Pacific Science (1976), Vol. 30, No. 2, p. 167–175
Printed in Great Britain

Present Knowledge of the Systematics and Zoogeography of the Order Gorgonacea in Hawaii[1]

RICHARD W. GRIGG[2] AND FREDERICK M. BAYER[3]

ABSTRACT: Past knowledge of the order Gorgonacea in Hawaii is based almost exclusively on the collections of the United States Fish Commission steamer *Albatross* in 1902, which contain 52 species. Recent efforts to investigate the ecology of precious coral have produced a new collection based on 183 dredge hauls and 10 dives with a submersible. This program is collectively referred to as the Sango Expedition. Of 59 species of gorgonians obtained by the Sango Expedition, 13 are considered to be new species and 28 new geographic records, bringing the total number of species considered to be present in Hawaii to 93 species.

In contrast to the high diversity of gorgonians in the West Indies and the Indo-West-Pacific, the faunal list in Hawaii must still be considered depauperate. This is especially true in shallow water (< 75 m), where only one species is known. Although climatic deterioration during the Pleistocene could account for the scarcity of gorgonians in shallow water at the present time, this factor is unlikely to have affected deeper species. Furthermore, one would expect to find a modern complement of an ancestral fauna in shallow water if it had existed, as is true in the case of reef corals. The paucity of gorgonians in Hawaii may be due to isolation, which appears to have been a particularly effective barrier in shallow water. It is suggested that the only accessible route to Hawaii for gorgonians has been in deep water where, in the past, there were numerous stepping stones that may have aided dispersal. Moreover, chemical and physical gradients in deep water are relatively low. Why more deepwater species have not migrated into shallow water in Hawaii may be a reflection of their stenotypic character.

EARLY KNOWLEDGE of gorgonian corals in Hawaii was based primarily on the collections of the United States Fish Commission steamer *Albatross* in 1902. No other significant collections were made until 1970, when a major research effort to investigate the distribution and abundance of precious corals in the Hawaiian archipelago began at the University of Hawaii. This program, collectively referred to as the Sango Expedition, has produced a large and diverse collection of deepwater corals and other benthic invertebrates taken between the islands of Hawaii and Midway. The numbers of new species and new records of gorgonian corals from the Hawaiian Islands obtained by the Sango Expedition are an indication of the inadequacy of prior knowledge of this fauna. These measures may also be a general indication of the extent of our knowledge of other taxonomic groups of deep-sea benthos inhabiting rocky bottoms in the Pacific. In this paper, the depth distribution of gorgonians in Hawaii is also considered and zoogeographic implications are discussed.

[1] Contribution UNIHI-SEAGRANT-JC-77-03 of the University of Hawaii College Seagrant Program. This research was supported by the Office of Sea Grant, grant no. 04-3-158-29. Manuscript received 19 June 1975.

[2] University of Hawaii, Hawaii Institute of Marine Biology, Post Office Box 1346, Kaneohe, Hawaii 96744. Present address: National Oceanic and Atmospheric Administration, National Sea Grant Program, 3300 Whitehaven Street, NW, Washington, D.C. 20235.

[3] University of Miami, Rosenstiel School of Marine and Atmospheric Science, 10 Rickenbacker Causeway, Miami, Florida 33149. Present address: Smithsonian Institution, National Museum of Natural History, Department of Invertebrate Zoology, Washington, D.C. 20560.

METHODS

Dredging was the primary means of collection. Of the three types of dredges used (tangle nets, pipe dredges, and chain dredges), tangle nets proved to be by far the most efficient. Tangle nets consist essentially of hanks of netting or rope tied to heavy objects (rocks, heavy bars, metal rings, etc.). The heavy objects serve to keep the nets on the bottom and break off the coral, which becomes entangled in the netting. Pipe dredges and chain dredges are designed to collect rocks and therefore frequently hang up on the bottom; tangle nets are built to ride over the bottom and cover a larger area.

Part of the Sango collection was obtained with the use of a small two-man submersible, *Star II*, which was equipped with a coral harvesting assembly including a coral cutter, mechanical arm, and basket (Grigg, Bartko, and Brancart 1973). All submersible dives were made off Makapuu, Oahu, at depths from 350 to 396 meters. As of June 1974, the Sango collection represents material collected from 183 dredge hauls and 10 submersible dives.

Systematics

Table 1 is a list of all species in the order Gorgonacea collected by the Sango Expedition. Also included in Table 1 is geographic information (locality and depth) and references for those species that have been collected by previous expeditions. Fifty-nine species are represented in the Sango collection, only 18 of which previously were known from Hawaii. About two-thirds of the collection (41 species) represent either new records or new species in Hawaii. All species except the chrysogorgids (four species) have been examined by the second author. Of the 59 species, 21 have been positively identified. Identification of the remaining 38 must await further research. Nonetheless, all species have been compared with those previously described from Hawaii, and only 18 match these descriptions.

Forty-one species, therefore, can be considered either new species or new species records in Hawaii. This represents a 79-percent increase over the previously known faunal list of 52 species of gorgonians in Hawaii (see below). Of the 41 new records in Hawaii, 13 are possibly new species while the remaining 28 are considered to be new geographic records. If these figures prove to be reasonably accurate, and if they are representative of the existing knowledge of other faunal groups on rocky bottoms in the Pacific basin at similar depths ($350 \pm$ several hundred meters [upper bathyal zone, Hedgepeth 1957]), future large collections of such organisms might contain about 25 percent new species and 50 percent new geographic records. Obviously, the extent to which these estimates might apply to other localities in the Pacific depends largely on the extent of previous exploration in such areas. The shallow seas that border Indonesia, for example, have been extensively sampled (expeditions include the Siboga Expedition, the Challenger Expedition, Swedish Deep Sea Expedition, the Galathea Expedition, the Investigator, the Snellius, and others) and, therefore, fewer new species and geographical records would be expected to be discovered there.

The 52 species known in Hawaii prior to the Sango Expedition were all obtained by the steamer *Albatross* in 1902. Most were described by Nutting (1908). Three other gorgonians described by Verrill (1928) have not been included because their origin is uncertain. In recent years, the second author has reexamined the entire Albatross collection and found many errors and misidentifications. Although this work is unpublished, a synopsis of it is presented in Table 2. Of the 47 species of Gorgonacea described by Nutting, 44 are recognized as good species. There are eight additional species in the Albatross collection that were not described by Nutting (Bayer 1956; unpublished manuscript), including six species of *Corallium*, *Keroeides mosaica*, and one paramuriceid in the genus *Pseudothesea*. The addition of these to the initial 44 species brings the total fauna prior to 1970 to 52 species.

Twenty-eight changes in Nutting's original descriptions are now suggested: nine family name changes, eight generic and specific name changes, nine generic name changes, and 12 specific name changes (Table 2). One species, described by Nutting as a gorgonian, *Menella grandiflora*, is a stoloniferan. Since Nutting's

TABLE 1

SPECIES IN THE ORDER GORGONACEA COLLECTED BY THE SANGO EXPEDITION

FAMILY AND SPECIES	GEOGRAPHIC LOCALITY	DEPTH RANGE (m) AND METHOD OF COLLECTION	REFERENCES
Coralliidae			
Corallium laauense Bayer	Kauai, Hawaiian Islands	365–531 (D + S)	Sango Expedition
	Molokai, Hawaiian Islands	511–580 (D)	Bayer 1956
Corallium regale Bayer	Oahu and French Frigate Shoals, Hawaiian Islands	365–564 (D + S)	Sango Expedition
	French Frigate Shoals, Hawaiian Islands	704–719 (D)	Bayer 1956
Corallium tortuosum Bayer	Hawaiian Islands (many stations)	216–408 (D + S)	Sango Expedition
	Molokai and Hawaii, Hawaiian Islands	167–386 (D)	Bayer 1956
Corallium secundum Dana	Hawaiian Islands (many stations)	350–564 (D + S)	Sango Expedition
	Hawaiian Islands (many stations)	231–280 (D)	Bayer 1956
Anthothelidae			
Anthothela nuttingi Bayer	Hawaiian Islands (many stations)	340–465 (D)	Sango Expedition
	Oahu, Hawaiian Islands	1387–1820 (D)	Bayer 1956
Briareidae			
Paragorgia sp., possibly	Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
P. regalis Nutting	Japan	coastal abyssal	Kükenthal 1924
Paragorgia sp., probably new	Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Keroeididae			
Keroeides mosaica Bayer	Kona, Hawaii, Hawaiian Islands	215–465 (D)	Sango Expedition
	Molokai, Hawaiian Islands	167–386 (D)	Bayer 1956
Acanthogorgiidae			
Paracanthogorgia sp., possibly	Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
P. paramuricata Verrill	Ceylon	? (D)	Kükenthal 1924
Acanthogorgia sp., possibly	Makapuu, Oahu, Hawaiian Islands	215–564 (D)	Sango Expedition
A. striata Nutting	North Celebes, Banda Sea, Japan	80–304 (D)	Kükenthal 1924
Paramuriceidae			
Villogorgia sp., possibly new	Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Villogorgia sp., probably new	Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Villogorgia (= *Perisceles*)	Lanai and Brooks Banks, Hawaiian Islands	315–412 (D)	Sango Expedition
arbuscula (Wright & Studer)	Japan	631 (D)	Kükenthal 1924
Villogorgia sp. (?)	Makapuu, Oahu, Hawaiian Islands	344–463 (D)	Sango Expedition
Paramuricea hawaiiensis	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Nutting	Kauai, Hawaiian Islands	924–1241 (D)	Nutting 1908
Paramuricea sp. (?)	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Paramuricea sp. (2)	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Paramuricea sp. (2)	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Placogorgia sp., probably new	Makapuu, Oahu, Hawaiian Islands	340–465 (D)	Sango Expedition
Placogorgia (= *Discogorgia*)	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
sp., probably *P. dendritica* (Nutting)	Malay Archipelago	75–94 (D)	Nutting 1910
Bebryce brunnea (Nutting)	Makapuu, Oahu, Hawaii	350–396 (S)	Sango Expedition
	Molokai, Maui, and Hawaii, Hawaiian Islands	167–386 (D)	Nutting 1908
Swiftia sp., probably new	Makapuu, Oahu, Hawaiian Islands	340–365 (D)	Sango Expedition

TABLE 1 (*cont*).

FAMILY AND SPECIES	GEOGRAPHIC LOCALITY	DEPTH RANGE (m) AND METHOD OF COLLECTION	REFERENCES
Paramuriceidae (*cont.*)			
Swiftia sp., probably new	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Thesea sp., probably *T. ramosa* Nutting	Brooks Banks, Hawaiian Islands Japan	313–399 (D) 193 (D)	Sango Expedition Kükenthal 1924
Pseudothesea sp. (?)	Makapuu, Oahu, Hawaiian Islands	335–375 (D)	Sango Expedition
Pseudothesea sp., probably *P. placoderma* Nutting	Barbers Point, Oahu, Hawaiian Islands Flores Sea	182 (D) 73 (D)	Sango Expedition Nutting 1910
Pseudothesea (= *Paracis*) sp., probably *P. orientalis* (Ridley)	Kona, Hawaii, Hawaiian Islands Mauritius	350–396 (S) 147 (D)	Sango Expedition Kükenthal 1924
Paracis miyajimai (Kinoshita)	Hawaiian Islands (many stations) Japan	362–531 (D) ? (D)	Sango Expedition Kükenthal 1924
Paracis spinifera (Nutting)	Makapuu, Oahu, Hawaiian Islands Japan	350–396 (S) 188 (D)	Sango Expedition Kükenthal 1924
Echinogorgia sp. (?)	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Anthomuricea tenuispina Nutting	Kauai, Hawaiian Islands Niihau, Hawaiian Islands	428–531 (D) 581–688 (D)	Sango Expedition Nutting 1908
Anthomuricea sp., possibly *A. divergens* Kükenthal	Brooks Banks, Hawaiian Islands Japan	381–426 (D) 200	Sango Expedition Kükenthal 1924
Anthomuricea sp., possibly *A. reticulata* Nutting	Kahoolawe, Hawaiian Islands Flores Sea	362–421 (D) 40 (D)	Sango Expedition Nutting 1910
Anthomuricea sp. (?)	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Plexauridae			
Eunicella sp., probably new	Oahu, Hawaiian Islands	275–495 (D)	Sango Expedition
Cyclomuricea flabellata Nutting	Makapuu, Oahu, Hawaiian Islands Oahu, Hawaiian Islands	350–396 (S) 71–333 (D)	Sango Expedition Nutting 1908
Isididae			
Keratoisis sp., probably *K. nuda* Wright & Studer	Hawaiian Islands (many stations) Fiji	344–463 (D + S) ? (D)	Sango Expedition Kükenthal 1924
Keratoisis flabellum Nutting	Makapuu, Oahu, Hawaiian Islands Kauai and Hawaii, Hawaiian Islands	405–465 (D) 346–428 (D)	Sango Expedition Nutting 1908
Keratoisis sp., new	Lanai, Hawaiian Islands	305–565 (D)	Sango Expedition
Acanella sp. (?)	Hawaiian Islands (many stations)	215–565 (D + S)	Sango Expedition
Primnoidae			
Callogorgia gilberti Nutting	Hawaiian Islands (many stations) Kauai and Hawaii, Hawaiian Islands	215–565 (D + S) 409–960 (D)	Sango Expedition Nutting 1908
Callogorgia sp., possibly *C. tuberculata* Versluys	Makapuu, Oahu, Hawaiian Islands Sulu Islands	350–396 (S) 522 (D)	Sango Expedition Kükenthal 1924
Callogorgia sp., new	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Callogorgia sp. (?)	Kaena Point, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Plumarella sp., possibly new	Brooks Banks, Hawaiian Islands	384–432 (D)	Sango Expedition
Narella sp., probably new	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
Narella sp., probably *N. megalepis* Kinoshita	Hawaiian Islands (many stations) Japan	215–564 (D) ? (D)	Sango Expedition Kükenthal 1924

TABLE 1 (*cont.*)

FAMILY AND SPECIES	GEOGRAPHIC LOCALITY	DEPTH RANGE (m) AND METHOD OF COLLECTION	REFERENCES
Primnoidae (*cont.*)			
Narella sp., new	Nihoa, Hawaiian Islands	353–417 (D)	Sango Expedition
Calyptrophora sp., possibly new	Makapuu, Oahu, Hawaiian Islands	344–454 (D)	Sango Expedition
Calyptrophora clarki Bayer	Oahu, Hawaiian Islands	965–1275 (D)	Sango Expedition
	Hawaii, Japan, East Indies	12–1264 (D)	Bayer 1951
Calyptrophora agassizii Studer	Hawaiian Islands	965–1145 (D)	Sango Expedition
	Oahu and Kauai, Hawaiian Islands	781–1014 (D)	Nutting 1908
Calyptrophora japonica Gray	Brooks Banks, Hawaiian Islands	216–432 (D)	Sango Expedition
	Japan, Fiji, Malay Archipelago	400–1300 (D)	Kükenthal 1924
Calyptrophora wyvillei Wright	Kauai, Hawaiian Islands	779–823 (D)	Sango Expedition
	Kauai, Hawaiian Islands	744–780 (D)	Nutting 1908
Candidella helminthopora Nutting	Oahu and Nihoa, Hawaiian Islands	353–627 (D)	Sango Expedition
	Oahu, Molokai and Maui, Hawaiian Islands	38–1820 (D)	Nutting 1908
Thouarella sp., possibly *T. typica* Kinoshita	Makapuu, Oahu, Hawaiian Islands	350–396 (S)	Sango Expedition
	Japan	173–187 (D)	Kükenthal 1924
Chrysogorgiidae			
Metallogorgia melanotrichos (Wright & Studer)	Kure Island, Hawaiian Islands	840–1200 (D)	Sango Expedition
	Kauai and Oahu, Hawaiian Islands	183–1385 (D)	Nutting 1908
Chrysogorgia sp., possibly *C. japonica* (Wright & Studer)	Pearl and Hermes Reef, Hawaiian Islands	750–1050 (D)	Sango Expedition
	Japan	3375 (D)	Kükenthal 1924
Chrysogorgia sp., probably *C. stellata* Nutting	Gardner Pinnacles, Hawaiian Islands	830–922 (D)	Sango Expedition
	Molokai and Oahu, Hawaiian Islands	646–675 (D)	Nutting 1908
Iridogorgia sp. (?)	Brooks Banks, Hawaiian Islands	745–925 (D)	Sango Expedition

NOTE: *D*, collected by dredging; the range of the depth of the dredge haul is given; *S*, collected with the submersible *Star II* at depths from 350 to 396 meters.

work in 1908, the spelling of two genera has also changed, *Ceratoisis* to *Keratoisis* and *Caligorgia* to *Callogorgia*. The taxonomic changes suggested in Table 2 will be considered tentative until full species descriptions have been published. Nevertheless, they indicate the degree to which the present knowledge of the order Gorgonacea in Hawaii is in need of revision. In addition, positive identification of 38 species in the Sango collection will require much further work.

Depth Zonation and Zoogeography

The paucity of gorgonians and alcyonarians on shallow Hawaiian reefs was noted by Verrill (1928). Although much of the early collecting in Hawaii was limited to deep water (the shallowest collection of the *Albatross* in Hawaii, for example, was 10 fathoms), a great deal of collecting effort in shallow water in recent years has failed to produce the diverse gorgonian fauna typical of so many other shallow seas in Polynesia, Micronesia, and the Indo-West-Pacific. Indeed, only one species is known from depths less than 75 m in Hawaii, compared with 93 species found at depths below 75 m. This ratio of shallow-water to deep-water gorgonians is not typical of other areas of the world where gorgonians are abundant. In the West Indies, of 167 species known, 41 percent are found in shallow water (< 50 m) (Bayer 1961). In the East Indies, 42 percent of the 225 species of Gorgonacea collected during

TABLE 2

NAME CHANGES OF SPECIES OF GORGONACEA IN THE ALBATROSS COLLECTION

NAME GIVEN BY NUTTING 1908	NAME SUGGESTED BY BAYER
Family Briareidae	Family Paragorgiidae
Paragorgia nodosa Koren & Danielssen	*Paragorgia dendroides* Bayer, 1956
Family Gorgonellidae	Family Melithaeidae
Verrucella bicolor Nutting	*Acabaria bicolor* (Nutting)
Family Suberogorgiidae	Family Keroeididae
Keroeides gracilis Whitelegge	*Keroeides pallida* Hiles
Family Muriceidae	Family Anthothelidae
Clematissa alba Nutting	*Anthothela nuttingi* Bayer, 1956
Family Muriceidae	Family Keroeididae
Paramuricea aequatorialis Wright & Studer	*Keroeides pallida* Hiles
Clematissa verrilli Wright & Studer	*Keroeides pallida* Hiles
Muricella tenera Ridley	*Keroeides fallax* Bayer, 1956
Family Muriceidae	Family Paramuriceidae
Clematissa tenue Nutting	*Villogorgia tenuis* (Nutting)
Echinomuricea brunnea Nutting	*Bebryce brunnea* (Nutting)
Family Acanthogorgiidae	Family Acanthogorgiidae
Acanthogorgia armata Verrill	*Acanthogorgia* sp.
Family Primnoidae	Family Primnoidae
Amphilaphis biserialis Nutting	*Thouarella biserialis* (Nutting)
Amphilaphis regularis Wright & Studer	*Thouarella regularis* (Wright & Studer)
Stenella helminthophora Nutting	*Candidella helminthophora* (Nutting)
Stachyodes angularis Nutting	*Calyptrophora angularis* (Nutting)
Stachyodes regularis Wright & Studer	*Narella studeri* (Versluys)
Stachyodes dichotoma Versluys	*Narella* sp.
Stachyodes bowersi Nutting	*Narella bowersi* (Nutting)
Calyptrophora versluysi Nutting	*Calyptrophora agassizii* Studer
Calyptrophora japonica Gray	*Calyptrophora clarki* Bayer, 1951
Family Chrysogorgiidae	Family Chrysogorgiidae
Lepidogorgia gibbosa Nutting	*Iridogorgia superba* Nutting
Lepidogorgia spiralis Nutting	*Radicipes spiralis* (Nutting)
Chrysogorgia flexilis (Wright & Studer)	*Chrysogorgia japonica* (Wright & Studer)
Chrysogorgia lata Versluys	*Chrysogorgia papillosa* Kinoshita
Chrysogorgia spiculosa (Verrill)	*Chrysogorgia* sp.
Chrysogorgia elegans (Verrill)	*Chrysogorgia* sp.
Chrysogorgia curvata Versluys	*Chrysogorgia* sp.
Metallogorgia squarrosa (Wright & Studer)	*Chrysogorgia squarrosa* (Wright & Studer)
Family Isididae	Family Isididae
Lepidisis longiflora Verrill	*Lepidisis* sp.
Acanella eburnea (Pourtales)	*Acanella* sp.

NOTE: Family sequence and affinities from Kükenthal (1924).

the Siboga Expedition were taken from water less than 50 m in depth (Bayer 1961). A tabulation of all gorgonians listed by Kükenthal (1924) from the seas between Indonesia, the Philippines, New Guinea, and northern Australia gives a ratio of shallow-water (< 75 m) to deepwater (> 75 m) species of 157 to 125 (56 percent shallow). While the gorgonian fauna in deep water around Hawaii appears to be somewhat depauperate relative to the Indo-West-Pacific, the shallow-water fauna is virtually nonexistent.

The low diversity of gorgonians in Hawaii can probably be attributed to isolation of the archipelago. In fact, the marine invertebrate fauna of Hawaii is considered in the main to be an attenuated Indo-West-Pacific fauna which has been present long enough to have speciated

(Edmondson 1940). If the depauperate gorgonian fauna in Hawaii can be attributed to isolation, then the extraordinarily low ratio of shallow to deeper water forms suggest that at least during some period of the history of the archipelago there were far fewer barriers in deep water. In the past, dispersal of benthic organisms may have been aided by numerous guyots and seamounts at moderate depths between the western Pacific and Hawaii (Menard and Hamilton 1963). The Marcus-Necker Rise, for example, connects the Hawaiian archipelago with the Mid-Pacific Mountains. Although many of the seamounts and guyots on the Marcus-Necker Rise are presently too deep to serve as stepping stones for most species considered in this paper, many of these structures were near, at, or even above the surface during the early Tertiary (Menard and Hamilton 1963). If this route did serve as a distributional corridor for deepwater species, it is puzzling why shallow-water forms did not also migrate unless, of course, there was insufficient habitat available in shallow water in the Hawaiian chain during the early Tertiary. Indeed, Menard, Allison, and Durham (1962) consider the age of the Hawaiian Islands to be middle Tertiary. Other corridors to Hawaii from the western Pacific include routes by way of the Mapmaker Seamounts and the Shatsky Rise/Emperor Seamounts complex.

Most alcyonarian larvae are lecithotrophic, passive swimmers, remain close to the bottom during their larval life, and generally settle within a few days to a week (Thorson 1946). Of the gorgonians studied in Discovery Bay, Jamaica, most had larval lives between 2 and 10 days (Kinzie 1970: 4, pt. 2). Gohar (1940) investigated the larval development of some xeniid corals (order Alcyonacea) and found their larval life generally to be less than 1 week. Gohar discovered that the larvae of most xeniids sink immediately after they are expelled from a parent colony and that they tend to adhere to any solid support. He attributed their rarity on offshore islands in the Red Sea to this behavior. On the other hand, the ability of many invertebrate larvae to postpone settlement until a suitable substrate is encountered has been well documented (Wilson 1958). Larvae of the temperate gorgonian *Muricea californica* were maintained in the laboratory in the presence of substrate for over 2 months without settling (Grigg 1970). After 2 months, the larvae began to metamorphose even though they had not settled, indicating that this period was an upper limit to larval life.

Von Koch (as reported by Gohar 1940) also reported that the larvae of *Gorgonia cavolini* (synonymized with *Eunicella verrucosa* Pallas [Kükenthal 1924]) were able to retard settlement up to 1 month but not without abnormalities in development. These studies suggest that the normal pelagic life of most gorgonian corals is relatively short. This behavior may be characteristic especially of species which have evolved on islands where currents tend to transport larvae into open ocean; hence, natural selection should favor forms with short pelagic stages or more direct development (Abbott 1966). In deep water, it would be expected that this relationship would be less pronounced. Abyssal species, in general, have wider distributions and are more commonly cosmopolitan than are forms in shallower water (Ekman 1940). Also Deichmann (1936) found that, in general, shallow species in the order Gorgonacea are different at the specific level on opposite sides of the Atlantic, whereas deepwater species are the same. This pattern, however, may not necessarily be due to long pelagic stages of species in the deep sea but, rather, may be a reflection of the lack of steep physiochemical gradients that might otherwise act as barriers to dispersal. Indeed, many deep-sea benthic species lack a pelagic stage altogether (Mileikovskii 1962).

The lack of gorgonians in shallow water in Hawaii could also be due to extinction during the Pleistocene or earlier. The hermatypic coral genera *Acropora* and *Platygyra*, for example, were found in a drowned Miocene terrace in Hawaii (Menard, Allison, and Durham 1962), but are absent at the present time. Another example is the genus *Pocillopora*, which was present in the Caribbean during the Tertiary but has since become extinct there (Bayer 1953). Considering only the gorgonians in the Caribbean Sea, Bayer (1953) suggested that after closure of the Central American portals, climatic deterioration led to the extinction of all but the hardiest of species, which furnished a small nucleus of species that were ancestral to the present fauna in the Caribbean. Although climatic deterioration must remain a possible explanation of the dearth of shallow-water gorgonians in Hawaii, there is no evidence of this in the fossil record. Furthermore, one would expect to find a modern faunal complement of that fraction of the ancestral fauna that survived, rather than a single species. Of course, the climatic deterioration could have eliminated all shallow-water gorgonians in Hawaii. Were this the case, however, reef corals and other groups of tropical fauna in Hawaii should also have been killed off during the Pleistocene; Menard and Hamilton (1963) consider this possibility unlikely. Furthermore, Briggs (1966) argued that the relatively high endemism in modern Hawaiian fishes is evidence that faunal decimation did not take place in Hawaii during the Pleistocene.

If isolation is considered to be the cause of the depauperate gorgonian fauna in Hawaii, then the broad depth range (15–233 m) of the one species in shallow water (*Acabaria bicolor*) should be taken into account. This species may represent the first species to migrate upward from deep water rather than the only species to survive an antecedent climatic deterioration in shallow water. Deepwater species are generally stenotopic, which presumably is an adaptation to more constant conditions in the deep sea (Sanders and Hessler 1969). This fact may explain why more deep water taxa have not invaded shallow water in Hawaii.

In conclusion, interpretation of the available evidence suggests that the isolation of the Hawaiian Islands acts as an effective barrier in the dispersal of many species in the order Gorgonacea to Hawaii. In shallow water, this barrier appears to have been absolute. Paleogeographic studies of the tropical Pacific suggest that, in the past, numerous submerged seamounts and guyots between Hawaii and the western Pacific may have served as stepping stones for the dispersal of deepwater gorgonian corals.

ACKNOWLEDGMENTS

We would like to thank the staff of the National Museum of Natural History, Division of Lower Invertebrates, for making space and access to the type material in the collections at the Smithsonian Institution available to us. Because of the poor quality of many descriptions of species by early workers, we simply could not have identified some gorgonians positively without the aid of type material. Even then it was difficult to determine how much weight should be given to certain taxonomic characteristics. Only by looking at a large number of specimens can one determine the extent of intraspecific variation.

We would also like to thank the captains and crews of the University of Hawaii vessel *Teritu* and the submersible *Star II*. Mr. Bill Worcester and Jim Vansant provided invaluable assistance during most phases of the fieldwork.

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