The Crustacea Decapoda (Brachyura and Anomura) of Eniwetok Atoll, Marshall Islands, with special reference to the obligate commensals of branching corals[1]

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Introduction

The brachyuran decapod crustaceans of the Marshall Islands have been reviewed by Balss (1938) and by Miyake (1938, 1939). These reports stem from the German and Japanese occupations, respectively, the former being the result of the Pacific Expedition of Dr. Sixten Bock, 1917–1918, the latter the result of the Micronesia Expedition of Prof. Teiso Esaki, 1937–1938. According to Fosberg (1956, p. 1), Jaluit Atoll was the headquarters of both the German and the Japanese administrations, a fact that accounts for the preponderance of records from the southern Marshall Islands. Additional coverage of the southern Marshalls was provided by the 1950 Arno Atoll Expedition of the Coral Atoll Program of the Pacific Science Board, the decapod crustaceans collected by Dr. R. W. Hiatt having been reported by Holthuis (1953). Carcinologically speaking, the northern Marshalls are less well known, collections having been made only at Likieb Atoll by both Dr. Bock and Prof. Esaki and at Kwajalein Atoll by Prof. Esaki alone. Except for the shrimps, reported by Chace (1955), the extensive collections made in connection with Operation Crossroads in 1946–1947, which included Bikini, Rongelap, Rongerik, and Eniwetok atolls (Fosberg, 1956, p. 4), are at the U. S. National Museum awaiting study.

The collecting on which the present report is based was carried out at Eniwetok Marine Biological Laboratory during 1956–1961. Five separate but related collections comprise the material examined: (1) a small consignment of decapod and stomatopod crustaceans obtained by graduate students of the University of Hawaii in August and September, 1956; (2) simultaneous collections made by Donald J. Reish in 1956 and also in July, 1957; (3) a small collection, mostly from corals, made by A. H. Banner in February, 1957; (4) extensive collections made by F. C. Ziesenhenne and J. S. Garth in July, 1957, and again in July, 1959; and (5) small collections from individual coral heads made by E. S. Reese in January, 1960, and in April, 1961. To these may be added occasional collections made by Eniwetok-based scientists at atolls other than Eniwetok,

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particularly Bikini and Ailinginae. Assistance in collecting was provided at Eniwetok by L. Donaldson, E. Held, T. Goreau, R. Neshida, J. Coatsworth, A. Smith, J. Roberts, E. S. Reese, and R. A. Stevenson, at Bikini by D. J. Reish and F. C. Ziesenhenne, and at Ailinginae by R. Palumbo.

Collecting methods utilized included (1) intertidal collecting on the reef flat of ocean and lagoon sides on windward and leeward islands; (2) subtidal collecting of coral heads, both living and dead, by skin diving in 10–30 feet, lagoon side only; (3) dredging among coral patches on sandy bottom in 2–5 fathoms, lagoon side only; (4) examination of invertebrates other than corals (i.e., mollusks and echinoderms) for commensal species; and (5) night collecting with suspended light or flashlight.

The present survey has resulted in the collecting of 19 families, 81 genera, and 147 species (9 identified to genus only) of anomuran and brachyuran decapod crustaceans from the northern Marshall Islands, almost all collected at Eniwetok Atoll. Of the anomuran crabs in the present collection there are 5 families, 14 genera, and 35 species (7 identified to genus only). Of the brachyuran crabs there are 14 families, 67 genera, and 112 species (3 identified to genus only). The macruran decapods have been referred to other specialists and are not included in this report.

Of the Anomura, the family Paguridae numbers 8 genera and 21 species (6 identified to genus only). With the addition of the Coenobitidae, the Paguroidea number 10 genera and 27 species (7 identified to genus only). Land hermit crabs literally swarm over the higher and drier portions of the atoll, and because of their omnivorous habits have been utilized as indicators of radiation present in organic matter (Held, 1960). The Porcellanidae number 2 genera and 4 species; the Galatheidae number 1 genus and 3 species; the Hippidae have but 1 genus and species.

The Brachyura may be divided further into four major groups: oxystomatous and allied crabs, 5 families, 6 genera, and 8 species; oxyrhynchous or spider crabs, 2 families, 13 genera, and 14 species (1 identified to genus only); brachyrhynchous Cyclometopa, or cancroid crabs, 3 families, 39 genera, and 77 species (1 identified to genus only); and brachyrhynchous Catometopa, or grapsoid crabs, 4 families, 9 genera, and 14 species.

The disproportionate representation of the cancroid crabs is accounted for largely by the preponderance of the Xanthidae, which alone number 30 genera and 63 species. One reason for their great proliferation in tropic seas is the protection afforded them by the branching corals that flourish in warm waters. The shallow water Portunidae are next in point of abundance, numbering 7 genera and 12 species. They find ideal conditions for their mode of existence in the shallows of the reef flat and in the atoll lagoon. Attention will therefore be focused on the brachyuran and anomuran crustaceans of these habitats, which are unique to coral islands and their reefs.

Fig. 1. The plate-like *Turbinaria*, a member of the coral family Dendrophyllidae, showing shallow burrows made by the hapalocarcinid crab, *Troglocarcinus viridis*. (Photo courtesy of R. A. Stevenson).

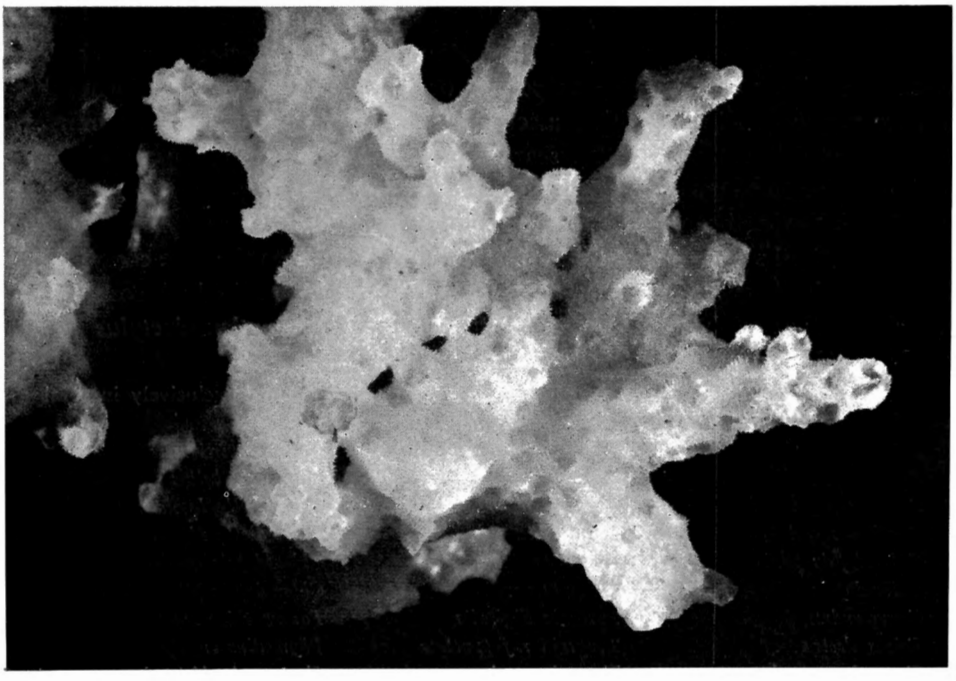

Fig. 2. The stony coral, *Pocillopora damicornis*, a member of the Pocilloporidae, showing respiratory openings of two coral gall crabs, *Hapalocarcinus marsupialis*, the females of which are imprisoned for life in their limestone cells.

Species found in Association with Corals

Among the oxyrhyncha, 6 species were collected in association with corals. Of these 5 were of the family Majidae, 1 of the family Parthenopidae. Of the 5 majid species 2 (or possibly 3) were found exclusively among corals, while 2 (or possibly 3) were found in other associations as well. Only *Tylocarcinus styx* was found both exclusively and commonly with corals, having been collected at 10 stations, at all of which *Acropora* was present. In only two of these was the coral living; at other stations it was noted as either overgrown or dead. It was concluded, therefore, that *Tylocarcinus* inhabits dead, and occasionally living, *Acropora* coral, and that there are no obligate commensals of living coral among Eniwetok Oxyrhyncha. The list follows:

Exclusively in coral	Not exclusively in coral
Majidae—*Paratymolus sexspinosus* (?)	Majidae—*Paratymolus sexspinosus* (?)
Schizophrys aspera	*Menaethius monoceros*
Tylocarcinus styx	*Perinea tumida*
Parthenopidae—*Harrovia elegans*	

Among the Brachyrhyncha, family Portunidae, 4 species were collected with corals. Of these 2 were more frequently taken free living or in other associations, while 2 were taken exclusively with coral. Although collected once in living *Acropora, Thalamitoides quadridens* is not considered an obligate commensal of living coral, since it occurs also in dead *Acropora,* and perhaps also in other corals. *Thalamita pilumnoides* was taken only in dead coral.

Exclusively in coral	Not exclusively in coral
Portunidae—*Thalamitoides quadridens*	*Thalamita admete*
Thalamita pilumnoides	*Thalamita picta*

Among the Brachyrhyncha, family Xanthidae, 37 species were taken in association with corals, either exclusively or predominantly. Of this number, 28 were not found in any other association, while 9 occurred at one or more non-coral stations as well. The search for the obligate commensals of living corals was therefore narrowed to the 28, and from these the greater number were excluded as having been found in dead coral only, or in dead as well as in living coral. The final number of 9 found only in living corals are the true commensals, although subsequent studies on collections made from individual coral heads have shown that to these the species of *Cymo* other than *melanodactylus* should be added. (See revised list at end of next section.)

Found exclusively in coral		Not found exclusively in coral
In dead or overgrown coral:	In living coral only:	
Actaea cavipes	*Cymo melanodactylus*	*Actaea superciliaris*
Actaea reppellii	*Domecia glabra*	*Carpilodes bellus*
Actaea rufopunctata	*Tetralia glaberrima*	*Chlorodiella laevissima*
Carpilodes coelatus	*Tetralia heterodactyla*	*Chlorodiella nigra*
Chlorodopsis pugil	*Trapezia cymodoce*	*Chlorodopsis areolata*
Chlorodopsis spinipes	*Trapezia danai*	*Chlorodopsis pilumnoides*
Cymo andreossyi	*Trapezia digitalis*	*Paraxanthias notatus*
Etisus electra	*Trapezia rufopunctata*	*Phymodius ungulatus*
Euxanthus exsculptus	*Trapezia speciosa*	*Zoozymodes biunguis*

Liocarpilodes armiger
Liocarpilodes integerrimus
Parapilumnus verrucosipes
Phymodius nitidus
Pilodius flavus
Planopilumnus vermiculatus
Pilumnus longicornis
Polydectus cupulifer

In coral of unknown condition:
Actaea speciosa
Cymo deplanatus

Studies of segregated Collections from individual Heads of Coral

The first collections of decapod crustaceans obtained from corals by diving in the lagoon at Eniwetok were indiscriminate. Since their objective was to determine the yield of this habitat in comparison with others, the material was treated like that from a shore station or a dredge haul, and specimens from several kinds of corals, both living and dead, were combined. Some 25 species of crabs were collected from corals of at least three genera (*Acropora, Pocillopora, Stylophora*) in July, 1957, but because of the mingling of the corals and the mixing of their commensals, it could not be determined from which kind of coral each had come, or whether from the dead base or the still growing terminal portion of the colony. Such information being essential in determining both host specificity and degree of attachment of commensal to host, which may vary from loosely to closely bound, a new approach to the problem was imperative.

Beginning in July, 1959, an attempt was made to segregate the crustacean collections according to the type of coral in which they were found and to distinguish between specimens found in dead coral and those found only in the living parts. This technique was further refined by E. S. Reese, who at the writer's instigation in January, 1960, and in April, 1961, made separate collections of crustaceans from individual coral heads, enclosing a piece of coral with each for later identification. These segregated collections number 30 and include representatives of the two principal families of the branching corals in which commensal decapods are found, the Acroporidae (10 species) and the Pocilloporidae (5 species), as well as the more massive Poritidae, Helioporidae, and Thamnasteriidae (1 species each). Coral identifications are by E. C. Allison, Geology Department, San Diego State College, and Museum of Paleontology, University of California, Berkeley.

The following are the corals examined for commensals, together with the number of collections from each, if more than one:

ACROPORIDAE (10 collections)
Acropora corymbosa (Lamarck)
Acropora cymbicyanthus (Brook)
Acropora echinata (Dana)
{*Acropora formosa* (Dana), or
Acropora acuminata (Verrill)
Acropora humilis (Dana) (2)

POCILLOPORIDAE (14 collections)
Pocillopora damicornis (Linnaeus) (3)
Pocillopora elegans (Dana) (2)
Pocillopora verrucosa (Ellis & Solander)
Pocillopora elegans and/or *verrucosa* (4)
Pocillopora eydouxi Milne Edwards & Haime
Seriatopora hystrix (Dana) (3)

Acropora hyacinthus (Dana)
Acropora paniculata (Verrill)
Acropora surculosa (Dana)
Acropora variabilis (Klunzinger)
DENDROPHYLLIDAE
Turbinaria danae Bernard
PORITIDAE
Porites andrewsi Vaughan
HELIOPORIDAE
Heliopora coerulea (Pallas)
THAMNASTERIIDAE
Psammocara (*Stephanaria*) *togianensis* Umbgrove

Among the crabs found only in living coral, the following preferences were apparent: (Number of times collected given in parentheses, if more than once).

Found only in ACROPORIDAE:
Cymo deplanatus
Cymo melanodactylus
Domecia glabra
Tetralia glaberrima[1] (11)
Tetralia heterodactyla (3)
Found only in DENDROPHYLLIDAE:
Troglocarcinus viridis
Found only in POCILLOPORIDAE:
Hapalocarcinus marsupialis (2)
Cymo andreossyi[2]
Domecia hispida
Trapezia cymodoce (5)
Trapezia ferruginea (7)
Trapezia digitalis group
Trapezia danai (3)
Trapezia rufopunctata

[1] Once in *Pocillopora damicornis*
[2] From an unsegregated collection, with *Acropora* also present

In general, the larger forms were found in the more robust Pocilloporidae, the smaller forms in the more delicate Acroporidae. Thus the *Trapezia* species occurred in the pocilloporid corals, the *Tetralia* species in the acroporid corals, although *Tetralia* was found once in *Seriatopora,* a finely branching member of the Pocilloporidae in which the spatial relationships found in the Acroporidae obtain. Again, while several of the larger *Tetralia* forms were found in the clump-type *Acropora,* only the smallest form (*T. glaberrima* var. *nigrifrons*) was found on the plate-type *Acropora,* where larger forms would lack concealment.

The *Trapezia* and *Tetralia* species were invariably found living in pairs, usually but a single pair to a head of coral. (Exceptions were the larger heads of *Pocillopora elegans,* where several pairs of *Trapezia* might occur, and the plate-like *Acropora* sp., which has no discrete unit as the head, and in which were found 27 males and 16 females of the small *Tetralia.*) The occupancy of a coral head by an adult pair of one species did not preclude its occupancy by the young of the same species, nor apparently by an adult pair of another species, together with their young. The way in which territoriality is established and defended is not known.

It will be noted that while all five species of *Trapezia* are restricted to the Pocilloporidae and the two species of *Tetralia* to the Acroporidae, the three species of *Cymo* and the two species of *Domecia* are distributed between these coral families. This suggests that the commensal habit is older and more firmly fixed in *Trapezia* and *Tetralia* than in *Cymo* and *Domecia.*

The coral gall crabs, family Hapalocarcinidae, are represented by *Hapalocarcinus marsupialis,* found thus far at Eniwetok only on *Pocillopora damicornis,* but known to form galls on other members of the Pocilloporidae, and by the minute burrowing crab, *Troglocarcinus viridis,* found only on the plate-like

Turbinaria danae, a member of the Dendrophyllidae. Close inspection of the many other types of corals found at Eniwetok Atoll would undoubtedly reveal additional hosts for *Hapalocarcinus* and additional species of *Troglocarcinus,* which are widely distributed in the Indo-west Pacific (Fize and Serène, 1957).

Species obtained by Dredging in the Lagoon

Sampling of the lagoon bottom by dredging was attempted on four occasions. Localities sampled were off Parry Island in the southeast part of the lagoon and off Aomon, Biijiri, and Rojoa islands in the northeast part of the lagoon. Dredging was done from an M-boat or an amphibious "duck" in depths of from 1 to 5 fathoms on sandy bottom. A triangular dredge frame with a 1-foot opening was used, with visual control to prevent fouling on larger clumps of coral. In such an emergency the 100-foot line could be tossed overboard with a life preserver attached and the dredge retrieved after circling with the boat.

Limited as were the hauls in number, duration, and scope, the dredged material contained 1 family, 6 genera, and 12 species of crabs not encountered in any other situation, plus several more occasionally found elsewhere but apparently most at home in this environment. Best represented were the Portunidae, with 4 species, and the Paguridae, also with 4 species. Among the Majidae two species were found nowhere else, as was one species of the Leucosiidae and one of the Parthenopidae.

Found exclusively in shallow dredging:

Portunidae—*Portunus granulatus*
Portunus longispinosus
Portunus orbicularis
Thalamonyx gracilipes
Majidae—*Huenia proteus*
Micippa philyra
Paguridae—*Dardanus scutellatus*
Dardanus wood-masoni
Dardanus sp.
Diogenes sp.
Parthenopidae—*Parthenope* sp.
Leucosiidae—*Ebaliopsis erosa*

The almost total absence of the Xanthidae from among dredged material is noteworthy because this family is represented so abundantly both intertidally and in coral. The small amount of hand dredging done has shown that the fauna of the lagoon bottom differs significantly from that of its exposed shore and promises the greatest reward for future investigation.

Conclusions

1. The collections of decapod crustaceans made at Eniwetok Atoll over the 1956–1961 five-year period, comprising 19 families, 81 genera, and 147 species of Brachyura and Anomura, compare favorably with those of the same groups collected by the Coral Atoll Survey of the Pacific Science Board (Holthuis, 1953), which numbered 21 families, 90 genera, and 180 species.

2. This gathering from a single locality of over 90 per cent as many families, 90 per cent as many genera, and 82 per cent as many species as were gathered at four widely separated western Pacific localities: Arno Atoll in the southern

Marshall Islands, Onotoa Atoll in the Gilbert Islands, Raroia Atoll in the Tuamotu Islands, and Saipan Island in the Marianas Islands, demonstrates the capacity of Eniwetok Atoll to support a great variety of crustacean inhabitants.

3. Of the collecting methods used for sampling the various habitats, which included shore collecting, skin diving in the lagoon, night collecting with light, and examination of invertebrates for commensals, the limited amount of dredging done revealed a significantly different fauna that bears further investigation.

4. The overwhelming representation in the atoll fauna of the family Xanthidae, which alone constituted 45 per cent of the genera and 56 per cent of the species of Brachyura collected, is believed in large part due to the protection afforded its smaller members by the branching corals.

5. Crustaceans collected from individually segregated coral heads showed 12 species of Xanthidae (and 2 of Hapalocarcinidae) to be obligatory commensals of living coral. Of these, 5 were found only on corals of the family Acroporidae, while 7 (and 1 hapalocarcinid) were found only on corals of the family Pocilloporidae.

6. The restriction of *Tetralia* to the Acroporidae and of *Trapezia* to the Pocilloporidae, with two or more species of each, suggests that the commensal habit is older and more firmly established in those genera than in *Cymo* and *Domecia,* which occur on both the Acroporidae and the Pocilloporidae, with one or more species on each.

7. The abundance of branching corals and of their associated decapod crustaceans makes Eniwetok Marine Biological Laboratory an ideal place for studies in those aspects of animal behavior related to symbiosis and commensalism, which it is hoped will be stimulated by this preliminary report.

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