Larval Behavior and Geographic Distribution of Coral Reef Asteroids in the Indo-West Pacific[1]

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Abstract.—Coral reef asteroids in the Indo-West Pacific faunal region may be divided into two groups, one widely distributed from continental areas to out among the scattered oceanic islands (widely distributed species) and the other found only along the continental land mass and proximal islands (continental species). A major difference in asteroid faunal compositions between Palau and Guam is the absence of the common continental species on the oceanic island of Guam. Larval development in four species, *Archaster typicus* and *Protoreaster nodosus* (continental species) and *Culcita novaeguineae* and *Acanthaster planci* (widely distributed species), shows marked similarities in morphology and rate of development when reared under similar conditions in the laboratory at Palau. The results from larval cultivation of these common asteroid species at Palau, Guam and in literatures suggest that the geographic distribution patterns might result from the modes of larval swimming behavior. Positive geotaxis in the continental species is in contrast with the negative geotaxis in the widely distributed species during most of their pelagic life span.

Introduction

The Indo-West Pacific possesses the most extensive marine faunal region with a homogeneous shelf fauna of high species diversity (Ekman, 1953). There is little endemism among the coral reef gastropods (Demond, 1957; Taylor, 1971) and asteroids (Marsh, 1974; Yamaguchi, 1975) on oceanic islands of this region. This low endemism and wide distribution of benthic animals has been attributed to passive dispersal of larvae by oceanic currents and to the lack of geographic isolation (Taylor, 1971). Scheltema (1968, 1971a, 1971b) has shown that some invertebrates produce "teleplanic" larvae in the tropical Atlantic. Closely related species in the Pacific may be assumed to produce similar long-distance larvae. However, there is information on larval development and behavior for only a small number of the Indo-West Pacific species (Thorson, 1961).

Abbott (1960) recognized two groups of species within the gastropod genus *Strombus* in the Indo-West Pacific and Caribbean: those restricted in distribution

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to the continental land mass or islands on the continental shelf and those distributed across the oceanic islands. Coral reef asteroids likewise may be divided into the continental and widely distributed species according to their distribution patterns. This paper considers the faunal compositions of the shallow water asteroids of Palau and Guam and the distribution patterns of four common asteroid species: *Archaster typicus, Culcita novaeguineae, Protoreaster nodosus,* and *Acanthaster planci* in relation to their larval behavior in the laboratory at Palau.

Materials and Methods

Specimens for breeding experiments and for distributional data on coral reef asteroids were collected in the Palau Islands in August 1974 and from May to July 1975. Collecting was limited to shallow water by daytime free or scuba diving. Aside from this sampling, the record of the asteroid fauna of Palau is comprised of Hayashi's (1938) report, a collection at the National Museum of Natural History (NMNH) made by "Project Coral Fish I" (Bayer and Harry-Roffen, 1957), and a collection in the Western Australian Museum (WAM) made by Mrs. L. M. Marsh. The above records and specimens are treated as the shallow water asteroid fauna of Palau for comparison with that of Guam (Yamaguchi, 1975) and the Marshalls (A. H. Clark, 1952, 1954).

Specimens of the four species, *Archaster typicus, Culcita novaeguineae, Protoreaster nodosus,* and *Acanthaster planci* in the NMNH and the Museum of Comparative Zoology of Harvard University (MCZ) were examined by the author and the data on these and the catalogued specimens at the British Museum (Natural History) (BM) and the WAM were compiled in order to construct the geographic distribution maps for each species. These four species normally inhabit shallow waters and are large and conspicuous enough to be easily collected so that the present compilation should give good indications of the distribution ranges for the four species.

During my 8 week visit from May to July 1975, the above four species were induced to spawn with injection of 1-methyladenine sea water solution in the laboratory at the Micronesian Mariculture Demonstration Center (MMDC), Palau. Cultures of less than 500 eggs were maintained in plastic beakers containing 750 ml of seawater. Embryos were kept in fresh seawater and changed every hour until after the development to vigorously swimming larvae had occurred. The density was then kept at 50 to 100 individuals per beaker. Subsequently, larvae were individually transferred daily to a new beaker with fresh seawater taken at the wharf of MMDC. No additional food was added to the seawater which was rich in phytoplankton.

For fully developed larvae, the blades of the seagrass *Halophila ovalis*, the surfaces of which were covered with epiphytic microalgae and fine sediments, were used as the settling substratum. A few isolated blades of *H. ovalis* were placed in the culture beakers with the fully developed brachiolariae for three to four days before counting the number of successfully settled juveniles.

Individual larvae were measured along the longest axis excluding paired arms. An ocular micrometer was used. During measurement, each larva was isolated in a depression slide with enough seawater to submerge the larva and to keep it still and straight. Twenty individuals per day were arbitrarily picked up from the culture beakers for the measurements and returned to the beakers immediately after the determination. The fully developed brachiolariae were difficult to measure because they contracted their bodies under the above conditions.

The transformation of asteroid larvae is gradual from gastrulae through bipinnariae to brachiolariae. Here, a larva is designated as a "bipinnaria" at the stage when the ciliary bands become clear and the feeding organs start functioning. "Brachiolaria" designates the stage when the three brachiolar arms develop. A fully developed larva has a dark-pigmented starfish primordium with developing ossicles and hydrocoel cavities and shows a "searching" behavior (Hyman, 1955; Henderson and Lucas, 1971; Yamaguchi, 1973) which indicates the readiness of a larva to settle if appropriate substrata were present.

Distributions of Continental and Widely Distributed Species

Although the asteroid faunas of Guam and Palau are both those of the Indo-West Pacific, the species compositions of the two islands are markedly different. Twenty-six species have been collected from Guam, but the Guamanian fauna lacks 10 of the 23 species reported from Palau (Table 1). Common species in Palau such as *Archaster typicus, Fromia monilis, Nardoa tuberculata,* and *Protoreaster nodosus* are absent in Guam and the Marshalls. There is no example of the reverse case, i.e., a species that is common in Guam but absent in Palau, except for a dubious species of *Linckia* (Yamaguchi, 1975; Strong, 1975), which may well be a variety of *Linckia laevigata.* The total number of asteroid species in Palau may rise to a much greater number if more extensive collections are made, but no new species have been found in the heavily collected waters of Guam since 1974.

The difference in faunal composition of asteroid species between Palau and Guam may be interpreted as a discontinuity between the distributions of two groups of species with disjunct ranges. The geographic ranges of *Archaster typicus* (Fig. 1) and *Protoreaster nodosus* (Fig. 2) are restricted to the continental region and the proximal islands while those of *Culcita novaeguineae* (Fig. 3) and *Acanthaster planci* extend to the oceanic islands. Other Indo-West Pacific coral reef asteroids which are not treated here can also be divided into the two patterns of continental and widely distributed species. Indeed, the asteroid species of Guam are mostly widely distributed species (Yamaguchi, 1975).

The majority of locality records for the continental species *Archaster typicus* and *Protoreaster nodosus* are enclosed within a triangle formed by Okinawa, Singapore and New Caledonia (Figs. 1 and 2). This strongly contrasts with the distribution patterns of the widely distributed species *Acanthaster planci* and *Culcita novaeguineae* (Figs. 3 and 4), which extend across the ocean to isolated oceanic islands. [*C. novaeguineae* is replaced in the Indian Ocean localities by the congener

Table 1. Asteroid species recorded from Micronesian islands.

Family and Species	Type of Geographical Distribution[1]	Relative Abundance[2]		
		Palau	Guam	Marshalls
Luidiidae				
Luidia savignyi	?	0	0	1
Astropectinidae				
Astropecten polyacanthus	Widely distributed	0	1	1
Archasteridae				
Archaster typicus	Continental	2	0	0
Oreasteridae				
Bothriaster prim genius	?	0	1	0
Choriaster granulatus	Widely distributed?	1	2	0
Culcita novaeguineae	Widely distributed	3	3	3
Protoreaster nodosus	Continental	3	(0)[3]	0
Ophidiasteridae				
Celerina heffernani	?	1	0	0
Cistina columbiae	Widely distributed?	0	1	0
Dactylosaster cylindricus	Widely distributed	0	1	1
Fromia milleporella	Widely distributed	1	2	2
Fromia indica	Continental	2	0	0
Fromia monilis	Continental	3	0	0
Fromia sp.	?	0	1	0
Gomophia egyptiaca	Widely distributed	0	2	0
Leiaster leachi	Widely distributed?	0	2	0
Linckia guildingi	Widely distributed	1	1	1
Linckia laevigata	Widely distributed	3	3	2
Linckia multifora	Widely distributed	3	3	3
Linckia pacifica	Widely distributed	0	1	0
Linckia sp.	?	0	3	0
Nardoa tuberculata	Continental	2	0	0
Nardoa sp.	Continental ?	1	0	0
Neoferdina cumingi	Widely distributed	0	1	1?
Noeferdina offerti	Continental	1	0	0
Ophidiaster granifer	Widely distributed	2	3	3
Ophidiaster robillardi	Widely distributed	3	2	1
Ophidiaster squameus	Widely distributed	0	1	1
Asteropidae				
Asteropsis carinifera	Widely distributed	1	1	0
Asterinidae				
Asterina anomala	Widely distributed	1	2	2
Asterina cepheus	Widely distributed	0	1	1
Patiriella exigua	?	1	0	0
Acanthasteridae				
Acanthaster planci	Widely distributed	2	2	1
Mithrodiidae				
Mithrodia clavigera	Widely distributed	1	2	0
Echinasteridae				
Echinaster callosus	Continental ?	1	0	0
Echinaster luzonicus	Widely distributed	3	3	3

[1] Judged from the distribution table for the Indo-West Pacific asteroids (Clark and Rowe, 1971) and later information.

[2] A. H. Clark (1952, 1954) gave the number of specimens for each asteroid species from the Marshalls. Here, 3 is for those with more than 10 specimens, 2 is for 2 to 9 specimens, 1 is for one specimen, and 0 is for no specimens. The relative abundance ranks for Palau and Guam asteroids are similarly classified according to the number of specimens collected, i.e., 0 is for no record, 1 is for less than a few incidental specimens, 2 is for rare but more than a few specimens, and 3 is for common or abundant.

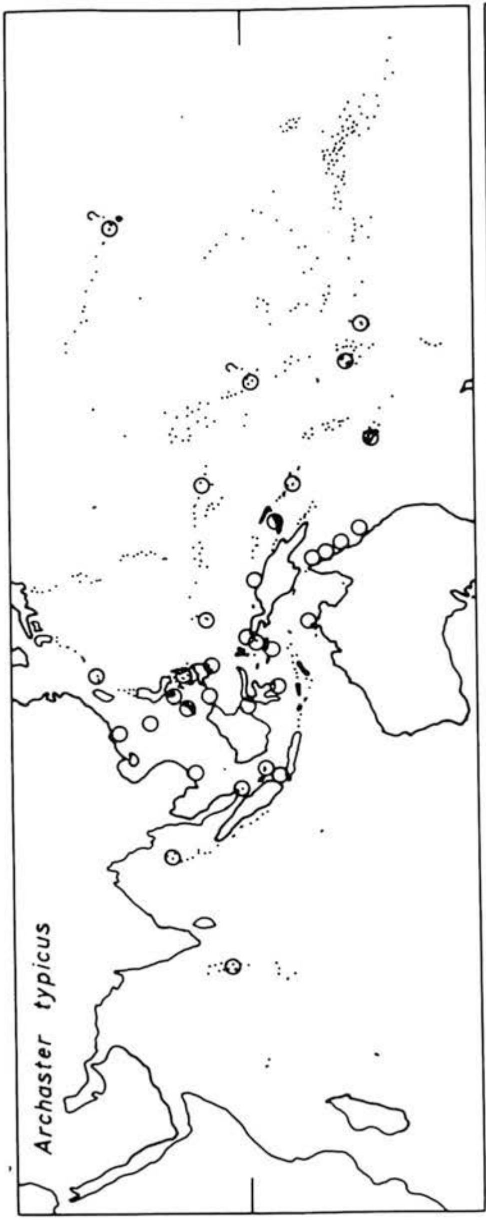
[3] Juvenile specimens were collected in 1945 but no further record exist.

Culcita schmideliana (Clark and Rowe, 1971). A specimen from the Cocos Keeling Atoll was identified by A. H. Clark (1950) as *Culcita novaeguineae* var. *grex* (NMNH E-7461). On my examination this appears to be an intermediate form between *C. novaeguineae* and *C. schmideliana*, having the strong conical spines, typical of the latter species, but distributed within the popular pore areas, the condition typical of the former species.

Both *Acanthaster planci* and *Culcita novaeguineae* are widely distributed throughout the tropical Pacific including Hawaii and many islands in southeastern Polynesia. *Acanthaster planci* is more widely spread in the Indian Ocean, reaching the Red Sea, and a very similar species *Acanthaster ellisii* is found in the eastern Pacific (Madsen, 1955; Dana and Wolfson, 1970) although its taxonomic status as a synonym of *A. planci* has been argued (Barham *et al.*, 1973; Glynn, 1973). Such wide distribution ranges are found in a few other coral reef asteroids such as *Linckia multifora, L. guildingi, L. laevigata* (excluding Hawaii), *Asteropsis carinifera,* and *Mithrodia clavigera* (replaced by *M. fisheri* in Hawaii) (Clark and Rowe, 1971). *Echinaster luzonicus* is found on the oceanic islands of the Pacific but is replaced by *Echinaster purpureus* in the Indian Ocean, just like the two species of *Culcita* mentioned above. These paired species may each constitute superspecies (Mayr, 1969) having a geographic segregation which is well-marked between the Western Pacific and the Indian Ocean.

The notable difference between the asteroid faunas of Palau and Guam may be attributed to the lack of common continental species in Guam. Furthermore, the asteroid species composition of the Marshall Islands indicates an additional attenuation of species diversity toward oceanic islands more remote from the continents. A. H. Clark (1952, 1954) reported 20 shallow water species of asteroids from the Marshalls, 15 of which are recorded on Guam. However, a close examination of the specimens at NMNH on which the above reports are based revealed that the total number of species from the Marshalls is likely to be 16 or 17 after correcting misidentified and probably overly split species. Thus, only one or two of the Marshallese species, i.e., *Luidia savignyi* and a juvenile asteroid (NMNH E-7288) questionably identified as *Fromia hemiopla* by A. H. Clark (1952), have not been found on Guam. All of the others have been recorded on Guam. Thus, about 40% of the total number of species found on Guam are not recorded from the Marshalls. However, this disparity may reflect only a sampling bias, with only 113 specimens available from the Marshalls compared to over 300 from Guam.

There are a few notable exceptions to the above geographic patterns which I should now discuss. A. H. Clark (1954) reported two collections of *Protoreaster nodosus* from Guam. The five specimens collected by D. G. Frey in November 1945 (NMNH E-7716) are all small juveniles with arm radius from 18 to 33 mm. The other was a single specimen identified by A. H. Clark as *P. nodosus* (NMNH E-7476), collected at Oca Point, Guam by D. H. Johnson in May 1945, but is in fact *Bothriaster primigenius* Doderlein. This specimen was 18 mm in arm radius. Three additional specimens of *B. primigenius* were found but no *P. nodosus* was



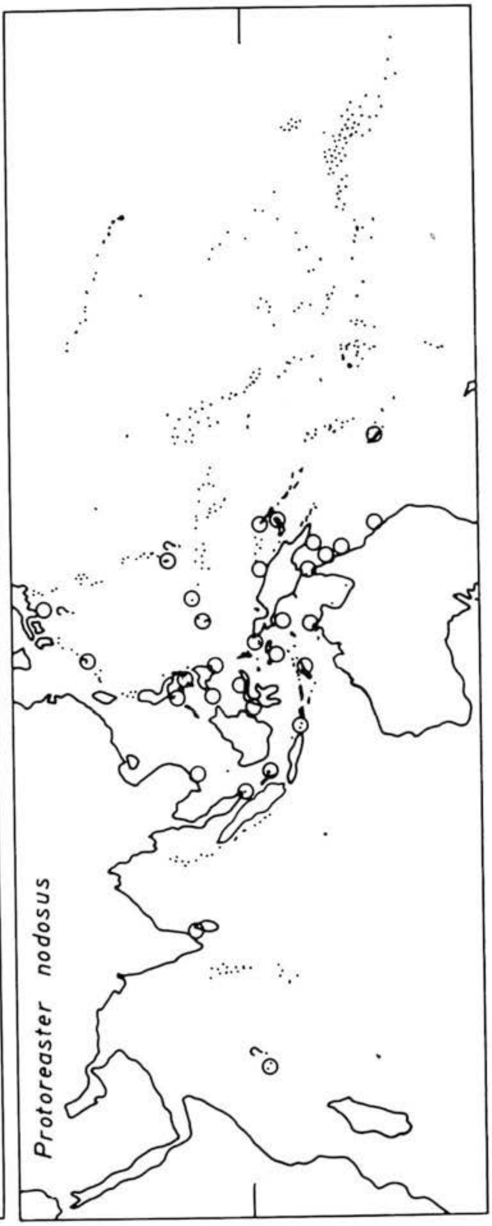
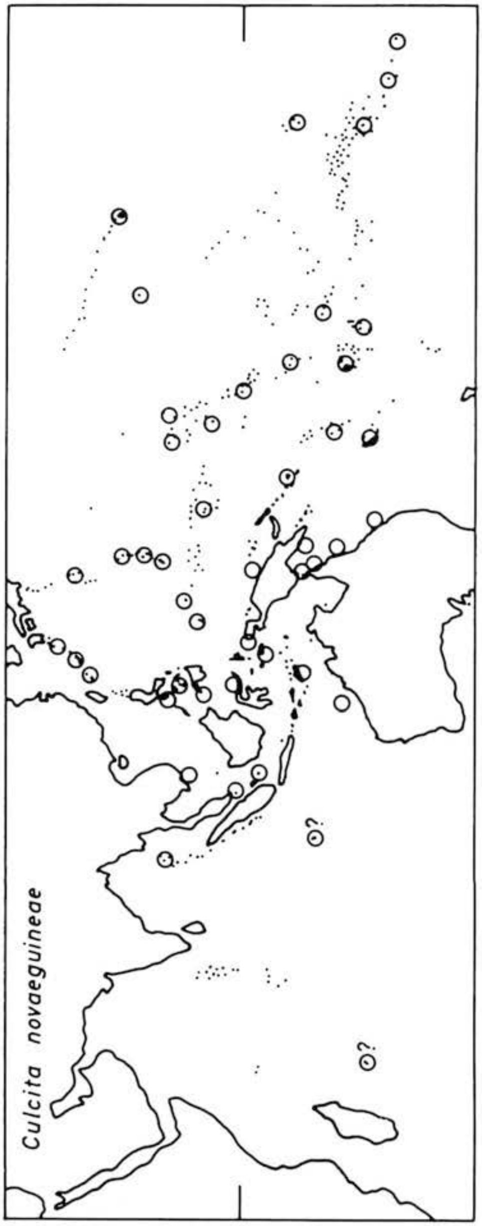


Fig. 1. Geographic distribution of *Archaster typicus*. Records from Hawaii and the Gilbert Islands (with question mark) are dubious (see text).

Fig. 2. Geographic distribution of *Protoreaster nodosus*. The record from southern Japan (Utinomi, 1962) is dubious because the illustrated specimen appears to represent *Pentaceraster* sp. That from Guam is problematical since there has been no record after the five juvenile specimens collected in 1945 (A. H. Clark, 1954). That from the Seychelles is dubious because the specimen (USNM 19698) has no data of collection on the label.



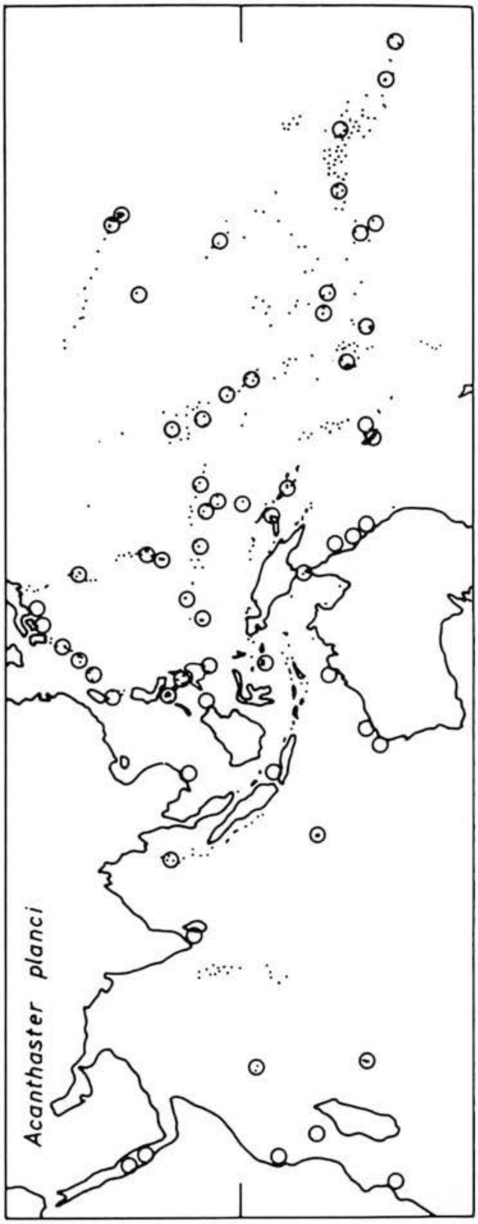


Fig. 3. Geographical distribution of *Culcita novaeguineae*. The specimen from the Cocos-Keeling Atoll was identified as a variety of *C. novaeguinea* by A. H. Clark (1950) but it appears to be an intermediate form between *C. novaeguineae* and *C. schmideliana* (see text). Livingstone (1932) gave a locality record of *C. novaeguineae* from the Mauritius without data.

Fig. 4. Geographical distribution of *Acanthaster planci*.

located on Guam in the recent collections. The juvenile specimens of *P. nodosus* which appeared on Guam shortly after World War II might represent a pseudo-population (Mileikovsky, 1971), perhaps carried by artificial means in the similar manner that U.S. Navy Barge YO146 transported many genera of molluscs from Guam to Hawaii (Burgess, 1970). It is safe to assume that *P. nodosus* has not established any selfsustaining population on Guam by 1975, although its juveniles were found about 30 years earlier.

The record of *Archaster typicus* in the literature from Hawaii (Fisher, 1906) is dubious for its specific identification as Fisher noted in the description. Also there is no recent record or specimen of *A. typicus* from Hawaii, i.e., no specimen in the B. P. Bishop Museum, Honolulu. The inclusion in the distribution record for *A. typicus* of the specimen from Onotoa Is., Gilberts (MCZ No. 62) is also questionable because the single specimen is very old and has no data on the label. Marsh (1974) did not report this species from southeastern Polynesia. The easternmost record of *A. typicus* may be that from Tonga (A. H. Clark, 1931) but there are discrepancies between this record and the description on the label of the specimen in NMNH (E-2949). On the other hand, there are three independent records from collections made within Fiji (NMNH and MCZ).

Reproductive Characteristics of Continental and Widely Distributed Species

There is little difference in egg sizes of the four species *Archaster typicus, Protoreaster nodosus, Culcita novaeguineae*, and *Acanthaster planci* (Table 2) and therefore between the two groups within the four species, i.e., continental and widely distributed species. The mean egg diameters for the four species fall within a narrow range from 182 to 205 microns. Maximum adult size varies among the different species, and the number of eggs per individual starfish varied from up to 170 thousands in *Archaster typicus* to over 7 million in *Culcita novaeguineae* from a single spawning induced by 1-methyladenine injection (Table 2). Among the asteroid species which produced planktotrophic larvae, egg diameters tended to converge at two levels, i.e., one around 190 to 200 μm in the four species mentioned above as well as in *Choriaster granulatus* and *Asteropsis carinifera*, and the others around 130 to 140 μm (i.e., about one third the volume of egg cell of the former size group) in *Linckia laevigata, L. multifora, L. guildingi, Leiaster leachi, Ophidiaster squameus, O. robillardi*, and *Mithrodia clavigera* (Yamaguchi, 1973 and unpublished data).

The early development of the four asteroid species is very similar (Figs. 5–8). The fertilized eggs undergo the typical sequence of holoblastic cleavage to form gastrulae which emerge from the egg membranes as swimming larvae in about half a day, showing nearly identical initial morphology and size. The gastrulae rapidly increase in length and then form feeding organs as early bipinnariae. Under the culture conditions utilized, the four species grow and develop at rather similar rates throughout the larval stages (Table 3). The brachiolariae of *Archaster typicus* develop three brachiolar arms which are more simple in structure than those of the other three species but otherwise are similar in gross morphology.

The rate of development in asteroid larvae is variable, both according to culture conditions and among individuals of the same culture batch (Lucas, 1973, 1975; Yamaguchi, 1973). The observed rate of development of *Culcita novaeguineae* in Guam is comparable to that in Palau, while *Acanthaster planci* developed more rapidly in Palau (see Yamaguchi, 1973 for comparison). In a preliminary observation in 1974, *Protoreaster nodosus* larvae were reared to early brachiolaria stage in 7 days so that the present result gave a similar rate up to this stage.

If the present results truly represent relative rates of development for the four species in Palau, the length of pelagic larval life tends to be shorter in the two continental species than in the two widely distributed species. However, the difference is only a few days between the two groups. The potential to prolong the pelagic life might be different between the two groups but it was not determined. This point remains as an open question, but the difference between the larval life spans of the two groups found in these observations is not considered sufficient to account for the segregated distribution patterns.

The only marked difference in larval behavior between the two groups was that larvae of the continental species swam consistently close to the bottom in the culture beakers when not disturbed, after attaining the early bipinnaria stage, while those of the widely distributed species remained geonegative up to the stage near metamorphosis. There was no evidence of phototaxis in the larvae of the four species. The larvae of continental species may not be widely transported if they remain semidemersal after the initial few days of early development because they may stand a good chance of being conserved around the rugged topography of coral reef structures. Mortensen (1938) reported that larvae of another continental species *Pentaceraster mammilatus* which is distributed along the east coast of Africa and the Red Sea, swam close to the bottom in his culture experiments. My observations with those of widely distributed species on Guam is consistent in that they are strongly geonegative (Yamaguchi, 1975). Thus, the larval swimming behavior of coral reef asteroids, so far as is known, is different with regard to geotaxis between the two groups. If a negative geotaxis is important for the long-distance dispersal of pelagic larvae, then larvae of continental species have little chance of spreading across the open ocean in surface currents.

In support of the above, crinoids in general appear to have a limited distribution. There are abundant and very conspicuous populations of many species of crinoids in Palau, but they are less abundant on Guam. Only three species of crinoids were recorded from the Marshalls (A. H. Clark, 1952). Attachment of crinoid larvae commences within a week or less for these species studied (Mortensen, 1937, 1938), so that only a limited capacity to extend their distribution across large areas of open ocean exists if most crinoid species produce similar larvae. Clark and Rowe (1971) indicated that most Indo-West Pacific crinoids are distributed around continental regions such as the East Indies, North Australia, and the Philippines. Palau clearly belongs to the continental region with respect to the faunal composition of shelf animals. Horikoshi (1971) made a comparison of molluscan

Table 2. Size and number of eggs spawned by four species of asteroids.

Species	Size[1] (mm)	Number of Eggs	Egg Diameter[2]
Archaster typicus	64	2.0×10^4	182 ± 6.4
	53	1.1×10^5	196 ± 6.0
	59	1.4×10^5	185 ± 7.6
	63	1.5×10^5	185 ± 6.0
	69	1.7×10^5	189 ± 7.2
Protoreaster nodosus	138	4.2×10^5	— —
	131	5.1×10^5	— —
	145	2.0×10^6	201 ± 6.4
Culcita novaeguineae	85	6.1×10^5	184 ± 4.9
	95	2.0×10^6	198 ± 6.4
	80	4.9×10^6	189 ± 5.5
	88	7.4×10^6	184 ± 5.0
Acanthaster planci	170	1.4×10^6	189 ± 7.2
	170	1.8×10^6	204 ± 6.0
	130	2.7×10^6	205 ± 6.9

1 Mean arm radius in mm, except the half diameter for *Culcita*.

2 Mean diameter in microns of 20 eggs measured after spawning, plus or minus one standard deviation.

Table 3. Chronology of development of four species of asteroids reared in the laboratory at Palau.

Developmental Stages[1]	*Archaster typicus*	*Protoreaster nodosus*	*Culcita novaeguineae*	*Acanthaster planci*
Fertilization	0	0	0	0
Early Gastrulae	0.4	0.5	0.5	0.6
Early Bipinnariae	1.8	2.0	2.0	2.0
Advanced Bipinnariae	4	4	8	5
Early Brachiolariae	6	7	11	7
Advanced Brachiolariae	8	10	13	12
Settlement	14	14	18	16

1 The figures are age of developmental stages in days when normally developed individuals attained the stage. Median water temperature was 28°C (extreme diurnal range 25–31).

fauna between oceanic and continental islands in the tropical Pacific but he considered Palau as representative of Micronesian islands which are mostly oceanic. Indeed, he did not find a significant difference in species diversity between Palau and the Bismarck Archipelago. This is probably because both belong to the continental fauna.

Discussion

Although the gap between the continental and widely distributed species appears to be clear, the range of distribution in widely distributed species varies considerably among different species. There are major variations reflecting the progressive attenuation of species diversity in relation to the distance of the oceanic

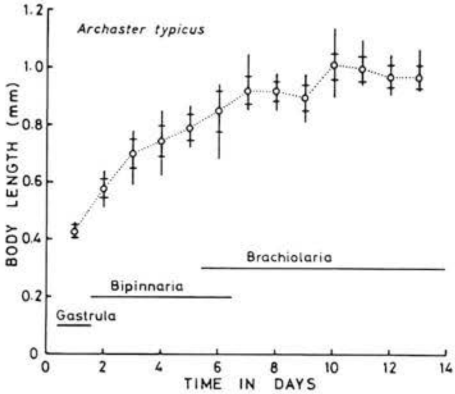


Fig. 5. Larval development of *Archaster typicus*. Growth in larval body length is indicated by means for 20 individuals with a standard deviation and range.

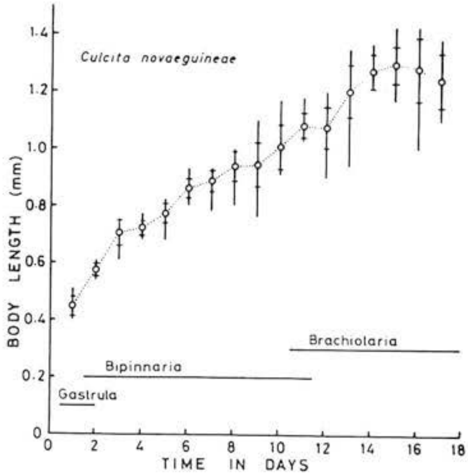


Fig. 7. Larval development of *Culcita novaeguineae*. Details as in Fig. 5.

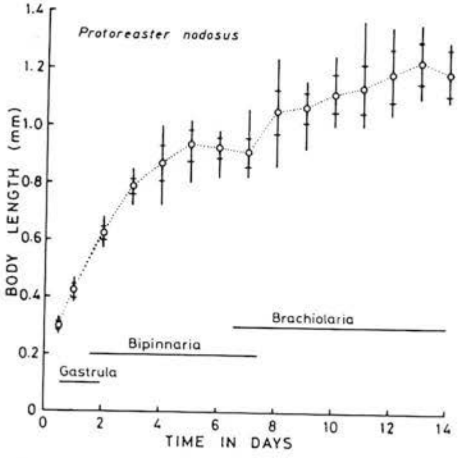


Fig. 6. Larval development of *Protoreaster nodosus*. Details as in Fig. 5.

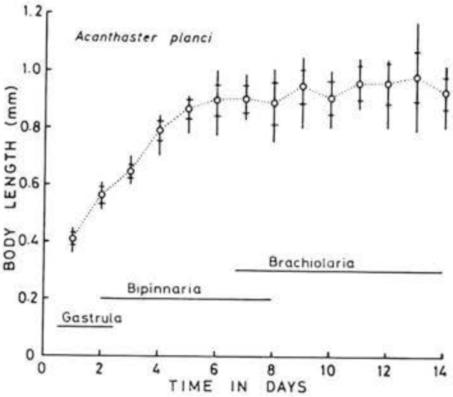


Fig. 8. Larval development of *Acanthaster planci*. Details as in Fig. 5. This culture batch may represent a poorly developed group of individuals because their success in metamorphosis was very poor.

island from the continental land mass (see Devaney, 1973; Marsh, 1974) and also the geographic segregation mentioned earlier for *Culcita* and *Echinaster* between the Western Pacific and the Indian Ocean.

It is intriguing that *Culcita novaeguineae* is replaced in the Indian Ocean by *C. schmideliana* while the distribution range of *Acanthaster planci* covers both oceans, although larval development is nearly identical in the two species. If the two species have evolved in a similar geological period, it may be hypothesized that there is a geographic barrier against gene flow between the Western Pacific and the Indian Ocean but that its effect on speciation of those species with ocean-wide distribution does vary. On the other hand, it may be postulated that geological age or the rate of speciation varied between the two taxa, i.e., the above difference in geographic distribution of the two species might indicate that the genus *Acanthaster* is more conservative in genetic drift or is younger than the genus *Culcita*.

There are a number of examples similar to the segregated distribution of *Culcita* in coral reef gastropods at the species level such as *Strombus luhuanus* and *S. decorus* (Abbott, 1960); *Drupa grossularia* and *D. lobata* (Emerson and Cernohorsky, 1973); *Cypraea eglantina* and *C. histrio* (Burgess, 1970); *Nassa serta* and *N. francolina* (Wilson and Gillett, 1971); and at the subspecies level such as the Western Pacific *Strombus gibberulus gibbosus* and the Indian Ocean *S. g. gibberulus* (Abbott, 1960). However, there are many more species of coral reef gastropods which are distributed throughout the Indo-West Pacific region as is *Acanthaster planci* so that the supposed barrier is only effective for a limited portion of the total fauna, even if it is real, and not the artifact of the taxonomy.

In conclusion, the coral reef asteroid species may be divided into two groups, continental and widely distributed, according to their distribution patterns in the Indo-West Pacific faunal region. There is a marked gap in asteroid fauna between Palau and Guam in Micronesia. The larval swimming behavior of the continental species is geopositive over most of the free-swimming period in contrast to the geonegative behavior of the widely distributed species, although there are many species of both groups yet to be observed for their development. If this is true for the unstudied species, the behavioral difference between the two groups might help perpetuate the segregation in the above major distribution patterns.

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Twenty-five additional references were used for the compilation of distribution data for the four asteroids in Figs. 1–4, but these references were not cited in the text. These references are available from the author upon request.

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