The Ecology of the Replacement of *Pseudosquilla ciliata* (Fabricius) by *Gonodactylus falcatus* (Forskål) (Crustacea; Stomatopoda) Recently Introduced into the Hawaiian Islands[1]

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ALTHOUGH KNOWLEDGE of the Hawaiian stomatopods was summarized by Townsley in 1953, the occurrence of a species of *Gonodactylus* not previously recorded from Hawaii (Kinzie, 1965) indicated a possible introduction and necessitated a revision of information on this group in Hawaii.

Previous workers, when discussing the Hawaiian stomatopods (Brooks, 1886; Bigelow, 1931; Edmondson, 1921; and Townsley, 1953), all indicated that *Pseudosquilla ciliata* (Fabricius) was the most common species. It was recorded as occurring on sand and mud flats as well as in coral heads. The only record of *Gonodactylus* from Hawaii before 1965 was *G. guerini* White, but this species was taken from deep water (Brooks, 1886; Edmondson, 1921; Townsley, 1953).

The stomatopod fauna of Hawaii prior to 1953 can be characterized as follows: *Pseudosquilla ciliata* was the dominant shallow water stomatopod. It was found in sand and mud flats, and was also the most common species living in dead coral heads. *P. ciliata* and occasional *P. oculata* Brullé (Townsley, 1953), were the only large (over 3 cm) stomatopods found living in coral heads.

In 1954, Townsley (personal communication) observed that a species of *Gonodactylus* was found in dead coral heads in Kaneohe Bay and on the reef at Waikiki. In 1958, Okamoto (in an unpublished class report at the University of Hawaii) reported two species of stomatopods that had not been described from the Hawaiian Islands. One was *G. hendersoni* Manning (as *G. demanii* Henderson), four specimens of which were taken in a fresh state from the stomach of one *Neothunnus macropterus* (Yellowfin tuna) caught near Oahu. The other species was *Gonodactylus falcatus* (Forskål).

Collections on the reefs at Waikiki in 1963 yielded a number of large *G. falcatus* as well as *G. hendersoni*. Further collections at other areas (Figs. 1 and 2) indicated that *G. falcatus* was by far the most abundant stomatopod in dead coral heads and *G. hendersoni* was fairly common in some areas. On the other hand, *Pseudosquilla ciliata* was not found in dead coral heads, but it was still abundant living within burrows in sand and mud flats.

From these facts it appears that the coral head habitat, once almost exclusively occupied by *P. ciliata*, was taken over completely by *Gonodactylus falcatus* in about nine years. This paper describes some of the results obtained while investigating this hypothesis and studying the origins, possible mode of introduction, and mechanism of replacement of *Pseudosquilla ciliata* by *Gonodactylus falcatus*.

DISTRIBUTION AND NOTES ON DESCRIPTION OF NEW HAWAIIAN SPECIES

Gonodactylus falcatus (Forskål)

A synonymy of *G. falcatus* is given by Holthuis (1941).

DISTRIBUTION: *G. falcatus* is widely distributed through the Indo-Pacific, ranging from the Red Sea (Forskål, 1775; Ingle, 1963) through the Indian Ocean to western Australia (Stephenson, 1962), northward to the Ryukyu Islands (Fukuda, 1910), Sagami Bay (Utinomi, 1961), and Tusima and Ogawara islands (Komai, 1927). *G. falcatus* occurs in the Pacific in Queensland (Stephenson, 1953), the Bonin

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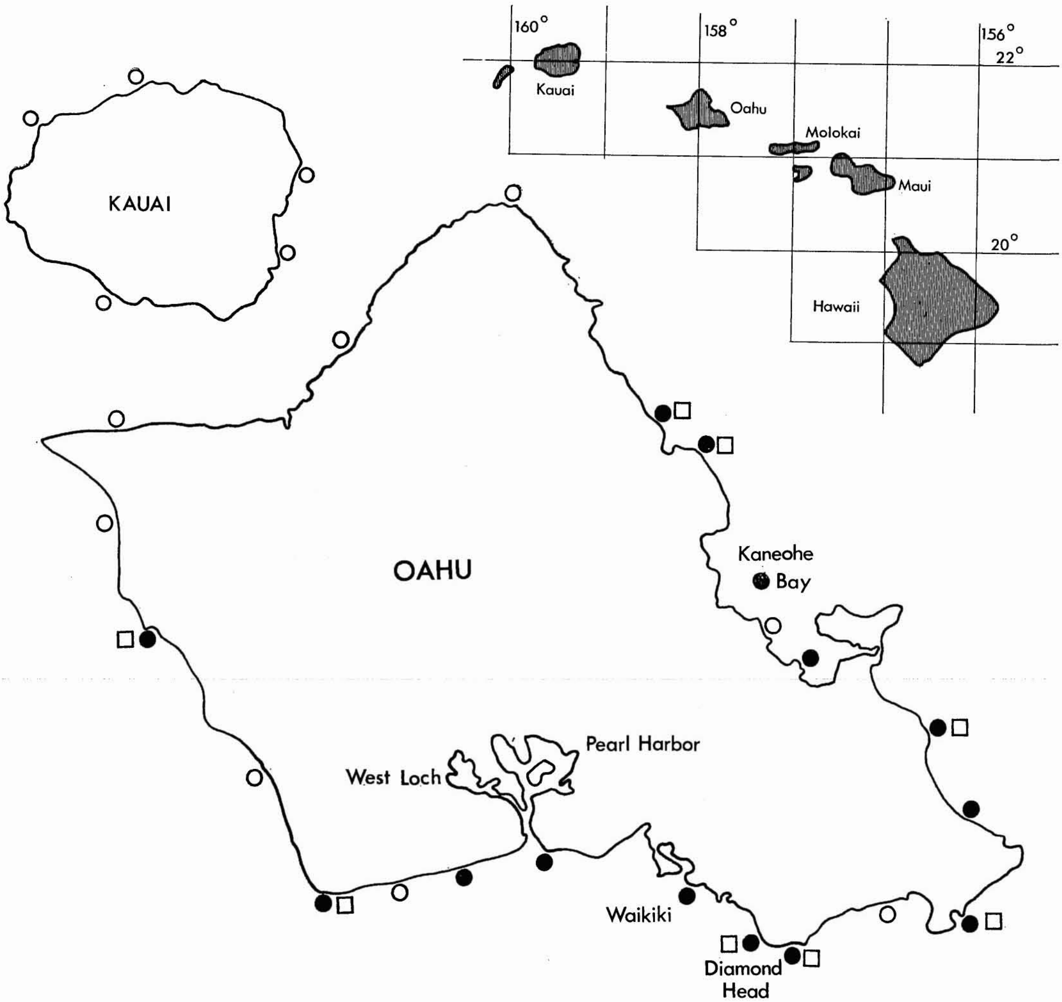

FIG. 1. Map of the Hawaiian Islands showing areas of collection on Oahu and Kauai. *Black circles* represent areas where *Gonodactylus falcatus* was found; *open squares* represent *G. hendersoni*; and *open circles* indicate collecting sites where no stomatopods were found.

Islands (Odhner, 1923), Saipan in the Mariannas (Holthuis, 1953), Truk in the Carolines (Komai, 1927), Eniwetok in the Marshalls (University of Hawaii collections), the Gilbert Islands (Holthuis, 1953), Rotuma (Borradaile, 1898), Fiji (Odhner, 1923), Samoa (Bigelow, 1931) and Hawaii (Kinzie, 1965).

MORPHOLOGICAL VARIATIONS: As Manning (1967:3) mentioned, the qualitative aspects of the telson morphology are important as taxonomic characters in this genus. Attempts to compare statistically the Hawaiian population with populations from other areas gave no conclusive indications of affinities of the Hawaiian population. This was due to the small size of the samples from most of the areas studied and the large variance of the statistics compared.

Qualitative comparisons indicated that the Hawaiian specimens had more inflated and rounded telson carinae than comparable individuals from Samoa, Palau, the Philippines, and the Red Sea. On the other hand *G. falcatus* from Queensland has slightly more inflated carinae than comparable Hawaiian specimens.

Serène (1954) has recognized *G. falcatus* var. *ternatensis* as a "dwarf race," with carinae of the telson and the sixth abdominal somite appearing more inflated, and sexual dimorphism expressed at a smaller size than in *G. falcatus s.s.* His descriptions and figures of this "dwarf race" show that it is similar to the Hawaiian specimens. However, Manning (1966:110) feels that until more is known the name *G. falcatus* should be used for specimens of this suggested race.

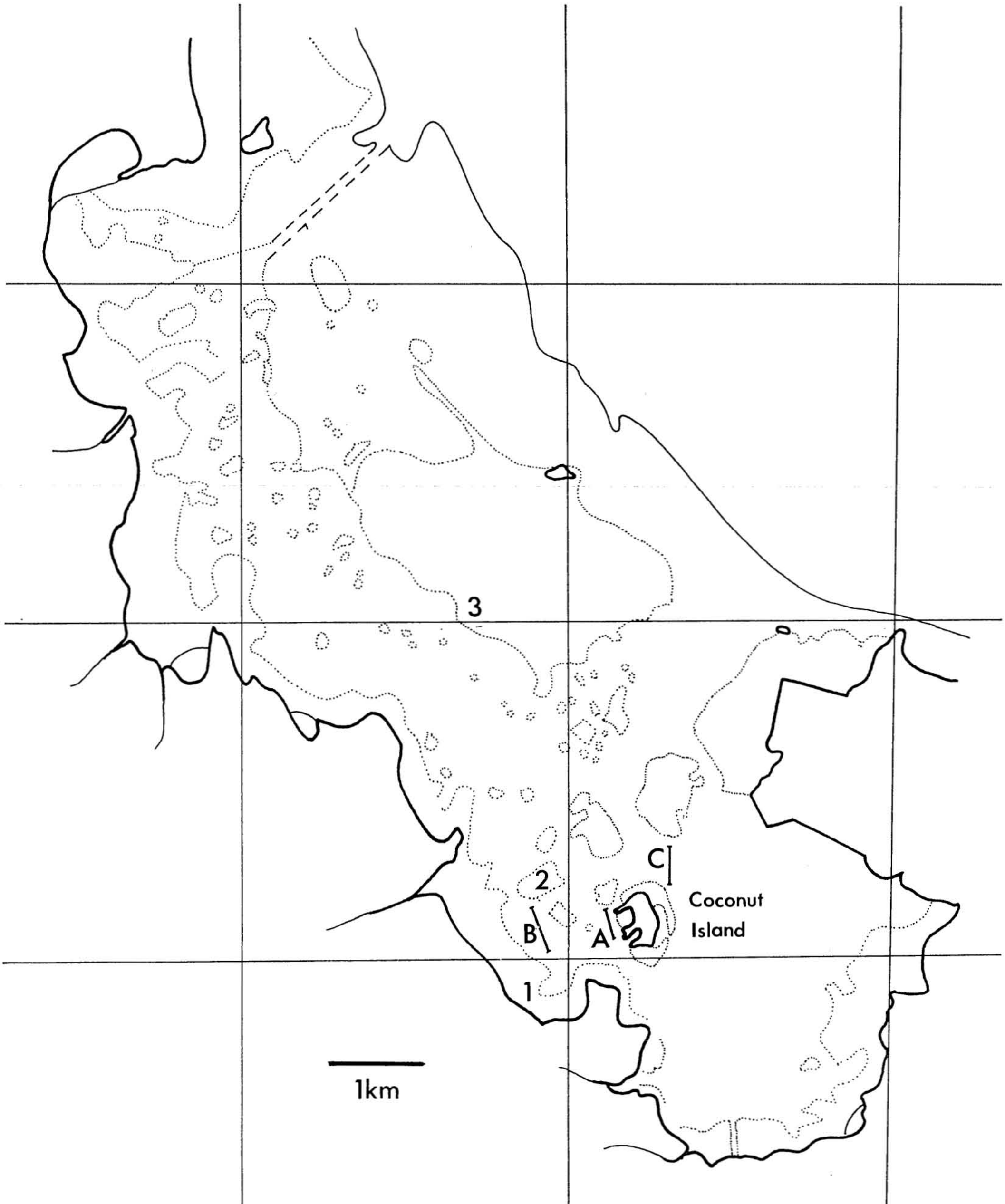

FIG. 2. Map of Kaneohe Bay showing plankton runs (*A*, *B*, and *C*), and collecting areas (*1*, mud flat; *2*, coral reef; *3*, sand flat).

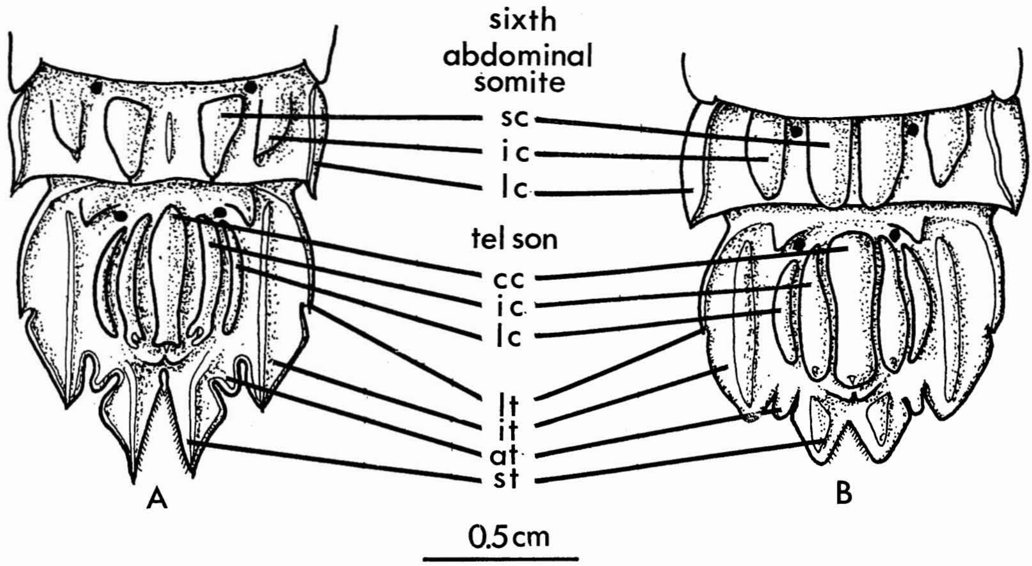

FIG. 3. Telsons of female (*A*) and male (*B*) *Gonodactylus falcatus* from Hawaii. *sc*, Submedian carinae; *ic*, intermediate carinae; *lc*, lateral carinae; *cc*, central carinae; *lt*, lateral teeth; *it*, intermediate teeth; *at*, accessory teeth; *st*, submedian teeth.

Although the specimens from the Philippines that were examined had narrow carinae, individuals with more rounded carinae also occur in the same area. Kemp (1915) stated that the majority of specimens from Bantayan, Puerto Galera, and Taytay in the Philippines belongs to "form B" which corresponds to Borradaile's var. *rotundus* (probably Serène's *ternatensis*), while one specimen is the narrow keeled type "form A" (= var. *ternatensis* deMan).

SEXUAL DIMORPHISM: Sexual dimorphism has been noted in *G. falcatus* by Bigelow (1931) and Serène (1954). The sexes are quite distinct in Hawaiian specimens. The females (Fig. 3*A*) have the carinae of the sixth abdominal somite and telson narrower and more sharply defined than those of males of corresponding size (Fig. 3*B*). However, as Serène has noted, this inflatedness and rounding of carinae and telson teeth increases with age, so care must be taken to insure that equal-sized specimens are being compared. The dimorphism of the dactyli is also pronounced in the Hawaiian population, with the females having the swelling of the base of the dactylus making a sharp angle with the shaft (Fig. 4*A*), while in the males the angle is less distinct (Fig. 4*B*); furthermore the tip of the dactylus of the females is sharply recurved, while that of the males is not. This dimorphism is developed at a small size in the Hawaiian population. The dactyli of a 43-mm male from the Philippines were indistinguishable from those of females from the same area, while in the Hawaiian collections specimens as small as 17 mm could be sexed by inspecting the dactylus.

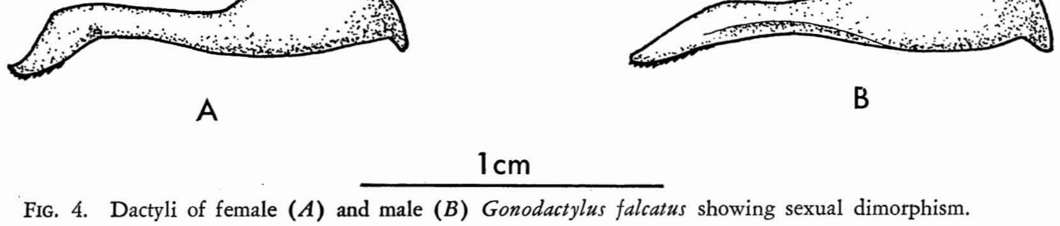

FIG. 4. Dactyli of female (*A*) and male (*B*) *Gonodactylus falcatus* showing sexual dimorphism.

Although it is difficult to describe unambiguously the coloration of the two sexes, there is a definite tendency for the larger males of the Hawaiian *G. falcatus* to be dark with dark green to black predominating. The females are reddish shading to brown in smaller individuals. In specimens under 35 mm both males and females are tan to brown.

Gonodactylus hendersoni Manning

Since the completion of the work reported in this paper, the second species of *Gonodactylus* found in Hawaii has been removed from *G. demanii* and named *G. hendersoni* by Manning (1967).

DISTRIBUTION: Burma, Indonesia, Queensland, Viet Nam, and Puerto Galera and Taytay in the Philippine Islands. On Oahu this species is most commonly found at Waikiki reef and off Diamond Head (Fig. 1). It has not been taken from Kaneohe Bay. Manning's description (1967) is based in part on Hawaiian material.

ORIGIN AND INTRODUCTION OF NEW HAWAIIAN SPECIES

Area of Origin

The almost simultaneous appearance of these two species in Hawaii indicates that they probably came from the same area at the same time. With this consideration in mind, localities where both *Gonodactylus falcatus* and *G. hendersoni* occur will be considered as possible areas from which the founding populations might have come.

Although *G. falcatus* occurs as far north as Japan, the most northerly reports for *G. hendersoni* are from Nha Trang in Viet Nam and Taytay and Puerto Galera in the Philippines. These two species co-occur further south in Queensland and to the west through Indonesia.

Means of Introduction

In discussing the introduction of marine invertebrates, larval transport and introduction of adults require separate consideration.

LARVAE: Although attempts to rear the larvae of *G. falcatus* were unsuccessful, the results indicated that the minimum pelagic life of the larvae of this species is about 22 days. This agrees with the findings of Gurney (1937) and Manning and Provenzano (1963). The great size attained by some stomatopod larvae taken at sea (Brooks, 1886:5ff.) suggests the possibility that stomatopods can prolong their larval life for an indefinite period, until proper conditions for metamorphosis are encountered. There is little concrete evidence to support this suggestion, however, and it must be considered as a tentative hypothesis until substantiating work has been done. If *G. falcatus* came to Hawaii as larvae the most likely possibility is that they were carried by the Kurashio current (Sverdrup, 1942:723). The probability seems slight that larvae of both *G. falcatus* and *G. hendersoni* were brought at the same time from as far as the northern Philippines by ocean currents.

ADULTS: Transportation of benthic adults over long distances would probably involve transport in or on ocean-going vessels. Newman (1963) suggested that the shrimp *Paelemon macrodactylus* was transported from the Orient to San Francisco Bay in the salt water system of a ship. Jones (1966) reports the introduction into Hawaii of the brackish-water copepod *Pseudodiaptomus marinus*, which had previously been recorded only in Japan. It is unlikely that this copepod was transported by ocean currents, since the time required would have covered several generations, and the species is restricted to brackish waters. Newman stated that the proper conditions for introduction by this method do not commonly occur, which would explain the infrequency of introduction of any species that cannot be transported on the exposed surface of a ship's bottom (Matsui, Shane, and Newman, 1964). The simultaneous introduction of both species of stomatopods in the saltwater system of a ship seems unlikely.

During World War II, the United States Navy used a number of barges constructed of concrete in their operations in the south and west Pacific. At the end of the war many of these barges were towed back from the localities where they had been used. Most of them were left in Guam, but some were towed as far as the Hawaiian Islands. They are now located, submerged, in West Loch at Pearl Harbor (Fig. 1) on Oahu. These barges were frequently used in the area of the Philippines and the South China Sea. The towed speed of these barges was about three knots, an uncommonly slow speed for sea-going vessels, but one that would not dislodge any organisms living in fissures or holes in the hull. The almost simultaneous appearance of *Gonodactylus falcatus* and *G. hendersoni*, soon after the arrival of these slow-moving barges from the area where they co-occur, is strong circumstantial evidence for their introduction by this means.

ECOLOGY OF REPLACEMENT

In investigating the mechanisms of replacement of *Pseudosquilla ciliata* by *Gonodactylus falcatus,* three parameters of the environment and biology of these species were compared: salinity tolerance, larval ecology, and behavior.

Salinity Tolerance

Both *Pseudosquilla ciliata* and *Gonodactylus falcatus* live on the shallow reef flat where fluctuations in salinity can be substantial. In an area such as Kaneohe Bay (Fig. 2) where the replacement of *Pseudosquilla ciliata* in coral heads by *Gonodactylus falcatus* is complete, the effect of differential salinity tolerance might have been important in effecting the replacement.

In May 1965, exceptionally low (0′ to –0.04′) tides occurred in the mornings during the first days of the month. During the night of May 2–3 there was a very heavy rainfall. Coconut Island in Kaneohe Bay reported 10.52 inches of rain during the night and morning, and a nearby weather station reported 21.61 inches. On May 7 surface salinities in the southern part of the bay ranged from 7.8 o/oo to 30.3 o/oo with an average surface salinity of about 20 o/oo. These lowered salinities showed a gradient from the surface to about 1.5 meters. Water in the southern part of the bay showed considerable dilution for at least two weeks. On May 5 a collection was made of dead animals that had washed up on a mud flat in the bay (Fig. 2, *1*). In this collection were 49 dead stomatopods of which 42 were *Pseudosquilla ciliata*, 5 were *Gonodactylus falcatus*, and 2 were *Lysiosquilla maculata.* On May 23 collections were made on a reef near Coconut Island (Fig. 2, *2*). All the coral on the surface of the reef was dead, and the characteristic fauna of amphinomid and polynoid worms, alpheid shrimp, and xanthid crabs was greatly reduced or entirely absent. The only exception to this reduction in numbers was *Gonodactylus falcatus.* In 20 liters of coral, 5 *G. falcatus* were found, which is about the normal number for samples of similar size from the reef. On July 17 all the loose coral was collected from an area 25 m^2 on the same reef. The fauna in these coral heads appeared to be returning to normal, though it was still noticeably reduced. From this coral, however, 69 *G. falcatus* were collected. Of the 42 females in the collection, 9 were carrying eggs.

Though qualitative, these observations suggest that *Gonodactylus falcatus* has a wider range of salinity tolerance than does *Pseudosquilla ciliata.* To test this hypothesis a series of tests on the differential salinity tolerance of these two species was performed. Two procedures were used. In the first, the animal was removed from seawater of normal salinity and placed directly into the water of the test dilution. In the second series, the animal was acclimatized for specified time intervals to increasing dilutions until the maximum dilution was reached. The second method probably more closely approximated the natural conditions where the amount of runoff, and hence dilution, increases gradually.

The results of these tests are shown in Table 1. In both series of experiments *Gonodactylus falcatus* exhibited a greater degree of salinity tolerance than did *Pseudosquilla ciliata.*

Larval Ecology

In order to obtain information on the breeding periods of *Gonodactylus falcatus* and *Pseudosquilla ciliata,* as well as the relative reproductive activity of these two species, investigations were carried out on the planktonic larvae of both species for a period of one year. Plankton tows were made at three areas in Kaneohe Bay from October 1964 to October 1965 (Fig. 2). Run A, close behind Coconut Island, was chosen to sample water from as close as possible to a reef where both species were known to be abundant. Run B was chosen to give a sample of the more inshore water of the reef system in the bay. Run C sampled water that had less contact with the inshore reefs and was more open to the waters of the ocean.

TABLE 1

RESULTS OF SALINITY TOLERANCE TESTS ON *Gonodactylus falcatus* AND *Pseudosquilla ciliata*

IMMEDIATE IMMERSION EXPERIMENTS

	Gonodactylus falcatus			*Pseudosquilla ciliata*		
% SEAWATER	NO. OF ANIMALS	LENGTH OF TEST	CONDITION AT END OF TEST	NO. OF ANIMALS	LENGTH OF TEST	CONDITION AT END OF TEST
75				2	indef.	alive
66				2	indef.	alive
66				1	4 days	dead
50	1	indef.	alive	5	90 min	weak
30	1	15 min	weak			

INCREMENTAL EXPERIMENTS

Gonodactylus falcatus				*Pseudosquilla ciliata*			
NO. OF ANIMALS	% SEAWATER 75	% SEAWATER 50	CONDITION AT END OF PERIOD	NO. OF ANIMALS	% SEAWATER 75	% SEAWATER 50	CONDITION AT END OF PERIOD
1	2 hr	indef.	alive	1	2 hr	3 hr	dead
				1	4 hr	19 hr	dead
				1	68 hr	indef.	alive
				1	6 hr	indef.	alive

	% SEAWATER				% SEAWATER			
	75	50	30		75	50	30	
1	1 hr	1 hr	25 min weak	1	68 hr	143 hr	2¼ hr	dead

The numbers of *Gonodactylus falcatus* and *Pseudosquilla ciliata* larvae are shown in Figure 5. The numbers of *Gondactylus falcatus* larvae taken during the year's sampling showed two peaks—one from October to January, and one from late March to mid-April—although larvae of this species were taken throughout the year. This was especially true of run C where all but three samples contained *G. falcatus* larvae in stage IV. *G. falcatus* larvae of stages III, V, and VI were taken only occasionally.

During most of the year *Pseudosquilla ciliata* larvae were either absent from the plankton samples or were represented by small numbers, generally less than *Gonodactylus falcatus*. However, during late spring coincident with the peak of *G. falcatus*, there was a peak in numbers of *Pseudosquilla ciliata* larvae taken in all runs.

If the year sampled was typical of the situation in Kaneohe Bay, *Gonodactylus falcatus* with its two periods of breeding activity would have a reproductive advantage over *Pseudosquilla ciliata* with only one. The fact that *Gonodactylus falcatus* larvae are generally more abundant might only be an indication that larger numbers of this species were present in Kaneohe Bay at the time the study was made, and might not be a measure of relative reproductive ability. However, *Pseudosquilla ciliata* was still very common on the sand and mud flats in the bay.

Behavior

It was observed in the field that *Gonodactylus falcatus* was apparently more aggressive than *Pseudosquilla ciliata.* Where *Gonodactylus falcatus* would snap readily with its raptorial claws when touched, *Pseudosquilla ciliata* would only occasionally strike. Whenever several *Gonodactylus falcatus* were put together in an aquarium with few places to hide, there was constant fighting and usually only the largest survived. This was found to occur even when the animals were only a little more than 2 cm long. On the other hand, *Pseudosquilla ciliata* indi-

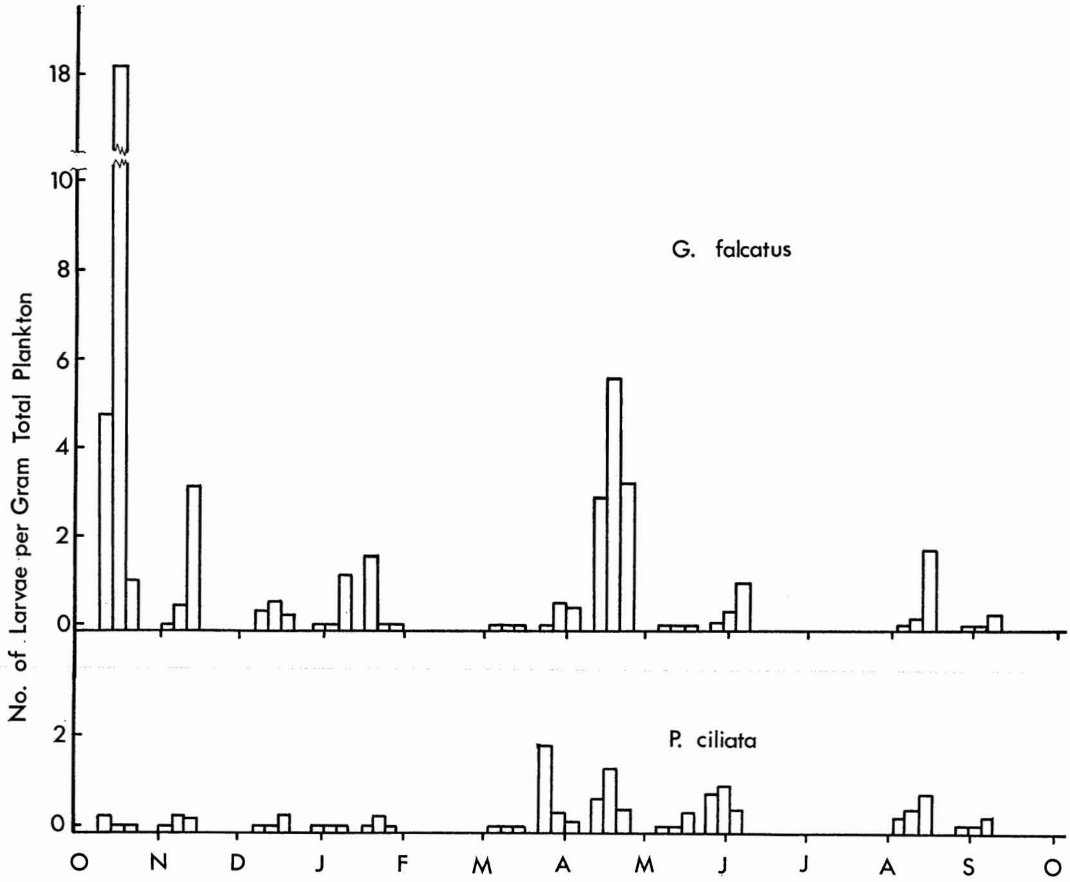

FIG. 5. Graph of numbers of stomatopod larvae taken in Kaneohe Bay during years 1964–1965. Each group of three bars represents one day's haul. The bars represent runs *A, B,* and *C* in that order.

viduals fought among themselves less frequently, even when the aquarium was fairly crowded. When put together in an aquarium, the *Gonodactylus falcatus* killed the *Pseudosquilla ciliata* even when the *P. ciliata* were considerably larger. This suggested the hypothesis that the greater aggressiveness of *Gonodactylus falcatus* might have been an important factor in its replacement of *Pseudosquilla ciliata* in the coral head habitat.

Most of the *Gonodactylus falcatus* collected for these studies were taken from dead heads of the coral *Porites compressa*. However, this species is also found in the dead bases of living heads of *Pocillopora meandrina* and from clumps of the coralline alga *Porolithon*, and occasional individuals have also been seen in bare rock or moving about on the surfaces of coral heads. When specimens of *Gonodactylus falcatus* were taken from coral heads they were consistently wedged between the branches of the coral near the base. They were usually found with the body flexed, the telson covering the anteroventral part of the body. In this position the sides of the animal are protected by the branches of the coral, the dorsal surface is covered by thick exoskeleton, and the ventral surface is within the curve formed by the animal doubling upon itself.

Pseudosquilla ciliata was taken from two types of habitat: from burrows which the animals had dug in fine muddy sand and silt, and from areas with a similar substratum but with a great deal of algal growth (Fig. 2, *3*), chiefly *Acanthophora*, where the animals were seen moving about on the bottom in shallow water. When

Pseudosquilla ciliata was observed in burrows, only the eyes and most anterior part of the body were visible. When disturbed, an animal would rapidly retreat into the burrow, and reappear after a few minutes. Since *P. ciliata* can be found in burrows in muddy bottoms and walking freely on the bottom, and since, prior to 1953, it was taken from coral heads, this species seems to have a wider range of possible habitats than does *Gonodactylus falcatus.*

The fact that coral heads were occupied by *Pseudosquilla ciliata* before 1953 suggested experimental comparison of agonistic behavior in relation to a "burrow." Ten trials were made to study the behavior of *P. ciliata* and *Gonodactylus falcatus* in relation to a glass vial placed in the sand in the bottom of an aquarium to simulate a burrow. Individuals of either species would readily enter the vial. However, if *Pseudosquilla ciliata* had entered the vial, it was invariably driven out by *Gonodactylus falcatus* when the second animal was placed in the aquarium (Table 2). *G. falcatus*, on the other hand, was never driven from a vial by *Pseudosquilla ciliata.*

When fighting, *Gonodactylus falcatus* curls its telson up under the ventral surface of the body in the same attitude as when it is in a coral head. While this is a very effective method of fighting when the animal is in a small crevice or hole, it leaves the animal unsupported when fighting in the open. When in the glass vial, *G. falcatus* blocks the opening with the telson, but its eyes are able to see out and the raptorial claws can be snapped out the opening. This position and method of defense is similar to that exhibited by *G. falcatus* living in coral heads.

Pseudosquilla ciliata, on the other hand, does not exhibit any such specialized fighting behavior, and it always fled from the vial when attacked by *Gonodactylus falcatus*. In their burrows in mud flats, the animals either retreated deeper inside or left the burrows if they were disturbed.

TABLE 2

SIZES OF *Gonodactylus falcatus* AND *Pseudosquilla ciliata* USED IN BEHAVIOR EXPERIMENTS (IN ALL CASES *G. falcatus* DROVE *P. ciliata* OUT OF THE VIAL AND WENT IN ITSELF)

EXPT. NO.	*Pseudosquilla ciliata*	*Gonodactylus falcatus*
1	5.0-cm male	4.5-cm male
2	6.3-cm female	4.0-cm female
3	5.5-cm male	4.5-cm female
4	5.5-cm male	4.0-cm female
5	5.3-cm male	4.3-cm female
6	5.5-cm male	4.3-cm female
7	6.0-cm male	6.0-cm female
8	5.5-cm male	5.0-cm male
9	7.0-cm male	5.0-cm male
10	6.8-cm male	5.0-cm female

DISCUSSION: The introduction of *Gonodactylus falcatus* into an area where *Pseudosquilla ciliata* was originally the dominant stomatopod affords an opportunity to study the effects of competition and competitive exclusion in a natural situation. *Gonodactylus falcatus* is a species specialized for living within the spaces between the branches of coral heads and similar habitats. This is borne out by the uniformity of situations in which it was found, and by its behavioral specializations. In the terminology of MacArthur and Levins (1964) it is a "coarse-grained" species, differentiating between this type of habitat and others less suitable. *Pseudosquilla ciliata* would be termed a "fine-grained" species in regard to habitat selection, because it will occupy a greater variety of habitats.

Both species are generally carnivorous, capturing prey by raptorial feeding. There appears to be ample food on the reef flats for animals of this trophic level within each of the habitat areas, and competition seems to be restricted primarily to obtaining a place to live. However, it must be emphasized that this conclusion was reached on a rather intuitive level and that, until more is known about the trophic structure of coral reef systems (see Kohn, 1959, and Hiatt and Strasburg, 1960), generalizing statements should be considered suspect.

The rapid replacement of *Pseudosquilla ciliata* by *Gonodactylus falcatus* verifies the prediction that the specialized species will exclude the generalist from the habitat for which the former is specialized (MacArthur and Levins, 1964). The wider salinity tolerance and greater reproductive activity of *G. falcatus* may have hastened the replacement, but probably the competition was primarily for living space, and behavioral differences were the deciding factor.

It can be further predicted that the presence of *G. falcatus* in Hawaii will not affect those populations of *Pseudosquilla ciliata* utilizing habitats other than coral heads, and that *Gonodactylus falcatus* will eventually spread to the coral head habitat in other islands in the Hawaiian Archipelago.

SUMMARY

1. Two species of *Gonodactylus*—*G. falcatus* (Forskål) and *G. hendersoni* Manning—occur on the island of Oahu in the Hawaiian Islands. The former is similar to the variety *ternatensis* using Serène's definition. *G. falcatus* is the most common species of stomatopod found in coral heads on Oahu. *G. hendersoni* is abundant in coral heads in some areas.

2. *Pseudosquilla ciliata* (Fabricius), which 14 years ago was the most common stomatopod in coral heads, is now not found in coral heads on Oahu.

3. It is suggested that *Gonodactylus falcatus* and *G. hendersoni* came to the Hawaiian Islands from the area of the Philippines or the South China Sea by means of concrete barges that were towed to the Hawaiian Islands at the end of World War II.

4. *G. falcatus* is more tolerant of lowered salinities than is *Pseudosquilla ciliata.* A heavy rainfall in Kaneohe Bay, which reduced surface salinities to as low as 22 per cent seawater, was more deleterious to the population of *P. ciliata* in the bay than it was to that of *Gonodactylus falcatus.*

5. Studies of the plankton of Kaneohe Bay indicate that while *G. falcatus* had two periods of breeding during the year sampled, *Pseudosquilla ciliata* had only one.

6. Comparisons of the aggressive behavior of *Gonodactylus falcatus* and *Pseudosquilla ciliata* indicate that the former is "more aggressive" and can drive the latter from a hole.

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