* in the shape of the body and the dactyls of the walking legs, but differs in the structure of the first two pairs of legs. One of the second legs resembles those of *C. superba* and produces a snap when the fingers are closed, while the other is smaller with a flattened chela (Fig. 2). The two very similar species, *J. japonica* (Ortmann, 1890) and *J. lucina* (Nobili, 1901), are distinguished by minor details of morphology (Patton, 1966) and are the smallest and least conspicuous of the *Acropora* associates. They are usually found attached to a coral branch up away from the base (Bruce, 1976a), but are good swimmers and very agile when disturbed.

PHILARIUS SPP./*PERICLIMENES LUTESCENS* GROUP. Although currently placed in two genera, these shrimps have a similar form, share several features (Bruce, 1982), and must be closely related. The much enlarged second legs are extended outwards with the claw open at intruders and are also used in locomotion as the animal crawls through the coral. *Philarius gerlachei* (Nobili, 1905) and *Philarius imperialis* (Kubo, 1940) typically attach to vertical coral branches, while the much larger *Periclimenes lutescens* (Dana, 1852) is found between branches at the base of the colony.

TETRALIA GROUP. These small crabs have a smooth, often brightly colored, exoskeleton, and were found within virtually all the *Acropora* examined. The species are readily distinguished by color (Patton, 1966) and morphology (Galil, 1986a, 1986b, 1988). *Tetralia cinctipes* Paulson, 1875, *T. fulva* Serène, 1984, *T. nigrolineata* Serène and Dat, 1957, *T. rubridactyla* Garth, 1969, and the less common, *Tetraloides nigrifrons* (Dana, 1852) were recognized in the present collections.

Tetralia have been found living within deformations in *Acropora* colonies (Eldredge and Kropp, 1982), but not in the present study. *Tetralia* are weak responders to invading specimens of the coral-

Table 1. Summary of occurrences of associated animals in collections of five species of *Acropora* at four Great Barrier Reef localities. (The number given is the number of corals in a particular collection that contained a given species of associate. Obligate associates are indicated by species name. Facultative associates are grouped as Other shrimp, crabs, etc.)

Collection:	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	Total number of occurrences
Coral species:	A. humilis			A. millepora					A. nasuta					A. valida	A. elseyi	
Collection site:	Heron I.	Lizard I.	Tijou R.	Heron I.	Keeper R. (shallow)	Keeper R. (6M)	Lizard I.	Tijou R.	Heron I.	Keeper R. (shallow)	Keeper R. (6 M)	Lizard I.	Tijou R.	Heron I.	Lizard I.	
No. of corals collected:	7	9	6	4	3	2	15	5	22	10	26	11	4	7	10	141
No. of corals that contained:																
Shrimp																
Coralliocaris graminea	1	—	—	—	—	—	—	—	5	—	—	3	—	2	1	12
Coralliocaris superba	2	4	4	1	2	—	12	3	13	4	4	8	2	1	5	65
Coralliocaris venusta	1	—	—	—	—	—	—	—	2	1	1	—	—	—	—	5
Jocaste japonica	1	1	2	2	—	1	8	5	—	2	4	6	4	1	—	37
Jocaste lucina	2	—	1	—	—	—	2	1	2	3	—	1	—	1	—	13
Philarius gerlachei	2	3	6	—	1	—	1	—	6	3	—	1	—	—	—	23
Philarius imperialis	—	3	—	—	2	—	3	1	2	2	2	3	—	—	—	18
Periclimenes lutescens	—	—	—	1	1	—	5	—	—	—	2	—	—	—	2	11
Other shrimp	3	4	—	1	1	1	1	—	4	4	5	1	—	—	2	27
Crabs																
Tetralia cinctipes	—	1	1	—	—	—	—	—	—	—	—	1	—	—	2	5
Tetralia fulva	4	7	2	3	—	2	13	4	15	9	23	9	4	4	8	107
Tetralia nigrolineata	1	2	—	1	—	—	1	—	5	1	3	3	—	1	6	24
Tetralia rubridactyla	2	2	3	—	3	—	1	1	2	1	—	—	—	2	1	18
Tetralia sp.	—	—	—	—	—	—	—	—	3	—	—	—	—	—	2	5
Tetraloides nigrifrons	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	2
Cymo deplanatus	1	2	—	1	1	2	9	3	4	4	4	7	—	—	3	41
Cymo melanodactylus	1	1	—	—	—	—	4	2	6	—	—	4	—	1	1	20
Domecia glabra	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	3
Other crabs	2	1	—	2	—	—	—	—	7	1	4	—	1	3	3	24
Other Crustacea	—	—	—	—	—	—	1	—	1	1	5	—	1	1	2	12

Table 1. Continued

| Collection:	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	Total number of occurrences
Coral species:	*A. humilis*			*A. millepora*						*A. nasuta*				*A. valida*	*A. elseyi*	
Collection site:	Heron I.	Lizard I.	Tijou R.	Heron I.	Keeper R. (shallow)	Keeper R. (6M)	Lizard I.	Tijou R.	Heron I.	Keeper R. (shallow)	Keeper R. (6 M)	Lizard I.	Tijou R.	Heron I.	Lizard I.	
No. of corals collected:	7	9	6	4	3	2	15	5	22	10	26	11	4	7	10	141
Fish																
Gobiodon axillaris	—	—	—	2	—	—	4	1	6	—	1	4	—	1	—	19
Gobiodon ceramensis	2	3	—	—	—	—	7	3	2	—	—	3	2	1	1	24
Gobiodon histrio	—	—	—	2	2	1	4	1	3	2	6	4	—	—	—	25
Gobiodon micropus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	9
Gobiodon quinquestrigatus	5	5	—	—	—	—	—	—	9	4	15	1	3	4	—	46
Gobiodon sp.	—	1	4	—	—	—	—	—	3	3	4	—	1	—	—	16
Caracanthus unipinna	—	—	—	—	—	—	2	5	1	—	—	1	2	—	—	11
Other fish	1	—	—	—	—	—	—	1	1	1	1	1	—	—	—	6
Coral volume (liters)																
Mean	4.5	4.6	3.6	4.1	7.0	3.7	6.4	5.9	4.7	5.3	4.6	7.4	5.1	4.1	1.9	
Median	2.9	3.9	4.1	4.4	6.0	—	6.1	5.2	3.5	5.1	4.6	7.8	4.6	3.6	1.7	
Species per coral																
Mean	4.7	4.7	4.0	4.0	4.3	3.0	5.4	7.2	4.6	5.2	3.2	5.6	5.3	3.6	4.6	
Median	4.0	4.0	4.0	4.0	4.0	—	6.0	7.0	5.0	4.5	3.0	6.0	5.5	4.0	3.5	
Obligate associate individuals per coral																
Mean	9.3	7.9	7.2	5.5	7.0	5.5	10.3	15.6	8.1	6.6	4.3	11.6	11.3	6.9	7.8	
Median	8.0	7.0	6.5	5.5	7.0	—	9.0	16.0	8.0	6.0	4.0	10.0	11.0	7.0	5.5	
Facultative associate individuals per coral																
Mean	6.0	0.7	0.0	1.0	2.7	0.5	0.3	0.4	1.4	1.4	0.8	0.2	0.5	0.7	1.2	
Median	0.0	0.0	0.0	0.5	0.0	—	0.0	0.0	1.0	1.0	0.0	0.0	0.0	1.0	0.0	
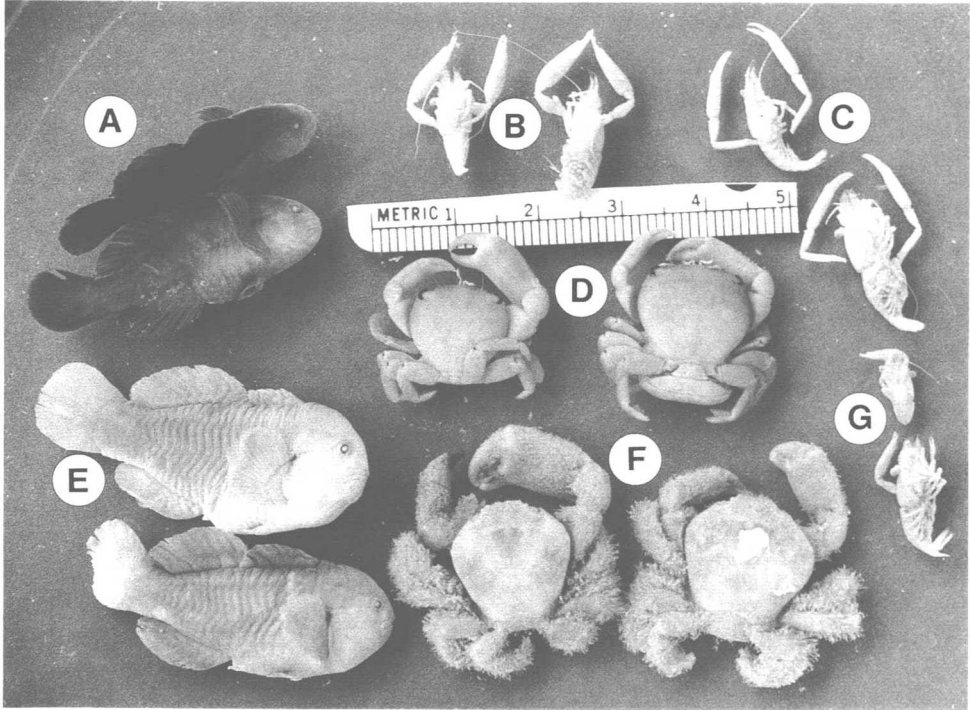
Figure 2.   Naturally occurring pairs of coral associate. (A) *Gobiodon quinquestrigatus.* (B) *Coralliocaris superba.* (C) *Philarius imperialis.* (D) *Tetralia fulva.* (E) *Gobiodon axillaris.* (F) *Cymo deplanatus.* (G) *Jocaste japonica.*

eating, crown-of-thorns starfish, *Acanthaster,* and do not show the vigorous nipping of tube feet seen in several species of *Trapezia* inhabiting pocilloporid corals (Pearson and Endean, 1969; Glynn, 1983).

The chelipeds of *Tetralia* and *Tetraloides* are quite dimorphic (Fig. 2). The smaller one is slender and mobile with long, thin, spoon-tipped fingers. The large cheliped is stout with relatively shorter tooth-bearing fingers and is relatively larger in males than females. In *Tetralia,* the large cheliped has a hair-filled depression on the outside of the palm that sweeps up coral mucus (Galil, 1987). The dactyls of the walking legs have a hoof-like ridge on their inner surface that seems well suited to grasping coral, and above this, rows of spines used in mucus gathering (Knudsen, 1967).

CYMO GROUP. These crabs have a shaggy appearance due to abundant hairs on the legs (Fig. 2) and, when disturbed, move through the colony in a slow, sloth-like manner. Continuing the sloth analogy, there is evidently considerable algal growth on the hairs, as most individuals dropped into alcohol in a collecting jar instantly generated a strong yellow-green color. The walking legs lack the specializations for coral life seen in *Tetralia.* The chelipeds are strongly dimorphic. The smaller one has rather slender spoon-tipped fingers and resembles the small chela of *Tetralia.* The larger chela is a heavy "crusher" with short, stout fingers. Two morphologically distinct species, *C. deplanatus* (Milne Edwards, 1873) and *C. melanodactylus* Dana, 1852, were abundant on Queensland *Acropora.*

GOBIODON GROUP. These small fish (Fig. 2) are predictable members of the *Acropora* community, with a pair inhabiting most coral heads (Table 2). Compared with typical gobies, they are quite laterally compressed and have eyes that tilt slightly upwards, seeming adaptations to life between vertical coral branches. *Gobiodon* individuals can be seen swimming within their coral when viewed underwater, but remain within it when the coral is collected or exposed by low tide.

Five *Gobiodon* species were recognized in this study. Two of these, *G. histrio* (Valenciennes, 1837), bright green with broad red cheek bars and rows of red spots on the body and *G. micropus* Günther, 1861, green with a pale patch and two dark bars above the eye, are figured in Randall et al. (1990). The most abundant species was *G. quinquestrigatus* (Valenciennes, 1837). Large individuals are dark brown, with an orange-red head bearing five thin blue stripes that remain visible in specimens pre-

Table 2. Size, frequency of occurrence, and population structure for the collections of common obligate associates (nine or more occurrences). Size in mm is mean for measured adult specimens (length from base of rostrum to tip of telson for shrimp, carapace width for crabs, and total length for fish). Frequency of occurrence data is derived from the 141 corals of Table 1.

Associate species	Size	Corals inhabited (No.)	Percent of occurrences consisting of differing numbers of individuals				
			1	2	3	4	5+
Shrimp							
Coralliocaris graminea	14	12	—	17	17	17	50
C. superba	15	65	31	63	6	—	—
Jocaste japonica	11	37	32	30	8	14	16
J. lucina	12	13	46	15	31	—	8
Philarius gerlachei	11	23	26	57	13	4	—
Ph. imperialis	12	18	39	61	—	—	—
Periclimenes lutescens	19	11	—	91	—	9	—
Crabs							
Tetralia fulva	11	107	9	85	3	—	2
T. nigrolineata	9	24	13	87	—	—	—
T. rubridactyla	9	18	11	89	—	—	—
Cymo deplanatus	11	41	44	51	2	2	—
C. melanodactylus	12	20	45	45	—	5	5
Fish							
Gobiodon axillaris	41	19	37	58	5	—	—
G. ceramensis	33	24	21	71	—	8	—
G. histrio	38	25	32	64	4	—	—
G. micropus	15	9	11	78	11	—	—
G. quinquestrigatus	28	46	30	63	2	2	2
Caracanthus unipinna	32	11	—	55	45	—	—

served in alcohol. In small specimens the head stripes are clearly visible, but the body is pale green. *G. ceramensis* (Bleeker, 1852) is the most drab-colored species, being uniformly light brown, except for a pale anterior ventral region. *G. axillaris* De Vis, 1884 has an olive green body with red cheek bars and a red line under the dorsal fin. Variation occurs in these most commonly encountered color patterns, and all species become paler at night. Comparison of the lengths of all paired specimens collected at Keeper, Lizard and Tijou Reefs revealed significant size differences (*t*-tests) between all species (Table 2).

The skin of *Gobiodon* lacks scales, is covered with a thick layer of mucus and contains clusters of toxin-producing cells (Hashimoto et al., 1974). Field observations by Lassig (1981) showed that *Acropora* colonies containing *Gobiodon* received far fewer bites from coral-eating butterfly fish (*Chaetodon* spp.) than did adjacent corals lacking these associates. However, *Acropora* cannot be absolutely dependent on defense by *Gobiodon*. Flourishing coral heads are found without them and *Gobiodon* rarely occurs on the plate-like *A. hyacinthus* and other species that by virtue of their shape are very exposed to predatory fish.

Two additional obligate associates of *Acropora* do not belong to the above groups. *Domecia glabra* Alcock 1899 is a little xanthoid crab. *Caracanthus unipinna* (Gray, 1831) is a small, laterally compressed fish, with a scaleless skin covered with small papillae. It is relatively deeper bodied and more muscular than the *Gobiodon* spp. and wedges itself between coral branches with opercular spines and pectoral fins (Hiatt and Strasburg, 1960; Schultz, 1966; Tyler, 1971; Randall et al., 1990). Hiatt and Strasburg (1960) state that this species does not leave its colony and feeds on other coral dwellers.

RESULTS

Associate Distribution Patterns.—ASSOCIATE ABUNDANCE AND DIVERSITY. When a colony of branching *Acropora* is examined under water, associates are frequently not apparent. Although 22 species of obligate associate, and numerous facultatives, were found in the present study, averaging the collections of Table 1 produces a coral with a volume of 4.9 l, but only 4.5 associate species and 9.1

individuals. This fauna is dominated by obligate associates. *Tetralia* crabs occurred on all 141 corals, while members of the *Gobiodon, Coralliocaris, Cymo, Philarius/Periclimenes lutescens,* and *Jocaste* groups were respectively present on 125, 77, 54, 48, and 46 of the corals examined. With regard to species, *T. fulva* was most common, occurring on 76% of the corals, followed by *Coralliocaris superba* on 46%, and *G. quinquestrigatis* on 33% (Table 1). Facultative associates, (that can be found in other habitats as well and indicated in the tables as Other shrimp, crabs, Crustacea and fish), were absent from most corals. However, the shrimp *Periclimenes amymone* sometimes occurred in large numbers; 29 individuals on a single coral produced the high mean for facultative associates in collection A of Table 1.

INTRASPECIFIC DISTRIBUTION PATTERNS. *C. graminea,* the *Jocaste* spp. and *Caracanthus unipinna* were frequently found in groups of three or more (Table 2). (Three males, i.e., animals with an appendix masculina, of *J. japonica* were found carrying small numbers of eggs, suggesting that this species is a protandrous hermaphrodite). The other associates occurred most often as a single male-female pair (Table 2). Pair members were generally quite large adults, and, in daytime collections, often found within a few centimeters of each other. In the decapods, the female pair member was usually larger. Several corals were found with a pair of *Tetralia* crabs among the branches and a juvenile underneath the coral holding to its base. Most other collections of three or more individuals of a normally pair-forming species involved several juveniles, or juveniles and a single adult.

Separation of a coral into regions or other features that restrict movement through it, seems to prevent the entire colony from being defended as a territory and allow co-existence of adult pairs. Thus, plates of *A. hyacinthus* with short, closely-spaced branches sometimes contained multiple pairs of *Tetralia,* while a large *A. humilis* from Lizard Island with an unusual branchless region in the center contained three pairs of *T. cinctipes* and two pairs of *C. melanodactylus,* with the conspecific pairs isolated in different regions of the colony.

It must be stressed that the data of Table 2 and the above discussion refer to relatively large and discrete *Acropora* colonies with a basal plate or closely spaced lower branches. Small corals, or those contributing to coral thickets, or open underneath, often lack associates or contain single individuals.

INTRAGROUP DISTRIBUTION PATTERNS. A typical open *Acropora* colony only contained adults of a single species per obligate associate group (Table 3). The great majority of co-occurrences of two species from within the same group, involved juveniles of one or both species. To test the hypothesis that the presence or absence of one member of a group influences the presence or absence of another, the abundance of group members among shallow-water corals was used to generate expected frequencies for the occurrence of 0, 1, 2, 3, or 4 group species per coral using a Poisson distribution (Table 3). Within each group, species were found together less frequently than expected by chance, i.e., the species within a group tended to avoid each other. These deviations were statistically significant for all but the *Jocaste* and *Cymo* groups.

The separation of a coral into regions that permitted co-existence of two pairs of the same species also allowed multiple pairs of the same group. Thus, the *A. humilis* with the branchless center mentioned above contained a pair of *T. fulva* and a pair of *T. rubridactyla,* in addition to the three pairs of *T. cinctipes.* Colonies of the rather small *A. elseyi* (Table 1:0) contained multiple members of the *Tetralia/Tetraloides* group (up to twelve individuals of three species). Only a single *Tetralia* pair would be found on much larger, "typical" *Acropora* heads. Two

Table 3. Occurrence of the six principal associate groups on "typical" shallow-water corals (Table 1). In each case, the observed distribution of the species of a group among the corals collected was compared with that generated by a Poisson distribution (in parentheses). The significance of deviations from random association of species was examined by chi-square tests. A. 96 collections of *A. humilis*, *A. millepora*, and *A. nasuta*. B. 49 collections of *A. humilis*, and *A. millepora*, since *Periclimenes lutescens* did not occur on *A. nasuta* (Table 1). C. 47 collections of *A. nasuta*. Some *Gobiodon* species were not found on *A. humilis* or *A. millepora* (Table 1).

Associate group	Species pool	Number of colonies that contained differing numbers of species from within the group					Probability
		0	1	2	3	4	
A. 96 corals							
Coralliocaris	3	33	59	3	1	—	0.001
		(47.3)	(33.5)	(11.9)	(2.8)	(0.5)	
Jocaste	2	57	35	4	—	—	N.S.
		(61.3)	(27.5)	(6.2)	(0.9)	(0.1)	
Cymo	2	51	38	7	—	—	N.S.
		(55.9)	(30.3)	(8.2)	(1.5)	(0.2)	
Tetralia	4	—	91	4	1	—	0.001
		(33.2)	(35.3)	(18.7)	(6.6)	(1.8)	
B. 49 corals							
Philarius/Periclimenes lutescens	3	22	24	3	—	—	0.05
		(26.6)	(16.3)	(5.0)	(1.0)	(0.2)	
C. 47 corals							
Gobiodon	4	6	31	10	—	—	0.001
		(15.9)	(17.2)	(9.3)	(3.4)	(0.9)	

features of *A. elseyi* seem responsible for this situation. Most importantly, the bases of the larger branches are often dead, creating sub-sets of live coral separated by dead coral barriers. These seem to be not readily crossed as each branch often contained its own *Tetralia* pair. Secondly, *A. elseyi* branches are thin, closely spaced, and contain sub-branches, that in addition to offering considerable shelter, must also interfere with movement through the colony. These natural experiments show that an *Acropora* colony can support more than two individuals per group and demonstrate that, for *Tetralia* at least, the one pair per group per colony rule is not the result of insufficient habitat or an absence of potential recruits. In an interesting exception to the one species per group rule, five large (mean volume = 9.8 l) *Acropora* colonies contained pairs of two species of *Gobiodon*. In each case, one of the species was *G. ceramensis*.

EFFECT OF THE HOST SPECIES. Although sample sizes are small, it does appear that most *Gobiodon* species are choosing among the species of *Acropora*. *G. ceramensis* was the only one collected from all five hosts (Table 1). Each other species was completely absent from one or more of the three intensively collected *Acropora*. The absence of the abundant *G. quinquestrigatus* from *A. millepora*, and of *G. micropus* from all corals except *A. elseyi*, are particularly striking. On the other hand, most decapods were found on all three *Acropora* species. *C. graminea* and *P. lutescens* provide possible cases of host discrimination, in view of their respective absence from *A. millepora* and *A. nasuta*.

Collection of associates from three *Acropora* species that do not form typical heads yielded results quite different from those of Table 1. Nine large colonies of *A. cuneata* (mean volume 12.5 l) with thick, widely spaced branches were collected from the reef flat at Heron Island. They contained a total of only 18 individual obligate associates (10 *Coralliocaris*, 3 *Jocaste*, 5 unpaired *Gobiodon*),

but more facultative associates (17 shrimp, 6 crabs and 21 fish). The faunas of "plates" of *A. hyacinthus* (Fig. 1) depended on the length and spacing of their vertical branches. Colonies with very short or very closely spaced branches lacked associates, those with more space sometimes contained multiple pairs of small *Tetralia* (often *T. cinctipes*), while taller colonies in sheltered habitats, although seldom containing *Gobiodon,* had a fauna approaching that of a "typical" head. The most surprising fauna was that of five side-attached, open colonies of *A. divaricata.* All contained *Trapezia cymodoce,* a usual associate of pocilloporid corals, and nothing else. In each case a pair was present, and on one, two juveniles as well.

EFFECT OF CORAL DEPTH. Colonies of *Acropora nasuta* collected from a depth of 6 m at Keeper Reef contained significantly fewer total associates than those obtained from shallow inter-tidal and barely subtidal locations (5.0 vs. 8.0, t = 2.89, P < 0.01; Table 1:K, J). The deeper *A. nasuta* had a smaller mean volume (4.6 vs. 5.3 l) than the shallow colonies, although not significantly so. In several cases their branches were more slender and closely spaced, which if anything, should increase the habitat for associates. Virtually every coral at each depth contained a pair of *Tetralia* and a pair of *Gobiodon.* Most of the decrease in total associates on the deeper corals was due to a marked reduction in the number of obligate shrimps and *Cymo* species (0.85 individuals per colony vs. 2.7 for the shallow corals, t = 3.90, P < 0.001). Interestingly, the three deep water corals with only a single, and thus perhaps transitory and less territorial specimen of *Tetralia,* averaged 2.0 individuals from the shrimp and *Cymo* groups, compared with 0.70 for the 23 colonies with a *Tetralia* pair.

GEOGRAPHIC PATTERNS. Although the relative frequencies of some associates on some corals varied considerably between localities (e.g., *Jocaste japonica, Cymo deplanatus,* and *Gobiodon quinquestrigatus* on the collections of *Acropora nasuta,* Table 1), the overall frequencies at the four sites were surprisingly similar. There was also considerable uniformity in the species lists. Of the 22 species recorded in Table 1, 18 were found at Heron Island, and another, *Domecia glabra,* was collected there previously (Patton, 1966). Thus only three species, *Tetralia cinctipes, Tetraloides nigrifrons* and *Gobiodon micropus,* seem to be restricted to more northerly (lower latitude) reefs.

Four of the eight possible comparisons (Table 1, H:D, H:E, H:G, M:J) between Tijou Reef and localities to the south showed significantly more obligate associate individuals per colony (*t*-tests) at Tijou. In no case did a Tijou collection have significantly fewer associates than another locality, nor were there any significant differences in coral volumes. Some, but not all, of this increase was due to the presence of the fish, *Caracanthus unipinna,* on half the *A. nasuta* colonies and all the *A. millepora* collected at Tijou Reef.

Stability of Associations.—In the short-term repeated examination of the associates inhabiting individual corals (Table 4), two-thirds of all the animals seen were on their host for successive observations and at least 12 of the 23 initially present seemed to be still there at the conclusion of observations 18 days later. On the other hand, seven pairs of decapod associates appear to have broken up during the observation period, and seven new pairs formed. Visual observation is, of course, less precise than collection and the amount of movement and pair rearrangement shown may be somewhat exaggerated. Still, the corals were fairly open and easy to observe and the numbers of associates found when the corals were

Table 4. Persistence of associates on four colonies of *Acropora* examined initially and 2, 4, 7, and 18 days after original observation. The five numbers indicate the number of individuals of each species present on each of the five observation days. Data were obtained by visual observation except for D18 when the associates were collected. Data for Day 4 for the *A. digitifera* colony were not recorded. All observations were made without knowledge of previous results.

Coral species: Coral volume (liters):	*A. nasuta* 0.64					*A. millepora* 1.2					*A. millepora* 3.6					*A. digitifera* 6.2			
Examination day:	0	2	4	7	18	0	2	4	7	18	0	2	4	7	18	0	2	7	18
Species of associate																			
Coralliocaris superba	1	1	1	2	2	–	–	–	–	–	–	2	2	1	1	1	1	1	1
Philarius spp.	–	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–	1	2	2
Periclimenes lutescens	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Other shrimp	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Tetralia fulva adults	2	2	1	2	2	2	2	1	2	2	2	2	1	2	1	2	2	2	2
T. fulva juveniles	–	1	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–
Trapezia cymodoce	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Cymo melanodactylus	–	–	–	–	–	1	2	1	2	2	1	1	–	–	–	1	1	–	–
Other crabs	1	–	1	1	1	–	–	–	–	1	1	1	1	2	2	–	2	1	1
Gobiodon axillaris	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–
G. histrio	2	2	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
G. quinquestrigatus	–	–	–	–	–	–	–	–	–	–	2	2	2	2	2	2	2	–	2
Species found	4	3	4	5	4	2	5	3	3	4	5	5	5	5	5	4	7	5	5
Individuals found	6	6	5	8	7	3	7	3	4	6	8	9	7	7	7	6	9	8	8
Individuals seemingly still present from previous observation	–	5	4	5	7	–	3	3	2	3	–	4	5	5	6	–	5	5	6
Number of apparent new arrivals since previous observation	–	1	1	3	–	–	4	–	2	3	–	5	2	2	1	–	4	3	2

collected at the end of the experiment differed little from those of the visual census. So, I expect that much of the indicated movement actually did take place.

Half of the pair break-up and formation events of Table 4 involved *Tetralia fulva*. In the longer term study of the duration of associations, only three of the eight corals that initially had a pair of *Tetralia* contained a pair of the same species when reexamined 13½ months later. For the six collections (Table 1:G, I, J, K, L, O) that contained eight or more pairs of *T. fulva*, only three of 12 possible instances (male:J; female:I, K) showed a significant correlation between crab carapace width and coral volume.

Gobiodon individuals on the other hand, may live with a particular coral for long periods. In the short-term study, two of three pairs were present over the 18 day observation period (Table 4). In the long-term study, five of the six corals with pairs of fin clipped *Gobiodon* contained pairs of the same species when reexamined 13½ months later, although only one of the 12 fish showed unambiguous indication of a previous fin clip. Before and after measurements of this fish, (and if they were indeed the same individuals, six other fish as well) showed little growth over this time period. In the two collections (Table 1) that contained eight or more pairs of a single species (*G. quinquestrigatus* on *A. nasuta*, Keeper Reef (6 m) and *G. micropus* on *A. elseyi*, Lizard Island, Table 1:K, O), the lengths of both pair members were significantly correlated with the volume of the host coral (r's > 0.75; N = 10, 8).

Recruitment.—In the winter-time recolonization experiment (Table 5), both 2 and 12 day recruitment periods generated significantly fewer obligate associates than were found in the initial collections. There were more obligate associates after 12

Table 5. Recruitment of associates into *Acropora* colonies on the reef flat at Heron Island, July–August, 1982. The initial inhabitants were removed from nine colonies (2 *A. humilis,* volumes of 3.2 and 4.5 liters; 3 *A. millepora,* 3.0, 4.8, 6.1; 3 *A. nasuta,* 0.9, 1.1, 5.0; 1 *A. valida,* 3.8). Subsequent collections were made from each coral at intervals of 2 or 12 days from the previous clearance. There were a total of 23 2-day collections and 9 (1 from each coral) 12-day collections. *Trapezia cymodoce,* a usual associate of pocilloporid corals is included with the facultative associates.

Species of associate	Initial collections (9)		Collections after 2-day recolonization period (23)		Collections after 12-day recolonization period (9)	
	Times found	Total individuals	Times found	Total individuals	Times found	Total individuals
Obligate associates						
Coralliocaris graminea	2	15	7	14	3	6
C. superba	3	6	1	1	—	—
C. venusta	—	—	2	2	—	—
Jocaste lucina	1	3	—	—	1	1
Philarius gerlachei	1	1	—	—	—	—
Tetralia fulva	6	12	7	10	4	5
T. nigrolineata	2	4	—	—	—	—
T. rubridactyla	1	2	1	1	—	—
Tetralia sp.	—	—	4	4	2	3
Cymo deplanatus	2	3	—	—	1	1
C. melanodactylus	2	3	3	3	2	2
Gobiodon histrio	5	10	—	—	1	1
G. quinquestrigatus	2	3	—	—	—	—
Gobiodon sp.	1	1	1	1	—	—
Facultative associates						
Other shrimp	2	2	5	8	5	7
Trapezia cymodoce	1	1	2	2	—	—
Other crabs	2	2	9	13	4	12
Other fish	—	—	4	6	3	3
Mean obligate associate individuals per coral		7.0		1.6		2.1
Mean facultative associate individuals per coral		0.6		1.3		2.4

than after 2 recruitment days, but not significantly so. Ovigerous females of most decapod obligate associates were found at all seasons and young individuals recently settled from the plankton are presumably present throughout the year. However, recruits were not abundant enough to immediately fill up emptied corals. Interestingly, there was a strong correlation between the initial abundance of the various species of decapod obligate associate and their abundance as subsequent recruits into the emptied corals ($r = 0.920$, N = 10). On the other hand, the recruitment by *Gobiodon* spp. was low in comparison to their initial abundance. *Gobiodon* nests were not specifically searched for within collected corals, but were noticed only irregularly. While all of the 27 *Tetralia* individuals that moved on to emptied corals (Table 5) were smaller than the 10.6 mm mean carapace width of paired specimens of *T. fulva,* two-thirds were larger than 5.3 mm, the size of the smallest paired egg-bearing female. Thus crabs either move between corals or can survive without a host for several molts. Two of the three largest immigrants were regenerating appendages, perhaps indicative of past territorial battles. The two immigrant *Gobiodon* seen in the recruitment experiment (Table 5) were much smaller than typical pair members.

In a July to September recolonization experiment with 14 *Acropora* colonies, six pairs of *Tetralia* spp. and five pairs of *Gobiodon* spp. were found at the end
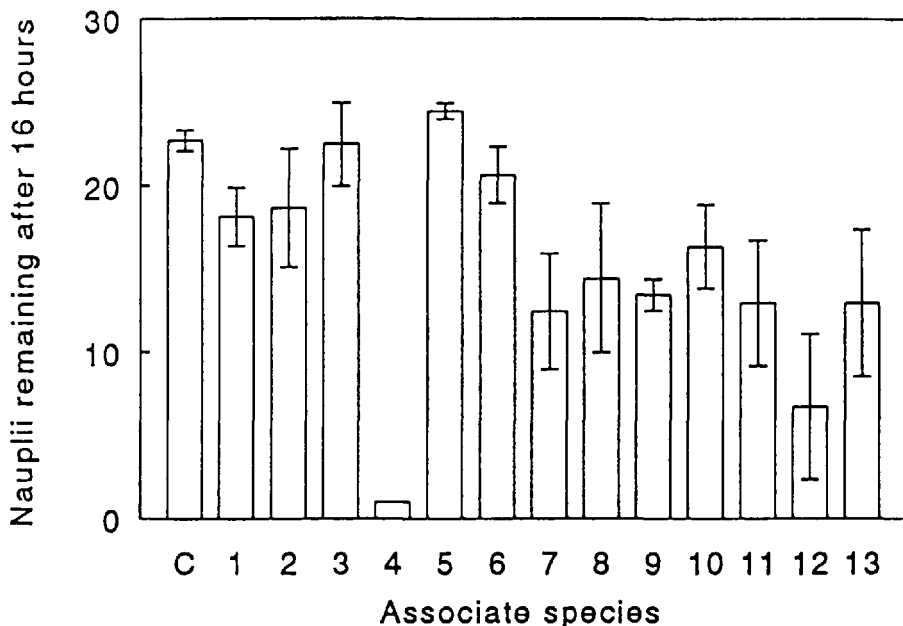
Figure 3. Capture of *Artemia* nauplii by coral associates. Bar shows the mean number of nauplii remaining after 16-h exposure to 25 nauplii (±SEM). C. Control, no associate present (16 replicates). 1. *Coralliocaris graminea* (7 replicates). 2. *C. superba* (3). 3. *Jocaste lucina* (2). 4. *Periclimenes amymone* (1). 5. *P. lutescens* (2). 6. *Philarius gerlachei* (3). 7. *Cymo deplanatus* (2). 8. *C. melanodactylus* (2). 9. *Tetralia fulva* (4). 10. *T. nigrolineata* (5). 11. *T. rubridactyla* (3). 12. *Gobiodon axillaris* (4). 13. *G. histrio* (4).

of the eight week period. (The 14 corals had contained seven pairs of *Tetralia* and five pairs of *Gobiodon* prior to their being emptied). The new pairs were adults of normal size, so either there is rapid growth of newly arrived juveniles or intercolony movement by adults.

Facultative associate individuals comprised nearly half (51/106, Table 5) of the animals found after 2- and 12-day recolonization periods. Their number of facultative associates per coral was greater in the recolonization collections than the initial ones, and significantly so for the 12-day recolonization period ($t = 3.12$, $P < 0.01$). Immigrants included at least 17 species of small, normally free-living, shrimp, crabs and fish.

Feeding and Activity.—Certain differences in the niches of the coral associates were apparent. In particular, the fish species are set apart from the decapods by their diurnal activity and more carnivorous food habits. *Gobiodon* kept in aquaria seemed alert and responsive during the day and quite inactive after dark. In laboratory experiments, several individuals ate coral tissue and most were active consumers of *Artemia* nauplii (Fig. 3). They seldom moved to catch a nauplius however, but instead inhaled them as they came by. *Gobiodon* could never be induced to eat pieces of fish. Stomachs of field collected specimens contained copepods (both free-living and coral parasitic species), coral tissue, and unidentified soft material. Stomachs of *Caracanthus unipinna* contained copepods and other zooplankton, unidentified soft material and probable fragments of coral tissue.

The decapod associates, on the other hand, seem quite inactive during the day.

In laboratory tanks, most became more active as light declined and tended to move upwards within their coral. The stomachs of field collected specimens of all species contained sand grains and spicule fragments intermingled with soft material. Although coral mucus was not voraciously consumed in every case where an associate was added to coral in the laboratory, all decapods except the *Cymo* spp., have appendage features that seem well-suited to mucus collection and most species were observed gathering it. Coral mucus and its contained debris would certainly seem to be the major food of the decapods. However, additional food sources are also utilized. *Cymo melanodactylus,* but no other decapod, was seen aggressively feeding on coral tissue. Suspension feeding is well-developed in the shrimp *Coralliocaris, Jocaste* and *Philarius* (Bruce, 1976a). The crab *C. deplanatus* also showed suspension feeding behavior, as specimens were seen to tilt back away from their coral branch, while the exopods of the maxillipeds beat rapidly and water currents entered the mouth region. Its food habits thus differs markedly from the con-generic *C. melanodactylus.* Judging by the capture of *Artemia* nauplii in laboratory experiments (Fig. 3), zooplankton would not seem to be an important food source for the shrimp obligate associates, but is utilized by the crab species and the shrimp facultative associate, *Periclimenes amymone.* A stomach of *Tetralia nigrifrons* was found containing seven zooea larvae, while a *C. deplanatus* in an aquarium was seen eating a still moving amphipod.

DISCUSSION

Community Nature.—The "typical" *Acropora* colony of this study is easily entered by small animals, and offers shelter and a variety of food sources. It is, of course, a living organism and thus a very distinct environmental patch, and one that must have at least some defenses against other species.

Although diverse free-living small fish and decapod Crustacea can live within a branching *Acropora,* most inhabitants come from a fairly large assemblage of obligate associates. Several factors seem to be involved. Clearly this is an attractive habitat, as there have been seven unrelated evolutions of dependance on *Acropora* (*Coralliocaris/Jocaste,* one each for the other four groups, and *Domecia glabra* and *Caracanthus unipinna*). Secondly, the size of an *Acropora* colony relative to the animals that inhabit it has allowed the evolution of species that can monopolize this resource to some degree. Thirdly, as will be discussed below, there are innate advantages to habitat restriction for small coral reef animals. And lastly, there has been considerable speciation within most groups.

Host Specificity.—Predation is particularly intense in tropical marine communities and is believed to be responsible for various differences between the structure and behavior of tropical species and their temperate counterparts (Johannes, 1978; Bertness et al., 1981). The high level of predation combined with the physical heterogeneity of reef environments make the location of mates particularly difficult for small benthic animals. This creates a situation favoring association with a larger species. A large host animal will release more target chemicals than a conspecific individual and can thus be located more easily. Providing that members of a species can survive on or near a potential host, those responding to host chemicals will find themselves in a situation where a mate is likely to be encountered without spending dangerous search time out in the world at large. I suspect that the effect of a host species in concentrating individuals, and thus facilitating reproduction, has been a major factor in the origin and diversification of the abundant associations that exist between small, benthic animals with internal fertilization (e.g., decapods, cyclopoid copepods) and the external surfaces

of large reef invertebrates. Once an association is established, selection will be expected to favor traits that suit the species to its particular host, or facilitate its ability to monopolize the host resource. The concept of host or habitat restriction in association with reproduction has been reviewed by Colwell (1986), who suggests that this process best explains the specificity for flower host found in hummingbird flower mites, while Rohde (1979) invokes it to account for the habitat restriction seen in monogenean parasites of fish gills.

The discrete and chemically recognizable habitat provided by a colony of branching coral, and the shelter and diverse food sources found there, can account for the repeated evolution of coral associated animals. The parallel, but distinct, faunas of obligate associates on *Acropora* spp. and the pocilloporid corals (Garth, 1964; Patton, 1966; Tyler, 1971) are probably best explained by the reproductive advantages of habitat restriction. For example, the crab *Trapezia cymodoce* is common on pocilloporid corals and belongs to a genus usually restricted to them, but can also live with *Acropora* (Patton, 1966; *A. divaricata* above). The other obligates should be equally adaptable.

The distribution data suggest that most *Gobiodon* species choose between various species of *Acropora*. Only in the case of *G. micropus* is there a possible ecological correlation with host choice, as this small species may be best suited to the narrow spaces between the branches of its host, *A. elseyi*. There is no comparable suggestion for the apparent avoidance of *A. millepora* by *G. quinquestrigatus,* or of *A. humilis* by *G. axillaris* and *G. histrio* (Table 1). If *Gobiodon* species are indeed more host specific than the decapod associates, this may reflect a greater age of association and thus more time for host restriction to evolve. Or, perhaps, the process of habitat restriction may have been able to proceed further in *Gobiodon,* because of the superior ability of fish to detect slight differences in environmental chemistry. Different species of anemone fish (*Amphiprion* spp.) can respond to chemicals produced by their own particular species of host anemone (Murata et al., 1986).

Since according to the reproductive advantage hypothesis, host structure or physiology is not the most important factor initiating host restriction, idiosyncratic host preferences, and differing "specificities" between local populations of wide-ranging associates, could be expected. (As an example among coral associates, the well-known shrimp associate of pocilloporid corals, *Alpheus lottini,* was abundant on *Pocillopora* and *Seriatopora* at Heron Island, but not found on *Stylophora* (Patton, 1966), whereas in east Africa (Edwards and Emberton, 1980) it was collected from 42 of 90 shallow water *Stylophora).* Once an association is established, further evolution can lead toward or away from greater host restriction, depending on the sensory abilities of the associate, changing relative abundances of host and symbiont, and the extent to which specializations for certain hosts have evolved.

Duration of Association.—Present data indicates differences between associate groups in the tenure of individuals on a given host. Short-term observations (Table 4) show fidelity between *Gobiodon* and their coral, and at least one fish inhabited the same coral for a year. The two largest collections of a single species showed significant correlations between fish length and coral volume. This is consistent with residence by a given pair that approaches the life span of the coral, but would be less likely if a coral housed successive pairs of fish during its life. Extrapolating from the growth rates of Connell (1973), some of the corals that I collected may have been growing for a decade. Although longer-term observations of individual corals are needed for proof, it does seem possible that *Gobiodon*

pairs may live for years within the same coral. On the other hand, the probable short-term break-up of pairs (Table 4), the 60% or greater turn-over in pairs during a 13½ month period, and the general lack of correlation between crab width and coral volume, all indicate that the equally coral-adapted *Tetralia* crabs have a briefer tenure on a particular coral, due to intercolony movement, and, perhaps also, shorter lifespan.

Restriction Of Associate Numbers.—While 20 species of obligate associate were collected at least five times, the 141 corals of Table 1 contained an average of only 4.5 associate species and 9.1 individuals. The chief causes of these rather sparse populations seem to be external predation, territorial behavior by established associates, and lack of recruitment by certain groups.

Except perhaps for the toxic *Gobiodon* species, all *Acropora* associates seem vulnerable to predation by the small fish seen probing around coral heads. Although the evidence is indirect, there are numerous indications of the effects of predation on associate communities. Identified obligate coral associates (chiefly *Trapezia* crabs), were found within 14 of the reef fish species dissected by Hiatt and Strasburg (1960). Closely branched colonies of *Acropora* contained more associates than did more open ones, including the much larger colonies of *A. cuneata*. Pocilloporid corals have a rather spherical growth form and thus provide more shelter than flatter "typical" *Acropora* colonies of equal volume. They tend to have more associates. For example, the medium-sized colonies of *Pocillopora damicornis* that I collected from Heron Island (Patton, 1974) had about the same mean volume as the *Acropora* of Table 1, but contained an average of 7.5 species and 20.8 individual associates, compared with the 4.5 species and 9.1 individuals on the *Acropora* colonies. Predation pressure also provides a likely explanation for the clustering of the decapod associates within the colony during the day, and their tendency to move towards the periphery at night when fish predation is less effective.

The most interesting factor influencing community composition is the colony defense exhibited by established associates. Although there are problems with inferring competition from distribution patterns, the evidence here seems clear cut. The numbers of facultative associates increased on corals whose obligates had been removed. Most obligates occur as single male-female pairs, and corals of various sizes typically contain no more than one adult pair per associate group. Yet, corals of similar size that are subdivided, or otherwise impede intra-colony movement, often contain several pairs of the species or group. Co-occurrences on "typical" *Acropora* colonies usually involved juveniles.

The five occurrences of a pair of *G. ceramensis* with a pair of another *Gobiodon* species are an interesting exception to the one pair per group rule. While the other three *Gobiodon* found on "typical" coral heads have prominent contrasting stripes on the sides of the head, *G. ceramensis* lacks head stripes and is a uniform tan-gray. Perhaps it does not arouse the aggressive behavior of other species and is thus able to coexist with them.

In the decapod obligate associates, the appendages presumed to be most important in agonistic encounters (one or both second legs in shrimp, "crusher" chela in crabs) are relatively larger than in free-living species. They are also better developed in males than females, which might suggest a greater male role in colony defense. However, pairs may well result from a male excluding other males and a female excluding other females, as has been shown for *Alpheus lottini* and *Trapezia* spp. associated with pocilloporid corals (Vannini, 1985; Huber, 1987).

Intra-group exclusion, in addition to restricting total associate numbers, also

contributes to unpredictability in community composition. At least for *Tetralia* and most *Gobiodon* species, there must be a "scramble" competition between the species of a group for occupancy of empty corals. Yet diversity within groups continues. In the most extreme case, reproductive pairs of *T. nigrifrons* and *T. rubridactyla* manage to become established despite the abundance of *T. fulva* on the reef and among potential recruits (Table 5).

There are indications of environment related changes in colony defense. *A. nasuta* from 6 m depth contained expected frequencies of *Gobiodon* and *Tetralia* spp., but significantly fewer other associates than shallow-water corals (Table 1: K, J). Corals produce less mucus in deeper water (Crossland, 1987). Enhanced territoriality by resident *Tetralia* on corals releasing less food is a possible explanation for the reduction in the other associate groups. Conversely, several of the collections from Tijou Reef contained more associates than those from the same corals on reefs to the south. Tijou Reef is on the edge of a narrow continental shelf and is more likely than the other collecting sites to be influenced by nutrient-rich upwelling water (Andrews and Gentien, 1982). Relaxed colony defense when food is abundant could result in higher associate densities. Depth related reductions in numbers have been noted among associates of pocilloporid corals (Edwards and Emberton, 1980; Gotelli and Abele, 1983; Chang et al., 1987), as have increases in facultative associates in areas of increased nutrient input (Abele, 1976; Kropp and Birkeland, 1982). Of course, these patterns could be produced by differences in recruitment and proof of a role for differential territoriality must await direct experiment.

The third major factor structuring the community of *Acropora* associates is the availability of recruits from the various groups. There is a high probability that a given coral will contain a pair of *Tetralia*, a pair of *Gobiodon* and specimens of *Coralliocaris,* and a lesser likelihood that it will contain members of other groups. As there is at present no evidence for negative interactions between members of different groups inhabiting the larger shallow-water *Acropora* heads, differences in group frequencies probably reflect differences in the availability of recruits.

Given the small sample sizes, the relative abundances of most obligate associates on the three "typical" *Acropora* species at the four collection sites (Table 1), are perhaps surprisingly similar. This suggests a pool of potential recruits that was quite uniform over a large area, and relatively stable between 1971 (Heron Island) and 1979 (the other sites). For the shrimp, *Coralliocaris graminea* however, there is good evidence of changes in abundance over time. In 1957 and 1958, this shrimp was present on 12 of 29 *Acropora* that I collected from Heron Island and Wistari Reef, and on 12 of 17 from two northern localities within the Barrier Reef. In the similar collections of Table 1, *C. graminea* was present on only 6 of 33 colonies of *A. humilis, A. millepora* and *A. nasuta* collected 14 years later at Heron Island and Wistari Reef, and on 3 of 63 shallow-water specimens of these corals collected 22 years later from the three northern sites ($\chi^2 = 31.93$). The *Acropora* species were not identified in the earlier collections, but were typical heads and must have consisted largely of the above three species. In 1992, *C. graminea* was once again abundant at Heron Island.

coral identification, to D. Hoese for *Gobiodon* identification and to J. Gatz for statistical advice. J. Gatz, R. Patton, D. Radabaugh, and a thoughtful anonymous reviewer provided helpful comments on various versions of the manuscript.

LITERATURE CITED

Abele, L. G. 1976. Comparative species richness in fluctuating and constant environments: coral-associated decapod Crustacea. Science 192: 461–463.

Andrews, J. C. and P. Gentien. 1982. Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: a solution to Darwin's question? Mar. Ecol. Prog. Ser. 8: 257–269.

Bertness, M. D., S. D. Garrity and S. C. Levings. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. Evolution 35: 995–1007.

Bruce, A. J. 1976a. Shrimps and prawns of coral reefs. Pages 37–94 *in* O. A. Jones and R. Endean, eds. Biology and geology of coral reefs, Vol. 3, Biology 2. Academic Press, New York.

————. 1976b. A report on some pontoniinid shrimps collected from the Seychelle Islands by the F. R. V. Mahine, 1972, with a review of the Seychelles pontoniinid shrimp fauna. Zool. J. Linn. Soc. 59: 89–153.

————. 1977. The hosts of the coral-associated Indo-West-Pacific Pontoniine shrimps. Atoll Res. Bull. 205: 1–19.

————. 1982. Notes on some Indo-Pacific Pontoniinae. XL. The rediscovery of *Periclimenes lifuensis* Borradaile, 1898 (Decapoda, Pontoniinae) and the establishment of its systematic position. Crustaceana 42: 158–173.

Chang, K.-H., Y.-S. Chen and C.-P. Chen. 1987. Xanthid crabs in the corals, *Pocillopora damicornis* and *P. verrucosa* of southern Taiwan. Bull. Mar. Sci. 41: 214–220.

Colwell, R. K. 1986. Community biology and sexual selection: lessons from hummingbird flower mites. Pages 406–424 *in* J. Diamond and T. J. Case, eds. Community ecology. Harper and Row, New York.

Connell, J. H. 1973. Population ecology of reef-building corals. Pages 205–245 *in* O. A. Jones and R. Endean, eds. The biology and geology of coral reefs, Vol. 2, Biology 1. Academic Press, New York.

Crossland, C. J. 1987. In situ release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. Coral Reefs 6: 35–42.

Edwards, A. and H. Emberton. 1980. Crustacea associated with the scleractinian coral, *Stylophora pistillata* (Esper), in the Sudanese Red Sea. J. Exp. Mar. Biol. Ecol. 42: 225–240.

Eldredge, L. G. and R. K. Kropp. 1982. Decapod crustacean-induced skeletal modification of *Acropora*. Proc. Fourth Int'l. Coral Reef Symp., Manila 2: 115–119.

Galil, B. 1986a. *Tetraloides*—a new genus of coral-inhabiting crabs. Crustaceana 50: 68–77.

————. 1986b. On the identity of *Tetralia cinctipes* Paulson, 1985 (Decapoda, Brachyura). Crustaceana 51: 97–102.

————. 1987. The adaptive functional structure of mucus-gathering setae in trapezid crabs symbiotic with corals. Symbiosis 4: 75–86.

————. 1988. Further notes on species of *Tetralia* (Decapoda, Trapeziidae). Crustaceana 54: 57–68.

Garth, J. S. 1964. The Crustacea Decapoda (Brachyura and Anomura) of Eniwetok Atoll, Marshall Islands, with special reference to the obligate commensals of branching corals. Micronesica 1: 137–144.

————. 1974. Decapod crustaceans inhabiting reef-building corals of Ceylon and the Maldive Islands. J. Mar. Biol. Assoc. India 15: 195–212.

————. 1984. Brachyuran decapod crustaceans of coral reef communities of the Seychelles and Amirante Islands. Pages 103–123 *in* D. R. Stoddart, ed. Biogeography and ecology of the Seychelles Islands. W. Junk, The Hague.

Glynn, P. W. 1983. Crustacean symbionts and the defense of corals: coevolution on the reef? Pages 111–178 *in* M. H. Nitecki, ed. Coevolution. The University of Chicago Press, Chicago.

Gotelli, N. J. and L. G. Abele. 1983. Community patterns of coral-associated decapods. Mar. Ecol. Prog. Ser. 13: 131–139.

Hashimoto, Y., K. Shiomi and K. Aida. 1974. Occurrence of a skin toxin in coral-gobies *Gobiodon* spp. Toxicon 12: 523–528.

Hiatt, R. W. and D. R. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30: 65–127.

Huber, M. E. 1987. Aggressive behavior of *Trapezia intermedia* Miers and *T. digitalis* Latreille (Brachyura:Xanthidae). J. Crust. Biol. 7: 238–248.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fishes 3: 65–84.

Knudsen, J. W. 1967. *Trapezia* and *Tetralia* (Decapoda, Brachyura, Xanthidae) as obligate ectoparasites of pocilloporid and acroporid corals. Pac. Sci. 21: 51–57.

Kropp, R. K. and C. Birkeland. 1982. Comparison of crustacean associates of *Pocillopora verrucosa* from a high island and an atoll. Proc. Fourth Int'l. Coral Reef Symp., Manila 2: 627–632.

Lassig, B. R. 1981. Significance of the epidermal icthyotoxic secretion of coral-dwelling gobies. Toxicon 19: 729–735.

Murata, M., K. Miyagawa-Koshima, K. Nakanishi, and Y. Naya. 1986. Characterization of compounds that induce symbiosis between sea anemone and anemone fish. Science 234: 585–587.

Patton, W. K. 1966. Decapod Crustacea commensal with Queensland branching corals. Crustaceana 10: 271–295.

—————. 1974. Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. Pages 219–243 *in* W. B. Vernberg, ed. Symbiosis in the sea. Belle W. Baruch Library in Marine Science No. 2. Univ. of South Carolina Press, Columbia.

Pearson, R. G. and R. Endean. 1969. A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. Fisheries Notes, Queensland Department of Harbours and Marine. 3: 27–55.

Randall, J. E., G. R. Allen and R. C. Steene. 1990. Fishes of the Great Barrier Reef and Coral Sea. Univ. of Hawaii Press, Honolulu. 507 pp.

Rohde, K. 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche segregation in parasites. Am. Nat. 114: 648–671.

Schultz, L. P. 1966. Fishes of the Marshall and Marianas Islands. Families Kraemeriidae through Antennariidae. U.S. Nat. Mus. Bull. 202(3): 1–165.

Tyler, J. C. 1971. Habitat preferences of the fishes that dwell in shrub corals on the Great Barrier Reef. Proc. Acad. Nat. Sci. Philadelphia 123: 1–26.

Vannini, M. 1985. A shrimp that speaks crab-ese. J. Crust. Biol. 5: 160–167.

Veron, J. E. N. 1986. Corals of Australia and the Indo-Pacific. Angus & Robertson, North Ryde. 644 pp.

————— and C. C. Wallace. 1984. Scleractinia of eastern Australia. Part V. Family Acroporidae. Australian Institute of Marine Science Monogr. Ser. 6: 1–485.

Wallace, C. C. 1978. The coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) in the central and southern Great Barrier Reef Province. Mem. Queensland Mus. 18: 273–319.

ADDRESS: *Department of Zoology, Ohio Wesleyan University, Delaware, Ohio 43015.*