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DECAPOD CRUSTACEANS INHABITING REEF-BUILDING CORALS OF CEYLON AND THE MALDIVE ISLANDS [1]

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ABSTRACT

Living corals were collected at Galle, Ceylon, and at ten localities in the Maldive Islands. Fiftyfive coral heads, 10 of the family Pocilloporidae and 45 of the family Acroporidae, were examined for decapod commensals. Shrimp found exclusivlely in *Pocillopora*, together with frequency of occurrence, if more than once, were *Alpheus lottini*(9), *Harpiliopsis beauprest* (5), *H. depressus* (5), *H. spinigera*, *Philarius* sp. (probably *gerlachei*, *Fennera chacei*, and *Thor maldivensis*. Crabs found exclusively in *Pocillopora* were *Trapezia cymodoce* (8), *T. ferruginea* (6), *T.* aff. *wardi* (3), *Domecia hispida* (3), *Trapezia areolata*, *T.* aff. *danai*, *T.* aff. *maculata*, *T.* aff. *tigrina*, and *Cymo quadrilobatus*. Shrimp found exclusively on *Acropora* were *Jocaste japonica* (17), *Coralliocaris superba* (3), *Jocaste lucina* (2), *Coralliocaris graminea* (2), *C. nudirostris*, *C. venusta*, and *Periclimines lutescens*. Crabs found exclusively or *Acropora* were *Tetralia glaberrima* (33), *T. heterodactyla* (19), *Cymo deplanatus* (13), *C. melanodactylus* (4), *Domecia glabra* (6), Crabs found in Ceylon but not in the Maldive Islands were *Trapezia* aff. *tigrina*, *T. areolata*, and *Cymo* (?) on *Pocillopora* and *Cymo deplanatus* on *Acropora*. Shrimp found in the Maldive Islands but not in Ceylon were *Philarius* sp. (probably *gerlachei*), *Harpiliopsis spinigera*, *Fennera chacei*, and *Thor maldivensis* on *Pocillopora* and *Coralliocaris nudirostris*, *C. superba*, *C. venusta*, *Periclimines lutescens*, and *Jocaste japonica* on *Acropora*. Crabs found in the Maldive Islands but not in Ceylon were *Trapezia* aff. *danai*, *T. digitalis*, and *T.* aff. *maculata* on *Pocillopora* and *Cymo deplanatus* and *C. melanodactylus* on *Acropora*. In the Maldive Islands *Tetralia glaberrima* and *T. heterodactyla* occurred in the proportion of 2:1, *Harpiliopsis depressus* and *H. spinigera* in the proportion of 3:1, and *Jocaste japonica* and *J. lucina* in the proportion of 8:1. Each head of *Acropora* usually supported a pair of *Tetralia:* either *T. glaberrima* or *T. heterodactyla* (19 times) or both (5 times). The occurrence in the same coral head of mated pairs of both, and of multiple numbers of both congeners of shrimp, was evidence of their specific identity, formerly in doubt.

INTRODUCTION

THE opportunity of studying at first-hand the decapod crustaceans commensal with reef-building corals of Ceylon and the Maldive Islands as a member of TE VEGA Cruise B of the International Indian Ocean Expedition (I.I.O.E.) was eagerly seized upon, for it was here that J. Stanley Gardiner collected the crabs that were reported by Borradaile (1901-1904), whose personal experience in the Indian Ocean was limited to a month of Minikoi. In former years it had been the writer's privilege to accompany Hancock expeditions to the Galápagos Islands, where among the comparatively limited coral fauna of the eastern Pacific a newspeciesof Borradaile's

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decapod genus *Maldivia* was discovered (Garth, 1939). Subsequently the writer explored the Marshall Islands in the western Pacific carcinologically, enumerating the decapods commensal with branching corals at Eniwetok (Garth, 1964). Investigation of the coral reef auna of the Maldive Islands, similarly situated on the Equator but half a world removed from the Galápagos Islands, promised some enlightening comparisons; while still other parallels might be drawn with a recently completed study of decapod commensals of branching corals of the Australian Great Barrier Reef (Patton, 1966).

As with the earlier expeditions of J. Stanley Gardiner (1901), TE VEGA took her departure from Colombo, Ceylon, on March 14, 1964. Two weeks were spent in the Maldive Islands, during which the atolls of Male, Fadiffolu, Milladummadulu, and Tiladummati of the eastern chain were visited. Following a return on March 30 to Cochin, India, and beginning on April 17, the Maldive Islands were again visited, at which time the atolls of North Malosmadulu and South Nilandu of the western chain and the southern most atoll of Addu were collected. No attempt was made to re-collect at Gardiner's localities, the purposes of the expedition as a whole being better served by stops at other locations. However, with the exception of Suvadiva Atoll, where TE VEGA encountered the S. E. monsoon, coverage of the islands was essentially complete. The writer departed on May 3 from Gan to Aden, while the vessel continued to Mauritius.

Sincere thanks are expressed to Dr. C. B. Goodhart of Cambridge University, England, who not only provided access to the Maldivian collections of the late L. A. Borradaile in the Museum of Zoology, but, by arranging overnight accommodations at Gonville and Caius College, re-created for the writer the atmosphere in which the late J. Stanley Gardiner lived and worked.

Although the brachyuran crab identifications are the writer's the assistance of Dr. R. Serène, UNESCO Marine Science Regional Expert, National Museum, Singapore, with species of the *Trapezia rufopunctata-maculata* grpup is gratefully acknowledged. Anomuran crabs were identified by Janet Haig, Allan Hancock Foundation, Univeristy of Southern California, Los Angeles. Alpheid shrimp were identified by Dora Mae Banner, Hawaii Institute of Marine Science, Honolulu, pontoniid shrimp by Dr. A. J. Bruce, Queensland Fisheries Research Institute-Redcliffe, Australia, and hi ppolytid shrimp by Dr. L. B. Holthuis, Rijksmuseum, van Natuurlijke Historie, Leiden.

Cruise B of TE VEGA, on which Dr. Dixy Lee Ray of Pacific Science Center Foundation, Seattle, was chief scientist, was supported by N.S.F. Grant G-17465. Travel to museums housing Maldivian and other Indian Ocean decapod collections was supported by N.S.F. Grant GB-3849.

The manuscript was read critically by Dr. A.J. Bruce, presently of the East African Marine Fisheries Research Organization, Mombasa, Kenya, whose pertinent suggestions were gratefully accepted.

CORALS COLLECTED IN CEYLON

Corals were collected by John S. Garth at Galle, Ceylon, on the southwest coast of the island. Of the 5 individual coral heads dismantled, 2 were POCILLOPORIDAE and 3 were ACROPORIDAE. These were identified by Dr. John W. Wells, Department of Geology, Cornell University, Ithaca, New York, as the following:

POCILLOPORIDAE : *Pocillopora elongata* Dana (1 collection)
Pocillopora elegans Dana (1 collection)

ACROPORIDAE : *Acropora* sp. cf. *corymbosa* (Lam.) (2 collections)
Acropora sp. cf. *conferta* (Quelch) (1 collection)

CORALS COLLECTED IN THE MALDIVE ISLANDS

Corals were collected by John S. Garth in the Maldive Islands at Dunidu Island, Male Atoll; Imma Island, Male Atoll; Mafilefuri Island, Fadiffolu Atoll; Kuludu Island, Milladummadulu Atoll; Ongu Island, North Mahlosmadulu Atoll; and Wilingili Island, Addu Atoll. Corals weer collected by Gary M. Beardsley in the Maldive Islands at Duwafuri Island, North Mahlosmadulu Atoll; Wala Island, South Nilandu Atoll; and Gan Island, Addu Atoll. Of the 50 individual cora heads dismantled, 8 were POCILLOPORIDAE and 42 were ACROPORIDAE, including 2 of which no sample was kept for identification. Corals were identified by Dr. John W. Wells as the following :

POCILLOPORIDAE: *Pocillopora wood-jonesi* Vaughan (5 collections)
Pocillopora eydouxi M. E. & H. (3 collections)

ACROPORIDAE : *Acropora humilis* Dana (24 collections)
Acropora sp. cf. *rotumana* (Gardiner)(5 collections)
Acropora sp. cf. *nasuta* (Dana) (3 collections)
Acropora convexa (Dana) (2 collections)
Acropora tenuis (Dana) (2 collections)
Acropora variabilis (Klunzinger) (2 collections)
Acropora hebes (Dana) (1 collection)
Acropora sp. cf. *diversa* (Alcock) (1 collection)

METHOD OF COLLECTING

Coral heads were selected at random for sampling and were hand carried to the beach, where they were set down on beach rock and dismantled piece by piece by taping with a geological pick or hammer. Decapod commensals were removed by hand or with forceps, those from each coral head being placed in a separate plastic jar, together with a small piece of the coral for later identification. Each coral was disposed of before collecting the next; however, some of the crabs invariably escaped into the substrate if it were creviced or rubbly. Also, it is believed that many shrimp escaped during the lifting and carrying of the coral over open water. It is suggested that future collecting be done from a skiff, and/or that the coral be enclosed in a platstic bag before lifting. Only in this way may one be sure that the entire assemblage is being sampled.

CORAL COMMENSALS COLLECTED IN CEYLON, WITH FREQUENCY AND MANNER OF OCCURRENCE

In *Pocillopora* Coral

Alpheus lottini Guérin : 2 occurrences, 1 single, 1 multiple
Harpiliopsis depressus (Stimpson) : 2 occurrences as single females, one ovigerous
Harpiliopsis beaupresi (Audouin) : 1 occurrence, multiple

Synalpheus, probably *charon* (Heller): 1 occurrence, fragmentary
Trapezia cymodoce (Herbst): 2 occurrences, 1 as mated pair with ovigerous female, 1 as unpaired ovigerous female
Trapezia ferruginea Latreille : 2 occurrences, 1 as mated pair, 1 as non-ovigerous female
Trapezia areolata Dana : 1 occurrence as mated pair with additional female present
Trapezia aff. *wardi* Serene : 1 occurrence, 0 as mated pairs
Trapezia aff. *tigrina* Eydoux & Souleyet : 1 occurrence, 0 as mated pairs
Domecia hispida Eydoux & Souleyet : 1 occurrence as mated pair with additional male present
Carpilodes margaritatus A. Milne-Edwards : 1 occurrence, 0 as mated pairs

In *Acropora* Coral

Coralliocaris graminea (Dana) : 1 occurrence as non-ovigerous female
Jocaste lucina (Nobili): 1 occurrence as non-ovigerous female
Tetralia glaberrima (Herbst): 3 occurrences, all multiple with ovigerous females present
Tetralia heterodactyla Heller : 1 occurrence, multiple, with ovigerous females present
Cymo melanodactylus Dana : 3 occurrences, 1 as mated pair with ovigerous female
Domecia glabra Alcock ; 1 occurrence as unpaired ovigerous female
Chlorodiella cytherea (Dana) : 1 occurrence, 0 as mated pairs
Paraxanthias notatus (Dana) : 1 occurrence, 0 as a mated pairs
Pilodius areolatus (Milne-Edwards) : 1 occurrence as mated pair, female non-ovigerous

CORAL COMMENSALS COLLECTED IN THE MALDIVE ISLANDS, WITH FREQUENCY AND MANNER OF OCCURRENCE

In *Pocillopora* Coral

Alpheus lottini Guérin : 7 occurrences, 6 as mated pairs.
Harpiliopsis beaupresi (Audouin): 4 occurrences, 3 multiple, 1 as non-ovigerous female
Harpiliopsis depressus (Stimpson) : 3 occurrences, 1 multiple, 2 single
Harpiliopsis spinigera (Ortmann) : 1 occurrence, multiple
Palaemonella rotumana (Borradaile): 1 occurrence as single male
Pericliminaeus cf. *spongicola* Holthuis : 1 occurrence as mated pair with ovigerous female
Philarius sp., probably *gerlachei* (Nobili): 1 occurrence, multiple, all juvenile
Fennera chacei Holthuis: 1 occurrence, multiple, with ovigerous females
Thor maldivensis Borradaile: 1 occurrence as mated pair
Synalpheus charon (Heller): 1 occurrence as mated pair
Trapezia cymodoce (Herbst): 6 occurrences, all as mated pairs with ovigerous females
Trapezia ferruginea Latreille: 4 occurrences, a total of 6 mated pairs (4 with ovigerous females)
Trapezia aff. *wardi* Serene : 3 occurrences, 2 as mated pairs with ovigerous females
Trapezia aff. *maculata* MacLeay : 2 occurrences as mated pairs (1 with ovigerous female
Trapazia aff. *danai* Ward: 1 occurrence as mated pair with ovigerous female
Trapezia digitalis Latreille : 1 occurrence as mated pair with ovigerous female

Domecia hispida Eydoux & Souleyet : 2 occurrences; as single, non-ovigerous females
Cymo quadrilobatus Miers : 1 occurrence as mated pair with non - ovigerous female

In *Acropora* Coral

Jocaste japonica (Ortmann): 17 occurrences, 9 multiple

Jocaste lucina (Nobili): 1 occurrence as single individual

Coralliocaris superba (Dana) : 3 occurrences, 2 as mated pairs, 1 multiple with ovigerous females

Coralliocaris graminea (Dana) : 1 occurrence as mated pair

Coralliocaris nudirostris (Heller) : 1 occurrence as single individual

Coralliocaris venusta Kemp : 1 occurrence as single ovigerous female

Periclimines lutescens (Dana) : 1 occurrenc as mated pair

Synalpheus charon (Heller): 1 occurrence as mated pair

Tetralia glaberrima (Herbst): 30 occurrences; 21 as mated pairs with ovigerous emales

(2 of the 21 with a second, unpaired ovigerous female present); 5 as unpaired ovigerous females; 3 as unpaired males; 1 multiple occurrence

Tetralia heterodactyla Heller : 16 occurrences; 10 as mated pairs (9 with ovigerous females); 3 as unpaired females (2 ovigerous); 3 as unpaired males

Cymo deplanatus A. Milne-Edwards: 12 occurrences; 9 as mated pairs (8 with ovigerous females); 2 as unpaired males; 1 as unpaired female

Cymo melanodactylus Dana: 3 occurrences; 2 as mated pairs (1 with ovigerous female); 1 as unpaired female

Domecia glabra Alcock : 5 occurrences; 2 as mated pairs: 3 as unpaired females (1 ovigerous)

Trapezia cymodoce (Herbst): 2 occurrences, 1 as single male, 1 as unpaired ovigerous female

METHOD OF TABULATING

The data obtained from field collections are presented in a series of Table each representing decapod crustaceans (crabs and shrimp) obtained from corals at a single locality in Ceylon (Teble 1) or in the Maldive Islands (Table 2—10). Numbers of coral heads of each group (pocilloporid and acroporid) examined for inquilines are shown parenthetically. Numbers of specimens of each decapod species recovered from an individual coral head are arranged in vertical columns under the name of the coral host. Tables 1—7 represent collecting by John S. Garth. Tables 8—10 represent collecting by Gary M. Beardsley, student member of TE VEGA Cruise B, who obtained by shallow diving corals containing species of both crabs and shrimp not otherwise represented and needed to complete the spectrum of decapod commensals. Total numbers of decapods collected from corals of each species at each locality sampled are carried to Master Table 1, showing the occurrence of obligate commensal decapods in branching corals of Ceylon and the Maldive Islands after non-obligate or facultative commensals have been eliminated for the reasons discussed.

TABLE 1

Galle, Ceylon

	POCILLOPORIDAE (2)			ACROPORIDAE (3)			
	P. elegans	*P. elongata*		*A. ramiculosa*	*A. ramiculosa*	*A. conferta*
Harpiliopsis beaupresi	0	11	*Coralliocaris graminea*	1	0	0
Harpiliopsis depressus	1	1	*Palaemonella rotumana*	1	0	0
Alpheus diadema	0	1	*Jocaste lucina*	1	0	0
Alpheus lottini	1	5	*Alpheus edwardsii* group	4	0	0
Athanas sp.	0	2				
Synalpheus sp.	f	0	*Synalpheus paraneomeris*	4	0	0
Pisidia sp.	0	1	*Pisidia* sp.	2	0	0
Porcellana gravelei	0	1	*Porcellana gravelei*	4	0	0
			Petrolisthes asiaticus	4	0	0
Cymo (?)	0	1	*Cymo melanodactylus*	4	1	0
Domecia hispida	0	3	*Domecia glabra*	1	0	0
Trapezia cymodoce	1	2	*Tetralia glaberrima*	14	7	12
Trapezia ferruginea	2	3	*Tetralia heterodactyla*	9	0	0
Trapezia areolata	0	4				
Trapezia aff. *tigrina*	0	3				
Trapezia aff. *wardi*	0	3				
Carpilodes margaritatus	0	1	*Chlorodiella cytherea*	1	0	0
			Pilodius areolatus	2	2	0
			Paraxanthias notatus	0	0	1

TABLE 2

Dunidu, Male

	POCILLOPORIDAE (4)				ACROPORIDAE (3)			
	P. woodjonesi	*P. woodjonesi*	*P. woodjonesi*	*P. eydouxi*		*A. humilis*	*A. humilis*	*A. nasuta*
Periclimenaeus sp.	0	0	0	1				
Palaemonella rotumana	0	0	0	1				
Harpiliopsis beaupresi	0	3	0	1	*Coralliocaris graminea*	0	2	0
Harpiliopsis depressus	0	0	1	0	*Jocaste japonica*	5	2	4
Alpheus eulimne	0	0	0	1	*Alpheus parvirostris*	1	0	0
Alpheus gracilipes	0	2	2	1				
Alpheus lottini	2	2	2	1				
Alpheus macrocheirus group	0	1	0	0				
Alpheus paragracilis	0	0	0	1				
Synalpheus sp.	0	0	f	0				
Petrolisthes penicillatus	0	2	1	1				
Cymo quadrilobatus	0	0	2	0	*Cymo deplanatus*	2	0	2
Domecia hispida	0	0	1	0	*Domecia glabra*	1	0	1
Trapezia cymodoce	2	2	3	2	*Tetralia glaberrima*	2	2	2
Trapezia ferruginea	0	3	4	0				
Trapezia aff. *danai*	0	0	2	0				
Trapezia aff. *wardi*	0	2	0	0				
Chlorodiella laevissima	0	0	2	0	*Chlorodiella laevissima*	0	1	0
Actaea polyacantha	0	0	0	1				
Actaea speciosa	0	0	2	0				
Phymodius sp.	0	1	1?	0				
Pilodius melanospinus	0	0	0	4				

TABLE 3

Imma, Male

POCILLOPORIDAE (2)			ACROPORIDAE (4)				
	P. woodjonesi	*P. woodjonesi*		*A. humilis*	*A. humilis*	*A.* unident.	*A.* unident.
Harpiliopsis beaupresi	0	4	*Coralliocaris superba*	2	0	0	0
Harpiliopsis depressus	0	1					
Alpheus crinites group	0	1					
Alpheus lottini	2	2					
Alpheus macrochirus	0	1					
			Cymo deplanatus	2	0	2	0
			Cymo malanodactylus	0	0	1	0
			Cymo quadrilobatus	0	0	1	0
Domecia hispida	1	0					
Trapezia cymodoce	0	2	*Tetralia glaberrima*	2	2	1	2
Trapezia ferruginea	0	2	*Tetralia heterodactyla*	0	0	3	1
Trapezia aff. *maculata*	2	0					
Trapezia aff. *wardi*	2	0					

TABLE 4

Mafilefuri, Fadiffolu

POCILLOPORIDAE (0)	ACROPORIDAE (1)	
		A. hebes
	Cymo melanodactylus	2
	Pilodius areolatus	1

TABLE 5

Kuludu, Milladummadulu

POCILLOPORIDAE (1)		ACROPORIDAE (1)	
			A. humilis
	P. eydouxi	*Jocaste japonica*	2
		Alpheus gracilis	1
		Tetralia glaberrima	2
Trapezia aff. *maculata*	1	*Trapezia cymodoce*	2
		Chlorodiella cytherea	1
		Cymo deplanatus	1

TABLE 6

Ongu, N. Mahlosmadulu

	POCILLOPORIDAE (0)	ACROPORIDAE (3)		
		A. humilis	*A. humilis*	*A. humilis*
Alpheus collumianus medius	1	0	0
Domecia glabra	0	0	1
Tetralia glaberrima	0	0	1
Tetralia heterodactyla	2	3	3

TABLE 7

Wilingili, Addu

	POCILLOPORIDAE (0)	ACROPORIDAE (6)				
		A. humilis	*A. humilis*	*A. humilis*	*A. nasuta*	*A. nasuta*	*A. diversa*
Coralliocaris nudirostris	0	0	1	0	0	0
Jocaste japonica	1	0	1	0	1	1
Cymo deplanatus	2	2	0	1	0	0
Domecia glabra	0	0	2	0	0	0
Tetralia glaberrima	2	0	1	0	0	0
Tetraila heterodactyla	1	2	0	2	0	0

TABLE 8

Duwafuri, N. Mahlosmadulu

	POCILLOPORIDAE (0)	ACROPORIDAE (5)				
		A. humilis	*A. humilis*	*A. humilis*	*A. humilis*	*A. rotumana*
Jocaste japonica	10	10	0	1	8
Alpheus gracilis	0	1	0	0	0
Chlorodiella laevissima	0	1	0	0	0
Pilodius spinipes	0	0	1	0	0
Tetralia glaberrima	2	0	3	0	2
Tetralia heterodactyla	2	2	0	1	0

TABLE 9

Wala, S. Nilandu

	POCILLOPORIDAE (1)		ACROPORIDAE (8)							
	P. eydouxi		*A. humilis*	*A. humilis*	*A. rotumana*	*A. rotumana*	*A. rotumana*	*A. rotumana*	*A. convexa*	*A. convexa*
Pericliminaeus cf. *spongicola*	2	*Periclimines lutescens*	0	0	0	0	0	0	2	0
Philarius sp. (prob. *gerlachei*)	10									
Harpiliopsis beaupresi	8	*Coralliocaris superba*	0	0	0	0	0	0	0	6
Harpiliopsis depressus	11	*Coralliocaris venusta*	0	0	0	0	0	0	1	0
Harpiliopsis spinigera	5									
Fennera chacei	4	*Jocaste japonica*	1	0	4	4	0	5	0	0
Thor maldivensis	2									
Alpheus lottini	2									
Synalpheus charon	2	*Synalpheus charon*	0	0	0	0	0	1	0	0
		Cymo deplanatus	0	0	0	2	0	1	0	0
		Cymo melanodactylus	1	0	0	0	0	0	0	0
Trapezia cymodoce	2	*Trapezia cymodoce*	0	1	0	0	0	1	0	0
Trapezia aff. *danai*	3	*Tetralia glaberrima*	2	0	2	2	0	2	2	13
Trapezia ferruginea	12	*Tetralia heterodactyla*	0	2	0	0	2	0	0	0
Trapezia digitalis	5									
Trapezia aff. *maculata*	6									

TABLE 10

Gan, Addu

	POCILLOPORIDAE (0)	ACROPORIDAE (11)									
		A. humilis	*A. humilis*	*A. humilis*	*A. humilis*	*A. humilis*	*A. humilis*	*A. humilis*	*A. variabilis*	*A. variabilis*	*A. tenuis*	*A. tenuis*
Coralliocaris superba		2	0	0	0	0	0	0	0	0	0	0
Jocaste japonica		4	0	0	0	0	0	0	0	0	0	0
Jocaste lucina		0	0	0	0	0	0	0	0	0	1	0
Cymo deplanatus		0	2	2	0	0	2	0	0	0	0	0
Cymo melanodactylus		0	0	0	0	0	0	0	0	0	0	2
Domecia glabra		0	2	0	0	0	0	0	0	0	0	0
Tetralia glaberrima		1	2	2	1	1	2	2	2	0	3	2
Tetralia heterodactyla		2	0	0	1	0	0	0	1	1	0	5
Pilodius melanospinus		1	0	0	0	0	0	0	0	0	0	0

MASTER TABLE

Decapod commensals collected from host corals at Galle, Ceylon, and in the Maldive Islands

	Galle, Ceylon		Dunidu, Male			Imma Male				Wilingili, Adu							Wala, S. Niladu				Gan, Addn		
	P. elegans	*P. elongata*	*A. ramiculosa*	*A. conferta*	*P. woodjonesi*	*P. eydouxi*	*A. humilis*	*A. nasuta*	*P. woodjonesi*	*A. humilis*	*A.* unident.	*A. hebes*	*P. eydouxi*	*A. humilis*	*A. humilis*	*A. humilis*	*A. nasuta*	*A. diversa*	*A. humilis*	*A. rotumana*	*P. eydouxi.*	*A. humilis*	*A. rotumana*	*A. convexa*	*A. humilis*	*A. variabilis*	*A. tenuis*
												Mafilefuri, Fadiffolu		Kuludu, Milladumma	Ongu, North Mahlosmadulu				Duwafuri, N. Mahlosmadulu								
Number of colonies seen	1	1	2	1	3	1	2	1	2	2	2	1	1	1	3	3	2	1	4	1	1	2	4	2	7	2	2
PALAEMONIDAE-PONTONIINAE																											
Periclimines lutescens																								2			
Pericliminaeus spongicola																					2						
Philarius gerlachei																					10						
Coralliocaris graminea			1				2																				
Coralliocaris nudirostris																1											
Coralliocaris superba										2														6	2		
Coralliocaris venusta																								1			

Fennera chacei																					4						
Harpiliopsis beaupresi		11			3	1			4												8						
Harpiliopsis depressus	1	1			1				1												11						
Harpiliopsis spinigera																					5						
Jocaste lucina			1																								1
Jocaste japonica							7	4						2		2	1	1	21	8		1	13		4		
HIPPOLYTIDAE																											
Thor maldivensis																					2						
ALPHEIDAE																											
Alpheus lottini	1	5			6	1			4												2						
Synalpheus charon																					2		1				
XANTHIDAE																											
Cymo deplanatus							2	2		2	2			1		4	1						3		6		
Cymo quadrilobatus					2						1																
Cymo melanodactylus			5	2								2				1						1					2
Cymo?		1																									
Domecia glabra			1				1	1						1		2						2					
Domecia hispida		3			1				1																		
Tetralia glaberrima			21	12			4	2		4	3			2	1	3	2	1	5	2		2	6	15	11	2	5
Tetralia heterodactyla			9								4				8	3	2		5			2	2		3	2	5
Trapezia areolata		4																									
Trapezia cymodoce	1	2			7	2			2					2							2	1	1				
Trapeaia aff. *danai*					2																3						
Trapezia digitalis																					5						
Trapezia ferruginea	2	3			7				2												12						
Trapezia aff. *maculata*									2				1								6						
Trapezia aff. *tigrina*		3																									
Trapezia aff. *wardi*		3			2				2																		

GARTH AND BEARDSLEY MALDIVIAN STATIONS COMPARED

The Gary Beardsley stations add 25 lots to the study, of which 5 are from Duwafuri Island, N. Malosmadulu Atoll; 9 are from Wala Island, S. Nilandu Atoll; and 11 are from Gan Island, Addu Atoll. Of these 24 are from *Acropora* coral, while only one is from *Pocillopora* coral.

Species of shrimp not encountered by John S. Garth are *Periclimines lutescens, Coralliocaris venusta,* and *Synalpheus charon* from *Acropora* and *Periclimin-aeus* cf. *spongicola, Philarius* sp.(probably *gerlachei*), *Harpiliopsis spinigera, Fennera chacei, Thor maldivensis,* and *Synalpheus charon* from *Pocillopora.* Species of crabs not encountered by John. S. Garth are *Pilodius spinipes* and *P. melanospinus* from *Acropora* and *Trapezia digitalis* from *Pocillopora.* Of the shrimp, *Fennera chacei* is a first record for the Indian Ocean (Bruce, 1965) and *Periclimin-aeus* cf. *spongicola* is probably a new species (A. J. Bruce, personal communication).

The Gary Beardsley collections serve to reinforce the findings based on the John Garth collections in the following ways: (1) The commonest crabs from *Acropora* were *Tetralia glaberrima* and *T. heterodactyla.* These were found 14 and 7 times, respectively, among Garth coral collections, but 20 and 10 times, respectively, among Beardsley coral collectinons. In both collections the frequcency of occurrence of *T. glaberrima* was twice that of *T. heterodactyla.* (2) The next most abundant crabs from *Acropora* were *Cymo deplanatus* and *C. melanodactylus.* These were found 7 and 2 times, respectively, among Garth collections, but 5 and 2 times among Beardsley collections. *C. deplanatus* is therefore three times as abundant as *C. melanodactylus,* in point of total c occurrence. (3) The commonest shrimps from *Acropora* were *Jocaste japonica* and *J. lucina* as previously reported by Bruce (1969b). These were found 8 and 1 times, respectively, in both Garth and Beardsley collections. The predominance of *J. japonica* over *J. lucina* in point of occurrence is therefore 8 to 1.

As to mated pairs, these occur for *Tetralia glaberrima* in 14 out of 19 cases (or 15 out of 20 if the occurrence of multiple pairs, noted below, is included), while for *T. heterodactyla* their occurrence is 6 out of 10 cases. Allowing for possible instances in which one of the pair was not recovered(the commonest cause being escape into the rocky or rubbly substrate), it seems reasonable to assume that each head of *Acropora* normally supports a mated pair of *Tetralia.* In 19 of the 24 heads examined it was either *T. glaberrima* or *T. heterodactyla;* in the remaining heads both were present. Of the 5 cases in which both species were present, mated pairs of both were present in 2, a mated pair one or the other in 2 more, while in only one case was a male of one found with a female of the other species. Again, while in 19 of the 24 heads examined not more than one pair of a given species of *Tetralia* was found, in the 20th (a 20-25 cm *Acropora*) there were 6 males and 7 ovigerous females of *T. glaberrima*! A similar multiple occurrence was noted by Patton (1967), who reported eleven pairs from a tightly branched coral colony.

Although the number of occurrences is far smaller, the pattern for *Cymo* is similar. Four out of 5 occurrences of *C. deplanatus* are of mated pairs, as is one of 2 occurrences of *C. melanodactylus.* Chances of escape for one of a pair of *Cymo* are less than for *Tetralia* because of their occupancy of a burrow in the base of the coral head; however, because of this it sometimesp roved impossible to extract one of a pair if the burrow was a deep one. The two species of *Cymo, C. deplanatus* and *C. melanodactylus,* did not occur in the same coral head, nor were multiple occurrences observed.

The occurrence in the same head of coral of mated pairs or multiple individuals of *Tetralia glaberrima* and *T. heterodactyla*, of *Harpiliopsis depressus* and *H. spinigera*, and of *Jocaste japonica* and *J. lucina* may be taken as clear evidence of the specific identity of each, a question formerly in doubt.

Although information on sex on many of the Pontoniinae is lacking, *Periclimines* is present as a mated pair in its single occurrence, as is *Pericliminaeus* cf. *spongicola*. The *Coralliocaris* species, *C. superba* and *C. venusta*, are present once each as mated pairs and once each in numbers (6 and 4, respectively) with ovigerous females present. Insufficient numbers of *C. graminea* were collected to confirm Patton's (1967) finding of twice as many females as males of that species in corals of the Great Barrier Reef. Among the Alpheidae, *Alpheus lottini* was collected 8 out of 10 times as mated pairs, twice as solitary individuals, while *Synalpheus charon* was paired in one of 2 occurrences. According to Dr. A. J. Bruce (pers. comm.), the presence of pairs or larger numbers of shrimp in a coral colony is largely a question of the size or degree of complexity of the coral head. Thus small heads or those with short, stout branches will often contain only a single pair of shrimps, whereas a larger head, or one with numerous, finely divided branches will produce many more.

CEYLON AND MALDIVIAN COLLECTIONS COMPARED

The inclusion of decapod commensals from coral collections at Galle, Ceylon, which lies in the same latitude as the northernmost atoll of the Maldive Islands but some distance to the east, serves to emphasize the similarities of coral communities from different localities, regardless of host species. Thus, while coral species collected from Gale and the Maldive Islands proved to be mutually exclusive, suggesting that two different suites of commensal inhabitants might be expected, the decapod species found in them were essentially the same. Only three coral commensal crabs, *Cymo*(?) *Trapezia areolata*, and *T.* aff. *tigrina*, were collected at Galle but not in the Maldive Islands, while three other coral commensal crabs, *T. digitalis*, *T.* aff. *danai*, and *T.* aff. *maculata*, were collected int the Maldive Islands but not at Galle. These, incidentally, were all found in *Pocillopora*, which, hile wless frequently sampled than was the more abundant *Acropora*, when encountered yielded larger heads with greater diversity of commensals. Shrimp found in the Maldive Islands but not in Ceylon were *Philarius* sp. (probably *P. gerlachei*), *Harpiliopsis spinigera*, *Fennera chacei*, and *Thor maldivensis* in *Pocillopora* and *Coralliocaris nudirostris*, *C. superba* and *C. venusta*, *Periclimines lutescens*, and *Jocaste japonica* in *Acropora*. Considerably more collecting must be done in both areas before it can be said that the absences noted were due to preferences of these decapod commensals for specific coral hosts.

CEYLON AND MALDIVIAN COLLECTIONS COMPARED WITH THOSE OF THE GREAT BARRIER REEF

The study with which the present one is most strictly comparable is that by Patton (1966) on decapod crustaceans commensal with branching corals of the Great Barrier Reef, Queensland. Corals examined by Patton were *Pocillopora damicornis* (Linnaeus) and *P. verrucosa* (Ellis & Solander), *Stylophora pistillata* (Esper) and *S. mordax* (Dana), and *Seriatopora hystrix* (Dana) of the Pocilloporidae; and *Acropora* alone of the Acroporidae, not identified to species.

Shrimp found by Patton to be obligate commensals of pocilloporid corals were *Periclimines amymone* and *P. inornatus* Patton (not Kemp) [now known as

P. madreporae Bruce], *Harpiliopsis beaupresi* and *H. depressus*, and *Fennera chacei* of the Pontoniinae; *Thor amboinensis* of the Hippolytidae; and *Alpheus ventrosus* and *Synalpheus charon* of the Alpheidae Crabs found to be obligate commensals of pocilloporid corals were *Cymo andreyossyi*, *Domecia hispida*, *Trapezia cymodoce*, *T. ferruginea*, *T. areolata*, *T. guttata* (the two latter as forms of *T. ferruginea*), *T. digitalis*, and *T. rufopunctata* of the Xanthidae.

Shrimp found by Patton to be obligate commensals of acroporid corals were *Periclimines amymone* and *P. lutescens*, *Philarius gerlachei* and *P. imperialis*, *Coralliocaris brevirostris*, *C. graminea*, *C. superba*, and *C. venusta*, *Jocaste japonica* and *J. lucina* of the Pontoniinae. Crabs found to be obligate commensals with acroporid corals were *Cymo melanodactylus* and *C. deplanatus*, *Domecia glabra*, *Tetralia glaberrima* (of which several forms were noted), and *T. heterodactyla* (including *T. heterodactyla fusca*.)

Patton (1966) concluded that the two coral families had quite distinct faunas of obligate commensals, only the single species *Periclimines amymone* occurring in both. This was also the conclusion of Garth (1964) regarding crabs commensal with branching corals at Eniwetok in the Marshall Islands. In comparing Patton's Queensland list with the writer's Ceylon and Maldive Islands lists it should be noted that *Alpheus ventrosus* Milne Edwards is a synonym of *A. lottini* Guérin, while *Trapezia maculata* MacLeay was considered a synonym of *T. rufopunctata* (Herbst) at the time of Patton's writing. *Thor amboinensis* de Man is apparently replaced in the Maldive Islands by *T. maldivensis* Borradaile, while *Coralliocaris brevirostris* may be similarly replaced by *C. nudirostris* (Heller). With these explanations, the remarkable similarity between the commensal decapod faunas of braching corals of the western South Pacific and Indian Oceans becomes apparent. The more extensive list of shrimps from Queensland may be due to the more numerous genera of pocilloporid corals examined, to more intensive collecting, or to the methods employed, which appear to have been more successful in capturing the full complement of shrimps than those of Gray Beardsley and the writer.

In the study mentioned, Patton (1966) described a number of colour forms of *Tetralia glaberrima*, several of which were recognised among the writer's Indian Ocean material, as well as among the earlier collections of Borradaile (Garth, in press), together with form *fusca* Serene and Pham Dat (1957) of *T. heterodactyla*. In the present paper these are grouped with the nominate forms for, although they may represent incipient species, they are not as well defined as are the better known "forms" of *Trapezia cymodoce*, which are now considered full species by most crustacean systematists.

CEYLON AND MALDIVIAN COLLECTIONS COMPARED WITH THOSE OF THE GALAPAGOS ISLANDS

A comparison of the present collections with those reported from the Galapagos Islands as occurring in branching corals (Garth, 1946) shows that an entire suite of commensals, those from *Acropora* corals, are missing. This is not surprising in view of the fact that the family Acroporidae is absent in the tropical eastern Pacific, whereas the Pocilloporidae is well represented. Of coral commensals common to the two regions, as well as to the Great Barrier Reef, *Fennera chacei* and *Harpiliopsis depressus* of the Pontoniinae, *Ailheus lottini*(=*A. ventrosus*) of the Alpheidae may be mentioned. These, together with *Trapezia ferruginea*, *T. digitalis*, and *Domecia hispida* of the Xanthidae, constitute the common element inhabiting the *Pocillopora* coral colony of both Indo-west Pacific and east Pacific Oceans. To these should

abedd ed the coral gall crab, *Haplocarcinus marsupialis* Stimpson. The xanthid carb *Maldivia galapagensis*, which inhabits *Pavona* coral, is closely related to *M. triunguiculata* (Borradaile) of the Maldive Islands. Unfortunately, neither this species nor *M. symbiotica* Borradaile, found on a gorgonian, were collected by Cruise B of TE VEGA.

SIGNIFICANCE OF PAIRING

The high incidence of mated pairs, with females in most cases ovigerous, is of particular significance with respect to the nature of the commensalism, the degree of host specificity, and the biological distinctness of the forms involved.

Nature of commensalism : In deciding whether the crab or shrimp is an obligatory commensal or a faculative one, two types of evidence were considered:(1) the obligatory commensal is rarely encountered outside of living coral, whereas the facul tative commensal is regularly and predictably found in other situations; (2) the obligatory commensal finds in the living coral its ultimate retreat for mating and reproduction; the facultative commensal, using the living coral only as one of several possible habitats, may, and frequently does, retreat to another of these, such as dead coral or coral rubble, for these purposes. Facultative commensals are therefore transients in living coral, and are more likely to occur there as single, non-breeding individuals than as mated pairs.

Host specificity : In those cases in which a choice is to be made between the host groups to which the commensal is to be assigned (*i. e.*, Pocilloporidae vs. Acroporidae), the coral group on which it occurs in breeding condition (the best evidence of which is she presence of mated pairs with ovigerous females) is more probably the true host than the one on which it occurs as single, non-breeding individuals.

Biological distinctness : When two forms of a given species of crab or shrimp are found on the same host coral, both as mated pairs, it is assumed that isolating mechanisms are operating to prevent cross-breeding. This is presumptive evidence for the biological or reproductive distinctness of the forms concerned. which would appear on this basis to be different species, rather than subspecies or varieties of the same species.

OBLIGATORY VERSUS FACULTATIVE COMMENSALS

In addition to those decapod species collectod only from living corals, and for this reason regarded as obligatory commensals, a number of decapod species collected among the branches of living corals were also found in other situations, such as as in dead coral, in coral rubble, in *Lithothamnion* nodules, or in sponges. From this circumstance, plus the fact that most were found as solitary individuals, rather than as mated pairs, it was concluded that they do not require living coral to sustain their life processes, that their occurrence on a particular coral was probably a matter of accident than of host preference, and hence that they were facultative symbionts at most, if not accidental inclusions in the coral milieu.

Among shrimp of the family Palaemonidae, subfamily Pontoniinae, *Periclimines elegans* was eliminated as an obligatory commensal of living coral by virtue of having been found in dead coral as well. Similarly, *Periclimінaeus* cf. *spongicola* was judged to be from sponges found among the coral branches, rather than from the coral itself (A. J. Bruce, *in litteris*). *Palaemonella rotumana*, although collected only in living coral, appears to have no host preference, having been found on

Pocillopora in the Maldive Islands and on *Acropora* in Ceylon. As regards shrimp of the family Alpheidae, only two species, *Alpheus lottini* and *Synalpheus charon*, are listed as obligate commensals, and of these *S. charon* occurs on both pocilloporid and acroporid corals. Also collected at Galle, Ceylon, on *Pocillopora* were *Alpheus didema* and *Athanas* sp. and on *Acropora* were *Alpheus edwardsi* group and *Synalpheus paraneomeris*. Collected in the Maldive Islands on *Pocillopora* were *Alpheus crinites* groups, *A. eulimne*, *A. gracilpes*, *A. gracilis*, *A. macrochirus*, *A. macrochirus* group, and *A. paragraclis;* and on *Acropora* were *Alpheus collumianus medius*, *A. crinites* group, *A. gracilis*, and *A. parvirostris*. Of these *Alpheus crinites* group and *A. gracilis* were found on both pocilloporid and acropoirid corals, hence are not host specific. Also, with the exception of *A. gracilipes*, all Maldivian alpheids except the two known obligate commensals mentioned were represented by single specimen, rather than pairs, suggesting that they are vagrants, likely to be found in other situations had collecting in non-coral habitats been sufficiently pursued.

Among crabs of the family Porcellanidae, *Porcellana graveleli* and *Pisidia* sp. were collected at Galle, Ceylon, from both *Pocillopora* and *Acropora* coral, indicating lack of host preference, P. *gravelei* from a lagoon as well. *Petrolisthes asiaticus* and *Pisidia* sp. were collected from both living and dead coral, showing them to be non-obligate. *Petrolisthes penicillatus* was collected in the Maldive Islands from living coral with a dead base and from hand-collecting on a reef, as was *Pagurus* (*Pagurixus*) sp., a hermit crab of the family Paguridae. *Calcinus rosaceus*, a hermit crab of the family Diogenidae, was collected from both *Pocillopora* and *Acropora* coral. It was concluded, therefore, either from lack of host specificity or from lack of need for living coral, that there were no obligate commensals present among these anomuran families.

Among crabs of the family Xanthidae, *Carpilodes margaritatus* was collected from *Pocillopora*, *Paraxanthias notatus* and *Pilodius areolatus* from, *Acropora* coral at Galle, Ceylon; whereas *Actaea polyacantha*, *A. speciosa*, and *Phymodius* sp. (*monticulosus* or *ungulatus*) were collected from *Pocillopora*, *Chlorodiella cytherea* and *Pilodius spinipes* from *Acropora*, and *Chlorodiella laevissima* and *Pilodius melanospinus* from corals of both general in the Maldive Islands. The *Chlorodiella*, *Paraxanthias*, *Pilodius*, and *Phymodius* species were found in dead as well as in living coral, leaving only the status of the *Actaea* and *Carpilodes* species in doubt, These occurred as solitary individuals, rather than as pairs, suggesting that they also should be regarded as facultative, rather than as obligatory symbionts of living coral.

CONCLUSIONS

1. Each head of *Acropora* normally supports a pair of *Tetralia*, which may be either *T. glaberrima* or *T. heterodactyla*, or occasionally both. Each head of the larger *Pocillopora* may support several pairs of *Trapezia* of one or more species.

2. When two or more congeners occur in the same type of coral, one is clearly dominant in a simple ratio: *Tetralia glaberrima* over *T. heterodactyla* in the proportion of 2:1; *Cymo deplanatus* over *C. melanodactylus* in the proportion of 3:1; *Harpiliopsis depressus* over *H. spinigera* in the proportion of 3:1; and *Jocaste japonica* over *J. lucina* in the proportion of 8:1.

3. The occurrence of mated pairs of both of these congeners in the same type of coral and often in the same coral head is evidence of their specific identity, in the case of the *Tetralia*, *Harpiliopsis*, and *Jocaste* species formerly in doubt.

4. The occurrence of mated pairs also supports the obligatory nature of the commensal relationship, the facultative commensals more frequently occurring as solitary, non-breeding individuals.

5. Although corals were identified to species and decapod commensals from each were segregated, no decapod commensal appears restricted to a single species of coral. Rather, host specificity appears to be at the generic or family level. (See also Bruce, 1969a, p. 185.)

6. Of decapod genera known to be obligate commensals of branching corals, *Harpiliopsis*, *Fennera*, and *Trapezia* are limited to the Pocilloporidae, *Coralliocaris*, *Jocaste*, and *Tetralia* to the Acroporidae, with few exceptions.

7. Of decapod genera known to be obligate commensals of branching corals, *Cymo* and *Domecia* species are limited to one or other coral family: *Cymo quadrilobatus* and *Domecia hispida* to Pocilloporidae; *Cymo deplanatus*, *C. melanodactylus*, and *Domecia glabra* to Acroporidae.

8. Allowing for replacement species in a few instances and for the fact that fewer genera of corals were sampled, the commensal decapod fauna of branching corals in Ceylon and the Maldive Islands is in essential agreement with that of the Great Barrier Reef.

9. Although many decapod genera are common to the Indo-west Pacific and east Pacific Oceans, few species occur in both regions. Conspicuous among these are the obligate commensals of pocilloporid corals: *Fennera chacei*, *Alpheus lottini* (= *A. venusta*), *Harpiliopsis depressus*, *Domecia hispida*, *Trapezia ferruginea*, and *T. digitalis*.

10. The small number of the shrimp *Periclimines* collected and the total absence of the swimming crab *Thalamita* from coral collections suggests that many of these active forms were lost in hand-carrying the coral heads to the beach from shallow water. To insure a complete representation of the decapod commensal fauna, coral heads should be enclosed in plastic bags before being pried loose from the substratum.

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