FINAL REPORT

to

The Western Pacific Regional Fishery Management Council

on

MANAGEMENT ASPECTS OF THE BIOLOGY OF THE SPINY LOBSTERS, *Panulirus marginatus*, *P. penicillatus*, *P. versicolor*, and *P. longipes femoristriga* IN HAWAII AND THE WESTERN PACIFIC

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1.0 SUMMARY

1. Spiny lobsters began being fished commercially at Palau in 1966 and at Truk in 1968. The level of catch was comparable to that at Oahu during the subsequent years. The fishery is seasonal, peaking in the summer and decreasing during the winter. Changes in the lobster landings are correlated with patterns of prevailing winds which affect the accessibility of the lobsters, particularly *P. penicillatus*.

2. *Panulirus marginatus* is more likely to be captured by trap than *P. penicillatus*. Male and female *P. marginatus* are equally likely to be captured. Male *P. penicillatus* are more likely to be trapped than females. Female reproductive condition does not influence catchability in either species. The differences in the catchability of the two species are of considerable importance since they suggest how catch rates by trapping and total production per density might change with increased fishing pressure in the Northwest Hawaiian Islands.

3. *Panulirus penicillatus* is the largest of the four species of spiny lobster considered in this study. Males tended to be larger than females in all species except *P. longipes femoristriga*, the sexes of which did not differ in carapace length.

4. *Panulirus penicillatus* at Palau and Oahu and *P. versicolor* at Palau reproduce continuously at the same level throughout the year. About 40% of the females of both species are ovigerous in any month at both locations. Reproduction is probably continuous in *P. penicillatus* across its broad geographic distribution at mean seawater temperatures greater than about 23°C.

5. Female *P. penicillatus*, *P. marginatus*, and *P. versicolor* differ significantly in the relation of carapace length and fecundity. This relation does not differ in *P. penicillatus* at Palau and Oahu.

6. The total standardized crude reproductive rates of female *P. penicillatus* and *P. marginatus* do not differ. The total standardized crude reproductive rate of female *P. versicolor* is much greater than that of *P. penicillatus*. There was no difference in the total standardized crude reproductive rates of female *P. penicillatus* at Palau and Oahu.

7. The fishing pressure exerted on *P. penicillatus* at Oahu up to 1960-62 apparently had little effect on either the population size-structure or the total standardized crude reproductive rate of that species. This conclusion is based upon comparisons with *P. penicillatus* at Palau. There is no data available to determine whether changes in growth rate or abundance might have resulted from the fishing activity at Oahu.

8. The exoskeleton condition of *P. versicolor* at Palau varies significantly with season and sex. The cause of this seasonality is not clear at this time. Too few *P. penicillatus* were collected in pre-molt and recently molted conditions to permit quantitative treatment of the results. No molt information was collected at Oahu.

9. No single pattern serves to characterize the relationship of total weight and carapace length between the sexes in *P. penicillatus*, *P. marginatus*, and *P. versicolor*. Male *P. penicillatus* increase in total weight relative to carapace length at a greater rate than non-ovigerous females. Male *P. marginatus* weigh proportionately less relative to carapace length than non-ovigerous females. Male and non-ovigerous female *P. versicolor* do not differ in weight relative to carapace length.

10. Male and female *P. penicillatus* are generally heavier at all carapace lengths when fresh than when frozen or boiled. Male and female *P. versicolor* demonstrate no consistent weight loss due to freezing. Males and non-ovigerous females, however, are proportionately heavier at all carapace lengths when fresh than when boiled.

11. The relations of total length and carapace length and carapace width and carapace length for *P. penicillatus* and *P. versicolor* at Palau are provided. Related information was not collected for spiny lobsters at Oahu.

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2.3 ACKNOWLEDGEMENTS

This report is written as a planning document for use by the Western Pacific Regional Fisheries Management Council in arriving at a recommended plan for the management of spiny lobster fisheries. The preparation of this report has required the assistance and cooperation of a large number of individuals. My field study at Palau was conducted with the support of the Marine Research Division, Department of Research and Development, United States Trust Territory of the Pacific Islands. The U. S. Trust Territory Biology Laboratory at Palau provided use of laboratory facilities. Mr. Frank Yoshiharu, Manager, Palau Fishermen's Cooperative and Mr. Camillo Nocket, Manager, PIIS Island Fishermen's Cooperative provided the data on commercial landings of lobsters at Palau and Truk respectively. The Hawaii Division of Fish and Game provided the data collected during the study of spiny lobsters by Mr. Donald E. Morris at Oahu. Size frequency and sex ratio data for *P. penicillatus* from different locations across the Pacific and Indian Oceans were generously provided by numerous individuals including: Dr. Karl-Günther Reck, Estacion Cientifica Galapagos, Ecuador; Mr. Eyal Gilead, Tel-Aviv University, Israel; Mr. Gary Long, Mid-Pacific Marine Laboratory, Enewetak, Marshall Islands; Mr. Bruce Thompson, Department of Biological Sciences, University of Southern California; Mr. Steven West, Pacific Atoll Divers, Johnston Island; Koral Kings Dive Club, Midway Islands; and Mr. Charles Apuna, Canton Island. Ms. Laurie Tsuji assisted with the computer analyses. Drs. Roy Mendelsohn, Jeffrey Palaveno, Robert Skillman, and Tim Smith provided helpful advice on the statistical analyses. Ms. Sue Monden, Zoology Department, University of Hawaii prepared figures 2-27 and the illustration of *P. marginatus* in Figure 1. Mr. Takesi Suzuki of the U. S. Trust Territory Biology Laboratory prepared the illustrations of *P. penicillatus*, *P. versicolor*, and *P. longipes femoristriga* in Figure 1. Ms. Lori Yamamura and the secretarial staff of the Zoology Department, University of Hawaii typed the report. Computer analyses were performed at the University of Hawaii Computing Center. This work was conducted at the Zoology Department, University of Hawaii, with financial support provided by the Western Pacific Regional Fisheries Management Council. (Contract no. WP-78-204 to C. D. MacDonald).

3.0 INTRODUCTION

The Fishery Conservation and Management Act of 1976 (Public Law 94-265) provides for the United States Government's exclusive management of all fishery resources from 3 to 200 miles off U. S. territory. The Western Pacific Regional Fishery Management Council (WPRFMC) is responsible for developing management plans for fisheries off the coasts of Hawaii, American Samoa, Guam, and the Northern Mariana Islands. The present draft of the Spiny Lobster Management Plan principally reviews the known biological and ecological data about the spiny lobster species, *Panulirus marginatus* in Hawaii. That management plan is aimed solely at managing the fishery in the Northwest Hawaiian Islands (NWHI) which at the present time is based almost entirely on *P. marginatus* and is consequently based on the concept of a single-species fishery.

Panulirus penicillatus, however, is fished in equal abundance with *P. marginatus* at Oahu (Morris, 1968), although it does not currently constitute a significant proportion of the commercial catch in the Northwest Hawaiian Islands. Both species overlap in depth range and diet and successfully reproduce throughout the Hawaiian Archipelago (Morris, 1968; McGinnis, 1972; Cheney, 1976; MacDonald and Thompson, MS). The low relative abundance of *P. penicillatus* in the NWHI may be the result of unsuccessful competition with *P. marginatus* for critical resources where various refuges allow *P. penicillatus* to survive at least in small numbers. A reduction in numbers of *P. marginatus* as the fishery for that species develops could result in a preempting of resources by *P. penicillatus* with a subsequent substantial increase in the latter's abundance and economic importance. This possibility is enhanced if the trapability of P. marginatus is greater than P. penicillatus thereby resulting in differential fishing mortality between the two species. Fishing may have reduced the numbers of P. marginatus relative to P. penicillatus at Oahu where there has been a fishery since at least the early nineteen hundreds (Morris, 1968). In that possibility, the concept of single-species maximum sustainable yield as set forth in the present draft of the Spiny Lobster Management Plan will not be applicable to determining optimal harvesting levels of spiny lobsters in the NWHI. An understanding of the biology of P. penicillatus, sufficiently detailed to be directly comparable to what is known of P. marginatus, is required and a plan modified to manage a mixed-species fishery is needed.

Panulirus penicillatus, P. versicolor, and P. longipes femoristriga are of potential economic importance throughout American Samoa, Guam, the Northern Mariana Islands, the U. S. Trust Territory and, in short, the entire area presided over by the South Pacific Commission. MacDonald (1971) and George (1972) have urged that fisheries for P. penicillatus and P. versicolor be developed and George (1974) has concluded that P. penicillatus is the most likely species for commercial development in the Indo-West Pacific. Panulirus penicillatus is the central species of a number of commercial fisheries at Revillagigedo Island and the Galapagos Islands (Holthuis and Villalobos, 1962; Holthuis and Loesch, 1967), Palau and Truk (MacDonald, 1971), and Tonga and the Solomon Islands (George, 1972) and constitutes approximately half of all commercial catches in the southern Hawaiian Islands (Morris, 1968; McGinnis, 1972). The marketing of

P. penicillatus, P. versicolor, and P. longipes femoristriga could center at Pago Pago, Guam, and Saipan where strong demand can be expected from burgeoning urban populations and expanding tourist industries and where limited quantities of spiny lobsters are already being shipped for retail from neighboring island districts (MacDonald, 1971; George, 1972). There is insufficient information presently available, however, to effectively manage a fishery for these species anywhere within the jurisdiction of the WPRFMC.

This study of the biology of spiny lobsters in Hawaii and the Western Pacific was undertaken to provide information potentially needed for the management of spiny lobster fishing in the NWHI, elsewhere within the jurisdiction of the WPRFMC, and in the nearshore waters under the jurisdiction of the State of Hawaii and diverse other Pacific Island governments. The majority of effort was directed at P. penicillatus and P. versicolor at Oahu and Palau. Whenever deemed useful, however, additional analyses of P. marginatus were undertaken to directly integrate the results of this study with the present draft of the Spiny Lobster Management Plan. Panulirus longipes femoristriga was infrequently sampled and is treated only briefly in this report.

4.0 DISTRIBUTION AND PHYSICAL HABITAT OF SPINY LOBSTERS IN HAWAII AND THE SOUTH PACIFIC

4.1 Distribution

Four species of spiny lobsters are found around Pacific islands within the area of jurisdiction of the United States: *Panulirus marginatus*, *P. penicillatus*, *P. versicolor*, and *P. longipes femoristriga* (Morris, 1968; MacDonald, 1971)(Figure 1). *Panulirus marginatus* occurs only within the Hawaiian Islands. *Panulirus penicillatus* is widely distributed and occurs in the Western Red Sea, throughout the Indian Ocean, and across the tropical Pacific Ocean as far east as the Galapagos Islands. *Panulirus versicolor* and *P. longipes femoristriga* are generally limited to the oceanic islands of the Indo-West Pacific region. All but *P. longipes femoristriga* are of at least some economic interest across their range of distribution.

4.2 Physical Habitat

Around much of Hawaii, *P. penicillatus* is generally found in water from 1 to 5 meters deep and tends to favor exposed shorelines along windward coasts of the islands. At Oahu, however, *P. penicillatus* departs from its usual shallow depth range and is regularly found to much greater depths. In the Northwest Hawaiian Islands, a few *P. penicillatus* have been caught at depths of approximately 100 meters. *Panulirus marginatus* inhabits a broader range of depths than *P. penicillatus* and regularly ranges from shorelines to depths as great as 185 meters. The Hawaiian Islands have relatively limited development of coral reefs but three species of coral, *Porites compressor*, *P. lobata*, and *Montipora verrucosa*, are widespread and serve as shelter at least in the shallows (MacDonald, in prep.). Rubble and ledges are also used. At greater depths, submarine terraces provide suitable shelter.

At Palau, P. penicillatus occupies a limited range of similar habitats (MacDonald, 1971). This species is most often found within a very narrow strip along the seaward margins of reefs that are heavily buffeted by surf and strong winds. Although present in scattered abundance in all reef sectors, it is most common along reefs in the northeastern quarter. This species is found at depths of as little as 10 centimeters in areas of wave wash to depths of about 5 meters further seaward. It is found in greatest concentration at depths of 1-2 meters amidst breaking waves. Within this zone, P. penicillatus shelter within several species of mound-forming coral, along the walls of surge channels, and under ledges. Coral species that frequently provide shelter are Acropora smithi, A. oceolata, A. abrotanoides, A. polifera, and Pocillopora cydouxi. Panulirus penicillatus can also be found beneath rubble blocks on reef flats and along the windward sides of fringing reefs within the lagoon. Clear, cool, and well aerated seawater is characteristic of those locations. This species appears to avoid direct sunlight and stays deep within shelters. Panulirus penicillatus is extremely gregarious and as many as 18 lobsters of assorted sex, size, and maturity have been found within a single 1 meter diameter coral head.

At Palau, P. versicolor occupies a broad range of habitats and is found widely both outside and within the lagoon to depths of about 20 meters (MacDonald, 1971). Outside the reef, P. versicolor shelters beneath ledges and coral heads noticeably well below the surge zone. Inside the reef, it is commonly found within shelter afforded by corals on reef flats, lagoon slopes, and fringe and patch reefs. This species characteristically shelters within spacious holes at the bases of large coral heads, particularly Porites lutea. Turbid and non-turbid water appears to be tolerated equally well, but this species is characteristically found where water conditions are calm. This species is apparently unaffected by intense sunlight and individuals are often observed stationed almost fully exposed at the entrances of shelters. Panulirus versicolor is not gregarious and adults are rarely found sharing the same shelter.

At Palau, P. longipes femoristriga is found in habitats that broadly overlap those occupied by P. penicillatus and P. versicolor (MacDonald, 1971). This species is found in shallow water on the lagoon side of active reef margins among dense coral growth and to depths of several meters at the seaward mouths of passes through the reefs. It was also observed in wave-washed caves at the bases of limestone islands within the lagoon.

The three species at Palau, P. penicillatus, P. versicolor, and P. longipes femoristriga, are also found in similar habitats at different islands across the U. S. Trust Territory (MacDonald, 1971). This use of habitat is similar to that observed by George (1974) for the same species at other island locations across the Indo-West Pacific.

5.0 FISHING HISTORY AND SEASONALITY

5.1 Fishing History

The catch of spiny lobsters in the Hawaiian commercial fishery from around the main Hawaiian Islands has decreased dramatically from 1946 (Figure 2). The catch statistics are maintained by the Hawaii Division of Fish and Game and do not differentiate the two species, *P. penicillatus* and *P. marginatus*, that make up the spiny lobster catches. The fishing history around the major Hawaiian Islands is summarized in the present draft of the Spiny Lobster Management Plan.

Spiny lobsters began being fished commercially at Palau in 1966 and at Truk in 1968 (Figure 3). The commercial landings in Palau from 1967 through 1970 were comparable to landings at Oahu over the same period of time (Figure 2). These are the only years for which I was able to obtain these data. Information on commercial lobster landings at Palau were provided by the Palau Fishermen's Cooperative and do not differentiate the three species, *P. penicillatus*, *P. versicolor*, and *P. longipes femoristriga*, that make up the spiny lobster catches. During October 1969 - October 1970 when I sampled the catch, *P. penicillatus* and *P. versicolor* constituted the great majority of the lobsters caught and *P. penicillatus* accounted for more than half of all the lobsters landed.

The commercial catches of spiny lobsters at Palau are greater than at Truk (Figure 3). Information on commercial lobster landings at Truk were provided by the PIIS Island Fishermen's Cooperative which also does not differentiate the species that make up the spiny lobster catches. Lobsters marketed at Truk are sold live and spearing is discouraged. Because

P. penicillatus can be collected more readily alive at Truk than the other two species (see Fishing Methods, this report), it probably accounts for the majority of the lobsters caught at that location.

5.2 Fishing Methods

The fishing methods for spiny lobsters around the major Hawaiian Islands are summarized in the present draft of the Spiny Lobster Management Plan. Tangle nets and wire-mesh traps are customarily employed.

Spiny lobsters are fished commercially at Palau exclusively by spearing by divers during the day and at night. Small outboard skiffs are used to transport divers to areas where lobsters are known to be found. During the day, individual divers are dropped off at intervals of half to one or two miles apart and picked up at a later time. Lobsters are speared within their shelters and are strung through the tail on a line attached to a bamboo float which the divers tow while swimming. At night, lobsters are speared in the open. Fishing is done in the vicinity of an anchored boat with the aid of underwater lights. Lobsters are characteristically found beneath large coral heads (*Porites* sp.) and limestone rubble within the lagoon and in surge channels and dome-shaped colonies of *Acropora smithi* along the seaward margins of windward reefs. Broad expanses of reef are efficiently searched and all but very small lobsters are taken. *Panulirus penicillatus* is often sought after specifically because it can be found concentrated within a narrow band of characteristic habitat outside the reef. *Panulirus versicolor* is more commonly taken incidentally while spearfishing within the lagoon where it is very widely distributed and requires a much greater amount of searching.

Spiny lobsters are usually fished commercially at Truk by walking over reef flats at night. Panulirus penicillatus is almost exclusively caught. A lantern is used to illuminate lobsters in shallow water where they are captured by hand. The windward reefs fringing the northeast quadrant of the lagoon are generally preferred. These reef flats are broad and flat and relatively easy to fish. Limited observation indicates that the windward reef flats yield higher catches than reefs in leeward sections. This may be in part due to the relative ease of fishing permitted by the pavement-like surface of the windward reef flat, but observations that I made while diving outside the reef during the day indicate that habitat generally associated with P. penicillatus is much more common in windward than leeward reef sectors. Panulirus versicolor is usually only caught incidentally while spearfishing within the lagoon.

Both species of spiny lobsters are invariably caught by diving or reef-walking across much of their range in the South Pacific. MacDonald (1971) offers a broader account of how these fishing activities are distributed at islands across the U. S. Trust Territory and how fishing activities differ relative to island and reef topography.

5.3 Seasonality

Lobster landings are strongly seasonal at Palau and Truk (Figure 3). This seasonality is correlated with prevailing wind patterns. Catches are low from the end of November through May. During this period the prevailing wind is the northeast to east trade wind which makes fishing outside of the reef in that quarter very difficult. Panulirus penicillatus is most abundant along the seaward margin of reefs particularly in the northeast sector. From late December until early April calms are infrequent. Beginning in April the frequency of the trades decreases and east winds predominate. Calms increase and meet an annual maximum in June. Light and inconstant winds then prevail. Lobster catches increase dramatically. From July through October winds remain comparatively light and variable but blow from the southwest more than half the time. During this time, northeast reefs lie in the lee of the islands. Divers are then more easily able to search for lobsters in what is generally the surf line along seaward reef margins and the visibility of fishermen walking along the reef flats is greatly improved by the lack of disturbance of the water's surface. About the beginning of November winds back around to their prevailing winter direction again making lobster fishing difficult.

This seasonality in lobster landings is largely the result of the seasonal accessibility of P. penicillatus. Panulirus versicolor is primarily fished within the lagoon and is apparently caught at about the same rate throughout the year. The differences in the seasonal availability of P. penicillatus and P. versicolor at Palau are clearly demonstrated in the samples that I took from October 1969 through October 1970. These differences are most pronounced in the study of reproductive seasonality that follows.

6.0 GENERAL METHODS

6.1 Data Collection

I recorded biometric data and information on reproductive and exoskeleton condition for *P. penicillatus* and *P. versicolor* at Palau from commercial fishing catches during weekly market sampling at the Palau Fishermen's Cooperative from October 1969 through October 1970. Lobsters were measured either when they were landed in a fresh or boiled condition or after they had been frozen for several days to a week preemptory to being shipped to Guam. No lobster was measured more than once. I collected additional data by diving day and night throughout the year with fishermen in all districts at Palau. The areas fished were seldom deeper than 15-20 m.

I reanalyzed the data for *P. penicillatus* and *P. marginatus* at Oahu that was collected by Morris (1968). These data consist of biometric and reproductive information and were made available through the cooperation of the Hawaii Division of Fish and Game. The lobsters were collected by a commercial trap fisherman at monthly intervals from May 1960 through October 1962 in the area of Maunalua Bay on the southeastern coast of Oahu. The depth range fished was not specified but it is unlikely that it exceeded 20 m. Only those data recorded upon the initial capture of each lobster were used in this study to assure independence of sampling.

6.2 Measurements

6.2.1 Length

All lengths were measured to the nearest millimeter. Carapace length at Palau and Oahu was measured along the mid-dorsal line from the anterior end between the post-orbital spines to the posterior edge. Total length at Palau was measured along the mid-dorsal line from the anterior end of the base of the antenulles to the posterior margin of the telson. Carapace width at Palau was measured at the point of greatest breadth between the lateral margins of the carapace. Total length and carapace width were not measured at Oahu.

6.2.2 Weight

Total weight was measured to the nearest ounce wet at Palau and Oahu. However, the antennae were removed above their bases from all lobsters prior to weighing at Palau. This practice facilitated handling and shipping in the whole-animal industry at Palau and all antennae were necessarily removed before lobsters could be landed for sale. The autotomy of appendages is frequently unavoidable during the capture and handling of spiny lobsters. Accordingly, total weight was measured to the nearest ounce only to minimize this source of bias in the data. Lobsters that had numerous limbs missing were not weighed at Palau. It is uncertain how this potential source of error was managed at Oahu and it is assumed that badly damaged lobsters also were not weighed there. The weights of lobsters at Palau and Oahu cannot be directly compared because of the removal of antennae at Palau.

6.2.3 Reproductive Condition

The reproductive condition of female lobsters at both Palau and Oahu was recorded as: 1) bearing eggs (ovigerous); 2) bearing a spermatophore at the base of the fifth pair of walking legs (mated); or, 3) bearing neither eggs nor spermatophore. When females simultaneously bore a spermatophore and eggs they were recorded only as being ovigerous. The condition of the spermatophore was not recorded at Palau and the information collected at Oahu was insufficiently detailed to treat as anything other than presence or absence.

6.2.4 Shell Condition

The exoskeleton of both males and females at Palau were categorized by the scheme of Matthews (1962), Heydorn (1969), Mitchell et al. (1969), and Berry (1971, 1973): 1) Old Hard Shell (OHS) - exoskeleton hard with evidence of wear and encrusting organisms; 2) Old Soft Shell (OSS) - exoskeleton soft and pliable, ready to be shed; 3) New Soft Shell (NSS) - molt has just occurred with the new shell still soft and devoid of encrusting organisms; and 4) New Hard Shell (NHS) - exoskeleton hard with no signs of wear or encrusting organisms. No data on molt state were collected in the Oahu study.

6.2.5 Fecundity

At Palau, females bearing eggs were collected from several different areas around the major islands at different times throughout the year. The lobsters were selected to cover as wide a range of carapace lengths as possible. Females were not used if they had been strung through the tail upon capture as is customary in that fishery. This was done to minimize the possibility of egg loss during handling.

Newly spawned and late stage eggs were counted. While fresh, pleopods were removed with the egg mass still adhering. Each egg mass plus pleopods was fixed in 10% formalin and seawater and dried in an oven at approximately

150°C. After drying, the egg mass was rubbed over a fine mesh screen to break up the egg clusters and separate out the pleopods and any other non-egg material. The dried eggs were then weighed to the nearest mg on an electro-balance. Three replicate 0.1g sub-samples of eggs were taken from each individual and counted manually. The average of the three sub-samples was used to calculate the total number of eggs for each respective female by simple proportion. In this manner, the fecundity of each individual female was calculated by the average of egg counts of samples from that particular specimen and not by an average figure based on samples from other individuals. This method of estimating fecundity is similar to that of Kensler (1967) and Morgan (1972).

At Oahu, egg counts were done differently (Morris, 1968). A sample of eggs weighing approximately 1 g was removed from each of four females. Each sample was superficially dried, weighed to the nearest mg, and counted. All eggs on each female were dried and weighed in a similar fashion. The total number of eggs for each female was calculated by simple proportion using as the number of eggs per 1 g the mean of the 4 females. In this manner, the fecundity of each individual female was determined by using an average figure based on samples from other individuals. The average number of eggs per 1 g was calculated separately for each species.

7.0 GENERAL BIOLOGY AND ECOLOGY OF SPINY LOBSTERS IN HAWAII AND THE SOUTH PACIFIC

7.1 Differential Trapability

Independent sample proportions tests (Tate and Clelland, 1957) on tag-recovery data from *P. penicillatus* and *P. marginatus* at Oahu (Morris, 1968) reveal that trap catches are biased with respect to species, and with respect to sex for *P. penicillatus* (Table 1). Assuming that recapture rates are representative of the probability of each sex to enter a trap initially, male and female *P. marginatus* are equally likely to be recaptured. Male *P. penicillatus*, however, are significantly more likely to be sampled than females. There was no difference in the trapability of females in different reproductive conditions in either species. A comparison between the two species indicates that *P. marginatus* are significantly more likely to be captured by trap than *P. penicillatus*. Expressed differently, *P. marginatus* are equally likely to be caught regardless of sex, male *P. penicillatus* are 80% as likely to be caught as *P. marginatus*, and female *P. penicillatus* are only 35% as likely as *P. marginatus* to be caught.

Similar conclusions are obtained with alternative analyses. Snedecor and Cochran (1956) suggest considering the data as proportions of the animals which were tagged and subsequently recovered. The four proportions are then analyzed as a two-way analysis of variance with unequal numbers of observations in each cell (numbers tagged) using an arcsine transformation and invoking a theoretical value of the error sum of squares for the arcsine transformed proportions. Sokal and Rohlf (1969) suggest a three-way analysis of frequencies using a log likelihood ratio test statistic. The results of both of those tests clearly indicate that the trapability of lobsters varies by both species and sex in a complicated fashion. Inspection of the proportions recovered suggests that there is little difference in trapability between male and female P. marginatus, substantial difference between male and female P. penicillatus, and possibly little difference between P. marginatus and male P. penicillatus. Only the results of the independent sample proportions test are reported in their entirety due to the simplicity and directness of that analysis relative to the other two methods considered and in view of the close agreement in the results of all three analyses.

Since male P. penicillatus were about 2.27 times more likely to be captured than females, this is the factor by which the female sample was underestimated at Oahu. Correction yields an adjusted total sample of 692 females instead of 469 with the result that there were probably significantly more females than males in the population ($X^2 = 42.41$, d.f. = 1, $P \leq 0.001$). This is the opposite of what would be concluded based solely on trap-caught data in the absence of an assessment of differential catchability by sex. Additionally, the apparent equal abundance of the two species in the trap catches at Oahu very likely reflects a substantially higher abundance of P. penicillatus than P. marginatus.

This difference in the catchability of the two species is of considerable importance since it strengthens the possibility that the greater abundance of P. penicillatus at Oahu is the direct result of long-term fishing pressure. The differential removal of P. marginatus by trapping in the Northwestern Hawaiian Islands because of that species greater catchability could give P. penicillatus a comparative advantage in competing for critical resources as fishing continues and the industry expands. If P. penicillatus increases in abundance and P. marginatus decreases, catch rates by trapping and total production per unit density could be expected to decrease in the future.

7.2 Species Composition

The original conclusion that P. penicillatus and P. marginatus were approximately equally abundant at Oahu is probably wrong in view of the findings that these species are differentially catchable by trap. As already discussed, P. penicillatus was probably substantially more abundant than P. marginatus.

The Palau data were taken from 2,006 spiny lobsters collected over a thirteen month period between October 1969-1970. All lobsters were collected by diving. Of these, 62.5% were P. penicillatus, 36.2% were P. versicolor, and 1.3% were P. longipes femoristriga. A chi-square one-sample test reveals that P. penicillatus comprised a significantly greater proportion of the catch than P. versicolor ($X^2 = 139.74$, d.f. = 1, $P \leq 0.001$). Panulirus longipes femoristriga accounted for an inconsequential fraction of the total landings. During a survey of the spiny lobster resources that I conducted at Yap, Guam, Saipan, Truk, Ponape, and Majuro Atoll, subsequent to the Palau study, P. penicillatus accounted for better than 95% of the lobsters sampled. Panulirus versicolor was found in only relatively small numbers and P. longipes femoristriga was rarely seen.

7.3 Size and Sex Composition

7.3.1 *Panulirus penicillatus* at Palau and Oahu

The mean carapace length and variance of males at Palau were significantly greater than those of females (Table 2). Males and females combined ranged from 5.0 cm to 17.8 cm in carapace length with means of 11.3 cm and 7.9 cm respectively (Figure 4). The smallest ovigerous female was 6.9 cm in carapace length. The average carapace length of females in reproductive condition was 10.0 cm. The size frequency distribution of ovigerous females relative to total females is presented in Figure 4. Females at Palau were significantly more abundant in the smaller size classes and males were significantly more abundant in the larger (Table 3). Overall, there were significantly more females than males.

The mean carapace length and variance of males at Oahu were significantly greater than those of females (Table 2). Males and females combined ranged from 6.9 cm to 14.0 cm in carapace length with means of 10.4 cm and 9.8 cm respectively (Figure 4). The smallest ovigerous female was 7.8 cm in carapace length. The average carapace length of females in reproductive condition was 9.8 cm. The size frequency distribution of ovigerous females relative to total females is presented in Figure 4. Females at Oahu tended to be more abundant in the smallest size class and males were significantly more abundant in the larger (Table 3). Overall, there were significantly more males caught than females. The greater number of males than females, has been shown to be the result of the differential trapability between the sexes of this species. Upon correction for this bias, there were significantly more females than males.

The mean carapace length and variance of males at Palau were significantly greater than at Oahu (Table 4). There was no significant difference in mean carapace length of females at Palau and Oahu but the variance in carapace length was significantly greater at Palau. This species entered the fishery at a smaller minimum size at Palau than (5.0 cm and 6.9 cm respectively) at Oahu.

The differences in the size frequency distributions between Palau and Oahu, although significant, are not as pronounced as the differences in _P. marginatus_ between Midway Islands and Oahu (MacDonald and Thompson, ms). This is particularly true of the larger size classes of _P. penicillatus_ at Oahu which apparently have not been dramatically reduced by fishing. This finding is not surprising in view of the fact that _P. penicillatus_ is less likely to be trapped than _P. marginatus_ and is therefore likely to experience lower fishing mortality.

7.3.2 _Panulirus penicillatus_ across the Pacific and Indian Oceans

Size frequency information on _P. penicillatus_ was obtained from the literature, biologists, and dive clubs at different island locations across this species' entire east-west range of distribution. This was done to establish a broad perspective based on multiple comparisons from which to generalize about the population size-structure of this species. Lobsters were collected by diving and/or reef walking at all locations except Oahu where traps were employed. Prolonged or intensive fishing operations are known to have occurred only at Oahu and the Galapagos. A government moratorium on commercial fishing in the Galapagos stopped much of the lobster fishing at that location over the two year period prior to which the data were collected. The extent to which fishing occurs at Eilat is uncertain at this writing. The data from all these locations except Oahu and possibly Eilat, therefore, were sampled from relatively unfished stocks. The data were collected by trained biologists or recreational fishermen that were given careful instruction.

A comparison of the size frequency distribution of male and female P. penicillatus across this species range of distribution indicates that there are appreciable differences in the mean, maximum, and variance in carapace length at different island locations (Figure 5). Additional data which are too few to present graphically suggest that this species grows to a large size at Canton Island and at Kure Atoll (Table 5). The carapace length that this species attains at different locations clearly is not associated with the island type (high volcanic, low atoll, etc.) or the latitude or longitude of the island location. Water temperature would also thus appear to have very little direct effect (Figure 6). At all locations, there is a pronounced sexual dimorphism resulting in the predominance of males in the larger size classes and females in the smaller.

Sex ratios differed considerably (Table 6). In the majority of cases, males and females were equally abundant. At Palau, Yap, and Enewetak, however, males were more abundant than females. That situation could arise if shelter were limiting and competed for by males. Control of shelter would enable dominant males to provide access to females but to deny it to rival males. Such a situation could result in greater male mortality and a polygynous mating system in which females attracted to a male's shelter were retained as a harem. There is evidence to support this explanation for lobsters at Palau and Yap (MacDonald, 1971). At Oahu, Johnston Island, and the Galapagos, females outnumbered males. Trap bias accounts for the greater abundance of males sampled at Oahu where females probably outnumber males. It is uncertain what factors might be responsible for the skewed sex ratios at Johnston Island and the Galapagos.

7.3.3 *Panulirus versicolor* at Palau

The mean carapace length of males was significantly greater than females (Table 2). The variances did not differ between the sexes. Males and females combined ranged from 5.7 cm to 13.2 cm in carapace length with means of 9.8 cm and 9.3 cm respectively (Figure 7). The smallest ovigerous female was 8.2 cm in carapace length. The average carapace length of females in reproductive condition was 10.0 cm. The size frequency of ovigerous females relative to total females is presented in Figure 7. Females were significantly more abundant in smaller size classes and males were significantly more abundant in the larger (Table 7). Overall, males and females were equally abundant.

7.3.4 *Panulirus longipes femoristriga* at Palau

Mean carapace lengths and variances did not differ between males and females (Table 2). Males and females combined ranged from 5.2 cm to 10.3 cm in carapace length with means of 7.5 cm and 7.0 cm respectively (Figure 8). The smallest ovigerous female was 6.5 cm in carapace length. The average carapace length of females in reproductive condition was 7.0 cm. The size frequency of ovigerous females relative to total females is presented in Figure 8. Overall, males and females were equally abundant.

7.3.5 Interspecific Comparison at Palau and Oahu

The mean carapace length and variance of pooled male and female *P. penicillatus* were significantly greater than *P. versicolor* at Palau and *P. marginatus* at Oahu (Table 8). *Panulirus penicillatus* also clearly attains a much greater carapace length than *P. longipes femoristriga* at Palau (Table 2). *Panulirus penicillatus* was the largest of the four species sampled at Palau and Oahu.

7.4 Reproductive Seasonality

The reproductive seasonality of spiny lobsters at Palau and Oahu is shown by plotting the relative percentage of females sampled each month that were either ovigerous or that had mated and bore a spermatophore. The actual proportion of females that bore spermatophores may have been underestimated since females that simultaneously bore a spermatophore and eggs were recorded only as being ovigerous. The relative frequency of females bearing a spermatophore would therefore be underestimated to the extent that females copulated while bearing eggs. The seasonality of reproduction in these species is based largely on changes in the relative proportions of ovigerous females sampled each month since these estimates are the least likely to be biased. The corresponding proportions of females that bore spermatophores provide at least a minimal measure of how mating activities are distributed over the year. Ninety-five percent confidence intervals were calculated about the individual frequencies each month (Pearson and Hartley, 1966).

7.4.1 Panulirus penicillatus and P. versicolor at Palau and Oahu.

Panulirus penicillatus at Palau and Oahu and P. versicolor at Palau show very similar patterns of reproduction throughout the year (Figures 9, 10, 11). Analysis of variance indicates that there is no significant seasonal difference in the relative frequency of ovigerous or mated female P. penicillatus and P. versicolor at Palau or Oahu (Table 9). The evidence suggests that, on the average, about 40% of the females of both species are ovigerous, and at least about 30% mated in any month at both locations. The proportion of females that were either ovigerous or mated did differ significantly but these differences appear to effect the species and locations equally because there is insufficient evidence of a significant interaction (Table 7). If all females that copulate and bear a spermatophore subsequently ovulate and become ovigerous, mated and ovigerous females should be equally abundant over the year. In that case, about 10% of the females, probably bore eggs and spermatophores simultaneously each month since this is the difference between the average monthly proportion of females that were either ovigerous or mated. This means that about 10% of the females each month copulate while bearing eggs and that females probably are not required to molt between successive matings.

7.4.2 Panulirus penicillatus across the Pacific Ocean

Reproduction in P. penicillatus is probably continuous everywhere at mean seawater temperatures greater than about 23°C. This is generally the minimum monthly surface seawater temperature at Oahu where water temperatures are consistently lower than at Palau (Figure 12). Reproduction occurs at similar levels throughout the year at these two locations. It is uncertain how average seawater temperatures lower than about 23°C effect reproduction in this species although female P. marginatus at Midway Islands cease to bear eggs at temperatures below this amount. Chittleborough (1976) has demonstrated that female P. longipes cygnus from Western Australia repeatedly bear eggs in the laboratory at 23°C.

Taken together, these data suggest a strong correlation between seawater temperature and reproductive activity. This correlation does not imply causation as many other factors such as food availability and light levels may also be changing similarly. However, correlation itself affords a way of predicting the periodicity of reproduction in areas other than just those that have been sampled. Figure 13 depicts the broadly general area of the Pacific Ocean within the range of this species geographic distribution where reproduction is expected to be continuous throughout the year. Figure 13 indicates that reproduction in P. penicillatus is probably continuous throughout the year at most locations within U. S. jurisdiction or affiliation although it may be seasonal in the northernmost islands of the Hawaiian Archipelago.

7.5 Fecundity

The relationship between body size and number of eggs in marine malacostracans (e.g. crabs, lobster, shrimp, etc.) generally tends to be a linear function of the volume of the female (Jensen, 1958). In lobsters, fecundity is generally expressed as a function of carapace length. Herrick's law, which originated from studies of the American lobster (Homarus americanus) [Herrick (1909)], states that the number of eggs increases proportionately to the length of the body cubed. This is frequently expressed as a curvilinear relationship of the form $\gamma = ax^b$ (where γ=number of eggs; x = carapace length; b is approximately 3; and a is a constant). This curvilinear relationship has been assumed to be applicable to a variety of both true (Homaridae) and spiny lobsters (Palinuridae). However, there appears some reason to doubt the general applicability of the curvilinear relationship to all species of the Palinuridae (Morgan, 1972). In certain species a linear relationship appears to better fit the data than a curvilinear over the range of sizes examined. This matter remains to be resolved theoretically.

In the study of fecundity of spiny lobsters at Palau and Oahu, a greater amount of variability was explained in each species by a curvilinear rather than a linear relationship (Table 10). As a result, a curvilinear relationship is used throughout the study of fecundity in these species and for the calculation of reproductive rates that follow. For practical purposes both linear and curvilinear regression equations are presented in all cases (Table 10). The differences are not great. This table facilitates direct comparison with other species and summarizes the relationships presented in Figures 14, 15, 16 in this study. The analyses of covariance follow the methodology of Li (1964).

7.5.1 *Panulirus penicillatus* and *P. marginatus* at Oahu

Covariance analysis of the relationship of carapace length and fecundity in female *P. penicillatus* and *P. marginatus* at Oahu indicates that there is a significant difference between these species (Table 11). The regression lines have similar residual variances and regression coefficients (slopes) but significantly different elevations. These results indicate that *P. marginatus* produces proportionately more eggs than *P. penicillatus* over the entire size range measured. The curvilinear relationship between number of eggs and carapace length is presented for both species in Figure 14. The number of eggs carried over the range of carapace lengths measured was approximately 150,000 - 575,000 for P. penicillatus and 130,000 - 475,000 for *P. marginatus*.

7.5.2 *Panulirus penicillatus* and *P. versicolor* at Palau

Covariance analysis of the relationship of carapace length and fecundity in *P. penicillatus* and *P. versicolor* at Palau indicates that there is a significant difference between these species (Table 12) similar to that found for *P. penicillatus* and *P. marginatus* at Oahu.

Again, the regression lines have similar residual variances and regression coefficients but significantly different elevations. These results indicate that *P. versicolor* at Palau, like *P. marginatus* at Oahu, produces proportionately more eggs than *P. penicillatus* over the entire size range measured. The curvilinear relationship between number of eggs and carapace length is presented for *P. penicillatus* and *P. versicolor* in Figure 15. The number of eggs carried over the range of carapace lengths measured is approximately 150,000 - 550,000 for *P. penicillatus* and 500,000 - 1,100,000 for *P. versicolor*. *Panulirus versicolor* is clearly the most fecund of the three species examined.

7.5.3 *Panulirus penicillatus* at Palau and Oahu.

Covariance analysis of the relationship of carapace length and fecundity in female *P. penicillatus* at Palau and Oahu indicates that there are no significant differences between locations (Table 13). Since there is no evidence of geographical variation in the number of eggs carried, the data from Palau and Oahu can be combined to give pooled estimates of fecundity. The curvilinear relationship between number of eggs and carapace length is presented in Figure 16 for *P. penicillatus* at Palau and Oahu and for the pooled estimates from both locations. Related evidence from other studies demonstrates a similar lack of geographic variation in fecundity in *P. longipes* in Western Australia (Morgan, 1972) and *P. marginatus* in Hawaii (MacDonald and Thompson, ms).

7.6 Reproductive Rates

Reproductive rates were calculated following the general methodology of Fleiss (1973). The same methodology was used to calculate the reproductive rates in the draft management plan for spiny lobsters. The reader is referred to Appendix I in this report for a summary of the specific techniques. In general, three kinds of information were used: (1) the proportion of females in each size class; (2) the proportion of females that were ovigerous in each size class; and (3) the size-specific fecundity. Analyses of female reproductive rates in this report differ from those in the draft management plan in two important respects: (1) the proportion of females that were ovigerous in each size class was used rather than the proportion that carried spermatophores; and (2) the size-specific fecundity was used instead of the weight of the egg mass. These are direct measures for estimating female reproductive rates and are therefore preferred. The pooled relationship between fecundity and carapace length is used to calculate the reproductive rates of P. penicillatus females at Palau and Oahu. The rates are standardized by direct methods to allow comparisons between species and locations.

The data used to calculate the reproductive rates in these species are believed to be relatively free of bias. There is no apparent sampling bias of ovigerous females at Palau as might have been incurred by recreational divers at Midway Islands because lobsters in all shell and reproductive conditions are inadvertently speared by fishermen at Palau. I have presented evidence in this report indicating that the reproductive condition of spiny lobsters at Oahu does not effect their catchability by trap (Table 1). Additionally, the size-composition of females of all species at both locations shows no marked departure from an approximately normal distribution in either the hand- or trap-caught sample that might suggest that size influences the trapability of female lobsters at Oahu (Figures 4, 7, 8).

7.6.1 Panulirus penicillatus and Panulirus marginatus at Oahu.

The size-specific and standardized crude reproductive rates of P. penicillatus and P. marginatus at Oahu differ relative to the carapace length at which changes occur (Figure 17). The standardized rates are presented in Table 14. These reproductive rates are relatively low in P. pencillatus and P. marginatus until carapace lengths greater than 8.9 cm and 7.9 cm respectively are attained. Beyond these sizes reproductive rates of both species increase rapidly although those of P. penicillatus reach a much higher level than do those of P. marginatus. These rates are greatest at a carapace length of 10.0 - 10.9 cm in P. penicillatus and 9.0 - 9.9 cm in P. marginatus and decrease rapidly at larger carapace lengths in both species. The cumulative size distribution of the standardized crude reproductive rates demonstrates the noticeable size-related differences in the mid-range of the carapace lengths sampled and attests to the particularly greater relative importance of females in the larger size classes of P. penicillatus than P. marginatus. The overall level of reproduction, in both species, however, is similar. The standardized crude reproductive rate totals rounded to the nearest thousand do not differ between the species ($\chi^2 = 0.26$, d.f. = 1, $P \leq 0.90$) and it is possible that the size-related differences observed might not have appeared if the fishing mortality of P. penicillatus and P. marginatus females were the same. In that case, the highest standardized crude reproductive rate would probably be shifted to a smaller carapace length if only because more of the larger females would have been removed by fishing and a greater proportion of females would therefore be of a smaller average size.

7.6.2 Panulirus penicillatus and Panulirus versicolor at Palau

The size-specific and standardized crude reproductive rates of P. penicillatus and P. versicolor at Palau show some broadly similar patterns between the species relative to the carapace lengths at which changes occur (Figure 18). The differences in absolute value, however, are considerable. The standardized rates are presented in Table 15. These reproductive rates are relatively low in both species until a carapace length greater than 8.9 cm is attained. At larger sizes, the reproductive rates of P. versicolor increase more rapidly and clearly attain a much greater value than do those of P. penicillatus. These reproductive rates are greatest at a carapace length of 10.0 - 10.9 cm in both species and decrease rapidly at larger carapace lengths.

The cumulative size distribution of the standardized crude reproductive rates indicates the great relative importance of females in the larger size classes in maintaining an overall high rate of reproduction within both species (Figure 18). Additionally, it emphasizes the particularly large overall difference between the two species. A comparison of the standardized crude reproductive rate totals rounded to the nearest thousand indicates that P. versicolor attains a significantly much greater rate of reproduction than P. penicillatus at Palau (χ^2 = 27.28, d.f. = 1, $P \leq 0.001$).

7.6.3 Panulirus penicillatus at Palau and Oahu

The size-specific and standardized crude reproductive rates of P. penicillatus at Palau and Oahu are similar overall (Figure 19). The standardized rates are presented in Table 16. The only differences occur at carapace lengths of 10 cm and greater. These differences are due largely to the greater proportion of ovigerous females within the 10.0 - 10.9 cm size class at Oahu (Figure 20) since the proportion of females within a size class and the size-specific fecundity remain the same at both locations. While not statistically significant, the greater proportion of ovigerous females in the 10.0 - 10.9 cm size class at Oahu may have occurred in compensation to the greater long-term fishing pressure at Oahu relative to

Palau (Figure 2). Although compensation is only one of several possible causes that could account for this difference, it bears directly on the question of what effect exploitation would exert on rates of reproduction. All possible explanations are difficult to prove and should be considered with caution.

The cumulative size distribution of the standardized crude reproductive rates demonstrates the overall similar level of reproduction in *P. penicillatus* at Palau and Oahu (Figure 19). The standardized crude reproductive rate totals rounded to the nearest thousand do not differ significantly between locations ($\chi^2 = 0.25$, d.f. = 1, $P \leq 0.90$).

7.6.4 Adjusted Crude Reproductive Rates at Palau and Oahu

Crude reproductive rates were calculated with the size-specific schedules for *P. penicillatus* females at Palau in combination with the Oahu size class proportions to judge what effect increased fishing pressure at Palau might have on the total crude reproductive rate there. This exercise is based on the assumption that the difference in the size frequency distributions of female *P. penicillatus* at Palau and Oahu (Table 4, Figure 4) is related to the history of lower levels of exploitation at Palau than at Oahu (Figure 2). Lower fishing pressure could account for a greater relative abundance of large female lobsters at Palau although Figure 4 clearly demonstrates that the differences in carapace length are not great at the two locations. In fact, the variances differ but the means do not (Table 4).

The total adjusted crude reproductive rate obtained at Palau was lower than the total crude rate from Oahu (Table 17). Rounded to the nearest thousand, these totals did not differ significantly ($\chi^2 = 0.39$, d.f. = 1,

$P \leq 0.90$). The total adjusted crude rate did not change appreciably from the original total crude rate at Palau which was also lower than that at Oahu to begin with (Table 16). The effect of the adjustment, however, was a tendency to increase the total rate at Palau. The results of these calculations suggest that, if differences in size composition at Palau and Oahu are related to differences in fishing pressure, a decreased average size comparable to that occurring at Oahu in 1960-62 when these data were collected might be readily sustained without appreciably lowering the total crude reproductive rate of P. penicillatus at Palau. There may even be a tendency toward compensation resulting in the total reproductive rate increasing upon the removal of the largest size classes by fishing. However, caution must be exercised since there are no hard data yet available to firmly support any conclusion that compensation will indeed accompany increased fishing pressure. The fishing pressure exerted on P. penicillatus at Oahu up to 1960-62, however, apparently had little effect on either the population size structure or the rate of reproduction of that species.

7.7 Molt Cycles at Palau

Molt cycles are difficult to ascertain in spiny lobsters. The molt state differs over a continuum and categorization based on macroscopic examination of the exoskeleton is necessarily subjective. In addition, lobsters are less likely to be sampled in immediately pre- and post-molt conditions when shells are soft than in the intermolt condition when shells are hard. This is because lobsters spend much less time in the softshell than the hardshell condition (e.g. Berry, 1971) and because they remain relatively inactive and tend to be reclusive when soft (e.g. Lindberg, 1955). Lobsters in the old soft shell, new soft shell, and new hard shell stages of the molt cycle were combined since they are all indicative of at least the approximate period when molting occurs. This is standard procedure in certain other studies of molting in spiny lobsters (Berry, 1971, 1973). To the extent that I could ascertain by working closely with and interviewing fishermen, there was no hesitation to spear and market lobsters in any molt condition.

7.7.1 *Panulirus penicillatus*

Too few *P. penicillatus* were collected in immediately pre-molt and recently molted conditions to permit quantitative treatment of the results. Less than 2% of all *P. penicillatus* sampled was in a soft or new hard shell condition that was indicative of molting. This species characteristically resides deep within shelters in areas of strong surge that are frequently wave-swept. Searching is difficult even under the best of conditions. If lobsters are more reclusive while molting they would be much more difficult to find. The difficulty ordinarily associated with searching for this species and any tendency for a lobster to become secretive when soft probably accounts for the very low number of pre- and post-molt *P. penicillatus* recorded.

7.7.2 *Panulirus versicolor*

Molting and recently molted *P. versicolor* were collected in sufficient numbers to afford comparisons with lobsters in the intermolt condition. Approximately 13% of all *P. versicolor* sampled was in an old soft, new soft, or new hard shell condition indicative of pending or recent molting activity. This species characteristically resides within large open shelters in the lagoon that afford fishermen comparatively ready accessibility. This behavior of the animal probably accounts for the greater number of molting P. versicolor that were collected than P. penicillatus. This level of molting activity is within the range characteristic of spiny lobster populations in the field (Berry, 1971; 1973).

The results of a three-way test of independence (Sokal and Rohlf, 1969) of season, sex, and molt state of P. versicolor are presented in Table 18. The sexes were sampled proportionately in all seasons. Molt state varies significantly with season. Molting occurred more frequently in the spring and summer than in the fall and winter. The significant interaction between season, sex, and molt state indicates that these three factors do not vary together. This lack of independence is apparently the result of different seasonal patterns of molting between the sexes (Figure 21). The cause of any such seasonality is not clear at this time. Water temperature and reproductive activity are probably not directly involved because they vary only slightly over the year at Palau (Figures 11, 12). Molting is strongly associated with growth and any seasonal influences that effect growth are certain to be related to seasonal differences in molting. The frequency of molting did not differ significantly between the sexes (Table 18).

Any tendency for males to molt at a lower rate than females (Figure 21), however, is attributed to the significantly greater size attained by males than females (Table 2). The frequency of molting in crustaceans is generally inversely correlated with size.

7.8 Morphometric Relationships and Predictive Regression Analysis

The use of linear regressions is widespread in fishery research. In recent years, however, the question has been raised whether predictive or functional regression analysis should be used (Ricker, 1973). Although the arguements for functional regression are well founded statistically, the momentum to continue to use predictive methods is extremely great. In addition to the sheer weight of the literature that has customarily used predictive regression, there is no generally popular substitute for the analysis of covariance which uses predictive regression statistics in the comparisons of linear relationships. The choice between functional regression and predictive regression is largely a matter of personal judgement. Ricker (1973 - Table 8) acknowledges that predictive regression is still appropriate in situations where both x and y variables are subject to natural variability and to measurement error and when the sample is taken randomly from a bivariate normal population. Because these regression analyses were performed to permit prediction of y from x, and to enable direct comparisons with similar analyses on spiny lobsters in the literature, predictive regression was used. In all instances the variables approximate a bivariate normal distribution at least in form and are subject to natural variability and measurement error.

For those who would still prefer functional regression, results are presented that will enable the calculation of functional regression equations. The sums of squares of the x and y deviations and the means of the dependent and independent variables are provided for each function in the covariance tables. Appendix II explains how this information can be used to calculate functional regression equations. These methods may also be applied to the derived linear regression of fecundity on carapace length in section 7.5. The necessary information is provided in Tables 11, 12, and 13.

Regression was used to estimate the body weight: carapace length relation for spiny lobsters at Palau and Oahu. This relation is commonly expressed in the form:

$$w = a(CL)^b$$

where w = body weight and CL = carapace length

Since this is non-linear, the variables were transformed using natural logarithms to permit comparison by analysis of covariance. This changes the relation to the form:

$$\ell n\ w = \ell n\ a + b\ (\ell n CL)$$

Estimates, however, may be needed in terms of untransformed variables. Just taking antilogarithms of values from a log-log regression line or function can lead to biased estimates. Approximate methods to test for bias were used (Beauchamp and Olson, 1973). In all instances in which logarithmic transformations were performed the results of the predictive regression analyses represent virtually unbiased estimates of the expected values. Covariance analyses were done to compare primarily the regression coefficients and elevations of the functions examined. All analyses of covariance follow the methodology of Li (1964).

7.8.1 Carapace Length and Total Weight at Oahu

The relationship of total weight to carapace length can differ within a species depending upon the sex and the reproductive condition of sexually mature females. The following analyses use fresh weights only.

Male P. penicillatus increase in weight relative to carapace length at a greater rate than do non-ovigerous females (Table 19). Ovigerous females are proportionately heavier than non-ovigerous females at all carapace lengths (Table 20).

Non-ovigerous female P. marginatus are proportionately heavier than males at all carapace lengths (Table 21). Ovigerous females are proportionately heavier than non-ovigerous females at all carapace lengths (Table 22).

Male P. marginatus are proportionately heavier than male P. penicillatus at all carapace lengths (Table 23). Non-ovigerous female P. marginatus increase in weight relative to carapace length at a greater rate than do non-ovigerous P. penicillatus (Table 24).

A summary of the derived linear regression equations used in the co-variance analyses for the relationship of carapace length and total weight fresh from P. penicillatus and P. marginatus at Oahu is provided in Table 25. Regression equations relating carapace length and total weight of males and non-ovigerous females combined are provided for each species. In practice, these pooled regression equations will probably be the most useful despite their statistical differences. The length:weight relationships for P. penicillatus and P. marginatus at Oahu are presented collectively in Figure 22.

7.8.2 Carapace Length and Total Weight at Palau

Male P. penicillatus increase in weight relative to carapace length at a greater rate than do non-ovigerous females (Table 26). Ovigerous females are proportionately heavier than non-ovigerous females at all carapace lengths (Table 27).

Male and non-ovigerous female P. versicolor do not differ in weight relative to carapace length (Table 28). Non-ovigerous females increase in weight relative to carapace length at a greater rate than do ovigerous females (Table 29).

Male P. versicolor increase in weight relative to carapace length at a greater rate than do male P. penicillatus (Table 30). Non-ovigerous female P. versicolor increase in weight relative to carapace length at a greater rate than do non-ovigerous female P. penicillatus (Table 31).

A summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length and total weight fresh from P. penicillatus and P. versicolor at Palau is provided in Table 32. Regression equations relating carapace length and total weight of males and non-ovigerous females combined are provided for each species. The length:weight relationships for P. penicillatus and P. versicolor at Palau are presented collectively in Figures 23.

7.8.3 Effect of Freezing and Boiling on the Relationship of Carapace Length and Total Weight at Palau

Male, non-ovigerous female, and ovigerous female P. penicillatus were proportionately heavier at all carapace lengths when fresh than when frozen (Tables 33, 34, 35). Male and non-ovigerous females were also proportionately heavier at all carapace lengths when fresh than when boiled (Tables 36, 37). However, ovigerous female P. penicillatus increased in weight relative to carapace length at a greater rate when boiled than when fresh (Table 38). A summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length and total weight from frozen and boiled *P. penicillatus* at Palau is provided in Table 39. These length:weight relationships are presented collectively in Figure 24.

Male and non-ovigerous female *P. versicolor* were not heavier fresh than when frozen at any carapace length (Tables 40, 41). There was no apparent weight loss due to freezing. Ovigerous females were proportionately heavier at all carapace lengths when fresh than when frozen (Table 42). Male and non-ovigerous females were proportionately heavier at all carapace lengths when fresh than when boiled (Tables 43, 44). Data are not available for ovigerous females that were boiled. A summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length and total weight from frozen and boiled *P. versicolor* at Palau is provided in Table 45. These length: weight relationships are collectively presented in Figure 25.

7.8.4 Carapace Length and Total Length at Palau

Non-ovigerous female *P. penicillatus* and *P. versicolor* increase in total length relative to carapace length at greater rates than do males (Tables 46, 47). A summary of the linear regression equations used in the covariance analyses for the relationship of carapace length and total length from *P. penicillatus* and *P. versicolor* at Palau is provided in Table 48. The relationship of carapace length and total length for male and female *P. penicillatus* and *P. versicolor* at Palau is presented in Figure 26.

7.8.5 Carapace Length and Carapace Width at Palau

Male *P. penicillatus* increase in carapace width relative to carapace length at a greater rate than do females (Table 49). Male and female

P. versicolor do not differ in carapace width relative to carapace length (Table 50). Pooled male and female P. penicillatus and P. versicolor did not differ in carapace width relative to carapace length (Table 51). A summary of the linear regression equations used in the covariance analyses for the relationship of carapace length and carapace width from P. penicillatus and P. versicolor is provided in Table 52. The relationship of carapace length and carapace width for pooled male and female P. penicillatus and P. versicolor at Palau is presented in Figure 27.

8.0 LITERATURE CITED

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9.0 Appendices

9.1 Appendix I - Calculation of Reproductive Rates

To calculate the reproductive rates, each sample is divided into I size classes (i=1,-----I). P_i is the proportion of females in each sample that fall in class i. C_i is the reproductive rate specific to each size class i. The reproductive rate is the proportion of females that are ovigerous in each size class adjusted for the size-specific fecundity. Following the methodology of Fleiss (1973), the total crude reproductive rate (C) for each population is:

$$C = \sum_{i=1}^{I} C_i P_i$$

where $C_i = \left(\frac{\text{\# ovigerous in size class i}}{\text{\# in size class i}}\right) \times \left(\begin{matrix}\text{fecundity} \\ \text{in size class i}\end{matrix}\right)$

and $P_i = \left(\frac{\text{\# in size class i}}{\text{total \#}}\right)$

When crude reproductive rates from two populations are compared, differences can arise in relation to size distribution and size-specific rates. If the two populations are not similarly constituted, a direct comparison of the overall rates may be misleading. The critical relationships are demonstrated as follows.

Given that:

1) $c = \sum_{i=1}^{I} c_i p_i$ denotes the crude rate of one population;

2) $C = \sum_{i=1}^{I} C_i P_i$ denotes the crude rate of another population; and

3) $d = c - C$ denotes the difference between the two crude rates

the difference (d) between the two crude rates can be expressed as:

$$c - C = \sum_{i=1}^{I} \frac{p_i + P_i}{2} (c_i - C_i) + \sum_{i=1}^{I} \frac{c_i + C_i}{2} (p_i - P_i)$$

difference between size-specific rates (d_1) | difference between population distributions (d_2)

where p_i, c_i, and P_i, C_i are, respectively, the size class proportions and size-specific rates from the two samples.

For a given summarizarion of the differences between two schedules of size-specific rates (d_1) the apparent difference (d) between the two populations may vary according to the differences between the two population distributions (d_2). It is therefore important to compare both the size-specific rates themselves and the crude rates "standardized" to remove effects due to differences in population distribution. Direct standardization is applied by choosing a standard population, P_{si}, calculating $c_{si} = \sum_{i=1}^{I} c_i P_{si}$ and $C_{si} = \sum_{i=1}^{I} C_i P_{si}$, and comparing. In direct standardization, the standard distribution is usually the combination of the two samples.

9.2 Appendix II - Calculation of Functional Regression Equations

In functional regression

$$y = u + vx$$

$$v = \pm\sqrt{\frac{\Sigma y^2}{\Sigma x^2}}$$

$$u = \bar{y} - v\bar{x}.$$

See Ricker (1973) for greater detail.

Table 1.- Results of independent sample proportions test (Tate and Clelland, 1957) on tag-recovery data from *Panulirus penicillatus* and *Panulirus marginatus* at Oahu. Expected cell frequencies are included in parentheses.

Within Species Comparisons

Difference between sexes

Panulirus penicillatus

	Male	Female	Total
Recovered	(75.6) 96	(46.4) 26	122
Not-recovered	(465.4) 445	(285.6) 306	751
Total	541	332	873

χ^2=16.82; P≤0.001

Panulirus marginatus

	Male	Female	Total
Recovered	(109.8) 116	(120.2) 114	230
Not-recovered	(378.2) 372	(413.8) 420	792
Total	488	534	1022

χ^2=0.86; no difference

Difference between reproductive conditions

Panulirus penicillatus

	Ovigerous	Non-ovigerous	Total
Recovered	(9.5) 6	(14.5) 18	24
Not-recovered	(110.5) 114	(169.5) 116	280
Total	120	184	304

χ^2 = 2.28; no difference

Panulirus marginatus

	Ovigerous	Non-ovigerous	Total
Recovered	(43.8) 47	(65.2) 62	109
Not-recovered	(146.2) 143	(217.8) 221	364
Total	190	283	473

χ^2 = 0.51; no difference

Between Species Comparison

	P. penicillatus	*P. marginatus*	Total
Recovered	(162.2) 122	(189.8) 230	352
Not-recovered	(710.8) 751	(832.2) 792	1543
Total	873	1022	1895

χ^2=22.7; P≤0.001

Table 2. Sample sizes, means, and variances in carapace length for four species of spiny lobsters at Oahu and Palau. Differences in means and variances between males and females are tested for each species at each location (t' after Snedecor and Cochran, 1967).

	Carapace Length (≥5.0 cm)											
	Males			Females			Mated Females			Combined Sexes		
Location	n	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n	$\bar{x}$	s^2
Panulirus marginatus												
Oahu	411	8.92	1.37	473	8.81	1.13	338	8.93	1.06	884	8.86	1.25
Panulirus penicillatus												
Oahu	469	10.43	1.76	305	9.81	1.11	184	9.80	1.00	774	10.19	1.59
Palau	442	11.32	4.96	811	9.88	1.55	438	10.03	1.28	1253	10.39	3.22
Panulirus versicolor												
Palau	367	9.75	2.51	359	9.27	226	209	9.95	1.12	726	9.51	2.44
Panulirus longipes femoristriga												
Palau	14	7.51	2.50	12	6.98	0.55	2	6.95	0.41	26	7.27	1.61

Tests of Differences Between Sexes

Species	Location	t' (d.f.)	F (d.f.)
P. marginatus	Oahu	1.50(836)	1.21*(410,472)
P. penicillatus	Oahu	7.16*(742)	1.58*(468,304)
P. penicillatus	Palau	12.51*(594)	3.21*(441,810)
P. versicolor	Palau	4.20*(723)	1.11 (366,358)
P. longipes femoristriga	Palau	1.48 (25)	1.35 (13,11)

* significant difference ($P \leq 0.05$)

Table 3. Population size-structure of *Panulirus penicillatus* at Palau and Oahu.

Palau

Carapace Length (cm)

	≤7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	13.9-13.9	≥14.0	All
Total	82	175	274	320	194	88	62	58	1253
% Male	40.2	21.7	21.2	21.6	33.5	68.2*	98.4*	100.0*	35.3
% Female	59.8	78.3*	78.8*	78.4*	66.5*	31.8	1.6	0.0	64.7*

* significant difference ($P \leq 0.05$)

Oahu

Carapace Length (cm)

	≤7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	12.0-12.9	≥13.0	All
Total	18	107	231	205	136	61	16	774
% Male	27.8	48.6	61.5*	50.2	71.3*	88.5*	100.0*	60.6*
% Female	72.2+	51.4	38.5	49.8	28.7	11.5	0.0	39.4

significant difference (* $P \leq 0.05$; + $P \leq 0.10$)

Table 4. Tests of Differences in means and variances in carapace length of *Panulirus penicillatus* at Palau and Oahu. Comparisons are between locations (t' after Snedecor and Cochran, 1967).

Sex	t' (d.f.)	F (d.f.)
Males	7.18*(708)	2.82* (441,468)
Females	0.92 (640)	1.39* (810,304)

* significant difference ($P \leq 0.05$)

Table 5. Summary statistics for size composition of *Panulirus penicillatus* at Canton Island and Kure Atoll. Sexes are pooled.

		Carapace Length (cm)				
Location	n	min	max	$\bar{x}$	s^2	Source
Canton Island	9	10.00	20.32	13.72	12.39	C. Apuna (per. comm.)
Kure Atoll	7	7.8	16.5	12.9	9.9	C. MacDonald

Table 6. Summary of numbers of *Panulirus penicillatus* collected at different islands acorss the entire breadth of this species' geographical distribution. Chi-square values test deviations from a 1:1 sex ratio.

	Males	Females	χ^2	Source
Enewetak	37	78	14.62*	G. Long (per. comm)
Ponape	12	14	0.15	C. MacDonald
Truk	29	37	0.97	C. MacDonald
Saipan	41	28	2.45	C. MacDonald
Yap	5	15	5.00*	C. MacDonald
Palau	442	811	108.67*	C. MacDonald
Eilat	25	29	0.30	E. Gilead (per. comm.)
Galapagos	2920	2175	108.94*	K. Reck (per. comm.)
Fiji	97	115	1.53	R. George (1971)
Johnston	26	5	14.23*	S. West (per. comm.)
Midway	17	9	2.46*	B. Thompson (per. comm.)
Oahu	469	305	17.37*	D. Morris (1968)

* significant difference ($P \leq 0.05$)

Table 7. Population size-structure of *Panulirus versicolor* at Palau.

	Palau Carapace Length (cm)							
	≤6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9	≥12.0	All
Total	53	79	116	166	176	105	29	726
% Male	35.8	46.8	56.0	42.8	47.7	63.2*	80.9*	50.6
% Female	64.2*	53.2	44.0	57.2	52.3	36.8	20.0	49.4

* significant difference ($P \leq 0.05$)

Table 8. Tests of differences in means and variances in carapace length of *Panulirus penicillatus* and *Panulirus versicolor* at Palau and *Panulirus penicillatus* and *Panulirus marginatus* at Oahu (t' after Snedecor and Cochran, 1967). Comparisons are between species at each location. Sexes are pooled.

Species	Location	t' (d.f.)	F (d.f.)
P. penicillatus *P. versicolor*	Palau	11.41*(1685)	1.32* (1252,725)
P. penicillatus *P. marginatus*	Oahu	22.58*(1556)	1.28*(773,883)

* significant difference ($P \leq 0.05$)

Table 9. Comparisons of the percent of females that were ovigerous or mated each month for *Panulirus penicillatus* and *Panulirus versicolor* at Palau and Oahu. Two-way Model I analysis of variance with unequal but proportional subclass numbers (Sokal and Rohlf, 1969). Calculations were based only on monthly samples of five lobsters or more. The data are presented as arcsin $\sqrt{p}$

Source of variation	d.f.	ss	ms	F
Subgroups	5	1525.95	305.19	
B (species/location, rows)	2	294.08	147.04	2.50
A (repro. cond., columns)	1	1060.41	1060.41	18.02*
AxB (interaction)	2	171.46	85.73	1.46
Within subgroups (error)	56	3296.36	58.86	
Total	61	4822.61		

* significant difference ($P \leq 0.001$)

Table 10. Curvilinear ($y = ax^b$) and linear ($y = a + bx$) regression equations and their respective measures of best fit for the relationship of number of external eggs and carapace length for three species of spiny lobsters at Palau and Oahu.

Location	Species	Regression Equation	n	r^2
Palau	*P. penicillatus*	$y = 865.11\ x^{2.62}$	23	0.8959
		$y = -481336.0 + 85884.2x$		0.8854
	P. versicolor	$y = 2007.87\ x^{2.52}$	12	0.7478
		$y = -1169870.0 + 185434.0x$		0.7459
Oahu	*P. penicillatus*	$y = 596.39\ x^{2.71}$	10	0.7277
		$y = -346621.0 + 67984.2x$		0.6209
	P. marginatus	$y = 452.62\ x^{2.96}$	11	0.9123
		$y = -574639.0 + 98699.1x$		0.8729
Palau and Oahu (pooled)	*P. penicillatus*	$y = 976.97\ x^{2.55}$	33	0.8219
		$y = -420773.0 + 78242.6x$		0.7878

y = number of eggs; x = carapace length (cm)

Table 11 - Analysis of covariance for the relationship of carapace length and fecundity from female *Panulirus penicillatus* and *Panulirus marginatus* at Oahu. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(fecundity)					
Species	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevati[on]
P. penicillatus	10	2.3403	0.1723	0.4673	1.7415	2.7123	12.7388	12.5472	0.0593			
P. marginatus	11	2.2054	0.1565	0.4626	1.4997	2.9566	12.6350	12.8249	0.0147			
										4.0402	0.1373	8.7820*

* significant difference ($P \leq 0.025$)

Table 12 - Analysis of covariance for the relationship of carapace length and fecundity from female *Panulirus penicillatus* and *Panulirus versicolor* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(fecundity)					
Species	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevatio
P. penicillatus	23	2.2721	0.5666	1.4841	4.3389	2.6190	12.7139	12.7690	0.0215			
P. veriscolor	12	2.3335	0.1024	0.2559	0.8493	2.4998	13.4915	13.3906	0.0210			
										1.0276	0.0578	126.1553*

* significant difference ($P \leq 0.001$)

Table 13 - Analysis of covariance for the relationship of carapace length and fecundity from female *Panulirus penicillatus* at Palau and Oahu. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(fecundity)					
Species	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevati
Palau	23	2.2721	0.5666	1.4841	4.3389	2.6190	12.7139	12.7680	0.0215			
Oahu	10	2.3403	0.1723	0.4673	1.7415	2.7123	12.7388	12.6100	0.0593			
										2.7528	0.0360	4.9648

Table 14. Size-specific, crude, and standardized crude reproductive rates of *Panulirus penicillatus* and *Panulirus marginatus* at Oahu.

	Standard Distribution (N=778)	*P. penicillatus* (N=305)			*N. marginatus* (N=473)		
		Size-specific	Crude	Standardized Crude	Size-specific	Crude	Standardized Crude
Size Class (cm)	P_{Si}	C_i	C_iP_i	C_iP_{Si}	C_i	C_iP_i	C_iP_{Si}
≤6.9	0.02	0.00	0.00	0.00	1,119.68	33.59	22.39
7.0-7.9	0.14	4,153.05	166.12	249.18	27,433.00	5,760.93	3,840.62
8.0-8.9	0.26	33,118.42	5,961.32	5,630.13	84,595.43	25,378.63	21,994.81
9.0-9.9	0.29	71,243.27	20,660.55	19,235.68	103,895.14	30,129.59	30,129.59
10.0-10.9	0.21	155,986.26	51,475.47	49,915.60	83,925.50	10,071.06	17,624.36
11.0-11.9	0.07	35,532.06	4,619.17	5,329.81	6,108.82	183.26	427.62
≥12.0	0.01	-----	-----	-----	-----	-----	-----
	1.00		82,882.63(C)	80,360.40(=C direct)		71,557.06(=C)	74,039.39(=C direct)

Table 15. Size-specific, crude, and standardized crude reproductive rates of female *Panulirus penicillatus* and *Panulirus versicolor* at Palau.

	Standard Distribution (N=778)	*Panulirus penicillatus* (N=811)			*Panulirus versicolor* (N=359)		
		Size-specific	Crude	Standardized Crude	Size-specific	Crude	Standardized Crude
Size Class (cm)	P_{Si}	C_i	C_iP_i	C_iP_{Si}	C_i	C_iP_i	C_iP_{Si}
≤6.9	0.04	0.00	0.00	0.00	0.00	0.00	0.00
7.0-7.9	0.07	3,329.74	166.49	233.08	0.00	0.00	0.00
8.0-8.9	0.16	37,048.37	6,298.22	5,927.74	30,666.47	4,293.31	4,906.64
9.0-9.9	0.27	90,006.23	24,301.48	24,301.68	214,952.22	55,887.58	58,037.10
10.0-10.9	0.29	133,292.19	41,320.58	38,654.74	262,084.71	68,142.02	76,004.57
11.0-11.9	0.14	87,235.18	13,957.63	12,212.93	169,745.34	18,671.99	23,764.35
≥ 12.0	0.03	19,169.31	766.77	575.08	34,946.78	698.94	1,048.40
			86,811.37(=C)	81,905.25(=C direct)		147,693.84(=C)	163,761.06(=C direct)

Table 16 - Size-specific, crude, and standardized crude reproductive rates of female *Panulirus penicillatus* at Palau and Oahu. Fecundities at both locations are pooled.

	Standard Distribution (n=1116)	Palau (n=811)			Oahu (n=305)		
		Size-specific	Crude	Standardized Crude	Size-specific	Crude	Standardized Crude
Size Class (cm)	P_{Si}	C_i	C_iP_i	C_iP_{Si}	C_i	C_iP_i	C_iP_{Si}
≤6.9	0.01	0.00	0.00	0.00	0.00	0.00	0.00
7.0-7.9	0.05	3,245.42	162.27	162.27	4,868.14	194.73	243.41
8.0-8.9	0.17	35,778.28	6,082.31	6,082.31	38,014.43	6,842.60	6,462.45
9.0-9.9	0.27	86,210.76	23,276.91	23,276.91	80,265.19	23,276.91	21,671.60
10.0-10.9	0.32	126,733.28	39,287.32	40,554.65	172,818.10	57,029.97	55,301.79
11.0-11.9	0.15	82,138.59	13,142.17	12,320.79	38,653.46	5,024.95	5,798.02
≥12.0	0.03	17,993.52	719.74	539.81	-----	-----	-----
			82,670.72 (=C)	82,936.74 (=C_{direct})		92,369.16 (=C)	89.477.27 (=C_{direct})

Table 17. - Comparison of Palau adjusted crude and Oahu crude reproductive rates of female *Panulirus penicillatus* (see text for details).

	Palau		Oahu
	Size specific	Adjusted crude	Crude
Size class (cm)	C_i	$C_i\ P_{oi}$ [1]	$C_i\ P_i$
≤ 6.9	0.00	0.00	0.00
7.0 - 7.9	3,245.42	129.82	194.73
8.0 - 8.9	35,778.28	6,440.09	6,842.60
9.0 - 9.9	86,210.76	25,001.12	23,276.91
10.0 - 10.9	126,733.28	41,821.98	57,029.97
11.0 - 11.9	82,138.59	10,678.02	5,024.95
		84,071.03 (=c)	92,369.16 (=c)

[1] P_{oi} = Oahu proportion

Table 18. Summary of three-way test of independence of season, sex, and molt state of *Panulirus versicolor* at Palau. Months are grouped into four seasons (S). Molt state (MS) is categorized intermolt or molt. The log likelihood ratio test (G-test) is used throughout.

Hypothesis tested	df	G
S x Sex independence	3	3.618
S x MS independence	3	14.238*
Spr. vs. Summ.	1	1.406
Fall vs. Wint.	1	1.054
Spr. + Summ. vs. Fall & Win.	1	21.824*
Sex x MS independence	1	1.014
S x Sex x MS interaction	3	18.736*
S x Sex x MS independence	10	37.606*

*significant difference ($P \leq 0.005$)

Table 19 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous female and male <u>Panulirus penicillatus</u> at Oahu. The data are presented as natural logarithms.

Sex	n	$\bar{x}$	Regression (sums of squares and products) Σx^2	Σxy	Σy^2	Regression coefficient	Dependent Variables (total weight) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	F Ratios Residual variance	Regression coefficient	Elevati
Female (non-ovigerous)	183	2.2773	2.4393	5.6446	14.0676	2.3141	6.6104	6.7068	0.0056			
Male	456	2.3357	7.4050	19.5758	54.6243	2.6436	6.7373	6.6931	0.0063			
										1.1395*	32.6148*	3.6637

* significant difference ($P \leq 0.05$)

Table 20 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous and ovigerous female *Panulirus penicillatus* at Oahu. The data are presented as natural logarithms.

Condition	n	$\bar{x}$	Regression (sums of squares and products) $\Sigma\chi^2$	Regression (sums of squares and products) $\Sigma\chi\gamma$	Regression (sums of squares and products) $\Sigma\gamma^2$	Regression: Regression coefficient	Dependent Variables (total weight): Unadjusted $\bar{y}$	Dependent Variables (total weight): Adjusted $\bar{y}$	Dependent Variables: Mean Square	F Ratios: Residual variance	F Ratios: Regression coefficient	F Ratios: Elevation
Non-ovigerous	183	2.2773	2.4393	5.6446	14.0676	2.3141	6.6104	6.6123	0.0056			
Ovigerous	118	2.2794	1.0555	2.4241	6.4620	2.2966	6.6813	6.6784	0.0077			
										1.3886*	0.0351	49.0228*

* significant difference ($P \leq 0.05$)

Table 21 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous female and male <u>Panulirus marginatus</u> at Oahu. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Sex	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Female (non-ovigerous)	278	2.1513	4.4873	11.9594	33.8497	2.6652	6.4638	6.5031	0.0072			
Male	402	2.1762	6.9202	18.9127	54.5224	2.7330	6.4784	6.4506	0.0071			
										1.0103	1.7591	63.0920*

* significant difference ($P \leq 0.05$)

Table 22 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous and ovigerous female Panulirus marginatus at Oahu. The data are presented as natural logarithms.

			Regression				Dependent Variables (total weight)			F Ratios		
			(sums of squares and products)									
Condition	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Non-ovigerous	278	2.1513	4.4873	11.9594	33.8497	2.6652	6.4638	6.5060	0.0072			
Ovigerous	190	2.1903	2.2056	5.6486	15.9748	2.5611	6.6322	6.5739	0.0080			
										1.1209	2.1348	67.0092*

* significant difference ($P \leq 0.05$)

Table 23 - Analysis of covariance for the relationship of carapace length and total weight fresh from male *Panulirus penicillatus* and *Panulirus marginatus* at Oahu. The data are presented as natural logarithms.

Species	n	$\bar{x}$	Regression (sums of squares and products) $\Sigma \chi^2$	$\Sigma \chi\gamma$	$\Sigma \gamma^2$	Regression coefficient	Dependent Variables (total weight) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	F Ratios Residual variance	Regression coefficient	Elevatic
P. penicillatus	456	2.3357	7.4050	19.5758	54.6243	2.6436	6.7373	6.5397	0.0063			
P. marginatus	402	2.1762	6.9202	18.9127	54.5224	2.7330	6.4784	6.7100	0.0071			
										1.1195*	4.2754	670.5574*

* significant difference ($P \leq 0.001$)

Table 24 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous female *Panulirus penicillatus* and *Panulirus marginatus* at Oahu. The data are presented as natural logarithms.

Species	n	$\bar{x}$	Regression (sums of squares and products) $\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Dependent Variables (total weight) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	F Ratios Residual variance	Regression coefficient	Elevatic
P. penicillatus	183	2.2773	2.4393	5.6446	14.0676	2.3141	6.6104	6.4345	0.0056			
P. marginatus	278	2.1513	4.4873	11.9594	33.8497	2.6652	6.4638	6.5972	0.0072			
										1.2887*	29.8598*	338.3064*

* significant difference (P $\leq$ 0.05)

Table 25. - Summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length (x) and total weight fresh (y) from <u>Panulirus penicillatus</u> and <u>Panulirus marginatus</u> at Oahu. $S\hat{y}$ represents the standard error of the estimate; S_b represents the standard error of regression coefficient. The symbolism is from Sokal and Rohlf (1969).

Group	Regression Equation	r^2	$S\hat{y}$	S_b	n
	<u>Panulirus penicillatus</u>				
Males	$\ell nY = 0.5626 + 2.6436\ \ell nX$	0.9474	0.0796	0.0292	456
Non-ovigerous Females	$\ell nY = 1.3405 + 2.3141\ \ell nX$	0.9285	0.0745	0.0477	183
Ovigerous Females	$\ell nY = 1.4464 + 2.2966\ \ell nX$	0.8615	0.0878	0.0855	118
Males and Non-ovigerous Females	$\ell nY = 0.7968 + 2.5461\ \ell nX$	0.9420	0.0803	0.0250	639
	<u>Panulirus marginatus</u>				
Males	$\ell nY = 0.5308 + 2.7330\ \ell nX$	0.9480	0.0842	0.0320	402
Non-ovigerous Females	$\ell nY = 0.7302 + 2.6652\ \ell nX$	0.9416	0.0846	0.0399	278
Ovigerous Females	$\ell nY = 1.0238 + 2.5611\ \ell nX$	0.9056	0.0896	0.0603	190
Males and Non-ovigerous Females	$\ell nY = 0.6506 + 2.6879\ \ell nX$	0.9404	0.0881	0.0260	680

Table 26 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous female and male Panulirus penicillatus at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Sex	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Female (non-ovigerous)	339	2.2875	5.2926	12.6922	33.7042	2.3981	6.5484	6.6864	0.0097			
Male	353	2.4003	13.7708	35.2433	93.3138	2.5593	6.8119	6.6704	0.0089			
										1.0919	10.7054*	4.1565

* significant difference ($P \leq 0.05$)

Table 27 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous and ovigerous female *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Non-ovigerous	339	2.2875	5.2926	12.6922	33.7042	2.3981	6.5484	6.5498	0.0097			
Ovigerous	283	2.2888	3.4149	8.0274	20.3596	2.3507	6.6148	6.6131	0.0053			
										1.8288*	0.6061	80.4547*

* significant difference ($P \leq 0.05$)

Table 28 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous female and male *Panulirus versicolor* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Sex	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Female (non-ovigerous)	75	2.2577	1.3164	3.8395	12.6138	2.9167	6.6148	6.5577	0.0194			
Male	254	2.2323	12.7894	34.1135	94.7510	2.6673	6.5210	6.5365	0.0149			
										1.2995	4.6608	1.6126

Table 29 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous and ovigerous female *Panulirus versicolor* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Non-ovigerous	75	2.2577	1.3164	3.8395	12.6138	2.1967	6.6148	6.6668	0.0194			
Ovigerous	54	2.3003	0.4394	1.0634	2.7847	2.4201	6.8454	6.7854	0.0041			
										4.7771*	6.2444*	32.2726*

* significant difference ($P \leq 0.05$)

Table 30 - Analysis of covariance for the relationship of carapace length and total weight fresh from male *Panulirus versicolor* and *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Species	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
P. versicolor	254	2.2323	12.7894	34.1135	94.7510	2.6673	6.5210	6.7816	0.0149			
P. penicillatus	353	2.4003	13.7708	35.2433	93.3138	2.5593	6.8119	6.6320	0.0089			
										1.6803*	6.7881*	249.4736*

* significant difference ($P \leq 0.05$)

Table 31 - Analysis of covariance for the relationship of carapace length and total weight fresh from non-ovigerous female *Panulirus versicolor* and *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

Species	n	$\bar{x}$	Regression (sums of squares and products) $\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Dependent Variables (total weight) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	F Ratios Residual variance	Regression coefficient	Elevatic
P. versicolor	75	2.2577	1.3164	3.8395	12.6138	2.9167	6.6148	6.6860	0.0194			
P. penicillatus	339	2.2875	5.2926	12.6922	33.7042	2.3981	6.5484	6.5354	0.0097			
										1.9998*	24.8237*	118.5614*

* significant difference ($P \leq 0.05$)

Table 32. - Summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length (X) and total weight fresh (Y) from Panulirus penicillatus and Panulirus versicolor at Palau. $S\hat{y}$ represents the standard error of the estimate; S_b represents the standard error of the regression coefficient. The symbolism is from Sokal and Rohlf (1969).

Group	Regression Equation	r^2	$S\hat{y}$	S_b	n
	Panulirus penicillatus				
Males	$\ell nY = 0.6688 + 2.5593\ \ell nX$	0.9666	0.0942	0.0254	353
Non-ovigerous Females	$\ell nY = 1.0628 + 2.3981\ \ell nX$	0.9031	0.0985	0.0428	339
Ovigerous Females	$\ell nY = 1.2346 + 2.3507\ \ell nX$	0.9268	0.0728	0.0394	283
Males and Non-ovigerous Females	$\ell nY = 0.8258 + 2.4977\ \ell nX$	0.9538	0.0965	0.0209	692
	Panulirus versicolor				
Males	$\ell nY = 0.5667 + 2.6673\ \ell nX$	0.9603	0.1221	0.0342	254
Non-ovigerous Females	$\ell nY = 0.0299 + 2.9167\ \ell nX$	0.8878	0.1392	0.1214	75
Ovigerous Females	$\ell nY = 1.2785 + 2.4201\ \ell nX$	0.9242	0.0637	0.0961	54
Males and Non-ovigerous Females	$\ell nY = 0.5148 + 2.6932\ \ell nX$	0.9510	0.1272	0.0338	329

Table 33. - Analysis of covariance for the relationship of carapace length and total weight from fresh and frozen male *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	353	2.4003	13.7708	35.2433	93.3138	2.5593	6.8119	6.8090	0.0089			
Frozen	62	2.3929	3.6935	9.7096	26.5257	2.6288	6.7086	6.7253	0.0167	1.8785*	1.4072	36.8995*

* significant difference ($P \leq 0.05$)

Table 34. - Analysis of covariance for the relationship of carapace length and total weight from fresh and frozen non-ovigerous female Panulirus penicillatus at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	339	2.2875	5.2926	12.6922	33.7042	2.3981	6.5484	6.5555	0.0097			
Frozen	55	2.3087	1.0464	2.4764	6.2913	2.3667	6.5267	6.4835	0.0081	1.1932	0.0911	25.4562*

* significant difference ($P \le 0.05$)

Table 35. - Analysis of covariance for the relationship of carapace length and total weight from fresh and frozen ovigerous female *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	283	2.2888	3.4149	8.0274	20.3596	2.3112	6.6149	6.6341	0.0053			
Frozen	51	2.3426	0.5696	1.3989	3.8061	2.4560	6.6660	6.5540	0.0076	1.4261	0.9607	42.5168*

* significant difference ($P \leq 0.05$)

Table 36 - Analysis of covariance for the relationship of carapace length and total weight from fresh and boiled male Panulirus penicillatus at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	353	2.4003	13.7708	35.2433	93.3138	2.5593	6.8119	6.8213	0.0089			
Boiled	18	2.4761	0.4199	1.1114	3.2117	2.6466	6.8251	6.6344	0.0169			
										1.9027*	0.3365	53.5078*

* significant difference ($P \leq 0.05$)

Table 37. - Analysis of covariance for the relationship of carapace length and total weight from fresh and boiled non-ovigerous female *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	339	2.2875	5.2926	12.6922	33.7042	2.3981	6.5484	6.5505	0.0097			
Boiled	11	2.3161	0.1228	0.2316	0.5162	1.8865	6.3787	6.3265	0.0088	1.1016	3.2473	51.8437*

* significant difference ($P \leq 0.05$)

Table 38. - Analysis of covariance for the relationship of carapace length and total weight from fresh and boiled ovigerous female *Panulirus penicillatus* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	283	2.2888	3.4149	8.0274	20.3596	2.3507	6.6148	6.6087	0.0053			
Boiled	14	2.2338	0.1252	0.4498	1.6662	3.5935	6.2162	6.4045	0.0042	1.2744	35.4931	81.8677*

* significant difference ($P \leq 0.05$)

Table 39. - Summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length (X) and total weight (Y) from frozen and boiled Panulirus penicillatus at Palau. $S\hat{y}$ represents the standard error of the regression coefficient. The symbolism is from Sokal and Rohlf (1969).

Group	Regression Equation	r^2	$S\hat{y}$	S_b	n
FROZEN					
Males	$\ell nY = 0.4181 + 2.6288\ \ell nX$	0.9623	0.1291	0.0672	62
Non-ovigerous Females	$\ell nY = 1.0628 + 2.3667\ \ell nX$	0.9315	0.0901	0.0881	55
Ovigerous Females	$\ell nY = 0.9125 + 2.4560\ \ell nX$	0.9026	0.0870	0.1152	51
Males and Non-ovigerous Females	$\ell nY = 0.6135 + 2.5537\ \ell nX$	0.9549	0.1151	0.0517	117
BOILED					
Males	$\ell nY = 0.2720 + 2.6466\ \ell nX$	0.9159	0.1300	0.2006	18
Non-ovigeorus Females	$\ell nY = 2.0095 + 1.8865\ \ell nX$	0.8460	0.0938	0.2677	11
Ovigerous Females	$\ell nY = -1.8110 + 3.5935\ \ell nX$	0.9699	0.0645	0.1823	14
Males and Non-ovigerous Females	$\ell nY = 0.4936 + 2.5512\ \ell nX$	0.9179	0.1244	0.1469	29

Table 40 - Analysis of covariance for the relationship of carapace length and total weight from fresh and frozen male Panulirus versicolor at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	254	2.2323	12.7894	34.1135	94.7510	2.6673	6.5210	6.5694	0.0149			
Frozen	70	2.3163	1.6892	3.9505	9.9686	2.3386	6.6936	6.5396	0.0107			
										1.3901	11.4893*	3.0569

* significant difference ($P \leq 0.05$)

Table 41 - Analysis of covariance for the relationship of carapace length and total weight from fresh and frozen non-ovigerous female Panulirus versicolor at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	75	2.2577	1.3164	3.8395	12.6136	2.9168	6.6148	6.5897	0.0194			
Frozen	50	2.2362	0.8050	2.2499	6.7379	2.7949	6.5098	6.5459	0.0094			
										2.0690*	0.4813	3.7050

* significant difference ($P \leq 0.05$)

Table 42 - Analysis of covariance for the relationship of carapace length and total weight from fresh and frozen ovigerous female *Panulirus versicolor* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	54	2.3003	0.4394	1.0634	2.7847	2.4201	6.8454	6.8555	0.0041			
Frozen	42	2.3009	0.2603	0.6545	1.8181	2.5147	6.7836	6.7701	0.0043			
										1.0607	0.3515	41.1947*

* significant difference ($P \leq 0.05$)

Table 43 - Analysis of covariance for the relationship of carapace length and total weight from fresh and boiled male *Panulirus versicolor* at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	254	2.2323	12.7894	34.1135	94.7510	2.6673	6.5210	6.5239	0.0149			
Boiled	9	2.2641	0.1935	0.5279	1.5048	2.7284	6.3831	6.2993	0.0092			
										1.6223	0.0482	28.4945*

* significant difference ($P \leq 0.05$)

Table 44 - Analysis of covariance for the relationship of carapace length and total weight from fresh and boiled non-ovigerous female Panulirus versicolor at Palau. The data are presented as natural logarithms.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total weight)					
Condition	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Fresh	75	2.2577	1.3164	3.8395	12.6136	2.9168	6.6148	6.6209	0.0194			
Boiled	5	2.2910	0.1226	0.3466	1.0729	2.8275	6.5274	6.4391	0.0310			
										1.5997	0.0450	7.5283*

* significant difference ($P \leq 0.05$)

Table 45. Summary of the derived linear regression equations used in the covariance analyses for the relationship of carapace length (X) and total weight (Y) from frozen and boiled *Panulirus versicolor* at Palau. $S\hat{y}$ represents the standard error of the estimate; S_b represents the standard error of the regression coefficient. The symbolism is from Sokal and Rohlf (1969)

Group	Regression Equation	r^2	$S\hat{y}$	S_b	n
	FROZEN				
Males	$\ell nY = 1.2765 + 2.3386\ \ell nX$	0.9268	0.1036	0.0797	70
Non-ovigerous Females	$\ell nY = 0.2599 + 2.7949\ \ell nX$	0.9333	0.0968	0.1079	50
Ovigerous Females	$\ell nY = 0.9750 + 2.5147\ \ell nX$	0.9051	0.656	0.1286	42
Males and Non-ovigerous Females	$\ell nY = 0.9730 + 2.4723\ \ell nX$	0.9265	0.1050	0.0641	120
	BOILED				
Males	$\ell nY = 0.2057 + 2.7284\ \ell nX$	0.9570	0.0959	0.2180	9
Non-ovigerous Females	$\ell nY = 0.0496 + 2.8275\ \ell nX$	0.9135	0.1761	0.5029	5
Males and Non-ovigerous Females	$\ell nY = 0.1005 + 2.7858\ \ell nX$	0.9344	0.1203	0.2132	14

Table 46 - Analysis of covariance for the relationship of carapace length and total length from non-ovigerous female and male *Panulirus penicillatus* at Palau. The relationship is based on fresh lobsters only.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total length)					
Sex	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
Female (non-ovigerous)	339	9.93	487.43	1219.61	3235.11	2.50	28.88	30.54	0.54			
Male	352	11.23	1552.36	3398.16	7635.55	2.19	29.98	28.59	0.56			
										1.03	65.68*	985.11*

* significant difference ($P \leq 0.05$)

Table 47 - Analysis of covariance for the relationship of carapace length and total length from non-ovigerous female and male *Panulirus versicolor* at Palau. The relationship is based on fresh lobsters only.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(total length)					
Sex	n	$\bar{x}$	Σx^2	Σxy	Σy^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevatio[n]
Female (non-ovigerous)	75	9.64	116.03	393.31	1417.29	3.39	30.48	30.18	1.15			
Male	254	9.53	816.42	2332.43	6799.21	2.86	28.98	29.05	0.54			
										2.14*	42.68*	108.74*

* significant difference ($P \leq 0.05$)

48. Summary of the linear regression equations used in the covariance analyses for the relationship of carapace length (X) and total length (Y) from fresh *Panulirus penicillatus* and *Panulirus versicolor* at Palau. $S\hat{y}$ represents the standard error of the estimate; S_b represents the standard error of the regression coefficient. The symbolism is from Sokal and Rohlf (1969).

Group	Regression Equation	r^2	$S\hat{y}$	S_b	n
	Panulirus penicillatus				
Males	Y = 5.41 + 2.19 X	0.97	0.75	0.02	352
Non-ovigerous Females	Y = 4.04 + 2.50 X	0.94	0.74	0.03	339
Males and Non-ovigerous Females	Y = 7.34 + 2.09	0.92	1.16	0.02	691
	Panulirus versicolor				
Males	Y = 1.76 + 2.86 X	0.98	0.73	0.03	254
Non-ovigerous Females	Y =-2.21 + 3.39 X	0.94	1.07	0.10	75
Males and Non-ovigerous Females	Y = 1.31 + 2.93 X	0.96	1.00	0.03	329

Table 49 - Analysis of covariance for the relationship of carapace length and carapace width from male and female *Panulirus penicillatus* at Palau. The relationship is based on fresh lobsters only.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)				(carapace width)					
Sex	n	$\bar{x}$	ΣX^2	ΣXY	ΣY^2	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevati[illegible]
Male	146	11.46	686.02	541.25	437.23	0.79	9.03	8.26	0.07			
Female	357	10.08	453.52	344.82	278.41	0.76	7.98	8.28	0.05			
										1.55*	4.23	1.09

* significant difference ($P \leq 0.05$)

Table 50 - Analysis of covariance for the relationship of carapace length and carapace width from male and female *Panulirus versicolor* at Palau. The relationship is based on fresh lobsters only.

Sex	n	$\bar{x}$	Regression (sums of squares and products) Σx^2	Σxy	Σy^2	Regression coefficient	Dependent Variables (carapace width) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	F Ratios Residual variance	Regression coefficient	Elevation
Male	47	9.84	191.64	147.93	116.13	0.77	7.80	7.82	0.043			
Female	31	9.90	51.99	38.35	29.52	0.74	7.95	7.92	0.043			
										1.01	1.13	4.66

Table 51. - Analysis of covariance for the relationship of carapace length and carapace width from pooled male and female *Panulirus penicillatus* and *Panulirus versicolor* at Palau. The relationship is based on fresh lobsters only.

			Regression				Dependent Variables			F Ratios		
			(sums of squares and products)									
Species	n	$\bar{x}$	$\Sigma\chi^2$	$\Sigma\chi\gamma$	$\Sigma\gamma^2$	Regression coefficient	Unadjusted $\bar{y}$	Adjusted $\bar{y}$	Mean Square	Residual variance	Regression coefficient	Elevation
P. penicillatus	504	10.49	1339.91	1036.50	829.62	0.77	8.28	8.22	0.06			
P. versicolor	78	9.87	243.69	186.44	146.05	0.77	7.86	8.27	0.04			
										1.23	0.27	2.63

Table 52. - Summary of the linear regression equations used in the covariance analyses for the relationship of carapace length (X) and carapace width (Y) from fresh *Panulirus penicillatus* and *Panulirus versicolor* at Palau. $S\hat{y}$ represents the standard error of the estimate; S_b represents the standard error of the regression coefficient. The symbolism is from Sokal and Rohlf (1969).

Group	Regression Equation	r^2	$S\hat{y}$	S_b	n
	Panulirus penicillatus				
Males	Y = -0.02 + 0.79X	0.98	0.27	0.01	146
Females	Y = 0.31 + 0.76X	0.94	0.21	0.01	357
Males and Females	Y = 0.17 + 0.77X	0.97	0.24	0.01	504
	Panulirus versicolor				
Males	Y = 0.20 + 0.77X	0.98	0.21	0.02	47
Females	Y = 0.64 + 0.74X	0.96	0.21	0.03	31
Males and Females	Y = 0.31 + 0.77X	0.98	0.21	0.01	78

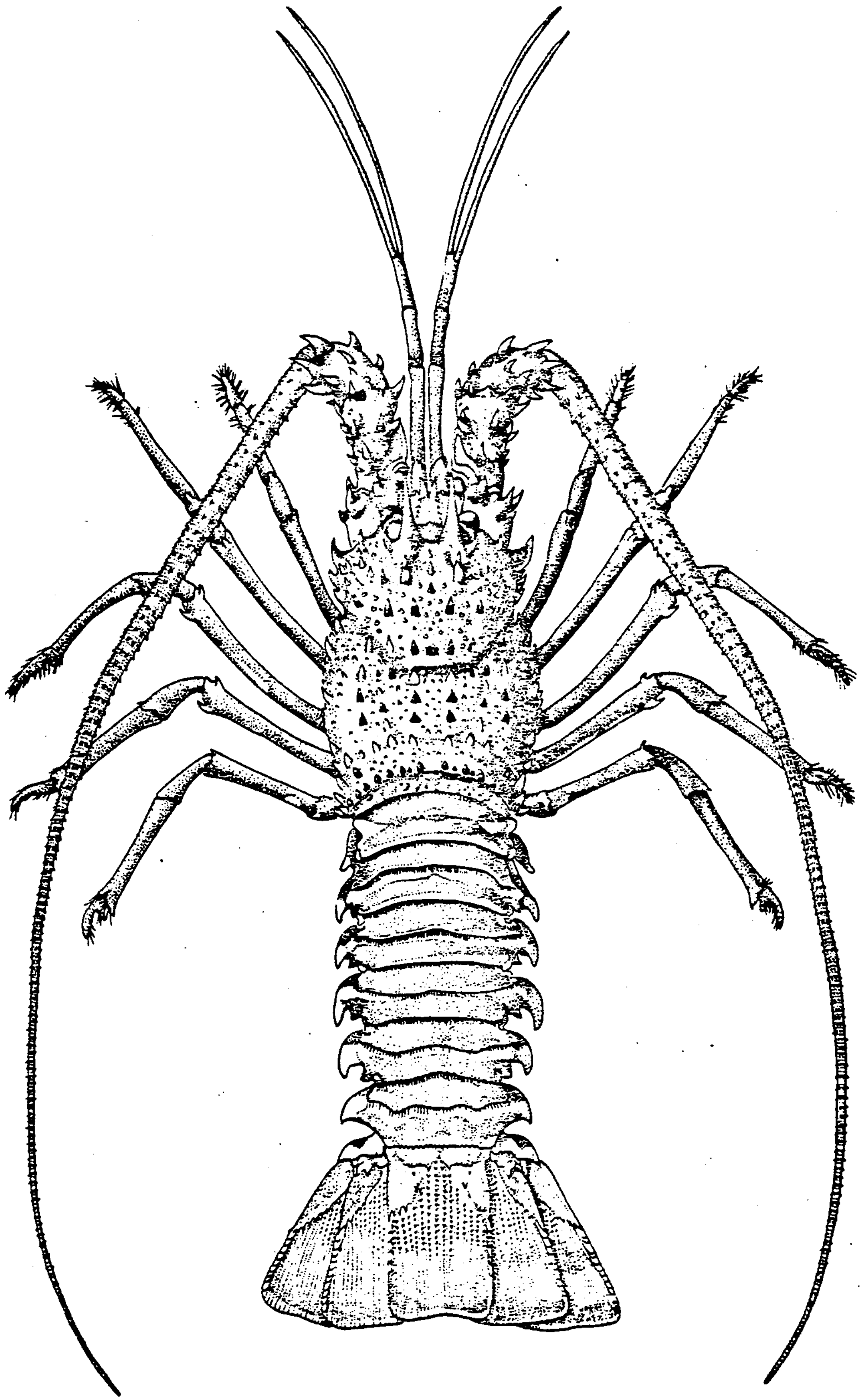

FIGURE 1. Spiny lobster species within the jurisdiction of the Western Pacific Regional Fishery Management Council. A. *Panulirus marginatus*.

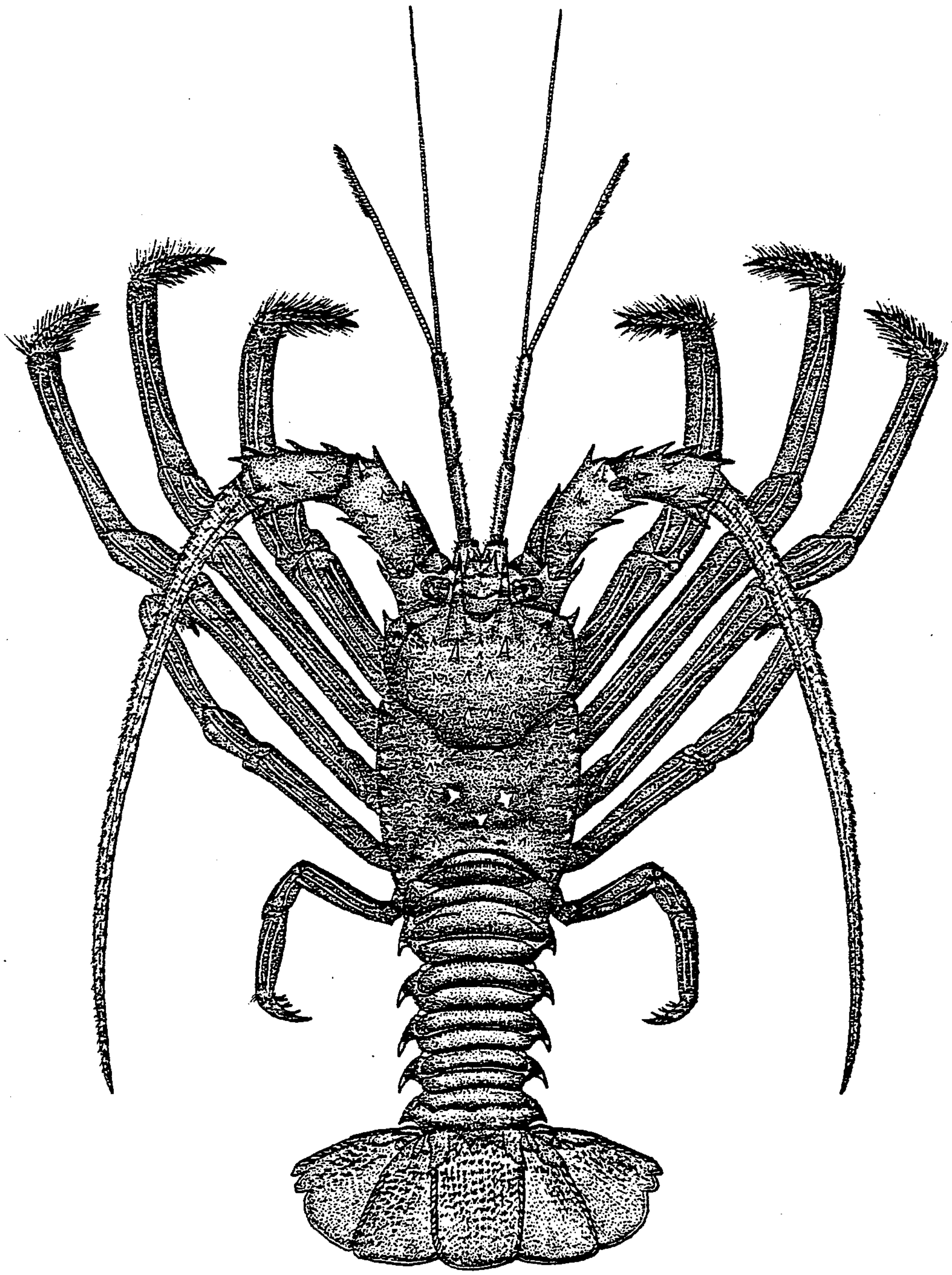

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FIGURE 1. B. Panulirus penicillatus

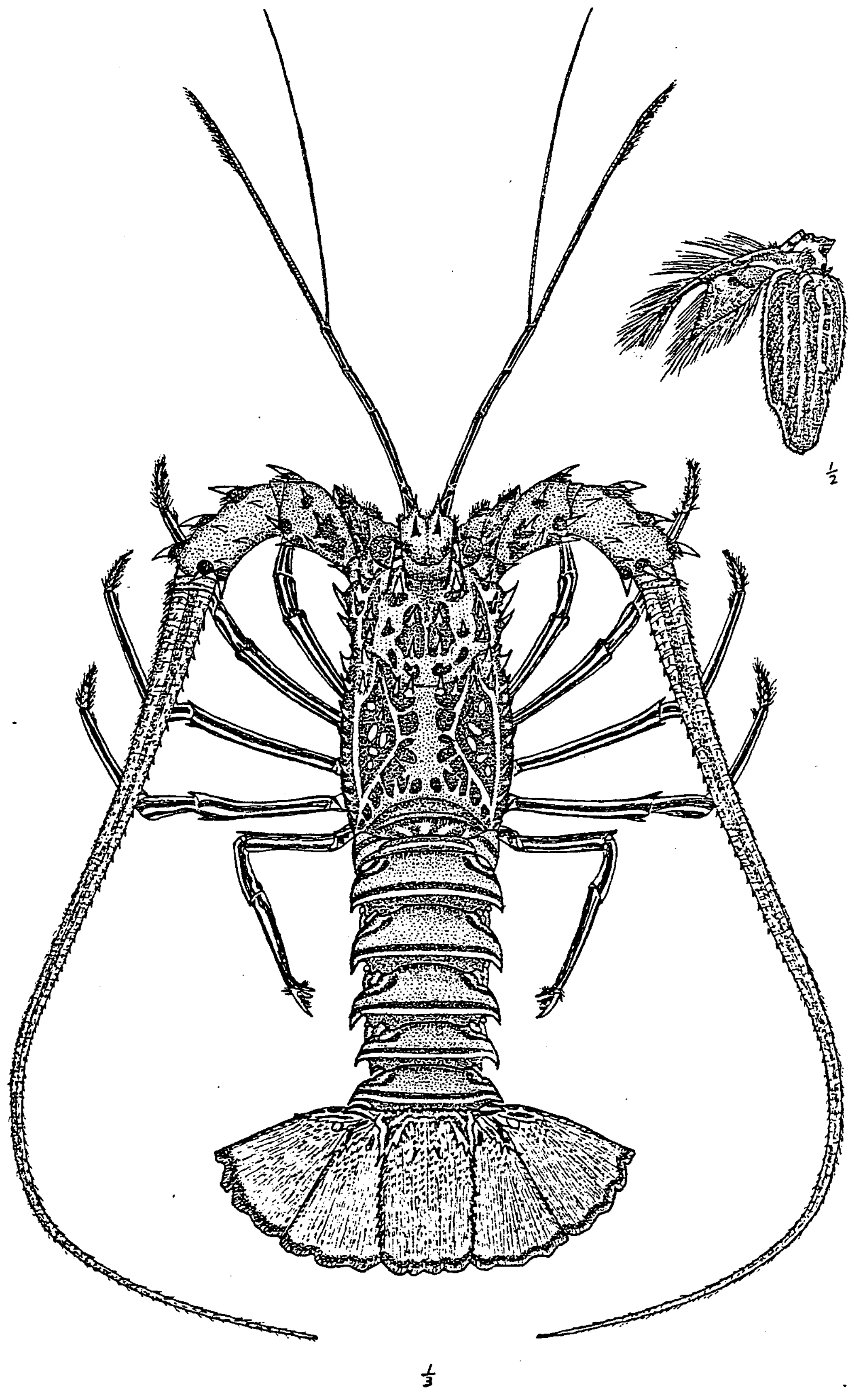

FIGURE 1. C. Panulirus versicolor

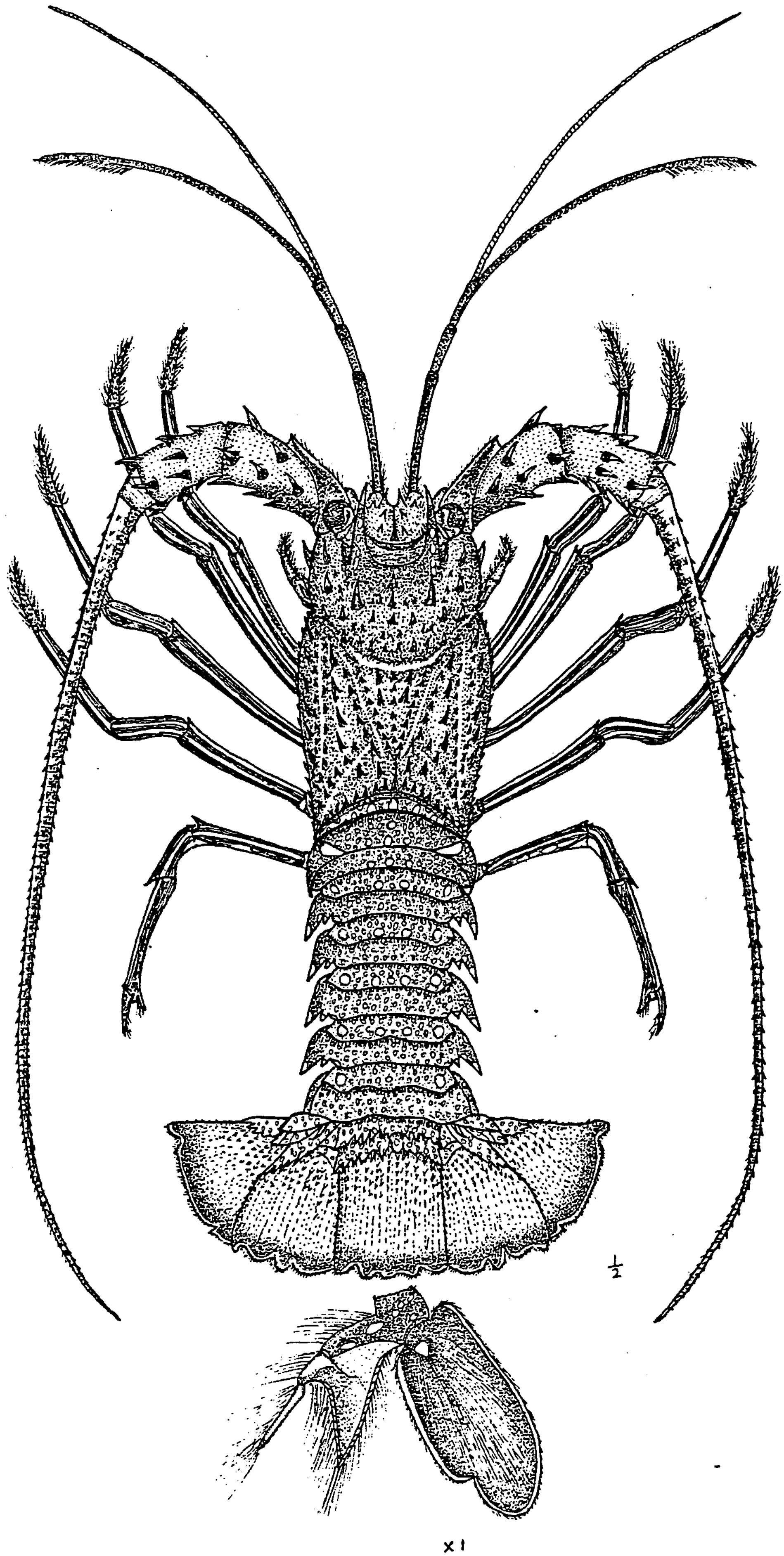

FIGURE 1. D. Panulirus longipes femoristriga

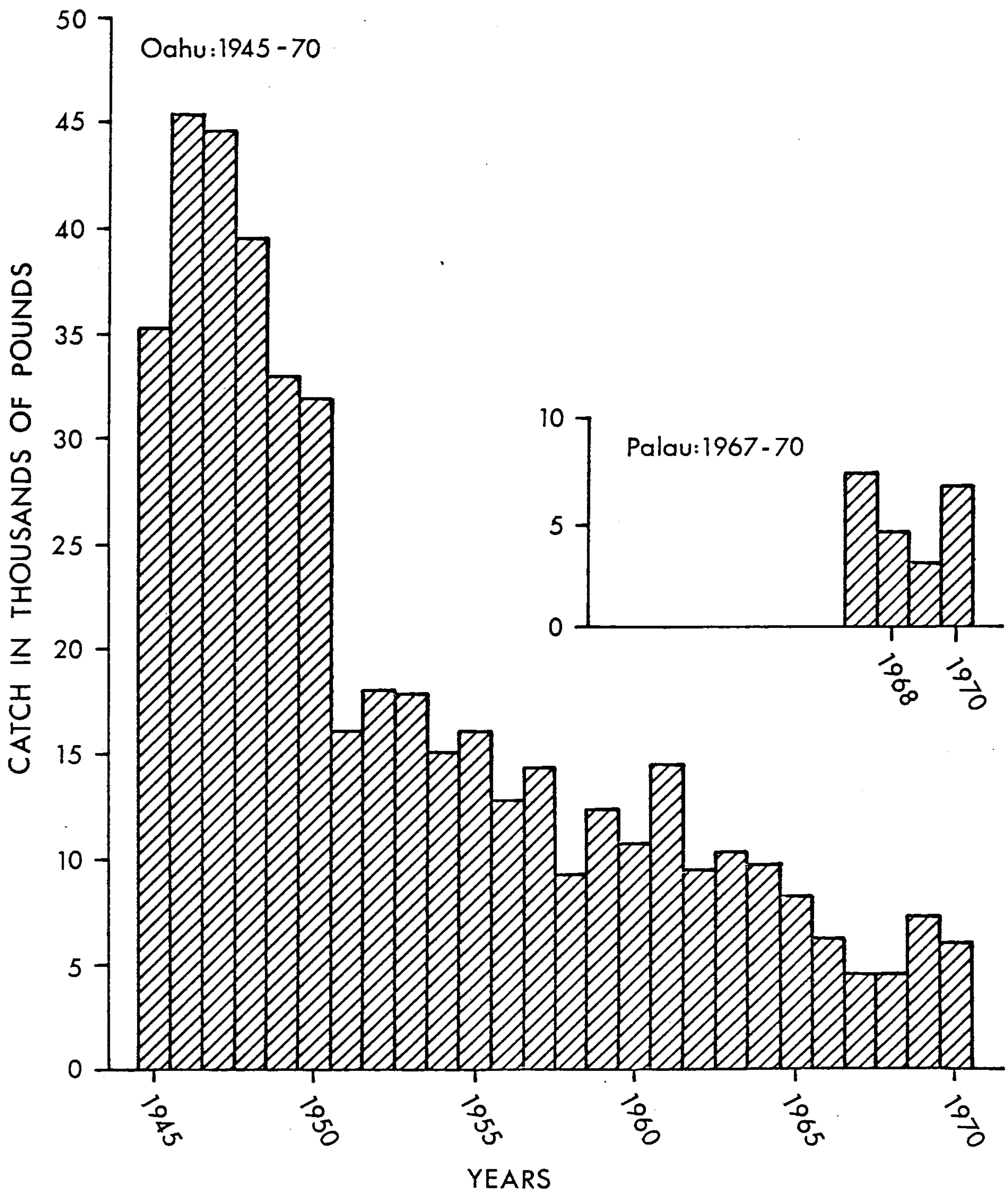

FIGURE 2. Annual commercial lobster landings of _Panulirus penicillatus_ and _Panulirus marginatus_ at Oahu and _Panulirus penicillatus_ and _Panulirus versicolor_ at Palau from 1945 to 1970.

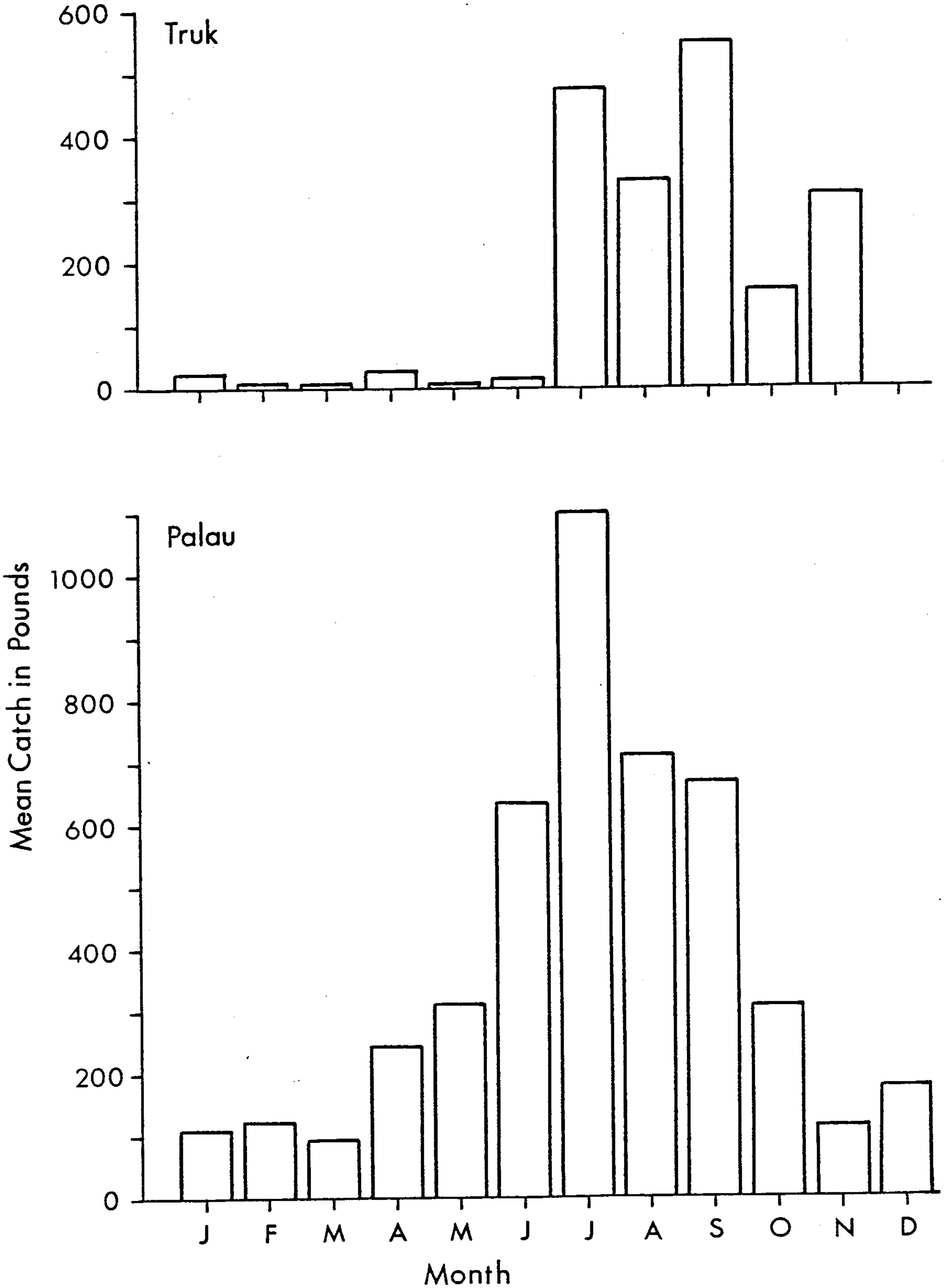

FIGURE 3. Mean monthly commercial lobster landings of *Panulirus penicillatus* and *Panulirus versicolor* at Palau and Truk.

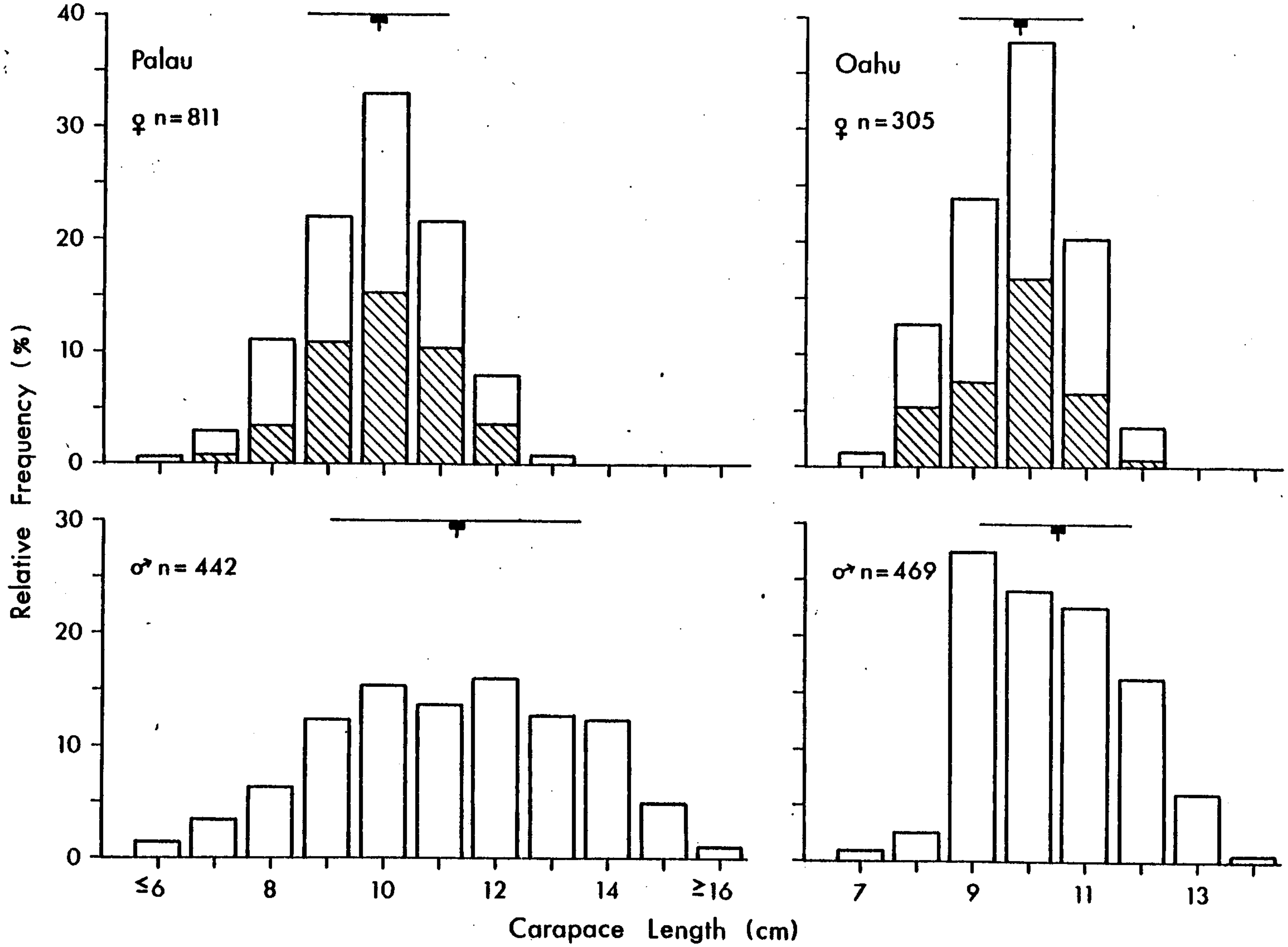

FIGURE 4. Carapace length frequency distributions of male and female *Panulirus penicillatus* at Palau and Oahu. The mean, standard error, and standard deviation are shown above each histogram. The shaded portions depict the proportions of females that were ovigerous, n = total sample size.

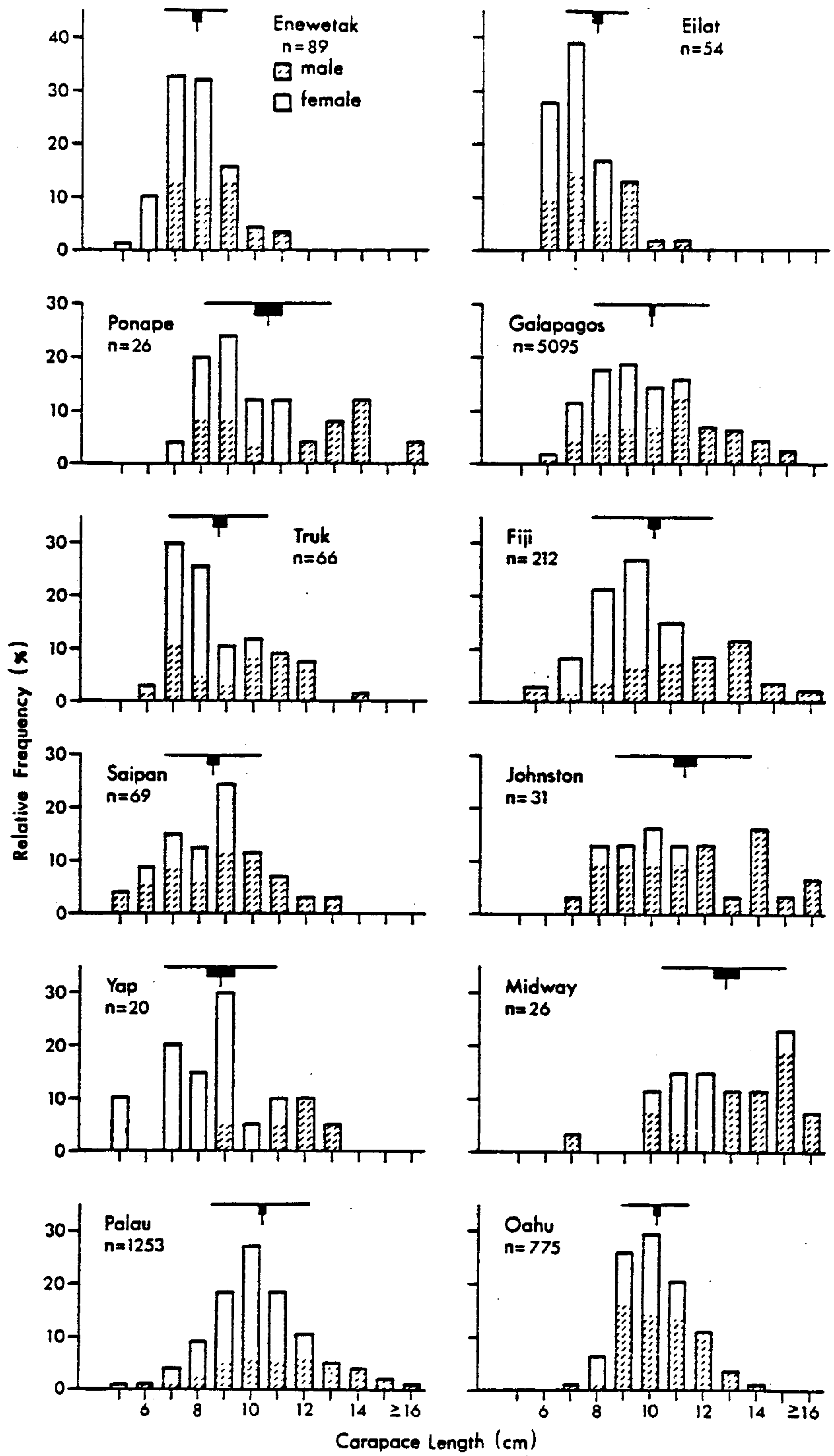

FIGURE 5. Carapace length frequency distributions of combined sexes of <u>Panulirus penicillatus</u> at different locations across the Pacific and Indian Oceans. The proportion of males and females within each size class is depicted by shading. Other details as in Figure 4.

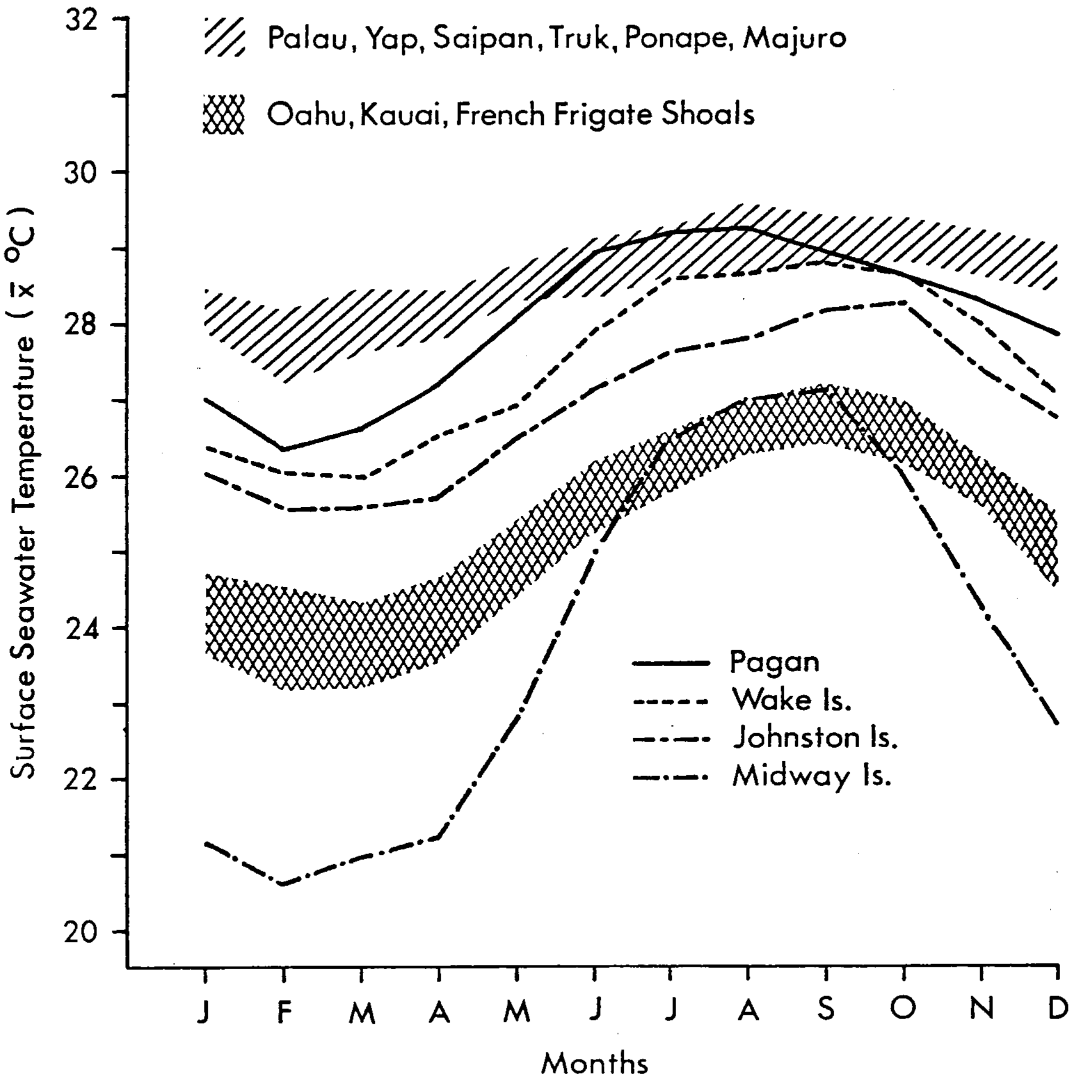

FIGURE 6. Seasonal surface seawater temperature at thirteen Pacific Island locations (U.S. Naval Weather Service Command, 1971).

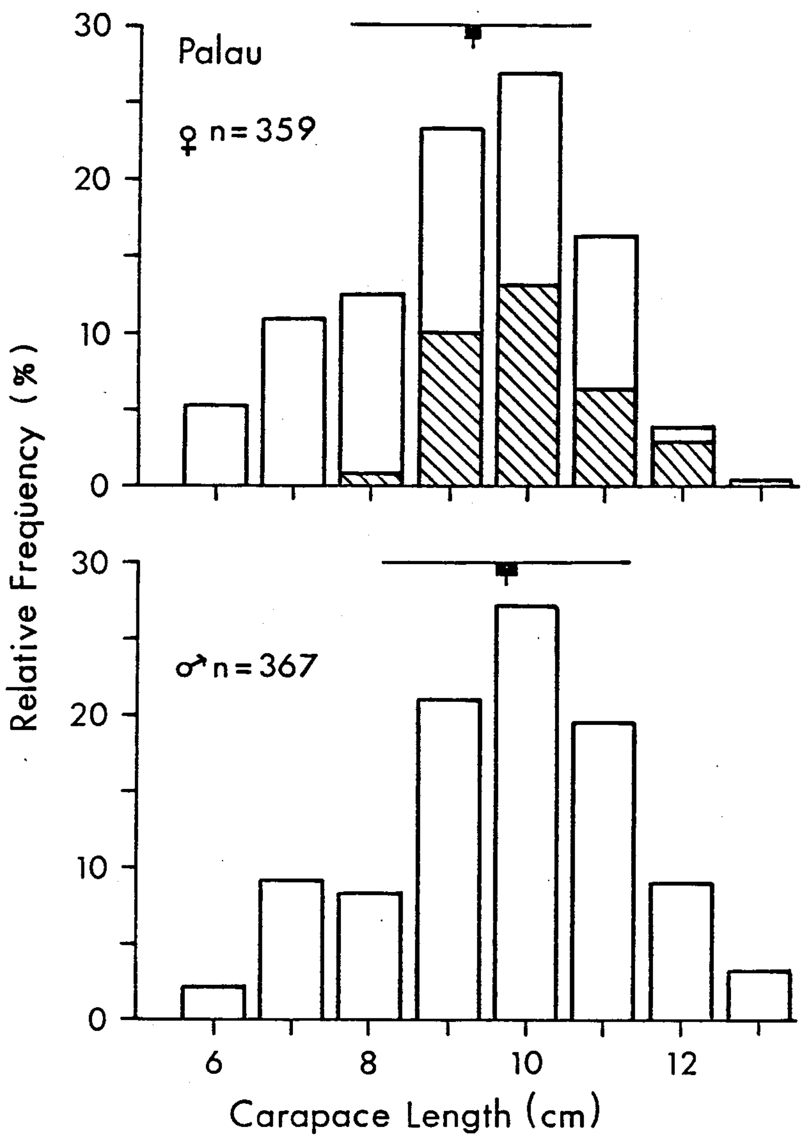

FIGURE 7. Carapace length frequency distributions of male and female *Panulirus versicolor* at Palau. Details as in Figure 4.

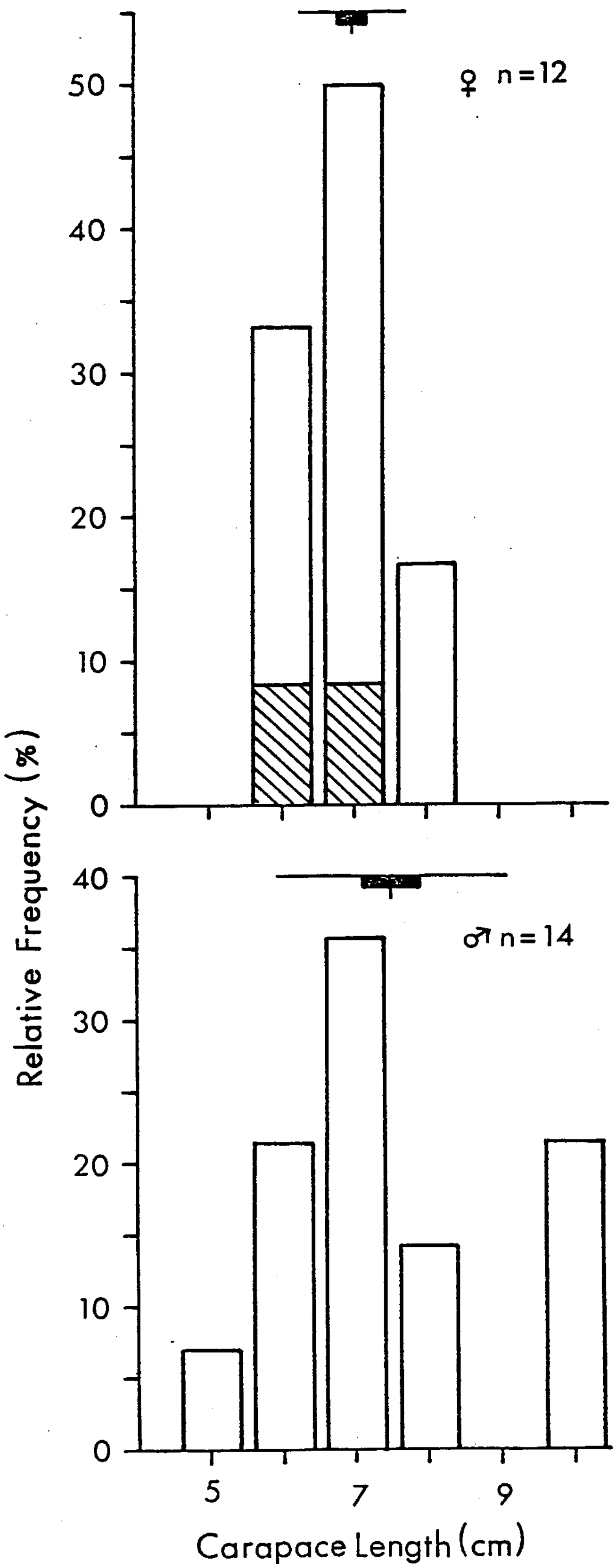

FIGURE 8. Carapace length frequency distributions of male and female *Panulirus longipes femoristriga* at Palau. Details as in Figure 4.

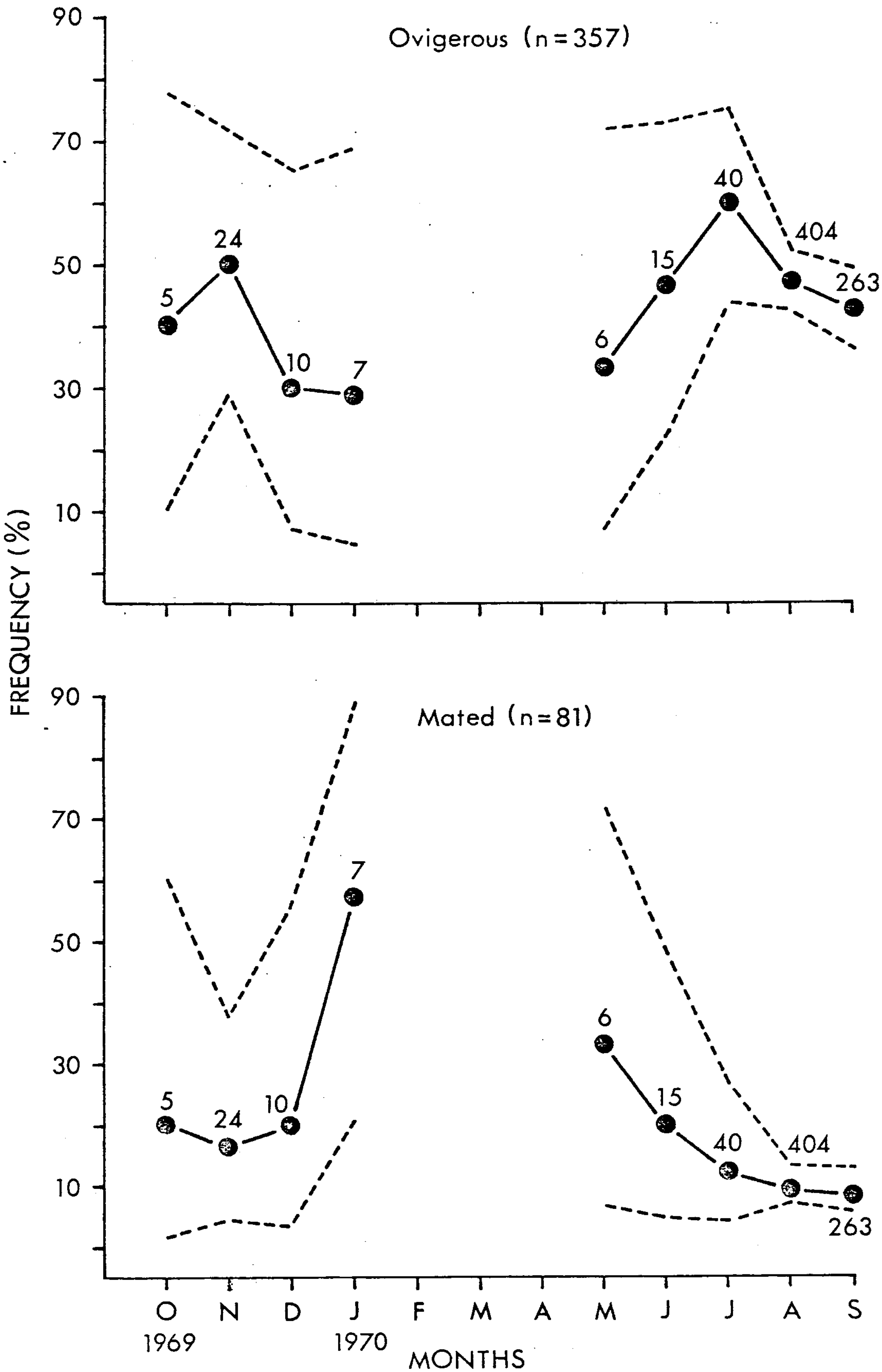

FIGURE 9. Seasonal changes in reproductive condition of female _Panulirus penicillatus_ at Palau. The broken lines represent 95% confidence limits about the estimates. Monthly sample size is included above each percent frequency. n = the total sample size of ovigerous and mated females respectively.

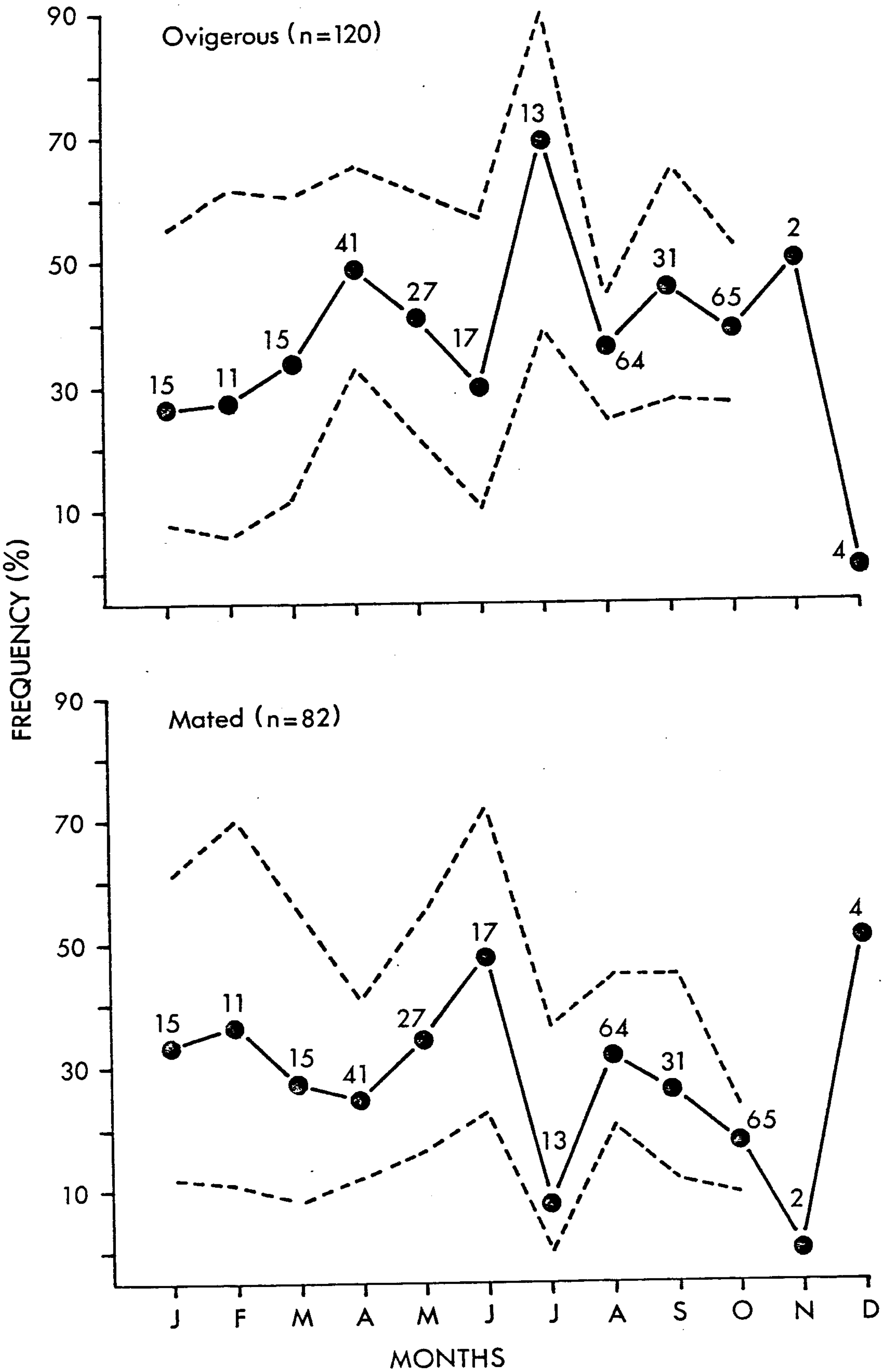

FIGURE 10. Seasonal changes in reproductive condition of female _Panulirus penicillatus_ at Oahu. Details as in Figure 9.

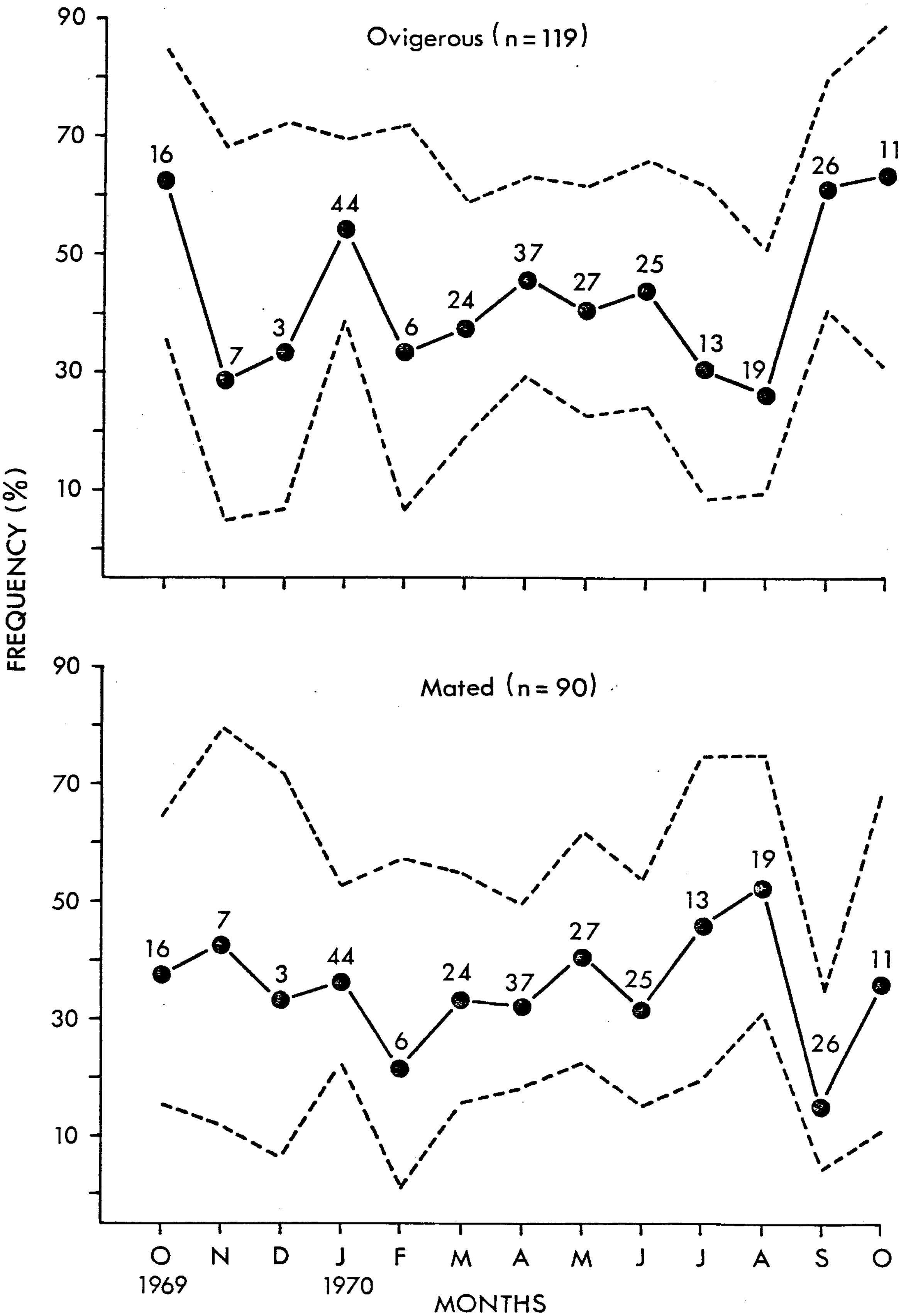

FIGURE 11. Seasonal changes in reproductive condition of female *Panulirus versicolor* at Palau. Details as in Figure 9

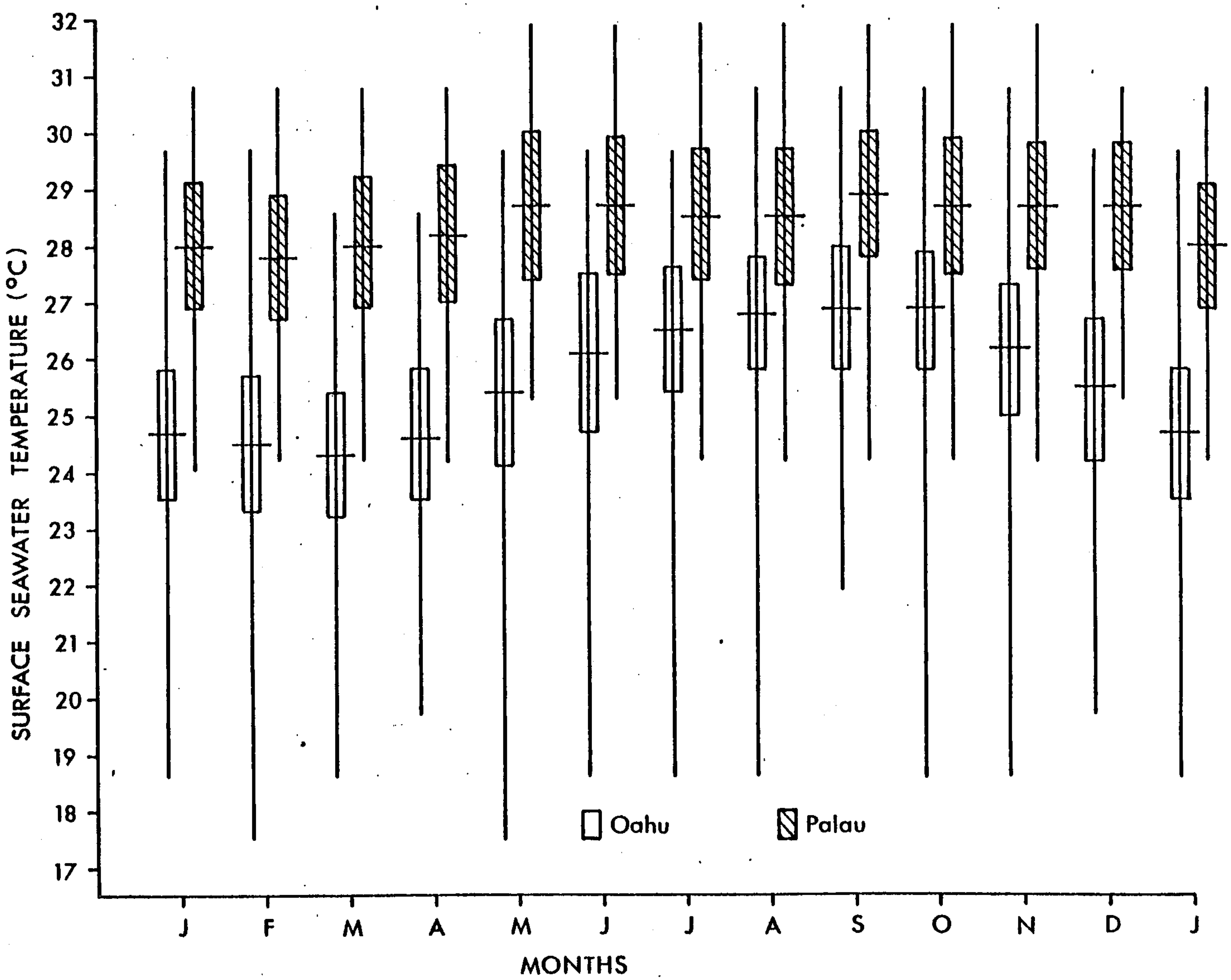

FIGURE 12. Seasonal changes in surface seawater temperature at Palau and Leeward Oahu. Leeward Oahu includes Maunalua Bay where the lobster data were collected at Oahu. The mean, standard deviation, and range are presented. Data are primarily from the period 1930-1970 (U.S. Naval Weather Service Command, 1971).

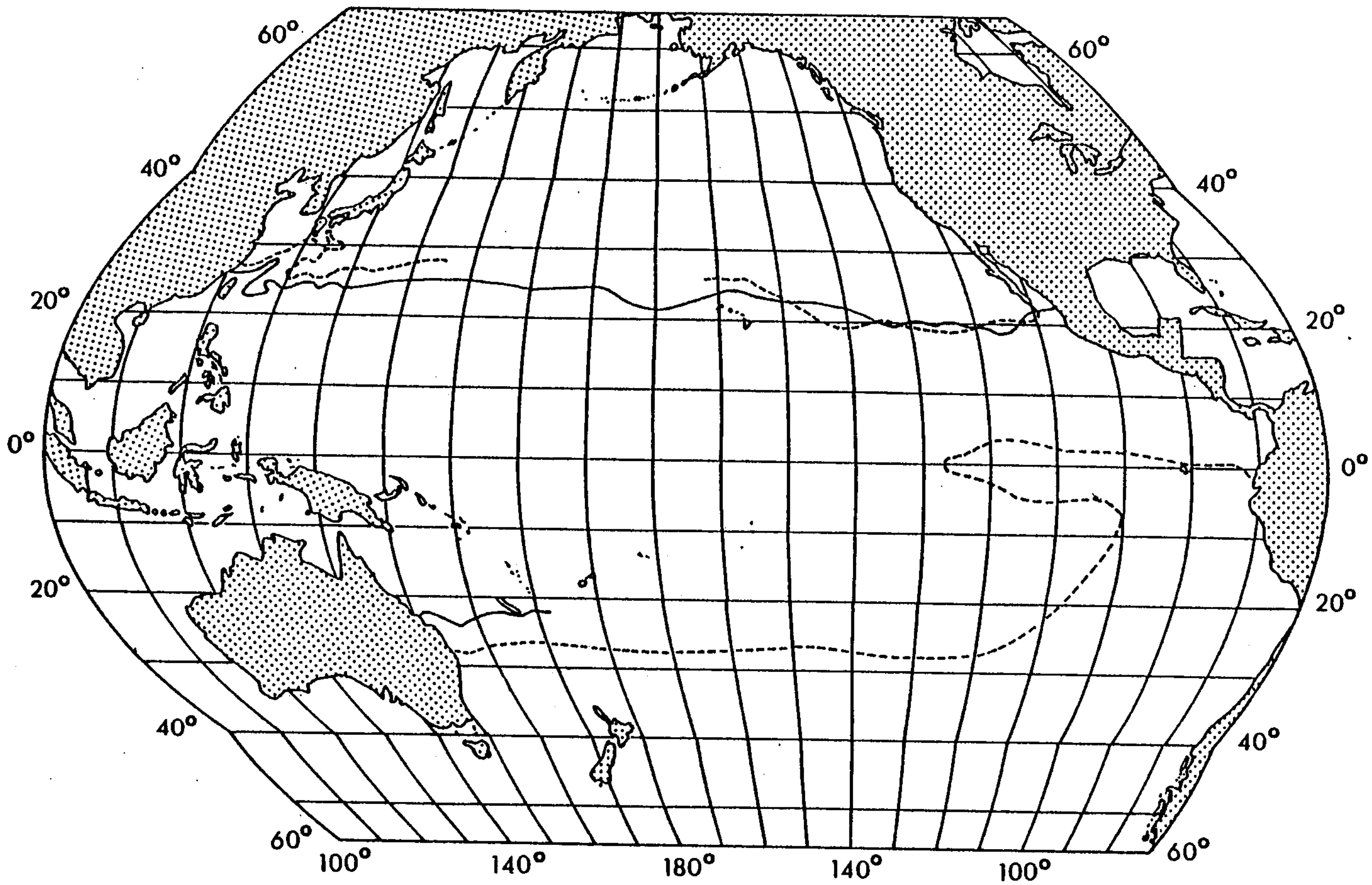

FIGURE 13. General area of the Pacific Ocean where reproduction in Panulirus penicillatus is expected to be continuous throughout the year. The area is defined by 22.5°C isotherms at 10m depth. The solid lines represent winter conditions and the broken lines represent summer conditions in the northern and southern hemispheres respectively. (re-drawn from Barkley, 1968).

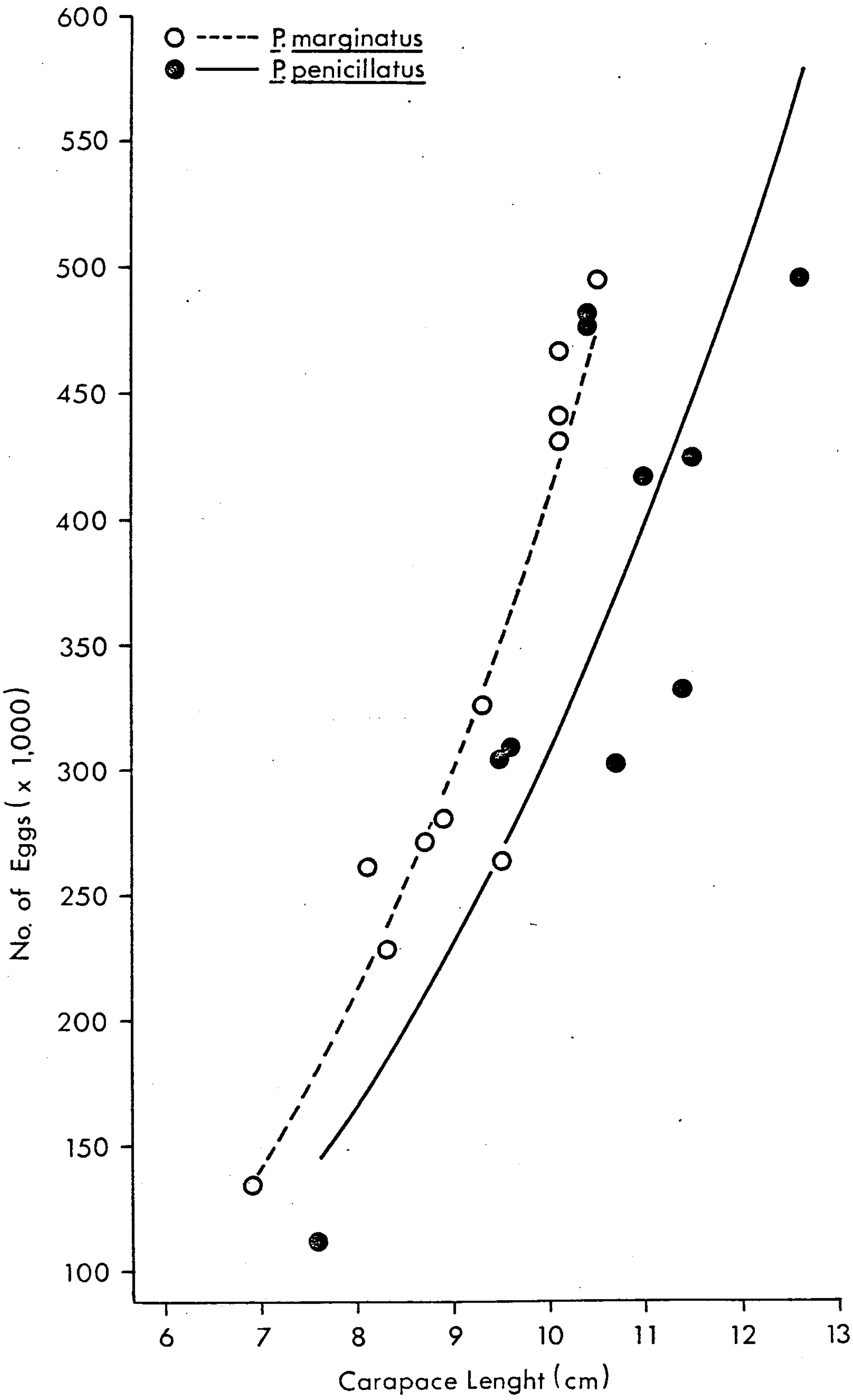

FIGURE 14. Regressions of fecundity on carapace length in female Panulirus penicillatus and Panulirus marginatus at Oahu.

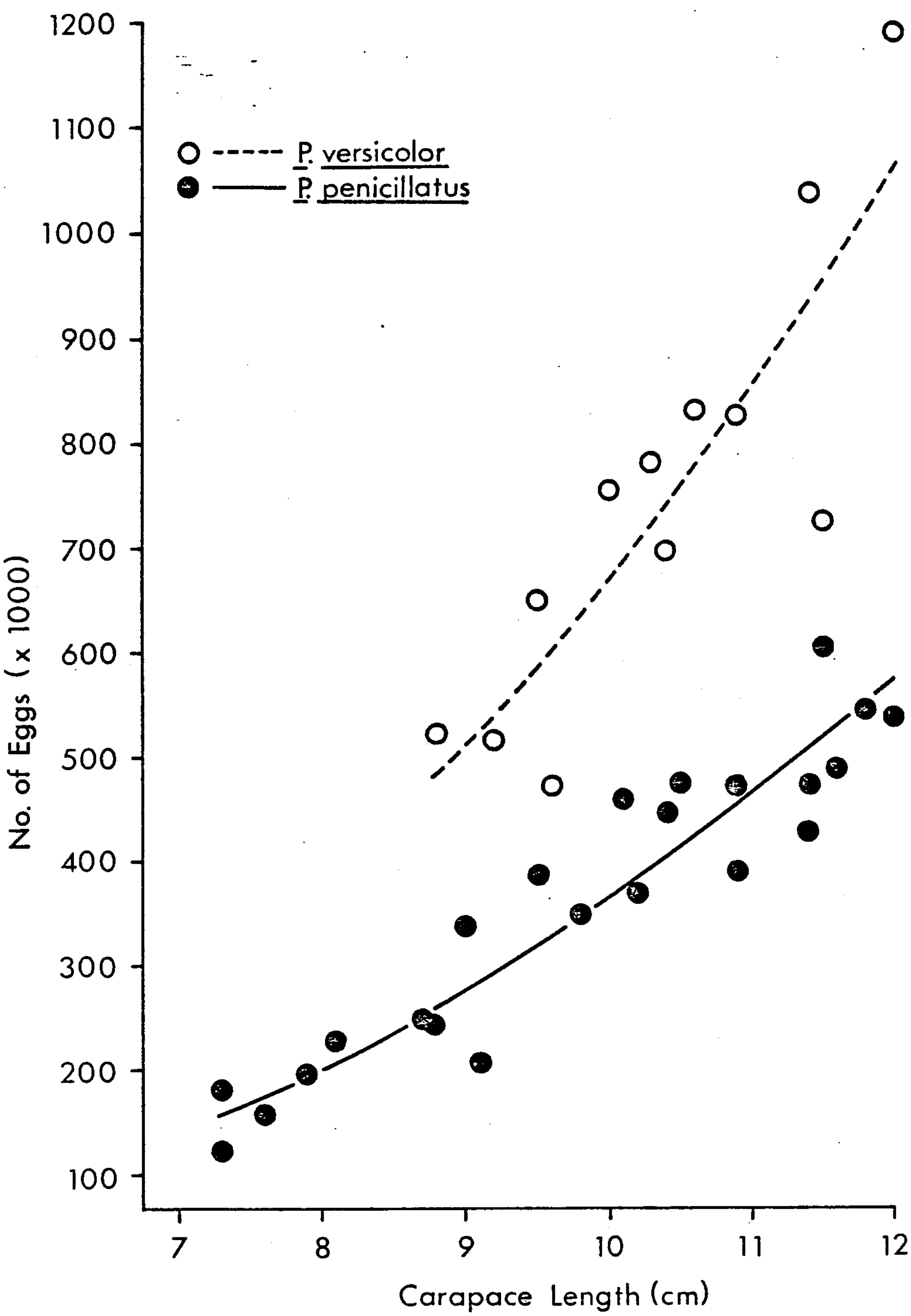

FIGURE 15. Regressions of fecundity on carapace length in female *Panulirus penicillatus* and *Panulirus versicolor* at Palau.

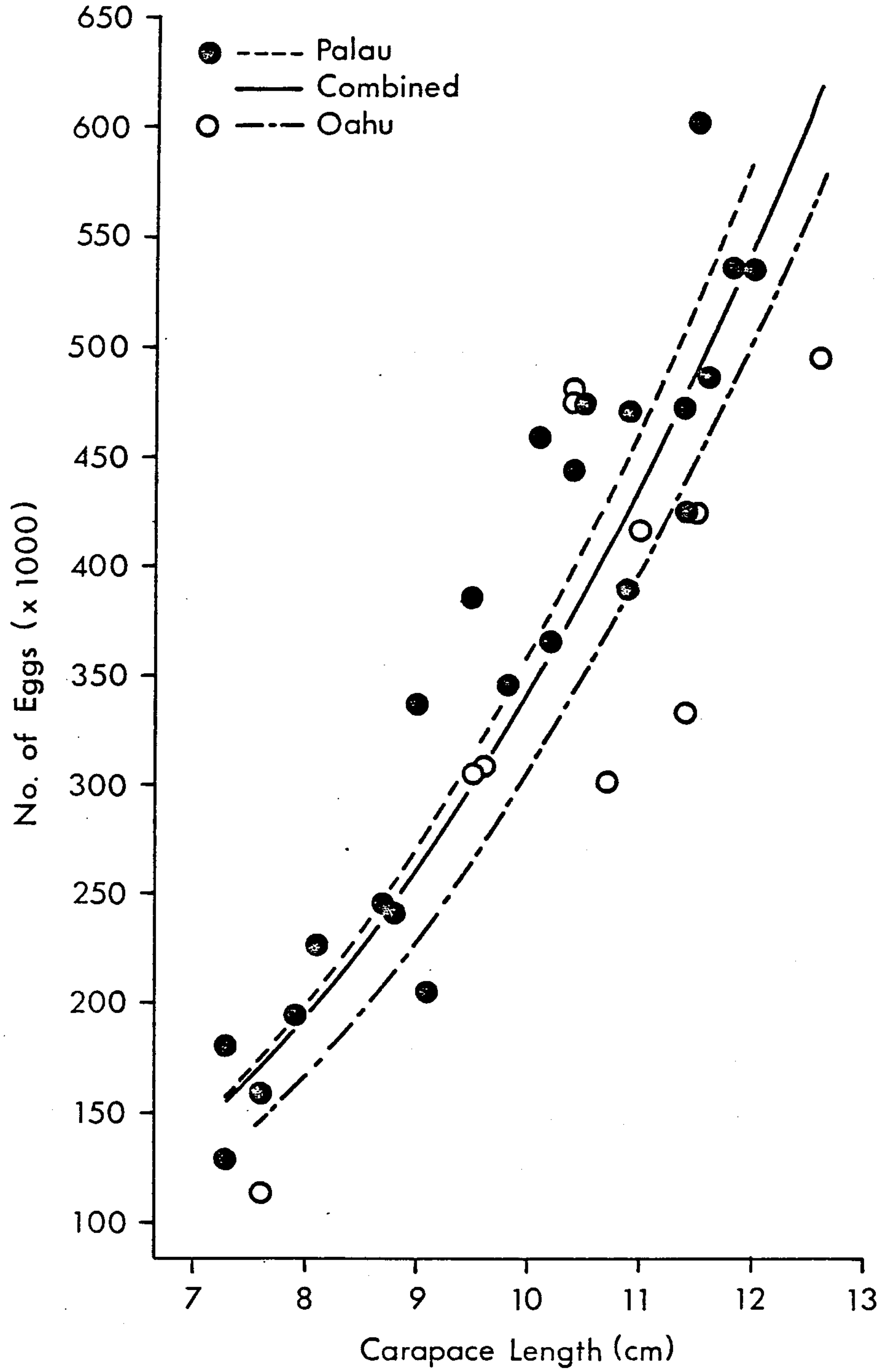

FIGURE 16. Individual and combined regressions of fecundity on carapace length in female Panulirus penicillatus at Palau and Oahu.

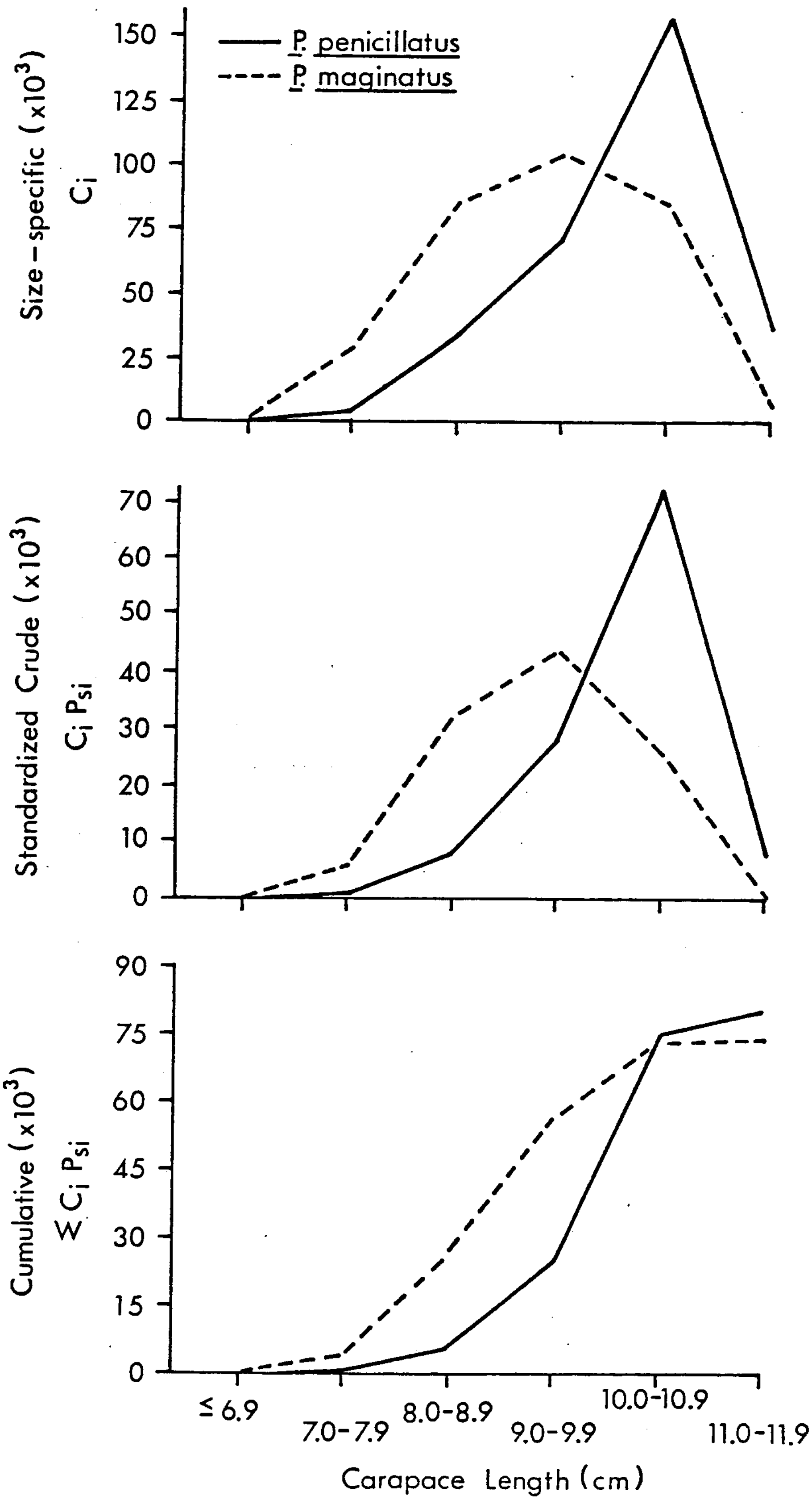

FIGURE 17. Comparison of size-specific, standardized crude, and cumulative standardized crude reproductive rates of female P. *penicillatus* and P. *marginatus* at Oahu.

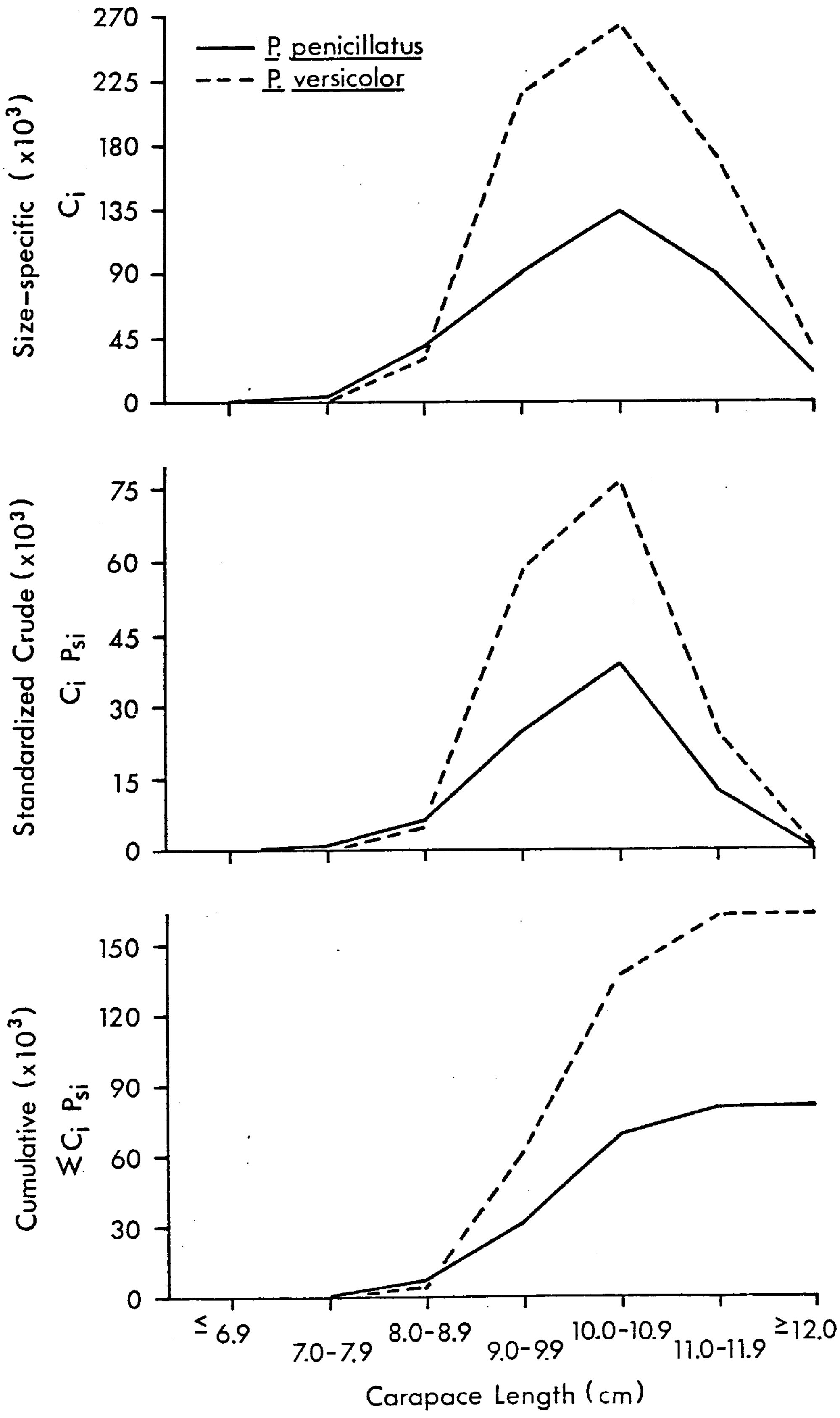

FIGURE 18. Comparison of size-specific, standardized crude, and cumulative standardized crude reproductive rates of female *Panulirus penicillatus* and *Panulirus versicolor* at Palau.

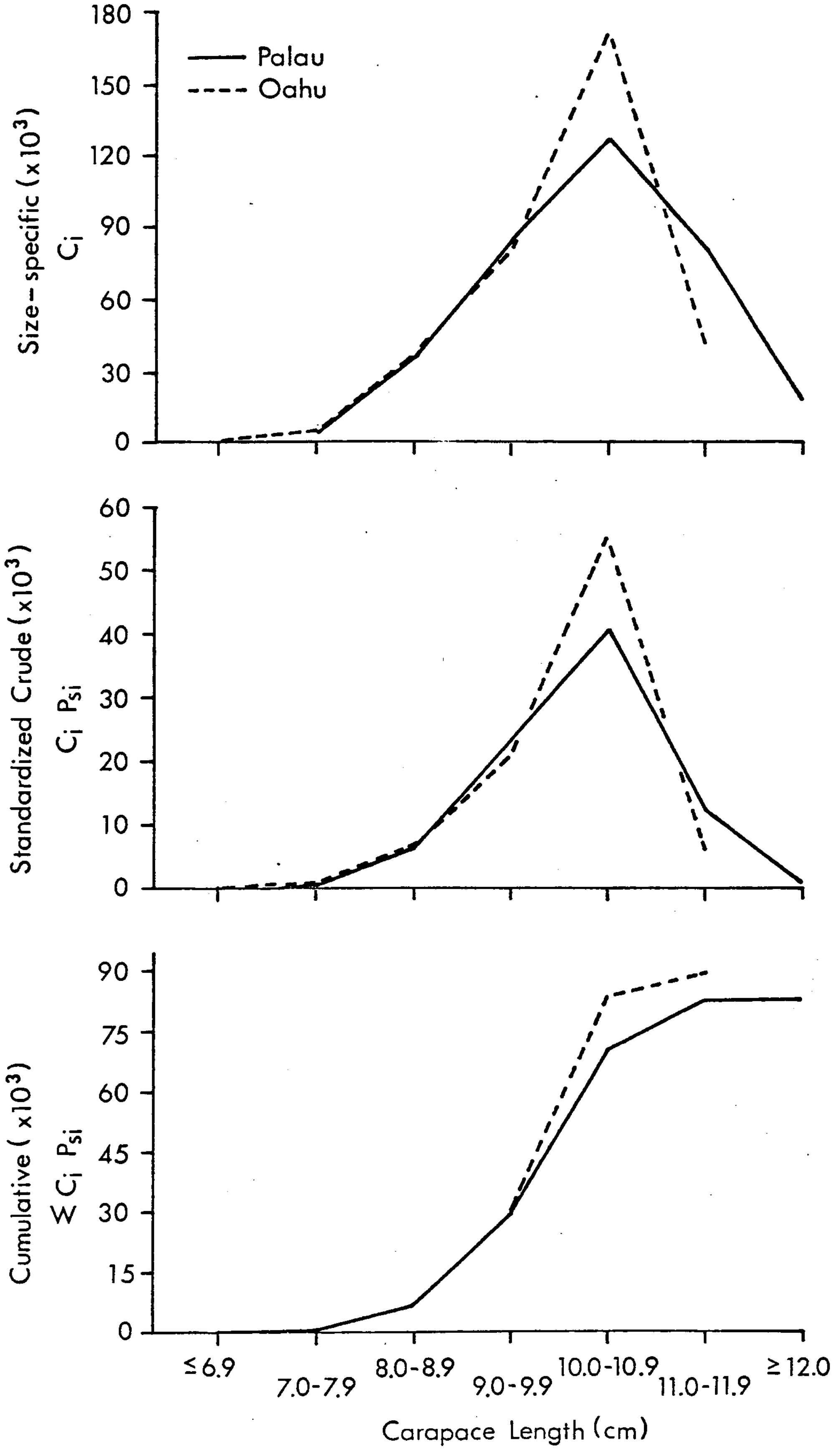

FIGURE 19. Comparison of size-specific, standardized crude, and cumulative standardized crude reproductive rates of female <u>Panulirus penicillatus</u> at Palau and Oahu.

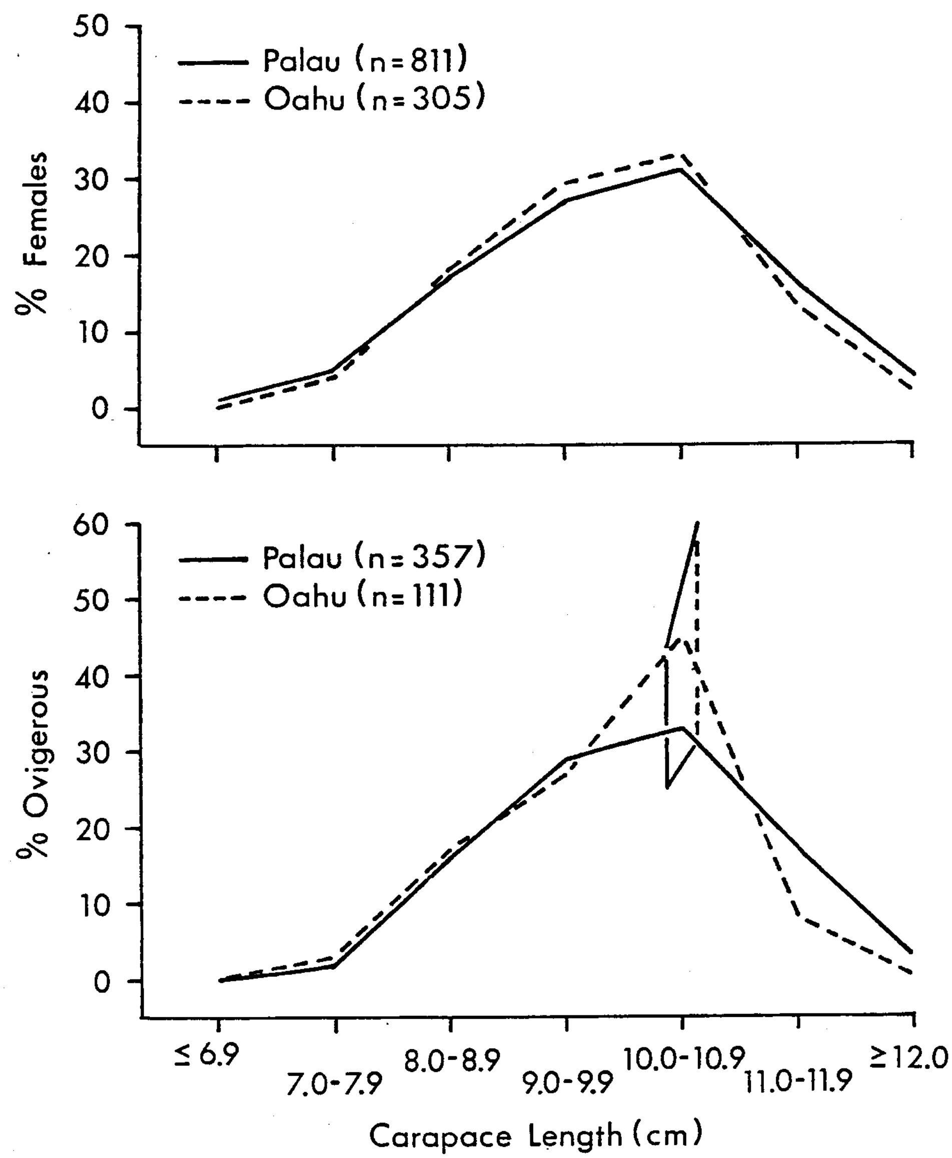

FIGURE 20. Comparison of size class proportions of total female and ovigerous female Panulirus penicillatus at Palau and Oahu. The 95% confidence envelope is plotted about the proportions of ovigerous females in the 10.0-10.9 cm size class at both locations.

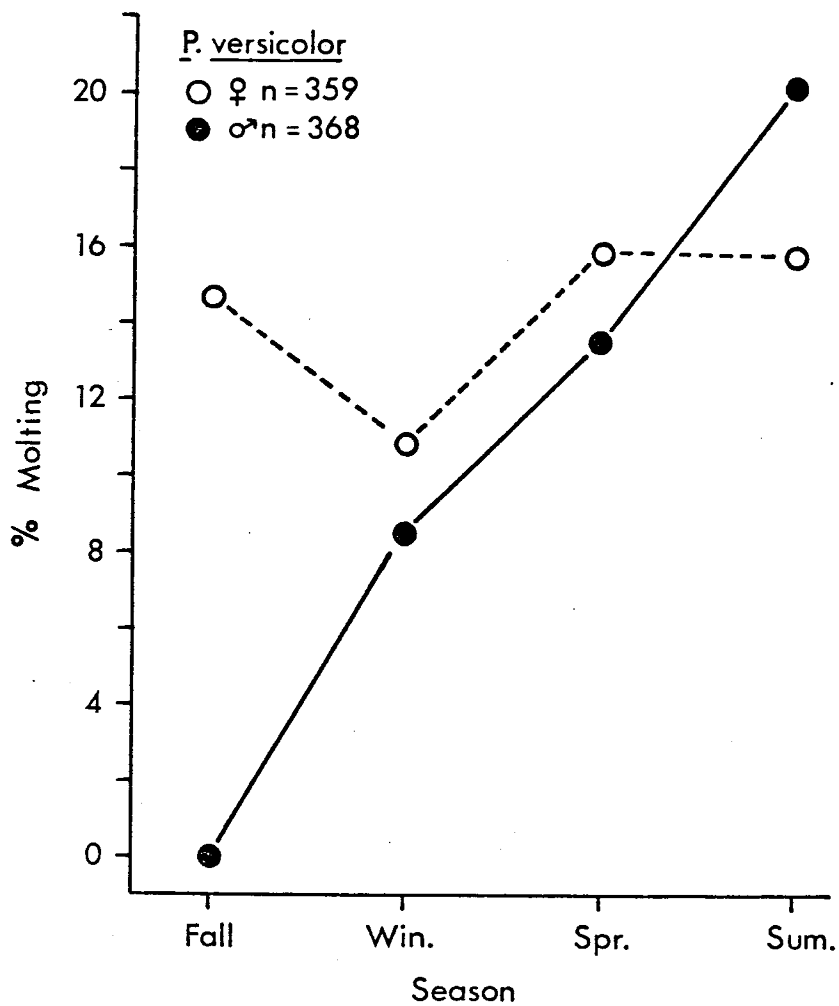

FIGURE 21. Seasonal changesin exoskeleton condition of male and female <u>Panulirus versicolor</u> at Palau.

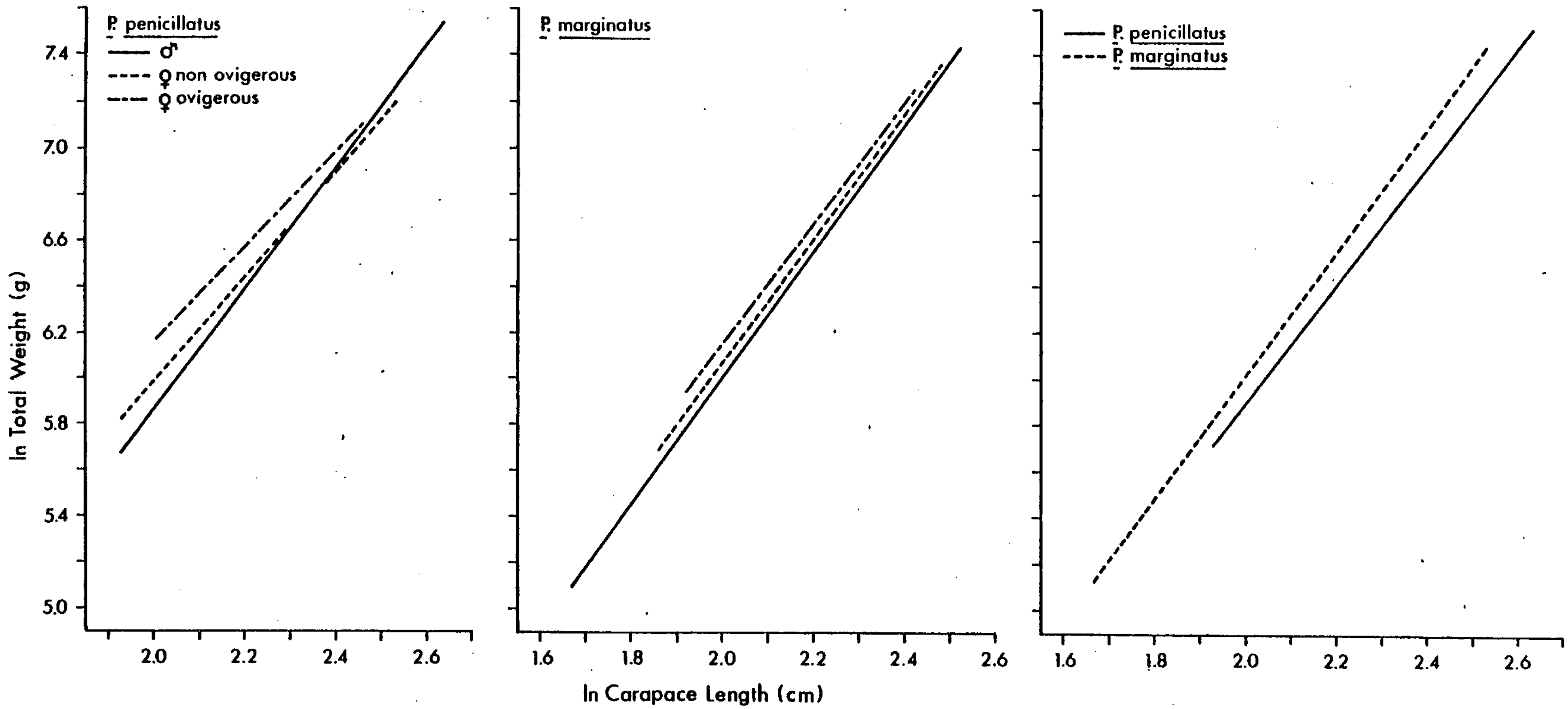

FIGURE 22. Regressions of total weight fresh on carapace length in male and ovigerous and non-ovigerous female <u>Panulirus penicillatus</u> and <u>Panulirus marginatus</u> at Oahu.

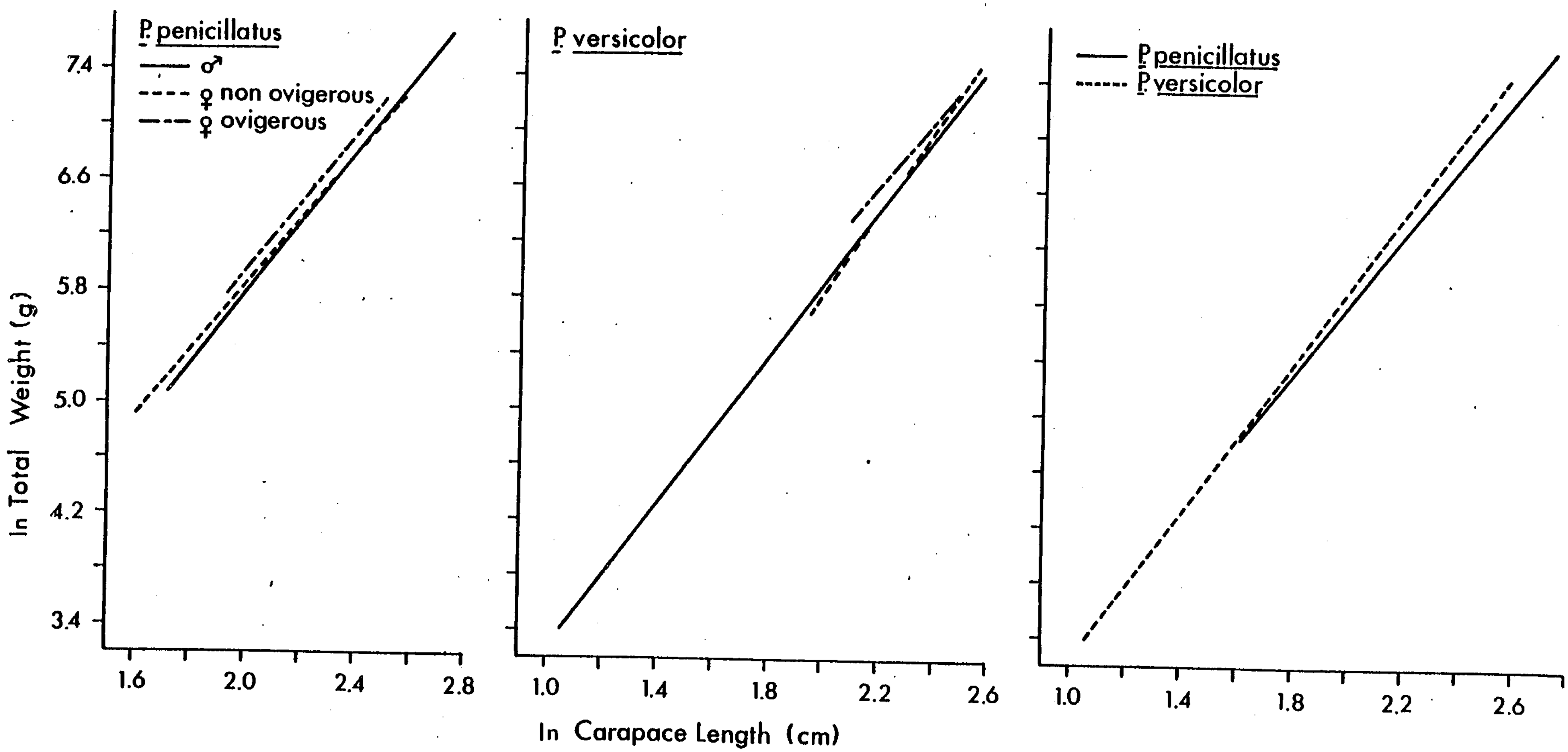

FIGURE 23. Regressions of total weight fresh on carapace length in male and ovigerous and non-ovigerous female _Panulirus penicillatus_ and _Panulirus versicolor_ at Palau.

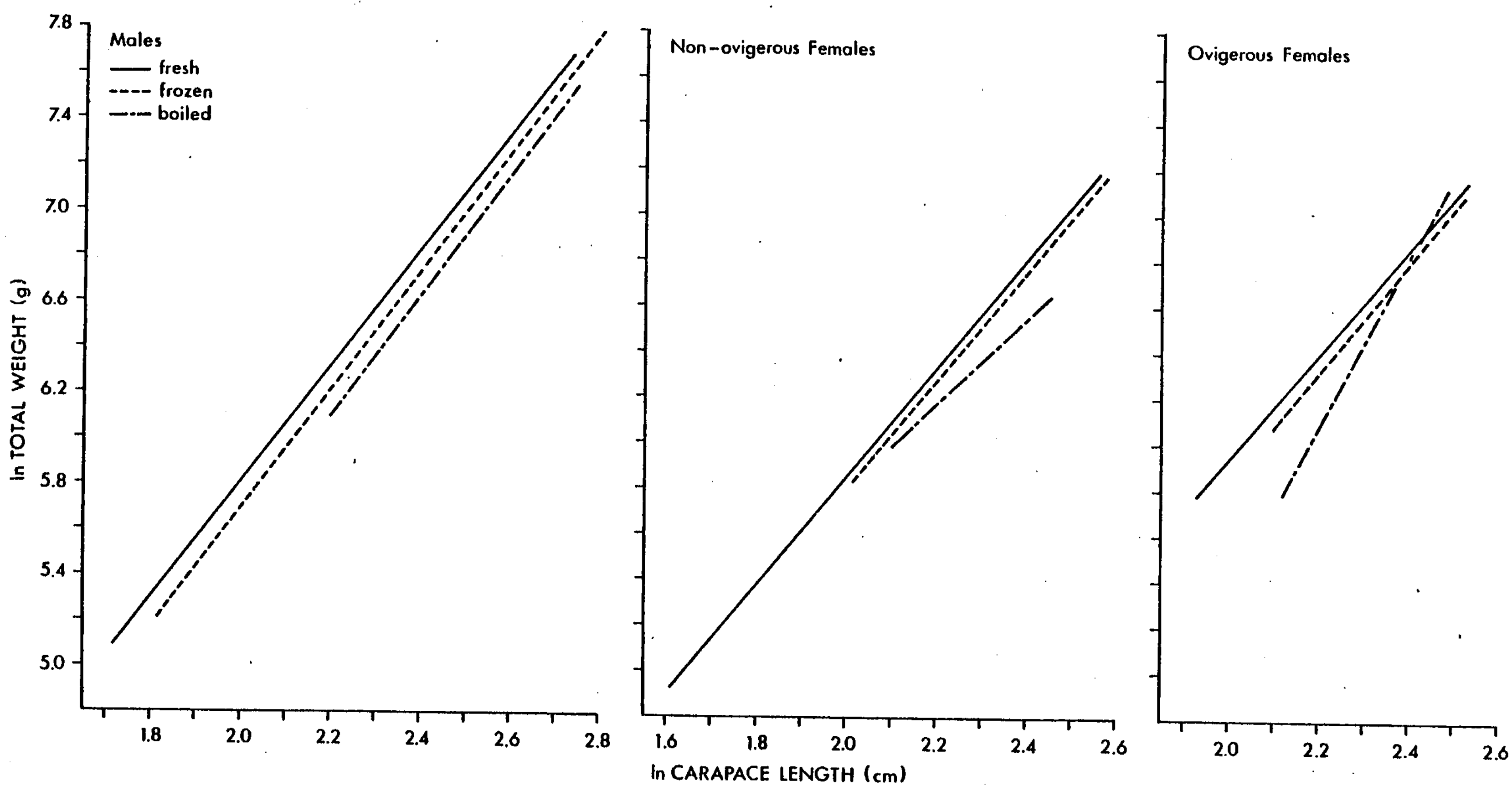

FIGURE 24. Regressions of total weight fresh, frozen, and boiled on carapace length in male and ovigerous and non-ovigerous female Panulirus penicillatus at Palau.

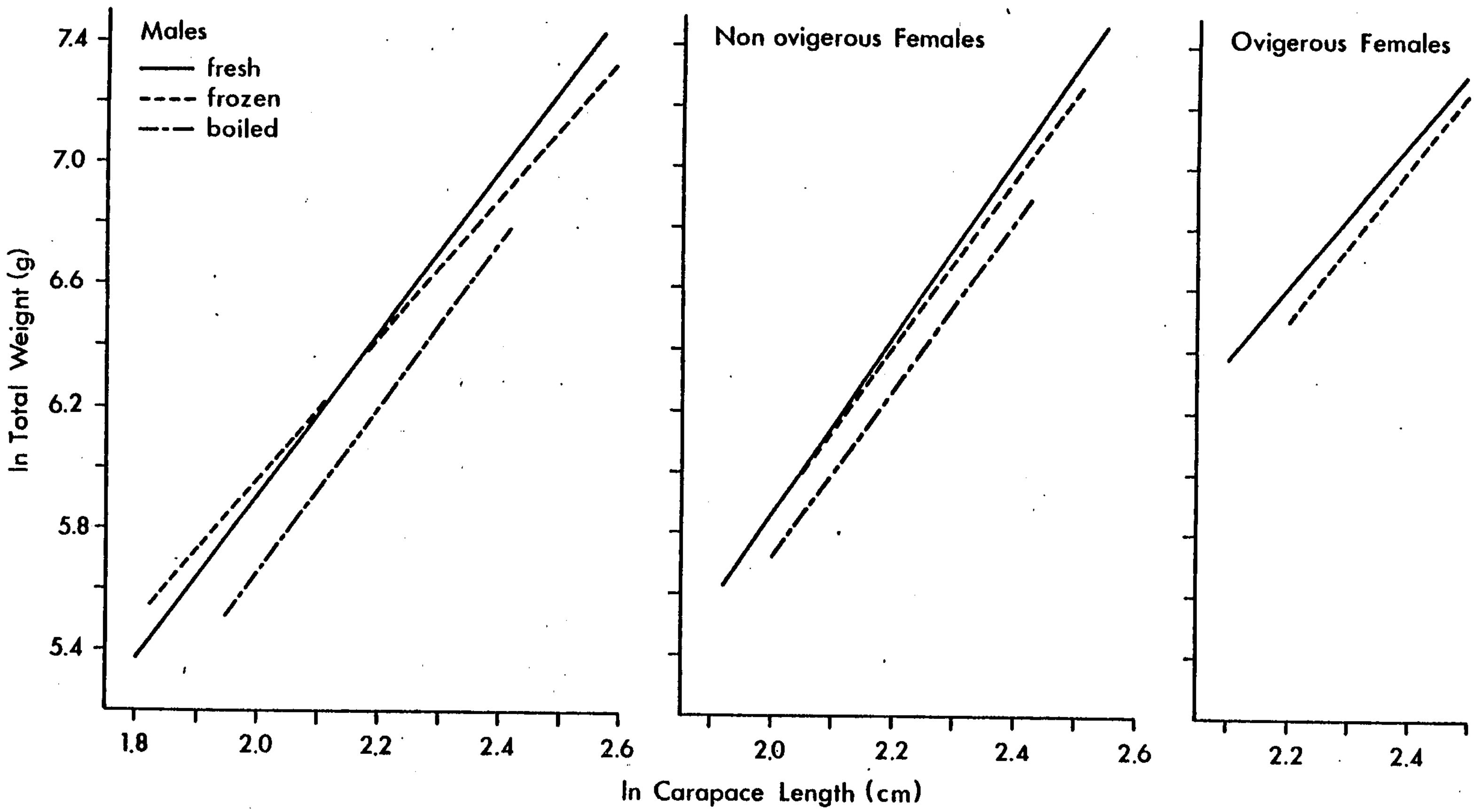

FIGURE 25. Regressions of total weight fresh, frozen, and boiled on carapace length in male and ovigerous and non-ovigerous female _Panulirus versicolor_ at Palau.

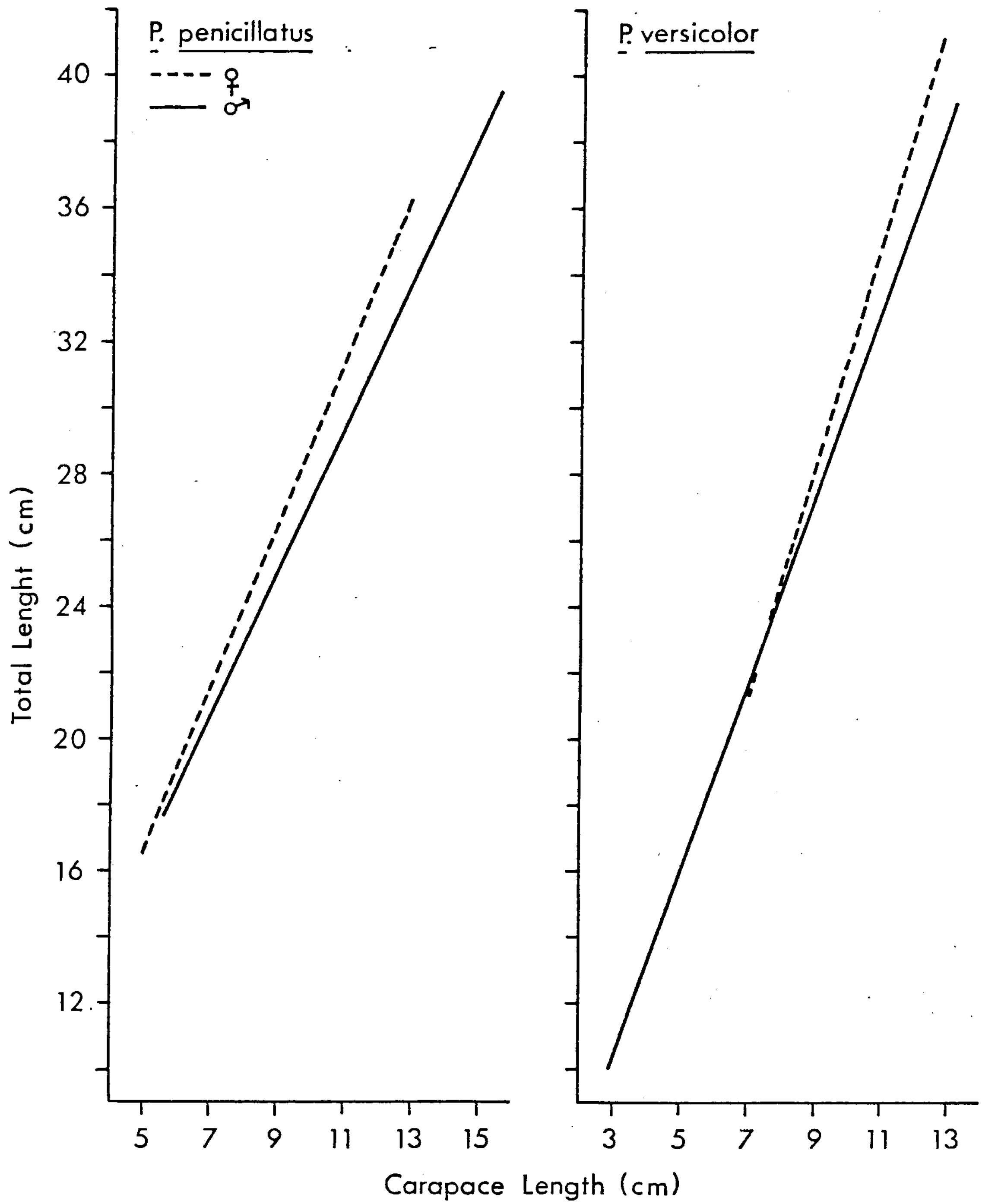

FIGURE 26. Regressions of total length on carapace length in fresh male and non-ovigerous female Panulirus penicillatus and Panulirus versicolor at Palau.

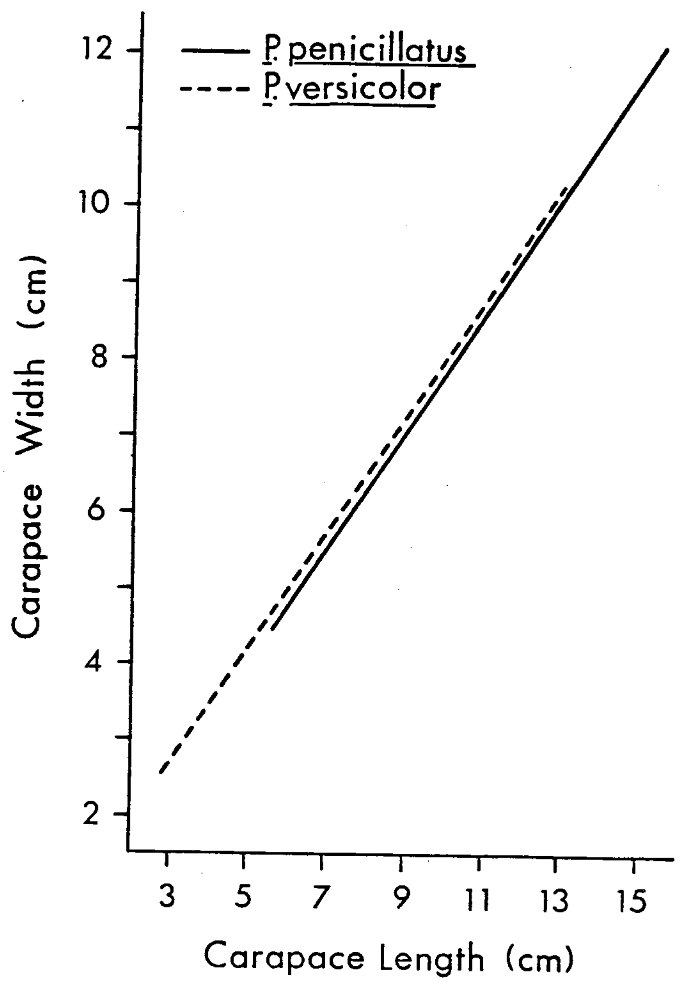

FIGURE 27. Regressions of carapace width on carapace length in pooled male and female Panulirus penicillatus and Panulirus versicolor at Palau. Measurements from fresh lobsters only.