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Title: The Occurrence and Natural Habitat of the Mangrove Crab, *Scylla serrata* (Forskal), on Ponape and Guam

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The natural habitat of the mangrove crab, *Scylla serrata* (Forskal) is described, and various physical data from habitats where mangrove crabs occur are presented. Physical data included temperature, dissolved oxygen, and salinity. *S. serrata* tolerated low dissolved oxygen levels in the field, as low as 0.7 ppm, and often experience extended periods of aerial respiration. Crabs occurred in zones of continuously variable salinity, but evidence indicated that larger individuals, especially large males, occurred more often in water of high salinity (greater than 25 ppt).

Gut analyses were performed on crabs from Ponape and Guam. Ponape individuals fed primarily on the bivalve *Geloina papua* (Lesson). Guam individuals fed mostly on a benthic grapsid crab, *Ptychognathus ishii* Sakai. Other food items are listed. Fish were rarely eaten.

Tagging studies indicated that crabs may remain in the same channel or river for up to one month or more.

A series of morphometric measurements were made on individuals captured in the field. There is a sexual dimorphism in cheliped size;

the growth rate of the male cheliped is faster than the growth rate of the female cheliped. The relationship of prey size and cheliped size as important factors regulating the distribution of mangrove crabs is discussed.

Crabs were maintained in small cubicles and in water of different salinity. Twelve individuals molted at least once and percentage increase in growth agreed well with growth data from work done elsewhere.

THE OCCURRENCE AND NATURAL HABITAT OF THE MANGROVE CRAB, SCYLLA SERRATA (FORSKAL), AT PONAPE AND GUAM

by

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TO THE GRADUATE SCHOOL:

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Introduction

The mangrove crab, Scylla serrata (Forskal), is the largest species of the crustacean family Portunidae known (Guinot, 1966). Estimates of its maximum size are in excess of 20 cm across the carapace, weighing more than 2 kgs (Guinot, 1967).

The natural range of Scylla serrata (Fig. 1) extends from Mossel Bay in South Africa (MacNae, 1968) along the east African coast including Mauritius and Madagascar (Barnard, 1950) to the Red Sea (Stephenson and Campbell, 1960). The range continues eastward to India and Sri Lanka (Jones and Sujansingani, 1952; Raphael, 1970; Chandy, 1973) and throughout Indonesia, the Philippines, and Malaysia (Arriola, 1940; Ong, 1966). Northward, it occurs in Thailand, China, and Taiwan (Tamura, 1966) and the northern limit is the mouth of the Tone River in Japan (Sakai, 1976). S. serrata is also found along the Australian coasts from Broome, West Australia north and east to Northern Territory and Queensland, and New South Wales to Port Jackson (Stephenson, 1972). It also occurs in New Zealand (Stephenson and Campbell, 1960) and the Pacific islands including the Caroline and Mariana Islands, Samoa, the Tuamotus (Bablet and Cayet, 1972), and Hawaii. It was successfully introduced into the latter from Samoa between 1926 and 1935 (Brock, 1960). This entire region encompasses an area referred to as the Indo-West Pacific (Ekman, 1953).

Wherever it occurs throughout the Indo-West Pacific it is a highly prized food and brings a high market price. In Guam alone, more than 93,000 individuals were imported between July 1975 and July 1976.

Because it is a widely sought delicacy, many fisheries have developed around it and commercial exploitation occurs in South Africa (Hill, 1976), Singapore (Thia-eng, 1974), India (Thomas, 1972) and on many of the Pacific islands. In addition to commercial fishing, S. serrata has been cultured in localized regions of the Indo-West Pacific (Arriola, 1940; Tamura, 1966; Raphael, 1970; Varikul, et al., 1972; Chen, 1975 (unpublished): Crab culture. Copy available at University of Guam Marine Laboratory). It is often cultured as a secondary product of milk-fish (Chanos chanos) ponds (Pillay, 1954; Guinot, 1967; Pagactipunan, 1972; Escritor, 1972).

The early life history of S. serrata has been completed with successful hatching of eggs from berried females through the five zoea and single megalopa stages to juvenile crab (Estampador, 1949b; Raja Bai Naidu, 1955; Ong, 1964; Brick, 1974; Hill, 1974). There is some general information regarding growth (Escritor, 1972; Pagactipunan, 1972; Varikul, et al., 1972), but precise growth and molting data are limited to only a few papers (Arriola, 1940; Ong, 1966; Raphael, 1970; DuPlessis, 1971 (unpublished): A preliminary investigation into the morphological characteristics, feeding, growth, reproduction and larval rearing of Scylla serrata Forskal, held in captivity. Copy available at University of Guam Marine Laboratory).

Adult S. serrata have been used for neural physiological and histochemical research. Many of the former have dealt with the statocyst and a series of papers were written describing the structure

and function of the statocyst and its neural connections to the eye muscle motor neurons (Okajima and Sandeman, 1972; Sandeman and Okajima, 1973a-b; Silvey, 1974; Silvey and Sandeman, 1976a-c; Silvey, et al., 1976). Another group of investigators studying the statocyst have monitored its neural response after experimental activation and inactivation of antennulary nerves (Sandeman, 1975; Fraser and Sandeman, 1975; Fraser, 1976a-b). Other papers dealing with the neurophysiology of this crab include a description of some of the neurosecretory cells and axon fibers in the central nervous system (Deshmukh and Rangneker, 1966) and a description of the close contact and excitation between the small nerve terminals in the brain neuropile and higher order central branches of the reflex-eye withdrawal motoneurons (Sandeman, 1971; Sandeman and Mendum, 1971).

The important amino acids in the blood of S. serrata have been identified (Krishnamurthy, et al., 1967), the blood plasma proteins have been used in comparative physiological studies with molluscs and other crustaceans (Rangneker, 1955), and the blood volume of S. serrata has been compared with other crustaceans (Rangneker, 1954). Additionally, the blood has been used as part of a study to determine whether the electrophoretic patterns of the haemolymph proteins might be useful as taxonomic characters (Lee and Lim, 1973; Maguire and Fielder, 1975).

The exoskeleton of Scylla has been studied and the molecular and protein arrangement of the cuticle described (Hackman, 1974 and 1975) and the amounts of certain amino acids in the cuticle are known (Airan

and Karat, 1953). The chitin from Scylla has been used in research involving the physical properties of crab shell (Hepburn, et al., 1975; Hepburn and Chandler, 1976).

In addition to these studies, S. serrata has been used in many endocrine experiments. The eyestalks of crustaceans are known to contain glands which secrete hormones essential for metabolism and growth (Carlisle and Knowles, 1959; Passano, 1960; Kleinholz, 1967) and experiments concerning these have been conducted on Scylla. Through eye-stalk ablation in S. serrata it has been shown that the x-organs in the eye-stalks are the site of synthesis for factors responsible for regulating blood sugar (Menon and Sivadas, 1967; Deshmukh and Rangneker, 1973) and oxygen consumption (Rangneker and Madhyastha, 1969), activating glycolytic enzymes (Rangneker, Vyanjoki, and Momim, 1975) and lipolytic enzymes (Momin and Rangneker, 1975a-b), controlling oxidative metabolism in the hepatopancreas (Nagbhushanam and Rao, 1968; Momin and Rangneker, 1976), stimulating glycogenolysis and accelerating glycogenesis (Rangneker and Momin, 1975a), maintaining high concentrations of calcium and sugar in the blood during proecdysis (Menon and Sivadas, 1968), causing an increase in weight and size of ovaries in females (Rangneker and Deshmukh, 1969) and increasing the weight of the testes, the diameter of the seminiferous tubules and number of cells per tubule in males (Rangneker, Madhyastha, and Latey, 1971). Additional histochemical work on localizing and describing oxidative enzymes in the hepatopancreas has been done (Momin and Rangneker, 1974; Rangneker and Momin, 1975b).

Some other physiological work has been carried out with S. serrata including the successful staining and description of cell organelles

(Bhattacharya, 1931) and ovaries (Baneriji, 1932), a study of the excretory system and relationship between the antennary glands and osmoregulation (Samuel, 1945), the activity of protease in the gut (Saha and Raychaudhuri, 1973), the discovery of chromatotrophorins in sinus gland extracts, optic ganglia, and other parts of the central nervous system (Deshmukh and Rangneker, 1965), and the recognition of 106 chromosomes in the diploid cell (Niiyama, 1942).

Scylla serrata has also been used as a test animal for neural work involving extracellular and intracellular recording of behavioral reflexes (Steinacker, 1975) and has been chosen as an indicator of radioactive contamination near a nuclear facility (Patel, Mulay, and Ganguly, 1975).

There appears to be some polymorphism among different geographic populations of S. serrata, and two authors have divided the genus into three species (Estampador, 1949a; Serene, 1951) although most recognize only one species (Stephenson, 1972; Sakai, 1976).

Despite its broad Indo-West Pacific distribution and popularity as a food item and research animal, there is a paucity of published information regarding the natural habitat of this crab. Most accounts are general descriptions (Musgrave, 1929; Arriola, 1940; MacNae and Kalk, 1958; Stephenson, 1972).

It is known to be primarily a brackish water animal and is the only portunid characteristically found in mangrove swamps (MacNae, 1968). It digs deep burrows (up to 5 m in depth) among the Avicennia roots or can be found lounging on Rhizophora roots or under rocks (Guinot, 1966). Besides mangrove swamps, it can be found in river mouths and estuaries, wherever brackish water and sandy mud bottoms occur. It is

often found far up freshwater rivers (Stephenson and Campbell, 1960) and in one report Scylla serrata was noted from Hankow, hundreds of miles up the Yangtse River in China (MacNae, 1968).

Although it is more common in brackish areas, it does venture into waters of higher salinity and is captured in open bays at depths greater than 7.0 m (Raphael, 1970; Brick, 1974). It has also been recorded from the island of North Keeling (Cocos Keeling atoll) where virtually no freshwater occurs (Gibson-Hill, 1948). Furthermore, specimens of S. serrata have been found in a fresh state in the stomachs of 30 tiger sharks which had been caught 20 km from the continental shelf and 50 km from the coast of Madagascar (Crosnier, 1962). It is known that female S. serrata migrate to the open ocean to spawn (Ong, 1966; Hill, 1974) but whether this species normally inhabits the open ocean is unknown. Some experimental work has been done raising larval and juvenile mangrove crabs under variable salinities and temperatures (Ong, 1964; Krishnamoorthy and Venkatramiah, 1971; Veerannan, 1972; Hill, 1974), but there is no information regarding the in situ range of these parameters.

In addition, there are very little data concerning natural crab populations. There are some brief accounts dealing with crab migrations (Crosnier, 1962; Day, 1969; Hill, 1974), but these refer primarily to the movements of ovigerous females to areas of higher salinity for spawning. There has been some work regarding crab movements in the field (Hill, 1975), but there is no information concerning the distribution of crabs, by sex or size, throughout the habitat.

The first objective of this study was to describe the natural habitat of Scylla serrata. This was accomplished by gathering in situ

physical data from habitats where mangrove crabs were known to occur. These measurements included the temperature, salinity, and dissolved oxygen of both surface and bottom waters. In these same areas field observations were made to describe the habitat of S. serrata, and a collection of the fauna living in the habitat was made to be considered as possible food items. The dominant flora was also noted. Finally, interviews with fishermen were conducted to gather valuable local knowledge about the natural history of the crab.

Secondly, in order to establish crab movements and distribution in the field, baited traps were used. Traps were set periodically at stations and captured crabs were tagged, measured, and released.

The third objective was to maintain crabs in the laboratory and to monitor growth increments and frequency of molting.

Finally, a series of morphometric measurements were made on crabs from five different geographic locations. These measurements were then statistically tested to see if there were any differences among them.

Materials and Methods

Natural Habitat

The field investigations were conducted at two different geographic locations: Ponape in the Eastern Caroline Islands (July - August, 1976) and Guam in the Mariana Islands (September, 1976 - January, 1977). At each of these two locations (Fig. 2), study areas were chosen where the habitat data would be taken and trapping conducted.

On Ponape, study areas were established in the Kamar area and at Takatik Island (Fig. 3); both of these areas are mangrove swamps. The physical data were taken primarily from these sites, however observations were made at three additional areas: Palikir, Patoi, and Sokehs (Fig. 3).

The sampling and trapping stations in the Kamar area were located along the shore of a major drainage channel and in two small rivers which emptied into the channel. The uppermost navigable reaches in the small rivers were designated as the "upper" zones. The areas halfway between the upper zones and the channel were designated the "middle" zones and the channel was designated as the "lower" zone (Fig. 4).

The sampling and trapping stations in the Takatik area were located in a small channel that historically had been continuous all of the way across the island of Takatik. However, when the Ponape airport was built, the middle of the island was filled and the channel was

permanently blocked. The stations for this study were located in the channel, from the southern entrance to approximately 600 m inland (towards the airport runway). This channel was considered to be a single zone (Fig. 4).

Three rivers were chosen as study areas at Guam: Pago River, Ylig River, and Talofofo River (Fig. 5). However, because of logistical difficulties and poor trapping success, sampling at the Pago and Talofofo Rivers was discontinued.

These three rivers all empty into the Pacific Ocean on the eastern shore of Guam (Fig. 5). The trapping and sampling stations in each river were located in different zones. These zones are defined as they have been for Kamar at Ponape, except the lower zones for the Guam study were the areas near the mouths of the rivers (Figs. 6-8).

The study areas for Ponape and Guam were accessible only by boat with outboard motor to carry personnel, instruments, and traps to and from the field.

Water temperatures were taken during both the rising and the falling tides by dipping out a water sample using a KAHLSICO engraved stem thermometer with PVC bucket frame for surface temperatures and using a Hydro Products XRB-135 VanDorn sampler to retrieve bottom water samples. The sample was brought immediately to the surface and a quantity was poured into the bucket thermometer for reading.

Salinity was obtained using an American Optical Goldberg refractometer with special scale for salinity (in parts per thousand). The VanDorn sampler, described above, was also used to collect water for the bottom salinity measurements.

Dissolved oxygen was measured using a Yellow Springs Instrument Company dissolved oxygen meter (Model 51 A) with 3.05 m probe. The meter was corrected for temperature and salinity, and the dissolved oxygen was recorded in parts per million.

An attempt was made to measure water turbidity using a secchi disc at the Ponape study areas, but the mangrove swamp channels were too shallow and the disc proved to be impractical. For Guam study areas, a bottom water sample was retrieved and brought to the Marine Laboratory for analysis using a HACH Model 2100 A turbidimeter. Bottom water samples on Guam were also taken for nitrate, nitrite, and phosphate analysis. The sample was retrieved using the VanDorn sampler and unit quantities were poured into linear polyethylene bottles. The water samples were packed in ice until brought to the Marine Laboratory where the water samples were frozen. The samples were later thawed and analyzed using methods described by Strickland and Parsons (1968) to determine reactive nitrite and nitrate (cadmium reduction method).

Faunal collections were made by walking through the swamps during low tides (Ponape) or collecting from the boat along the river banks (Guam); snorkelling in the channels and rivers was also done. Additionally, organisms other than S. serrata were occasionally found in the traps. All animals collected were preserved in either 70 percent ethyl alcohol or a 10 percent solution of formalin and identified to species where possible. Dominant vegetation was recorded in field notebooks.

Mark-Recapture

Two types of traps were used for capturing crabs. On Ponape, the traps were made from 12.7 mm galvanized screen and formed into the shape of a quonset hut. A 0.9 m x 1.5 m piece of screen was cut and laid flat. Then, measuring 0.9 m along the long side, the screen was folded up and the remaining 0.6 m x 0.9 m section formed the bottom, and the upfolded section was joined to the other end to form the quonset. A smaller entryway was made at each of the open ends by fastening pieces of wire screen to the sides forming an elliptical ramp leading into the trap and a cylindrical bait container was wired to the bottom. A small door was made in the top for access to the bait container, and a large door was made in the bottom to remove crabs. Both doors were fastened closed when the trap was in use.

The traps used on Guam were constructed from 6.3 mm black plastic screen (Takiron Trical Netting) and folded into rectangular boxes. The box traps were 0.8 m x 0.6 m x 0.3 m in size with flat ramps leading in from the open ends. Additionally, 0.8 m x 0.3 m rebar (6.3 mm diameter) frames were fastened to the ends to provide extra weight and support. Cylindrical bait containers were fastened with tire inner tube straps to the bottom of the trap. A large door was cut in the bottom of the trap for removing crabs and for access to the bait container. The bottom door was held closed by inner-tube straps when the trap was in use.

The traps were set on the bottom of the channels and rivers by attaching one end of a rope to the top of the trap and the other end to roots or vegetation along the bank. On Ponape, twenty permanent

trapping stations were established in the Kamar area and ten at Takatik Island (Fig. 4). On Guam, twelve trapping stations were established in Pago River (Fig. 6), twenty-five in Ylig River (Fig. 7), and twenty in Talofofo River (Fig. 8).

The Ponape traps were monitored for five or six day periods and checked twice daily if possible. On days when tides were too low the trapping stations were accessible only once a day.

Trapping on Guam was conducted for three day periods and traps were checked each day. In addition, 24-hour trapping periods were conducted at Ponape and Guam. During these periods, physical data (water temperature, salinity, dissolved oxygen, and depth) were recorded and the traps were checked every three hours.

Captured crabs were tagged by scratching a number on the carapace with a scriber. The respective length and width of carapace, and heights of right and left palm were measured to the nearest millimeter using vernier calipers. The wet weight was measured to the nearest 25 grams using an Ohaus spring scale. Also recorded were the sex, time, and station of capture before the crab was released.

Bait for the Ponape traps consisted of spoiled reef fish. On Guam, spoiled fish were used but other baits were tried including land snails (Achatina fulica), toads (Bufo marinus), and hermit crabs.

In addition to using traps on Ponape, a series of walking forays into the swamps were made. These expeditions were made during the low tides when crabs can be found sitting stationary on the mud or in deep oval-shaped burrows. Once a crab was found, indicating a suitable habitat, a quadrat 18.3 m wide and 45.7 m long (0.08 hectares) was

roped off, then the area was carefully searched for crabs and crab holes. Crabs found were measured as described above but were not tagged.

During the latter part of the trapping studies on Guam, 24 crabs were dissected and a gut analysis was made to see if different foods were being consumed by crabs from different parts of the river. Although the crabs were caught in baited traps, the bait was readily separated from other stomach contents. In addition, 28 individuals from Ponape were dissected for comparison.

Laboratory

Crabs used to obtain molting frequency and growth increment information were captured during the mark-recapture studies on Guam (Ylig and Talofofo Rivers only). Crabs were brought from the field to the Marine Laboratory and kept separated in a large holding tank.

The resin- and fiberglass-coated wooden holding tank was permanently separated into two parts by a resin-coated wood divider. One part was an open system with flowing seawater (10.8 ℓ/min) pumped from Pago Bay and with an ambient salinity of 31 parts per thousand (ppt) $\pm$ 2 ppt. The other was a closed system (9.0 ℓ/min) utilizing crushed coral filtration. Water was pumped from the drainage sump of the closed system into the bottom of a plexiglas box filled with crushed coral (0.6 m x 0.2 m x 0.25 m). The water was forced up through the filter and allowed to flow out the top of the filter box back into the holding tank. The salinity for the closed system was kept at 20 ppt $\pm$ 2 ppt. Temperatures were virtually the same for both parts and

varied from 27°C to 30°C. Dissolved oxygen levels were also identical and ranged from 5.6 ppm (parts per million) to 6.2 ppm for both.

The two parts were each divided into 18 cubicles, 16.5 cm x 24.1 cm x 10.1 cm. Resin-coated wood was used for the partitions. These partitions were placed loosely into position and water flowed between compartments. The partitions prevented crabs from fighting and injuring each other as well as providing protection from cannibalism following ecdysis. A resin-coated lid with 2.5 cm diameter holes was placed over the top.

Additionally, since these crabs are burrowers, a 3.0 cm thick layer of crushed coral was placed on the bottom of each of the cubicles. Individual crabs were placed in the cubicles and fed daily with chopped fish and shrimp. If a crab molted, the date was recorded and the shed carapace removed. The remainder of the exoskeleton was left for the crab as a source of calcium to expedite the hardening of the new shell.

Comparative Morphology

A series of morphometric measurements was made on crabs from Palau, the Philippines, Taiwan, Ponape, and Guam. Crabs from the first two locations are regularly imported to Guam and visits to local markets were made to measure them. The Taiwan crabs were part of a shipment sent to the Guam Fish and Wildlife Division, and crabs from the latter two locations were measured during the trapping studies previously described.

The measurements taken were the same as those recorded during the mark-recapture studies on Ponape and Guam and were measured with Vernier calipers to the nearest millimeter. The length of carapace is the

distance from the base of the third and fourth frontal lobes across the dorsal carapace surface to the most posterior point of the carapace. The width is the distance from the base of the eighth and ninth anterolateral teeth on one side of the carapace to the same position on the other side. The height of the palm is the distance normal to the axis of the palm, from the ventral surface to the base of the two spines at the distal end of the palm. Wet weights were measured using the spring scale and recorded to the nearest 25 grams.

Results

The Kamar study area lies within a major drainage area and freshwater runoff into the adjacent rivers and channel causes an extensive surface layer of freshwater to form. This layer accounts for the cooler water temperatures recorded at the surface for each station when compared with the respective bottom temperatures. The mean temperatures of both surface and bottom waters became progressively warmer from the upper to the lower zone and bottom water was significantly warmer ($p<.01$, t-tests) than surface water for all zones. Additionally, the bottom water from the lower zone was significantly different (warmer) at the 99% significance level ($t_{s[35]}= 4.37$) than bottom water from the upper zone. The mean surface temperatures ranged from 27.12°C to 27.21°C and mean bottom temperatures ranged from 28.18°C to 30.28°C for the upper and lower zones, respectively. Combining data for all Kamar zones, the range for surface temperatures was 25.4°C to 30.2°C and the range for bottom temperatures was from 26.3°C to 31.8°C. Tables 1 and 2 contain the ranges, means, and standard deviations of water temperature, salinity, dissolved oxygen and turbidity for all zones at Ponape and Guam.

Takatik Island is influenced by freshwater runoff and a brackish surface layer is present although there was no significant difference between the surface and bottom water temperatures ($t_{s[6]}= 0.86$). The temperature range for surface water at Takatik was from 27.0°C to

29.8°C (mean: 28.9°C) and bottom water temperatures ranged from 27.0°C to 32.0°C (mean: 30.08°C).

Water temperature trends for the Guam study areas were similar to those at Kamar. The warmest water for each river, both at the surface and the bottom, was recorded at the lower zones. In Ylig River there was no significant difference between surface and bottom water at the upper zone but the bottom temperatures at the middle and lower zone were significantly warmer ($p<.05$, t-tests) than the respective surface temperature. There was no significant difference between surface and bottom water temperatures at the upper zone and the respective water temperatures at the lower zone. The mean water temperatures at the lower zones were 29.8°C, 28.36°C, and 30.5°C and the mean bottom water temperatures were 30.63°C, 29.61°C, and 29.6°C for the Pago River, Ylig River, and Talofofo River, respectively. The upper zone surface water temperatures ranged from a mean low of 28.14°C (Ylig) to a mean high of 29.5°C (Pago).

The salinity for Kamar was also effected by the freshwater runoff as evidenced by the low surface salinities when compared to the respective bottom salinities; differences were at the 99% significance level for all zones. The mean salinity for the bottom water also decreased progressively from the lower to the upper zones. The mean bottom salinities were 24.47 ppt, 18.46 ppt, and 16.4 ppt for the lower, middle, and upper zones, respectively. The bottom salinity values between the upper and lower zones were different at the 99% significance level ($t_{s[35]}= 3.42$). Combining salinities for all zones at Kamar, the surface salinities ranged from 1.0 ppt to 28.0 ppt and bottom salinities ranged from 5.0 ppt to 30.0 ppt.

Salinity readings at Takatik Island showed no difference between surface and bottom water and ranged from 24 ppt to 26 ppt for both.

Salinities recorded from the Guam study areas were similar to those recorded at Kamar. The lowest mean salinities for surface and bottom waters were recorded at the upper zones and the highest mean salinities for surface and bottom waters were recorded at the lower zones. Lower zone bottom salinities ranged from a mean of 16.0 ppt (Talofofo) to a mean of 32.3 ppt (Pago) while upper zone bottom salinities ranged from a mean of 8.6 ppt (Talofofo) to a mean of 31 ppt (Pago). There was no significant difference in the bottom salinities between upper and lower zones in Pago and Talofofo. However, the upper and lower zone bottom salinities in Ylig were significantly different at the 99% significance level ($t_{s[17]}= 4.94$).

The dissolved oxygen in water at Kamar also varied among the zones. The mean dissolved oxygen levels for surface water were consistently higher than the respective mean dissolved oxygen level for bottom water; differences were significant for all zones ($p<.01$, t-tests). The highest mean dissolved oxygen level was 6.47 ppm and was recorded from the surface water at the lower zone. The surface water for the middle and upper zones had mean dissolved oxygen levels of 4.61 ppm and 3.86 ppm, respectively. Mean dissolved oxygen for bottom water increased from 2.19 ppm at the upper zone to 3.83 ppm at the lower zone; this difference was significant the 99% level ($t_{s[35]}= 5.29$).

There was no significant difference between the amount of dissolved oxygen in surface and bottom water at Takatik Island, although mean values of dissolved oxygen were lower for bottom water. The mean for surface water was 3.95 ppm and the mean for bottom water was 3.0 ppm.

The surface water at Guam study areas had higher mean dissolved oxygen levels than the respective bottom water, with the exception of the lower zone at Talofofo where bottom levels were higher. The mean dissolved oxygen for all zones in Ylig were significantly higher ($p<.05$, t-tests) in the surface water than the respective bottom water. There was no common gradient in mean dissolved oxygen among zones in the different rivers and mean dissolved oxygen levels for surface water ranged from a high of 6.8 ppm in the upper zones of Ylig and Talofofo to a low of 4.8 ppm at the middle zone of Pago. The highest dissolved oxygen level for bottom water was 7.8 ppm at Talofofo (lower zone) and the lowest was 2.9 ppm at Pago (middle zone).

The water turbidity at the Guam study areas fluctuated greatly. The upper and middle zones in Ylig had the clearest water sampled with a value of 1.2 ntu (nephelometric turbidity units) for each zone. These same two zones also had the most turbid water with turbidity readings of 25.0 ntu at each. The lower zones for Pago and Ylig had consistently clear water with mean turbidity values of 3.2 ntu and 3.28 ntu, respectively.

The phosphorus, nitrite, and nitrate data were obtained at Pago and Ylig only (Table 3). The highest level of reactive phosphorus was recorded at the lower zone in Pago and had a value of 0.0152 mg/ℓ. The lowest value was recorded from the upper zone at Ylig where less than 0.001 mg/ℓ was recorded.

The nitrite in the water was highest at the middle zone of Pago and had a value of 0.004 mg/ℓ. There was no detectable reactive nitrite at the upper and lower zones of Ylig.

The nitrate ranged from a high of 0.07 mg/ℓ in the water of the lower zone in Pago and a low of 0.01 mg/ℓ also in the lower zone in Pago.

The mark-recapture studies at Ponape were conducted primarily in the Kamar study area, but tagging was also accomplished in the Takatik study area. Ylig was the primary area for mark-recapture studies at Guam. A summary of the recapture data is presented in Table 4.

A total of fifty-six crabs were tagged in the Kamar area and of those, six were recaptured at least once. One of the six was recaptured one day after release and at the same time station where it had been released. Another crab was recaptured twenty-five days after release and at a station approximately 200 m from the release point.

A total of thirteen crabs were tagged in the Takatik area and of those, one was recaptured twenty-two days after release and at a point approximately 100 m from where it had been released.

In Ylig at Guam, sixty-five crabs were captured and of those forty-one were tagged and released, fifteen were dissected for gut analyses, and the remainder used in the growth studies. Five of the tagged crabs were recaptured. One of the five was recaptured one day after release and at the same station where it had been released. Another was recaptured twenty days after release and at a station approximately 400 m from the point of release.

Nineteen crabs were captured in Talofofo. Nine were used for gut analyses and the remainder were used in growth studies.

Two crabs were captured in Pago and both were tagged and released; neither was recaptured.

In order to identify potential food items of S. serrata, a collection of organisms from the different study areas was made. A complete list is in Table 5. Gut analyses were performed on 28 individuals from Ponape and 25 individuals from Guam. The gut contents and frequency are listed in Tables 6 and 7.

The most frequently (39%) consumed food by S. serrata from Ponape was the bivalve, Geloina papua (Lesson). This clam occurs in the mud of the mangrove swamps. I have observed residents on Ponape collecting this edible clam by wading into the mud, sometimes thigh deep, and probing for them with their bare feet. This particular clam species is an important part of the Ponapean legend explaining the occurrence of S. serrata on Ponape. The story describes how a large female crab swam to Yap Island and returned with the clam to Ponape as food for her young. I am skeptical about the swim, but the clam appears to be an important food item for S. serrata on Ponape. Crustaceans were also consumed by the crabs from Ponape (14%) as well as bits of vegetation (8%), and one individual contained fish vertebrae. The relatively high frequency of completely empty foreguts (20%) may reflect the greater occurrence of crabs preparing to molt, S. serrata cease feeding one to two days before molting. Since all of the Ponape crabs were collected from mud surface or from burrows during low tides, it seems possible that a high percentage were in the proecdysis (premoult) stage.

The most frequently consumed food for Guam crabs (36%) was grapsid crabs. Many different species of this family (Grapsidae) were collected from their small, supratidal mud burrows in the river bank and from foliage at the water's edge. One species of grapsid crab (Ptychognathus ishii Sakai) however, was only collected from the river bottom. This

species is small enough (carapace width about 1.0 cm) to pass directly through the screen mesh of the traps and was regularly observed feeding on the bait. On one occasion, during a night trapping session, over 50 individuals were collected from one bait container. This small crab occurred at all zones but was particularly common under rocks in the upper zone. It is believed to be the species of grapsid most commonly eaten by S. serrata (the others are primarily supratidal and not readily available).

The second most frequently consumed food item (16%) was the barnacle, Balanus eburneus Gould. Dense aggregations were found attached to nipa branches. When the tall nipa branches break, the basal portion remains attached to the main part of the tree. The end of the branch sinks to the bottom of the river where it becomes buried in the mud. This sunken branch provides a convenient substratum for barnacles; it is off the bottom but also deep enough to be in the more saline water of the river. The brackish water nerite, Nerita pulligera (12% frequency in the gut analysis), was collected from all three rivers, but it was never found in great abundance. Other food items with a frequency of 4% included a piece of a blade of Sargassum cristaefolium, sea urchin spines, and the limpet-like gastropod Septaria porcellana. The latter was collected at all zones but was not abundant. Fish parts were not found in any of the Guam crabs.

Nineteen crabs were kept in the holding tank at the Marine Laboratory, and of those eight molted once and four molted twice (Table 8). The mean percentage increase in carapace width was 16.2% (percentage increase = increase in width ÷ carapace width before molting x 100). The range of percentage increase was 9.6% to 24.0%

with the greatest increases from crabs with premolt sizes of 6.0 cm to 8.0 cm. There was no significant difference in percentage increase between crabs from the two different salinities.

The largest crab to molt successfully was 11.17 cm in width before molting and 12.63 cm in width after molting; this individual had been moved to a cubicle with twice the surface (from 39.7 cm^2 to 79.4 cm^2) area because of its larger size. The smallest crab to molt was 5.22 cm in width before molting and 6.13 cm after molting.

Molting occurred sporadically with one important exception. During one night, seven of eight crabs in the open system molted. The only exception was a crab that had molted four weeks earlier. The seven crabs that did molt were caught in different areas, ranged in premolt size of 6.03 cm to 11.17 cm, and had been in the holding tank for varying numbers of days. Two were females and five were males.

Scylla serrata exhibits sexual dimorphism in cheliped size. When the logarithm of the carapace width for females is plotted against the logarithm of the respective height of the dominant cheliped (Fig. 10), the resulting regression line has a slope of 1.073 (n=30, r=0.96). Since the slope is close to 1.0, the growth of the cheliped is isometric with the growth of the carapace. However, if the same graph is drawn for males (Fig. 10), the resulting slope is greater than 1.0 (n=39, r=0.99) and the growth rate appears to be exponential. As a result, larger male crabs have proportionally larger chelipeds than females.

The same data have been plotted without converting to logarithms to show the dimorphic trends more clearly (Fig. 11). From this graph it can be seen that the differences in cheliped sizes between sexes become more pronounced in the larger individuals.

Discussion

Natural Habitat

The Kamar study area is bordered by the Tawenjokola River on the west, a small tributary on the north and one on the south, and the increasing elevation prevents mangrove development on the east.

The tributaries are shallow, ranging from 1.0 to 2.5 m at mean higher high water. The trapping sites along the bank of the Tawenjokola River averaged 1.0 to 3.0 m in depth although the mid-channel depth was greater (to 5.0 m).

During high tides the substratum of this area is completely submerged, and it is believed that crabs are most active at this time, especially at night (personal interview, July 1976, with local fishermen, Ponape). The crabs forage for food among the roots of the mangrove trees.

Trees are the most common flora growing within the swamp and along the river channels. The mangrove tree, Bruguiera conjugata is common and is easily recognized by its bent, knee-like root projections. Other common trees are Xylocarpus granatum with massive roots which twist across the surface of mud; Sonneratia caseolaris the largest tree in the swamp with widespread roots which project straight up from the mud; and two species of Rhizophora: R. apiculata which grows within the swamp and is tall with long aerial roots and R. mucronata which grows on the seaward fringe of the swamp and is more stunted in growth

than the other species. These mangrove trees with their complex root systems entangle debris brought down by heavy rain or drifted in with the tides. Scavenging crabs search them for food.

As the tide falls, the substratum gradually becomes emerged and it is possible to walk across the swamp mud in search of crab burrows; the burrows are dug among the mangrove tree roots. This is the most common method used by local fishermen for catching crabs, especially when the tide is low immediately following the new and full moon high tides. Other authors have noted the occurrence of mangrove crabs in burrows (Musgrave, 1929; Verwey, 1930; Arriola, 1940; Guinot, 1966; MacNae, 1968) but the purpose of the burrow is uncertain. It may be a refuge made by crabs prior to molting or mating (the latter can be successful only when accomplished immediately after the female molts) and when abandoned they may be used by other crabs to escape exposure during the falling tide. I have found newly molted and hardened individuals of both sexes as well as mating pairs in separate burrows.

During emergence, crabs may actually become stranded on the mud. This has previously been unrecorded. Veerannan (1972) states that S. serrata is entirely water-bound. He concluded that aerial respiration is possible but that the gills of S. serrata are not suited for lengthy terrestrial exposure. The gill leaves (subunits of the gills) are held apart by water currents but in the air they collapse and drastically reduce the available surface area for oxygen diffusion (Veerannan, 1974). Crabs in the Kamar study area and at Takatik Island (where periodic submergence and emergence of the substratum also occurs) were often observed sitting on the mud or in shallow muddy pools, not

moving. S. serrata is not strictly water-bound as previously cited, but may experience periodic aerial exposure. Tolerance of low oxygen levels by S. serrata is further indicated by the low dissolved oxygen levels recorded for the bottom water at the upper and middle zones at Kamar (0.7 ppm and 0.8 ppm, respectively).

The Ylig River study area was confined to the river itself. It is one of the largest river systems on Guam (Wilder, 1976) and extends approximately 1.5 km to the west, inland from Ylig Bay. It is slightly deeper than the Kamar study area channels and averages 1.5 m in depth at the upper zone and 4.0 m at the lower zone; it varies from 3.0 to 6.0 m in width. The river banks are steep and during high tides they are not submerged, nor is there an emergent mud flat during low tides as was noted for the Kamar study area. The flora did not vary significantly along the river from lower to upper zones, but it was completely different from the mangrove swamp at Kamar.

Nypa fruticans was found growing at the water's edge, at all zones. Scattered but dense groves of Bambusa sp. grow on the bank, and in places they form a canopy over the river. The coconut tree Cocos nucifera, occurred sporadically along the entire length of the river and a few breadfruit trees, Artocarpus mariannensis, were noted. Leucaena sp. grows everywhere and its large limbs jut out over the water. In addition, Hibiscus tiliaceus, Pennisetum sp., and Delonix regia were noted from along the river.

Crabs caught in Ylig were captured solely by trapping. A few possible S. serrata burrows were observed, but crabs were never found inside them although it is possible they are used for molting and mating. The river bottom is littered with sunken logs and debris

washed in during heavy rains. Especially large accumulations of debris were noted where shore vegetation becomes entangled with drifting branches and on many occasions the river channel was completely blocked. S. serrata probably forages in these piles of debris, and crabs were observed on them at different times.

Scylla serrata is primarily a brackish water resident (Tinker, 1965; Ong, 1966; Tamura, 1966; Miller, 1975) and it penetrates deeper into estuaries than other Indo-West Pacific portunids (Stephenson, 1972). However, its ability to invade low salinity regions has not been well documented and is perhaps overestimated. In a study where S. serrata were adapted to 100% and 25% seawater (100% = 33 ppt S), it was found that crabs were more efficient in adapting, metabolically, to full strength seawater than to the freshwater (Krishnamoorthy and Venkatramiah, 1971). Another study showed that the enzyme ATP-ase was more thermostable at higher salinities (Krishnamoorthy and Venkatramiah, 1969). Trapping results from this study further emphasize an affinity for higher salinity. Many individuals were captured in an area where salinity never fell below 26.0 ppt (mean salinity: 31.2 ppt; Ylig River, low zone) and in two instances crabs were released and recaptured several days later in that same zone. There are also references to the presence of large numbers of crabs at river mouths after heavy rains, presumably driven downstream by freshwater and seeking a more favorable salinity (Stephenson and Campbell, 1960; MacNae, 1968).

S. serrata can tolerate low salinities but evidence indicates that it is adapted to higher salinities. However, if we consider the

early life history of this crab, the problem of salinity adaptation becomes more complex.

Fertilized females migrate to the open ocean, that is, to water of higher salinity, to spawn (Arriola, 1940; Ong, 1966). The eggs, approximately 2 million per female (Arriola, 1940; Ong, 1964), become attached to the endopodite setae under the abdomen and after a 12-day incubation period, hatch as free swimming zoeae (Raja Bai Naidu, 1955; Ong, 1964). Experimental rearing of the zoeae has shown that water temperatures above 25°C and salinities below 17.5 ppt causes high mortality (Hill, 1974); thus the zoeae are unsuited to estuarine conditions. However, the megalopa, which occurs after the fifth zoeal stage (about 21 days after hatching) grows at a faster rate in reduced salinities (Ong, 1964; Brick, 1974); the faster rate of development of the megalopa in reduced salinity suggests that the megalopa in nature moves shoreward into brackish water. Furthermore, Ong (1966) observed shorter intermolt periods for small crabs in water of reduced salinities.

The adult life of S. serrata is then spent in water of continuously variable salinity, but there is evidence that smaller individuals (carapace width of 2.0 to 8.0 cm) tend to be intertidal dwellers and larger individuals (10-20.0 cm in width) subtidal (letter dated 3 October 1976 from Mick Heasman, Department of Zoology, University of Queensland, St. Lucia, Queensland). Prasad and Tampi (1953) found a similar segregation between large and small individuals of the portunid, Neptunus pelagicus; larger specimens occurred in deeper water and smaller specimens occurred in shallower water.

A mangrove crab is generally a bottom dwelling animal, and, in deep water adjacent to an estuarine area or in channels, it would be exposed

to virtually full strength seawater. However, a crab in the shallow parts of an estuary would be within the consistently less saline surface waters and would rarely be subjected to full strength seawater. This type of environment was found at the Ponape and Guam study areas. I believe that smaller individuals remain in shallow water because the lower salinity is more suitable to juvenile growth. Studies have shown that for other crustaceans early growth may tolerate a wider salinity range and more pronounced salinity fluctuations than old mature individuals (Kinne, 1964). Furthermore, Estampador (1949a) divided this genus into more than one species by discussing the different habitats of large and small individuals; larger crabs inhabit water of higher salinity and smaller ones tolerate a wider range of salinity. Similar differences in S. serrata distribution have been reported from Taiwan (Chen, 1975 (unpublished): Crab culture; copy available at University of Guam Marine Laboratory). Trapping results from this study at Talofofo River support the more general observations of the latter two authors.

During storms and subsequent high surf conditions in Talofofo Bay, a sand bar is formed at the mouth of Talofofo River and the flow of water in and out of the river is minimized. Heavy rainfall associated with the storm is partially blocked from flooding out the river, and brackish water in the river may persist for days. Thus, the salinity in the Talofofo River is extremely variable from month to month (Randall, 1974). Mean bottom water salinity recorded for this study (November and December, 1976) did not exceed 16 ppt for any zone, but Randall (1974) recorded salinity as high as 30 ppt in the upper and middle zones and 32 ppt in the lower zone. All three zones have been

shown to have salinities as low as 2.8 ppt (Randall, 1974). Trapping for this study was done when there was no full strength seawater evident anywhere in the river. Coincidentally, of the 19 crabs captured during two separate periods, none were greater than 14.7 cm in width and 74% of them were less than 12.0 cm in width. Interviews with local fishermen however, indicate that very large crabs are caught, especially near the river mouth. I believe that the periodic reduction in salinity may cause larger crabs to migrate out into the bay where deeper, and hence more saline, conditions exist.

Another possibility which may affect crab distribution in the habitat is available food. S. serrata is best described as an opportunistic feeder; it feeds on almost anything organic. At Ponape for instance, it is reported to feed extensively on mangrove molluscs, especially bivalves (personal interview, July 1976, with local fishermen, Ponape) while a study done on the gut contents of 10 individuals from the Ganges River showed 95% of the crabs had been feeding on vegetation (Pearse, 1932). Other gut analyses confirm an omnivorous diet (Pillay, 1954; Hill, 1976).

Although S. serrata has been reported to be omnivorous, the Ponape and Guam specimens do not support this. It has also been reported to feed extensively on fish (Guinot, 1966; Thia-eng, 1974), but Hiatt (1944) did not find fish predation by S. serrata in Hawaiian fish ponds nor were fish an important part of the diet of crabs studied from Australia and South Africa (Hill, 1976). Only one of the 53 crabs from Ponape and Guam contained fish remains.

S. serrata from Australia and South Africa is reported to be a predator of sessile or slow-moving benthic macroinvertebrates, chiefly molluscs (Hill, 1976). This is true for crabs from Ponape and Guam, although the latter consumed more crustacea, especially grapsid crabs. No bivalves were recorded from the Guam study areas, whereas the barnacle, Balanus eburneus, and grapsid crabs, especially Ptychognathus ishii, are abundant. Although fish are available to S. serrata in the mangrove swamps of Ponape and in the rivers of Guam, their virtual absence in the gut might indicate the difficulty of catching highly mobile forms. This would certainly be true for large male crabs; observations in the laboratory of large males indicate that the male crabs are exceedingly powerful but extremely slow.

I performed a series of preliminary experiements where small reef flat bivalves, Quidnipagus palatam Iredale and individuals of the grapsid crab P. ishii were fed to crabs of different sizes. The food items, 5 bivalves or 5 crabs, were placed in aerated aquaria with the test animal. The food was introduced in the evening and checked the following morning.

Results showed that crabs with carapace widths ranging from 7.12 cm to 15.87 cm could successfully eat bivalves as small as 0.97 cm in length and 0.3 cm in height. However, the larger crabs often did not eat all of the food items whereas the smallest crabs consistently ate them all. Furthermore, observations showed a greater length of time necessary for the larger crabs to manipulate the small prey into the mouth. Bivalves of greater size (2.0 cm in length and 0.8 cm in height) were all eaten by each crab.

The experiments with grapsid crabs as food were accomplished in the same manner as with the bivalves, except a few small rocks were added to the testing aquaria. In the field, the river bottoms are not barren, smooth surfaces and it was felt that some sort of refuge was needed.

The results for the grapsid crab testing were similar to the results from the bivalve experiments. Grapsid crabs with a minimum carapace width of 0.72 cm and a minimum body thickness of 0.26 cm, were all eaten by the smaller test crabs. However, the larger test crabs often ate only one or two of the grapsids during the night, and on several occasions were not successful in eating any of them. Observations showed that the rocks were constantly moved around by the test animals while trying to capture the small grapsid crabs. The largest S. serrata tested (15.87 cm in width) chipped large pieces off the rocks while attempting to grab the elusive prey. On mornings when no grapsids had been eaten, the refuge was removed and the grapsids were successfully captured and eaten.

No work regarding prey size with S. serrata has been done, but these preliminary results indicate that small S. serrata, with small chelipeds, have a mechanical advantage over larger crabs when prey organisms are small, especially small, mobile forms. The smaller individuals can more efficiently exploit a smaller range of prey.

This may be further evidence for the size difference between brackish water residents and higher salinity residents. As the crab grows in width, the chelipeds also attain greater size, and in large male crabs, the cheliped becomes especially massive. No male crab with a carapace width greater than 15.0 cm was captured in any of the upper zones of the Guam study areas; the largest male captured in the upper

zone of Ylig was 11.41 cm in width. Females with carapace widths as great as 17.2 cm were captured in the upper zones. However, if the respective cheliped sizes of these crabs are compared, the male would have a cheliped of about 5.0 cm in height (largest cheliped) and the female with a width of 17.2 cm would also have a cheliped height of about 5.0 cm. No crab with a cheliped height greater than 5.0 cm was caught in any of the upper zones at Ponape or Guam. It is suggested that cheliped size as well as salinity tolerance is a factor regulating the separation of large and small crabs, especially males, in their natural habitat.

The distribution patterns noted in Ylig, where available prey organisms are small, exemplify this situation. Large female crabs (carapace width greater than 15.0 cm) have relatively small chelipeds when compared with males of equal carapace width. It is suggested that the larger males cannot efficiently feed in the river and instead forage into deeper water, perhaps on the reef flats on the north and south sides of Ylig Bay. The large females however, have smaller chelipeds and are successful at feeding efficiently in the river.

A study done on the incidence of the parasitic barnacle, Lepas sp. (Hashmi and Zaidi, 1965) in S. serrata, has important implications when discussing crab distributions. In that study, more than 100 crabs were dissected and approximately 90% of the crabs with a carapace width greater than 7.6 cm were infested with Lepas sp. This pedunculate barnacle settles on the gills and adjacent parts of the body cavity, and in heavily infested individuals the respiratory surface of the crab was severely reduced. The infestation caused sluggishness and in some instances death.

It was further noted in the study (above) that crabs collected from the deep sea were rarely affected by Lepas sp., whereas those collected from the creeks and mangrove areas were heavily infested. This suggests another reason why older (larger) individuals are more commonly found in the higher salinity water. Smaller individuals molt more often and, since the gills are also shed when the crab molts, the smaller crabs periodically rid themselves of this parasite. Larger individuals molt less frequently and parasitic infestation could become more dense, thus restricting the normal activity of the crab and perhaps causing death.

Other parasitic barnacles have been recorded from S. serrata: Dichelaspis maindroni (Pearse, 1932), Dichelaspis apeita (Pearse, 1933), Octolasmis spp. (MacNae and Kalk, 1958; Newman, 1960; Day, 1969), and Poecilasma sp. (MacNae and Kalk, 1958). Additionally, Octolasmis cor was common on gills of S. serrata from Truk Island (letter dated 3 January, 1977 from William A. Newman, Scripps Institution of Oceanography, La Jolla, California) and 27 of the 28 individuals from Ponape dissected for gut contents were also infested with O. cor. It is not known if any of these occurrences were distributed similar to the Lepas sp. infestations.

One more aspect which may be pertinent to the distribution of S. serrata in the field is the protection from predators afforded by the mangrove swamps and the rivers. S. serrata has few natural enemies and was the largest invertebrate commonly found in the mangrove swamps of Ponape and in the rivers at Guam. The only known natural predators are sharks (Crosnier, 1962), crocodiles (personal interview, September 1975, with local fishermen, Palua), mangrove snappers

(family: Lutjanidae) and groupers (family: Serranidae). At Ponape, fishermen told of an instance when a large (approximately 100 kgs) grouper was found dead in one of the small mangrove rivers. When the fish was cut open, three large S. serrata were found in the stomach. The crabs had been swallowed whole and had mortally wounded the fish by tearing the stomach and viscera. Other large fish and perhaps octopus may prey on crabs, especially migrating females, but in the mangrove muds the crabs are safe. Smaller S. serrata are more vulnerable than the larger individuals and perhaps the small ones remain in the mangrove for safety.

Cannibalism is another factor that may be important in regulating the abundance of mangrove crabs. Large S. serrata are known to eat smaller individuals, especially freshly molted ones (Arriola, 1940; Guinot, 1967). In one of my traps in Ylig, a large female was captured and also inside the trap were the remains of a smaller, partially devoured male crab. However, cannibalism does not always occur. I have often captured two crabs in my traps (two males, one male and one female, and two females) of different sizes that appeared to be feeding on the bait and no evidence of fighting, autotomized appendages or wounds in the exoskeleton, were observed. In two instances three crabs were captured in one trap; one trap with two males and one female and the other trap with two females and one male. Perhaps cannibalism is precipitated by a lower food supply in the habitat. It is not known how important cannibalism is in regulating the population density, but it must be considered as a limiting factor.

If food is plentiful, it seems less likely that fatal interspecific encounters will occur. However, when the food supply is limited

individuals are forced to roam farther seeking food. This increases the chance of meeting another individual, and encounters with conspecifics may result in some fighting activity and cannibalism may ensue. Furthermore, I believe that when available food is limited, in abundance or size of prey organism, it is the larger individuals which must forage more widely.

The possibility of crabs moving over great distances, either in search of food or to find more suitable living conditions has been investigated. Extensive tagging studies in South Africa (Hill, 1975) showed a maximum movement of 13.5 km in 3 weeks by a 12.0 cm male, but 68% of the recaptured crabs had moved less than 1 km from the site of tagging mean interval between release and recapture was 99 days. Tagging work in Australia has recently begun (letter dated 8 February, 1977 from Chris Lee, Fisheries Research Station, Deception Bay, Queensland) and preliminary results show that 93% of the recaptured crabs were collected within 1.0 km from the release site, and two individuals were caught 4.0 and 5.0 km away.

Tagging results from Ponape and Guam support the trends noted above; crabs are capable of considerable movement but tend to range over a limited area. The maximum movement for any crab during this study was 0.4 km in 20 days. Another individual traveled only 0.2 km in 25 days and one crab in Ylig, was recaptured in exactly the same place where it had been released 14 days earlier. The data indicate that S. serrata do not remain in any particular location for long periods of time, but may remain within the same river or channel for periods of up to 1 month or more. There does not appear to be any obvious territoriality.

Growth Studies

Scylla serrata is extensively cultured in many parts of the Indo-West Pacific, but much of the culturing takes place in poorly maintained ponds. The ponds undergo extreme variation in salinity and temperature, and the growth data and observations are misleading and difficult to interpret.

There have been some studies where individual crab growths were monitored under controlled conditions (Arriola, 1940; Ong, 1966; Raphael, 1970; DuPlessis, 1971 (unpublished): A preliminary investigation into the morphological characteristics, feeding, growth, reproduction and larval rearing of Scylla serrata Forskal, held in captivity. Copy available at University of Guam Marine Laboratory). I have graphed the mean percentage increase after molting for 2.0 cm size classes (Fig. 9). From the graph it can be seen that growth data obtained from my Guam specimens are similar to data from the other studies.

The mean percentage increase in carapace width is greater for smaller crabs (less than 8.0 cm) than for larger size classes. The percentage increase in width begins to decrease for crabs between 8.0 cm and 10.0 cm, and for crabs greater than 10.0 cm in width, the increase decreases dramatically.

These results are preliminary, but they do indicate that S. serrata can be maintained in relatively small cubicles and will grow (molt) under those conditions.

Sexual Dimorphism

The sexual dimorphism in cheliped height between sexes may be a factor regulating distribution of S. serrata in the natural habitat. I have already noted that no crab with a cheliped height greater than 5.0 cm was captured at any of the upper zones. In fact, of all crabs captured with a cheliped height greater than 4.0 cm (n=31), only three were captured in the upper zones.

The absence of large individuals in the upper zones may be due to metabolic problems experienced in the changing salinities of the zone. However, since large crabs were found in zones where salinity did fluctuate, I believe the absence of exploitable food items is a more important factor. No large potential prey organism was found in any of the upper zones. This implies that a large cheliped is disadvantageous in a habitat (zone) where prey organisms are small. Conversely, a crab with a small cheliped would have a selective advantage in such a habitat. Thus, large males cannot efficiently exploit the same food (small prey) as large females and competition between sexes for available food would be reduced.

The males must forage more widely in search of food, and, if food is scarce, the male may be forced to leave the relative safety of the estuary. Such a migration would reduce the possibility of cannibalism on resident juveniles or on females by the large males.

Conclusions

Scylla serrata (Forskal) is the largest portunid crab in existence and it occurs throughout the Indo-West Pacific. Its maximum size exceeds 20 cm across the carapace, and it may weigh more than 2 kgs.

It is primarily a brackish water animal, but larger individuals, especially large males, occur more often in waters of high salinity (greater than 25 ppt). Smaller individuals are more tolerant of brackish conditions and are characteristically found in shallow water.

Sexual dimorphism in cheliped size may be an important factor regulating mangrove crab distributions in nature. The male cheliped grows at a faster rate than the female cheliped. The large male crabs cannot efficiently exploit a habitat where prey organisms are small, and the males may be forced to forage outside the relative safety of the estuarine habitat. The large females, with a smaller cheliped, have an advantage over the males where available food is small.

S. serrata can tolerate very low dissolved oxygen levels (as low as 0.7 ppm) and they often experience extended periods of aerial respiration.

The primary food of S. serrata is benthic invertebrates, especially bivalves and grapsid crabs. The most commonly consumed food is probably a function of what is available. Ponape crabs feed mostly on the bivalve Geloina papua Lesson. Guam crabs feed most frequently on a benthic grapsid crab, Ptychognathus ishii Sakai. The barnacle,

Balanus eburneus Gould, and the nerite, Neritina pulligera (Linnaeus), are also important for Guam individuals. Fish are rarely eaten.

S. serrata is capable of wide ranging movements, but may remain in the same channel or river for up to one month or more.

Crabs can be successfully raised in individual cubicles of approximately 0.04m^2, with water salinities of 20 ppt or 30 ppt., and at a temperature of approximately 28^oC. Percentage increases are greater for individuals less than 8.0 cm in width. No significant difference in growth between the different salinities was noted.

Table 1. Ranges, means (in parentheses), and standard deviations of water temperature, salinity, dissolved oxygen, and turbidity for Guam study areas.

	Pago River	
	Surface	Bottom
Upper Zone		
Temperature (°C)	29.3-29.7 (29.5) N=2, S=0.28	30.8
Salinity (ppt)	5.0	30.0-32.0 (31.0) N=2, S=1.41
Oxygen (ppm)	5.1	3.8
Turbidity (ntu)		2.0-2.4 (2.2) N=2, S=0.28
Middle Zone		
Temperature (°C)	29.4-30.7 (30.0) N=2, S=0.92	30.5-31.0 (30.7) N=2, S=0.35
Salinity (ppt)	6.0	30.0-33.0 (31.5) N=2, S=2.12
Oxygen (ppm)	4.8	2.9
Turbidity (ntu)		1.5-2.5 (2.0) N=2, S=0.71
Lower Zone		
Temperature (°C)	29.3-30.8 (29.8) N=3, S=0.84	30.1-30.9 (30.63) N=3, S=0.46
Salinity (ppt)	4.0-6.0 (5.0) N=2, S=1.41	32.0-33.0 (32.3) N=3, S=0.58
Oxygen (ppm)	5.0-6.0 (5.5) N=2, S=0.71	3.3-6.0 (4.6) N=2, S=1.91
Turbidity (ntu)		2.0-4.5 (3.2) N=3, S=1.25

Table 1. (Continued)

	Ylig River	
	Surface	Bottom
Upper Zone		
Temperature (°C)	26.7-29.7 (28.14) N=9, S=1.28	26.7-30.7 (28.72) N=9, S=1.45
Salinity (ppt)	0.0-13.0 (1.44) N=9, S=1.33	0.0-28.0 (13.22) N=9, S=11.29
Oxygen (ppm)	5.2-8.2 (6.8) N=9, S=1.0	1.7-7.0 (4.87) N=9, S=2.05
Turbidity (ntu)		1.2-25.0 (7.56) N=5, S=10.02
Middle Zone		
Temperature (°C)	26.8-29.7 (28.01) N=8, S=1.23	27.8-30.8 (29.54) N=7, S=1.07
Salinity (ppt)	1.0-24.0 (3.0) N=8, S=1.51	22.0-32.0 (29.38) N=8, S=3.25
Oxygen (ppm)	5.3-7.0 (6.06) N=7, S=0.66	3.0-6.0 (4.03) N=7, S=0.97
Turbidity (ntu)		1.2-25.0 (7.7) N=4, S=11.55
Lower Zone		
Temperature (°C)	26.5-29.7 (28.36) N=10, S=1.16	28.4-30.9 (29.61) N=10, S=0.82
Salinity (ppt)	1.0-32.0 (3.2) N=10, S=1.48	26.0-34.0 (31.15) N=10, S=2.11
Oxygen (ppm)	5.0-6.7 (5.9) N=8, S=0.63	4.0-5.7 (4.74) N=8, S=0.58
Turbidity (ntu)		2.1-6.0 (3.28) N=5, S=1.58

Table 1. (Continued)

	Talofofo River	
	Surface	Bottom
Upper Zone		
Temperature (°C)	28.2-28.4 (28.3) N=2, S=0.14	27.8-28.6 (28.2) N=2, S=0.57
Salinity (ppt)	2.0-4.0 (3.0) N=2, S=1.41	2.0-20.0 (8.67) N=3, S=9.87
Oxygen (ppm)	6.6-7.0 (6.8) N=2, S=0.28	5.8-7.0 (6.4) N=2, S=0.85
Middle Zone		
Temperature (°C)	28.2-28.6 (28.4) N=2, S=0.28	28.6-28.8 (28.7) N=2, S=0.14
Salinity (ppt)	2.0-4.0 (3.0) N=2, S=1.41	10.0-22.0 (14.0) N=3, S=6.93
Oxygen (ppm)	5.8-6.0 (5.9) N=2, S=0.14	5.0 (5.0) N=2, S=0.0
Lower Zone		
Temperature (°C)	30.5	29.6
Salinity (ppt)	2.0-4.0 (3.0) N=2, S=1.41	12.0-20.0 (16.0) N=2, S=5.66
Oxygen (ppm)	5.5	7.8

Table 2. Ranges, means (in parentheses), and standard deviations of water temperature, salinity and dissolved oxygen for Ponape study areas.

	Kamar	
	Surface	Bottom
Upper Zone		
Temperature (°C)	25.5-29.4 (27.12) N=22, S=1.04	26.3-30.7 (28.18) N=22, S=1.42
Salinity (ppt)	1.0-18.0 (9.0) N=22, S=4.9	5.0-28.0 (16.4) N=22, S=7.6
Oxygen (ppm)	1.9-7.0 (3.86) N=22, S=1.6	0.7-4.4 (2.19) N=22, S=1.0
Middle Zone		
Temperature (°C)	25.4-30.2 (27.19) N=14, S=1.24	26.5-31.4 (28.76) N=14, S=1.6
Salinity (ppt)	1.0-11.0 (5.86) N=14, S=3.18	8.0-30.0 (18.64) N=14, S=8.29
Oxygen (ppm)	2.0-7.2 (4.61) N=14, S=1.77	0.8-3.8 (2.39) N=14, S=0.95
Lower Zone		
Temperature (°C)	25.5-29.7 (27.21) N=18, S=1.09	26.8-31.8 (30.28) N=15, S=1.45
Salinity (ppt)	0.0-7.0 (4.06) N=18, S=2.21	10.0-30.0 (24.47) N=15, S=6.13
Oxygen (ppm)	4.4-7.3 (6.47) N=18, S=0.65	1.8-4.9 (3.83) N=15, S=0.77

Table 2. (Continued)

	Takatik	
	Surface	Bottom
Single Zone		
Temperature (^{o}C)	27.0-29.8 (28.9) N=4, S=1.31	27.0-32.0 (30.08) N=4, S=2.41
Salinity (ppt)	24.0-26.01 (25.0) N=4, S=0.82	24.0-26.0 (25.0) N=3, S=1.0
Oxygen (ppm)	1.7-6.8 (3.95) N=4, S=2.5	1.4-5.0 (3.0) N=4, S=1.78

Table 3. Ranges, means (in parentheses), and standard deviations of reactive phosphate, reactive nitrite, and reactive nitrate for Pago River and Ylig River.

	Upper Zone	Middle Zone	Lower Zone
Pago River			
Phosphorus (mg/ℓ)		0.008-0.010 (.009) N=2, S=0.002	0.006-0.015 (0.011) N=4, S=0.005
Nitrite (mg/ℓ)	0.003	0.004	0.000-0.002 (0.001) N=2, S=0.001
Nitrate (mg/ℓ)	0.130	0.100	0.010-0.070 (0.04) N=2, S=0.042
Ylig River			
Phosphorus (mg/ℓ)	0.001-0.004 (0.003) N=4, S=0.002	0.005-0.006 (0.006) N=2, S=0.001	0.002-0.004 (0.003) N=4, S=0.001
Nitrite (mg/ℓ)	0.000 N=2	0.003	0.000 N=2
Nitrate (mg/ℓ)	0.013-0.075 (0.044) N=2, S=0.044	0.120	0.290-0.440 (0.037) N=2, S=0.011

Table 4. Summary of recapture data for Ponape and Guam study areas. K = Kamar, Ponape; T = Takatik, Ponape; Y = Ylig River, Guam.

Crab No.	Sex	Release		Recapture		Distance Traveled (m)	Days since release
		Date	Zone	Date	Zone		
K-1	F	7 July	Middle	8 July	Middle	0	1
K-2	F	7 July	Lower	13 July	Lower	60	6
K-3	F	8 July	Lower	13 July	Lower	90	5
K-4	M	10 July	Upper	14 July	Upper	150	4
K-5	M	11 July	Lower	14 July	Lower	100	3
K-3	F	13 July	Lower	19 July	Lower	90	6
K-6	M	18 July	Lower	12 August	Middle	200	25
T-1	F	8 July		30 July		100	22
Y-1	M	6 October	Lower	13 October	Middle	120	7
Y-2	M	13 October	Middle	14 October	Middle	0	1
Y-3	F	21 October	Lower	27 October	Lower	0	6
Y-4	M	14 October	Lower	28 October	Lower	0	14
Y-5	M	14 October	Upper	3 November	Lower	400	20

Table 5. Organisms collected from study areas on Ponape and Guam.

Ponape

Gastropoda	Bivalvia	Crustacea	Pisces
Littorina scabra (Linnaeus)	Barbatia sp.	Clibinarius sp.	Agoponidae sp.
Cerithium sp.	Geloina papua (Lesson)	Grapsidae spp.	Eleotridae sp.
Nassarius (Zeuxis) vitiensis (Hombron and Jacquinot)	Septifer sp.	Thalamita crenata Latreille	Gobiidae sp.
Nerita planospira Anton		Xanthidae sp.	
Nerita undata Linnaeus			
Patella sp.			

Guam

Achatina fulica Linnaeus		Balanus eburneus Gould	Apogonidae sp.
Neritina pulligera (Linnaeus)		Cardiosoma sp.	Gobiidae sp.
Septaria porcellana (Linnaeus)		Clibinarius strialatus	Lutjanidae spp.
		Grapsidae spp.	
		Ptychognathus ishii Sakai	
		Thalamita crenata Latreille	
		Uca sp.	

Table 6. Frequency of foregut contents of 28 mangrove crabs from Ponape. Crabs are arranged in 3.0 cm carapace width intervals. The number in parentheses is the number of crabs studied for the corresponding interval. The number of males (M) and females (F) are shown.

	9.01-12.0(4)	12.01-15.0(7)	15.01-18.0(17)	Total Frequency	Percent Frequency
Geloina papua (Bivalve)		1M	6M 4F	11	39
Empty	2M 1F	4M	3M	9	32
Chitin Fragments	1F	1M	3F	4	14
Vegetation			2M	2	8
Unidentifiable Ooze			2M	2	8
Fish Vertebrae			1M	1	4
Unidentified Gastropod		1M		1	4

Table 7. Frequency of foregut contents of 25 mangrove crabs from Guam. Crabs are arranged in 3.0 cm carapace width intervals. The number in parentheses is the number of crabs studied for the corresponding interval. The number of males (M) and females (F) are shown.

	6-9.0(2)	9.01-12.0(10)	12.01-15.0(9)	15.01-18.0(4)	Total Frequency	Percent Frequency
Grapsid crabs		3F 1M	3M 2F		9	36
Empty	1M 1F	1F		1M 1F	5	20
Unidentified gastropods		1F	1M 1F	1F	4	16
Balanus eburneus (Crustacean)			3M 1F		4	16
Vegetation			3M	1F	4	16
Nerita pulligera (Gastropod)		1F	2M		3	12
Chitin fragments		1F 1M			2	8
Sargassum cristaefolium (Algae)		1M			1	4
Urchin spines		1M			1	4
Septaria porcellana (Gastropod)		1F			1	4

Table 8. Summary of molting increments and frequency.

#	Sex	Carapace Width (mm)	Width Increase (mm)	% Increase	# of days in captivity before first molt	# of days between successive molts
1	M	52.2				
		61.3	9.1	17.4	88	
2	M	60.3				
		73.2	12.9	21.4	69	
3	F	71.2				
		82.0	10.8	15.2	77	
		95.5	13.5	16.5		61
4	F	72.6				
		90.2	17.6	24.0	68	
5	M	74.0				
		88.3	14.3	19.3	68	
6	M	78.7				
		91.0	12.3	15.6	94	
7	M	83.3				
		93.7	10.4	12.5	85	
		111.3	17.6	18.8		74
8	F	83.6				
		97.6	14.0	16.7	84	
9	M	87.7				
		100.2	12.5	14.3	92	
		113.8	13.6	13.6		57

Table 8. (Continued)

#	Sex	Carapace Width (mm)	Width Increase (mm)	% Increase	# of days in captivity before first molt	# of days between successive molts
10	M	88.1				
		100.0	11.9	13.5	88	
		116.6	16.6	16.6		72
11	M	105.0				
		115.1	10.1	9.6	45	
12	M	111.7				
		126.3	14.6	13.1	75	
Ylig Specimen	M	85.7				
		112.2				121
		132.9	20.7	18.4		105

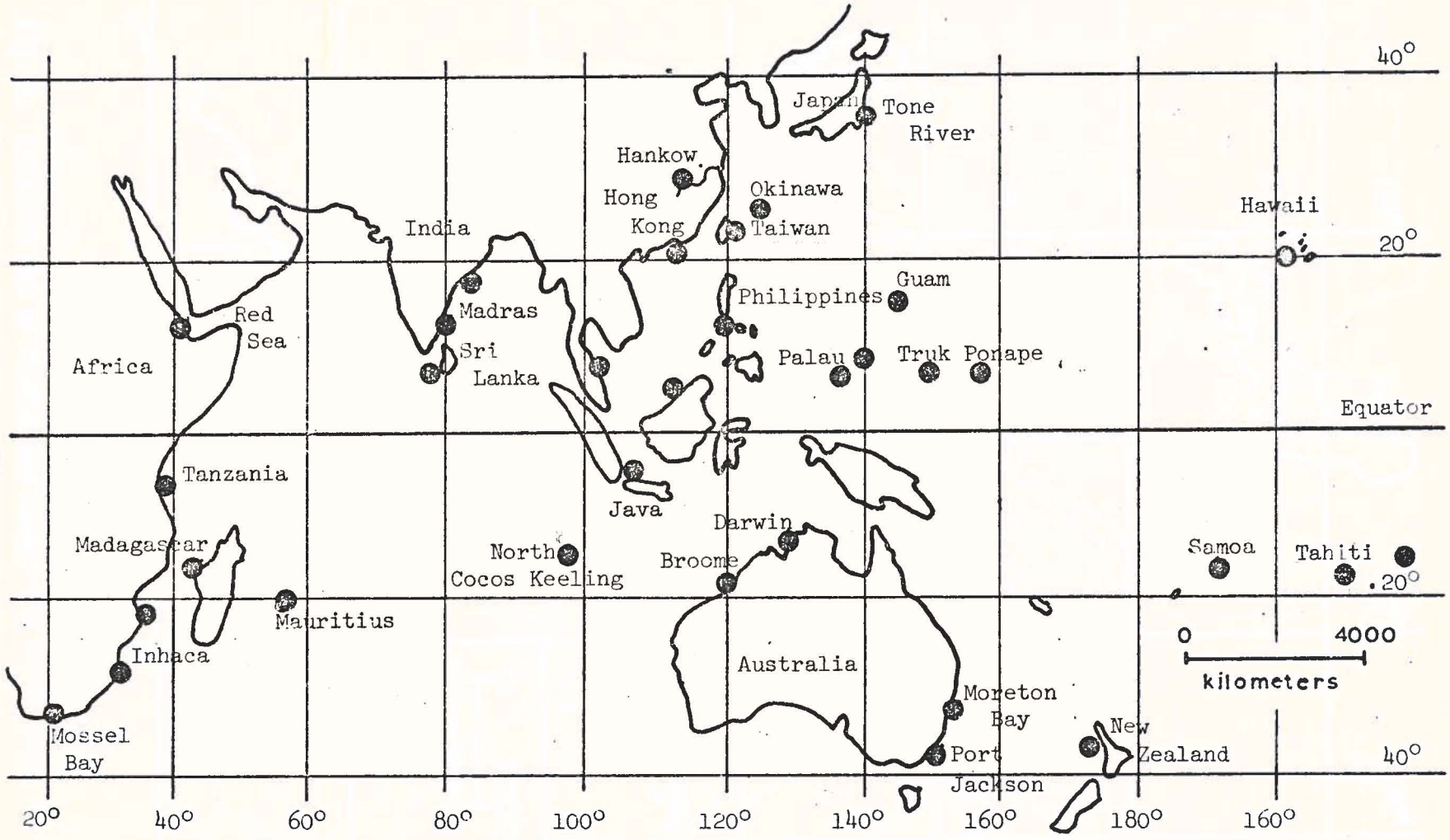

Fig. 1. Range distribution of Scylla serrata.

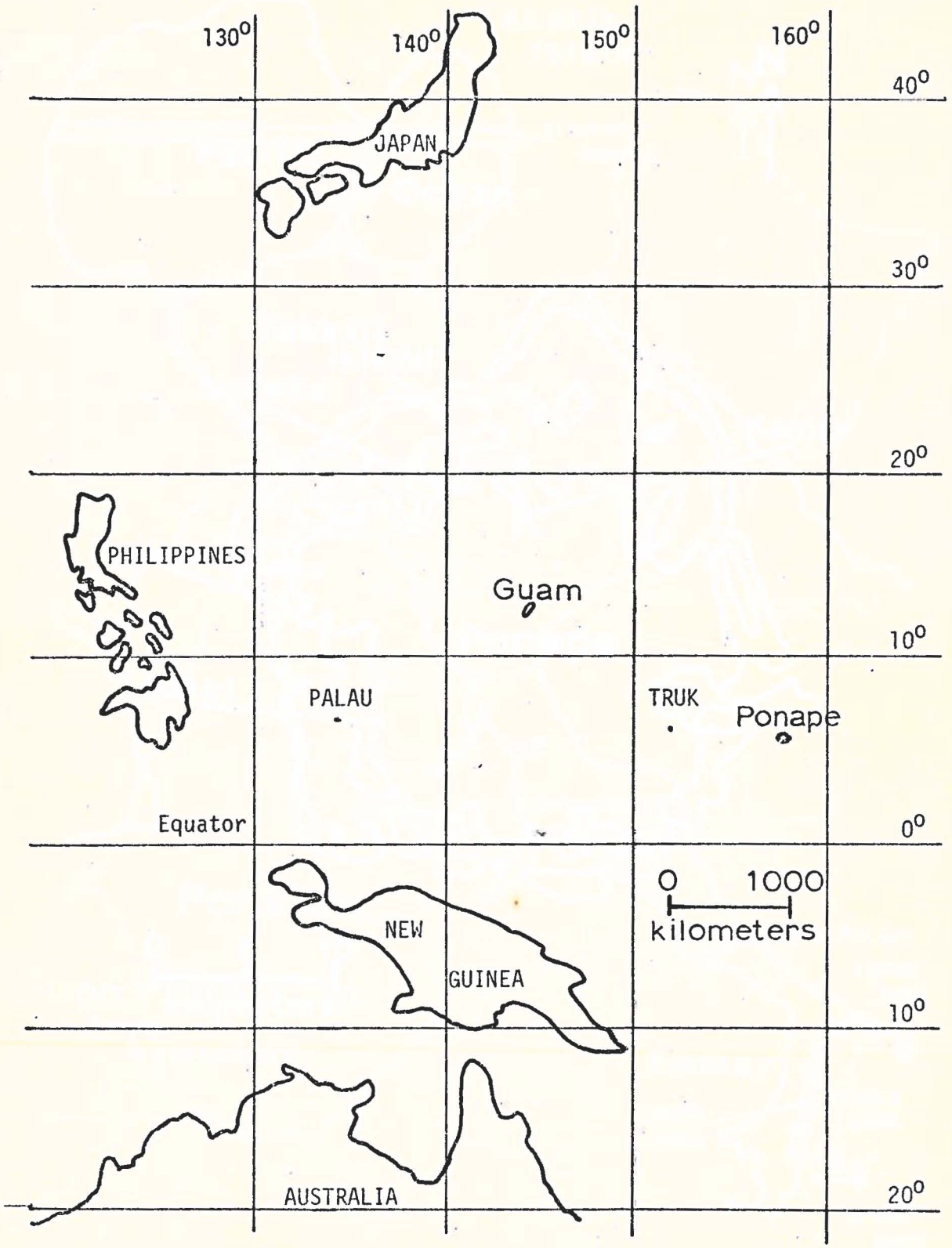

Fig. 2. Location map of Ponape and Guam.

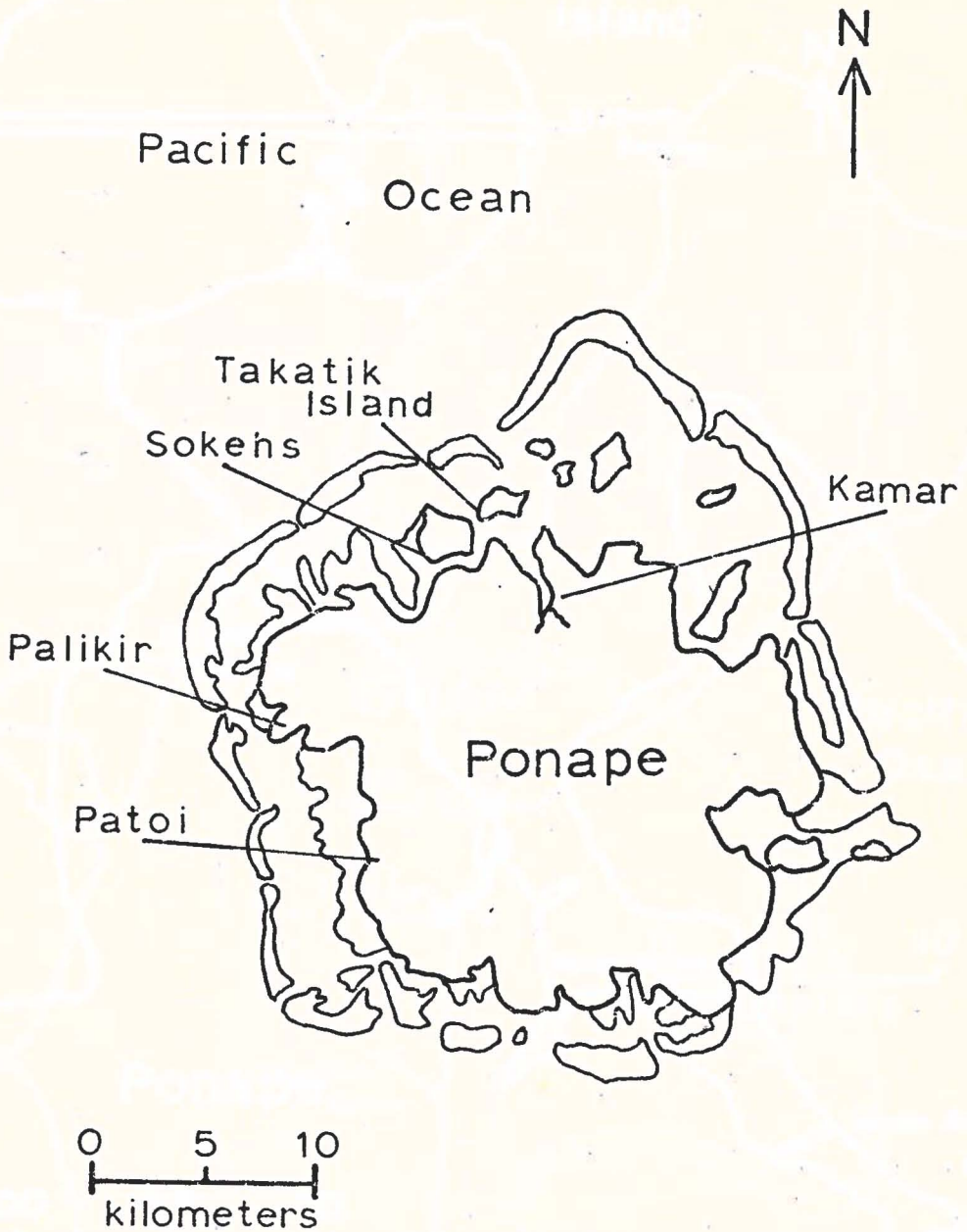

Fig. 3. Location map of observation sites and study areas at Ponape.

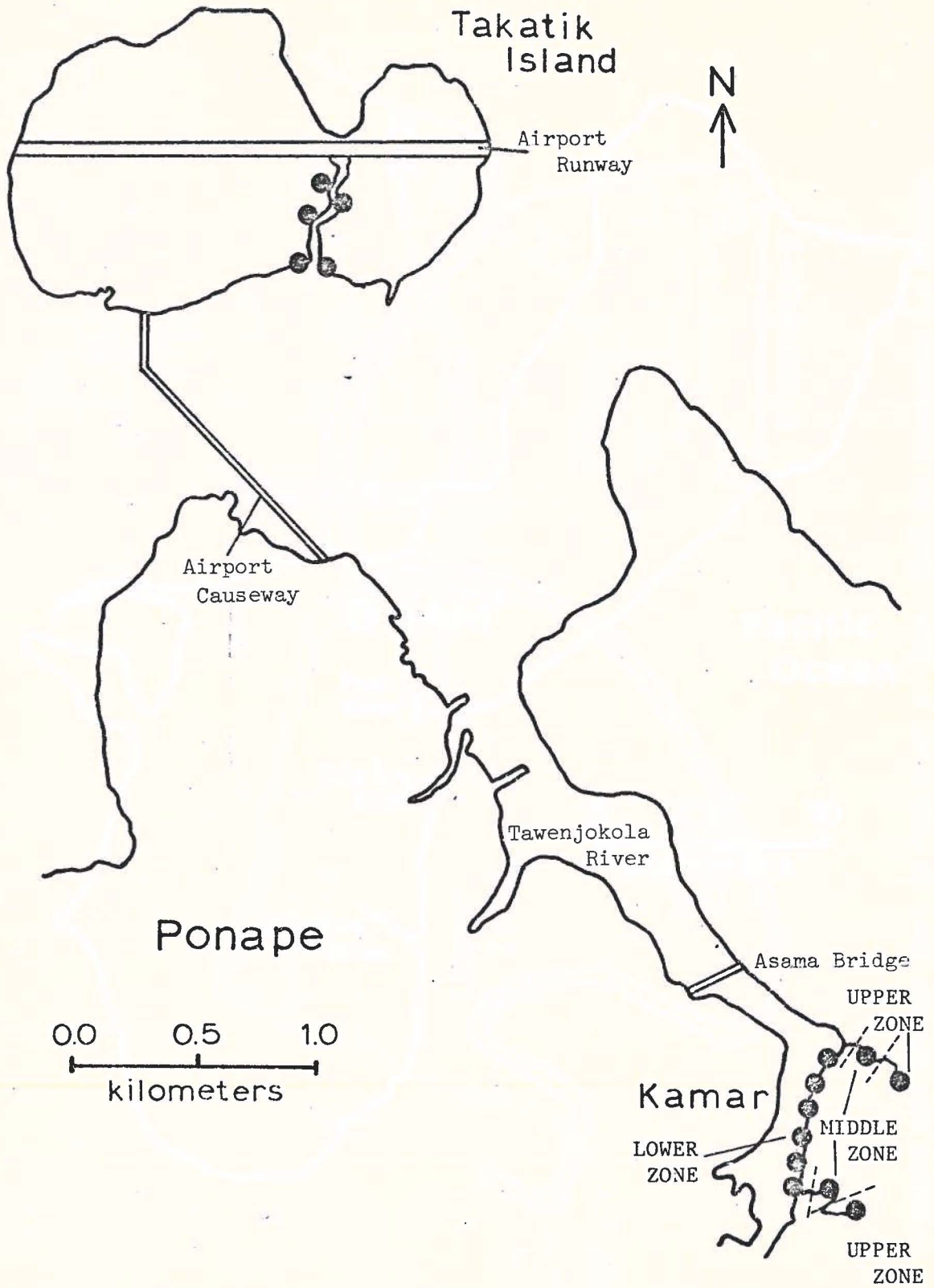

Fig. 4. Trapping stations and zones in the Kamar study area and trapping stations in the Takatik Island study area. Each dot represents two stations.

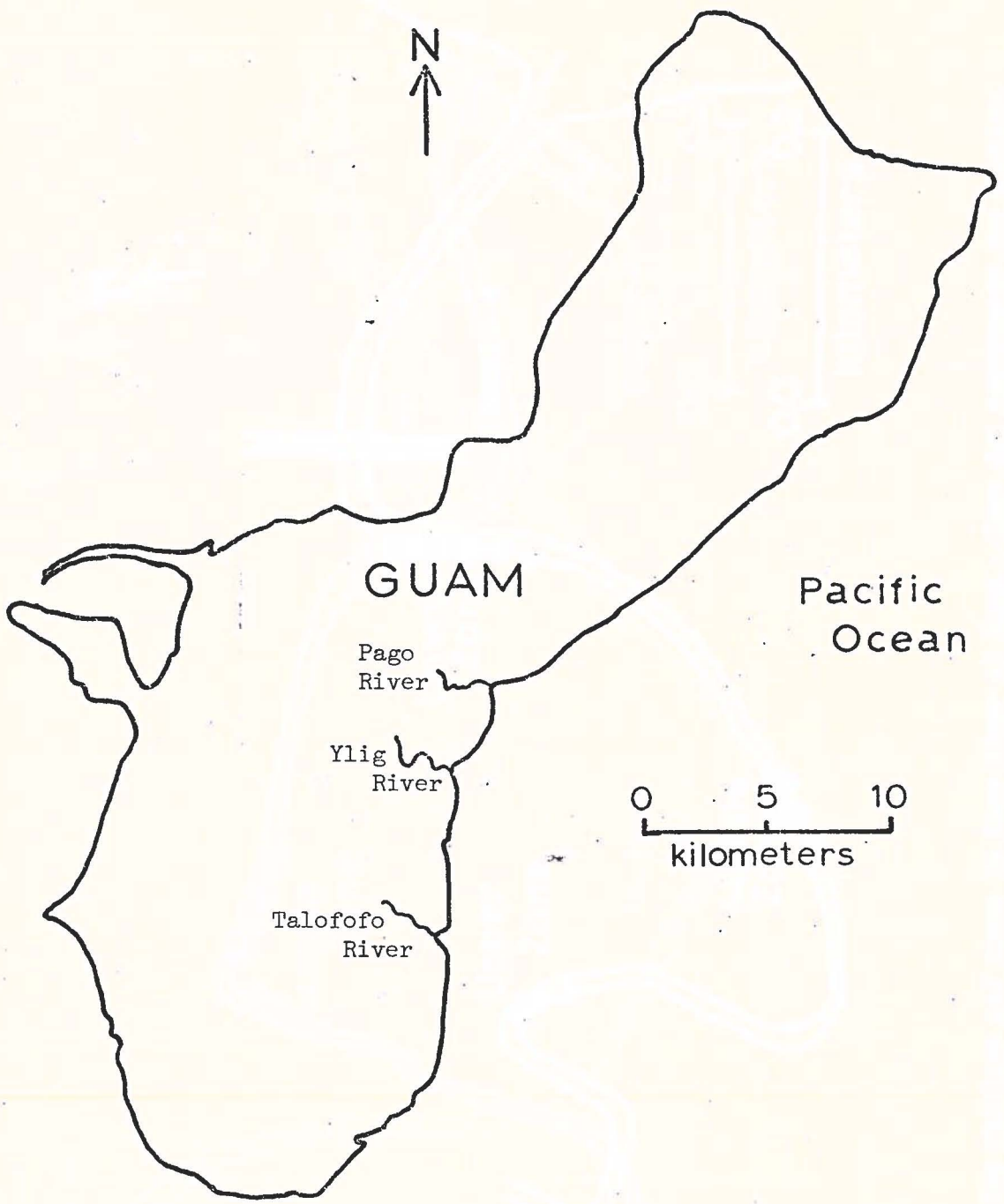

Fig. 5. Location map of study areas at Guam.

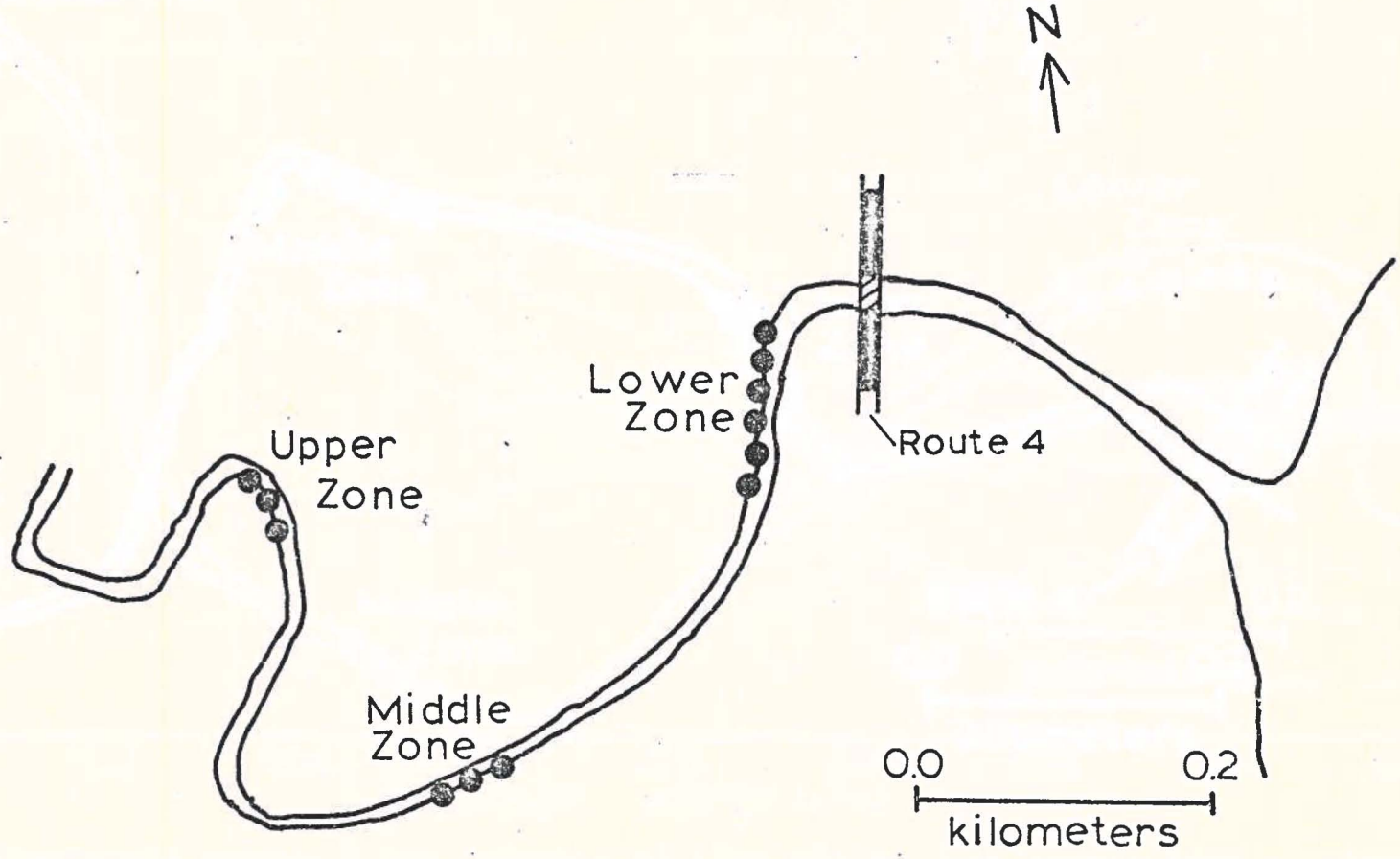

Fig. 6. Trapping stations and zones in Pago River at Guam. Each dot represents one station.

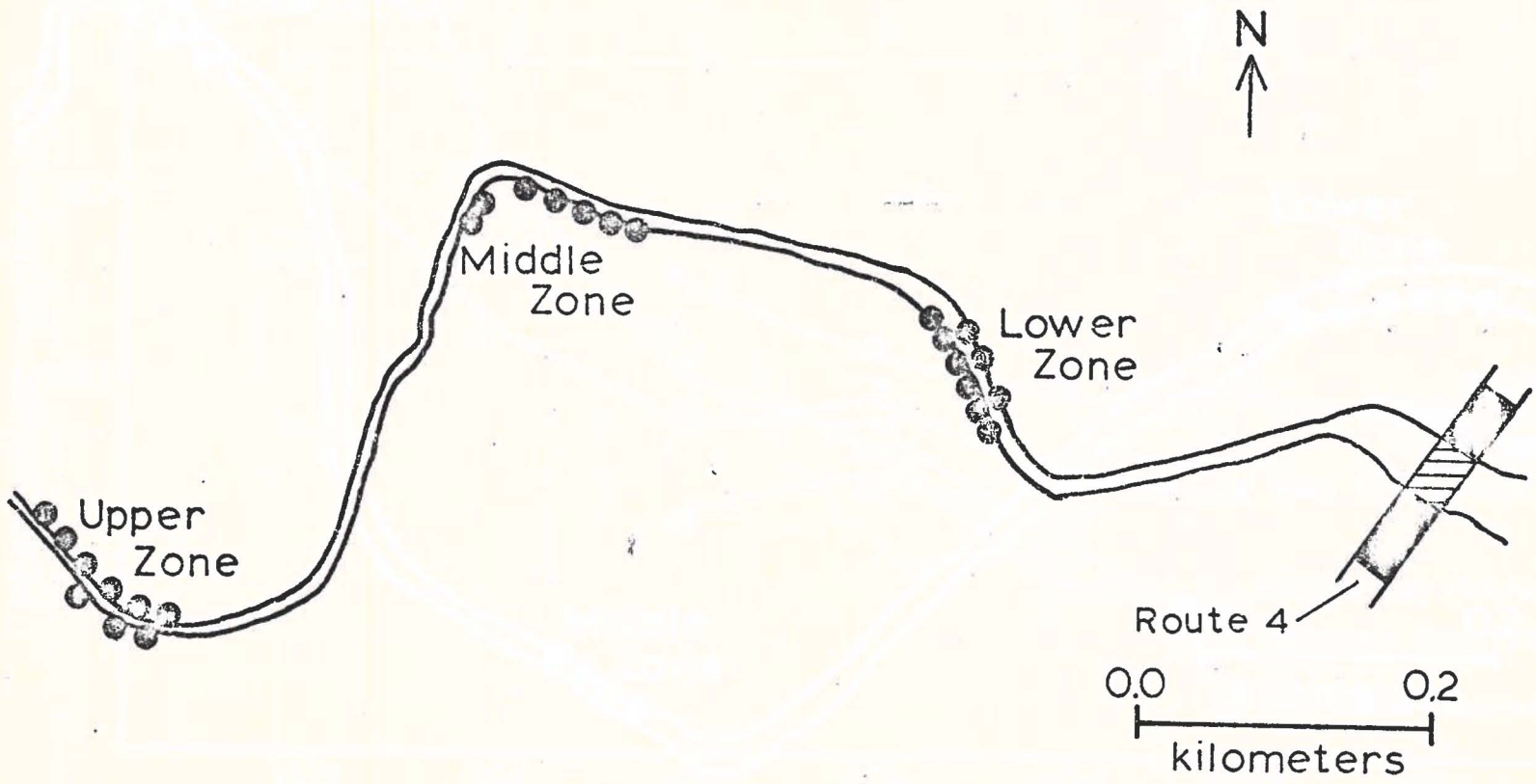

Fig. 7. Trapping stations and zones in Ylig River at Guam. Each dot represents one station.

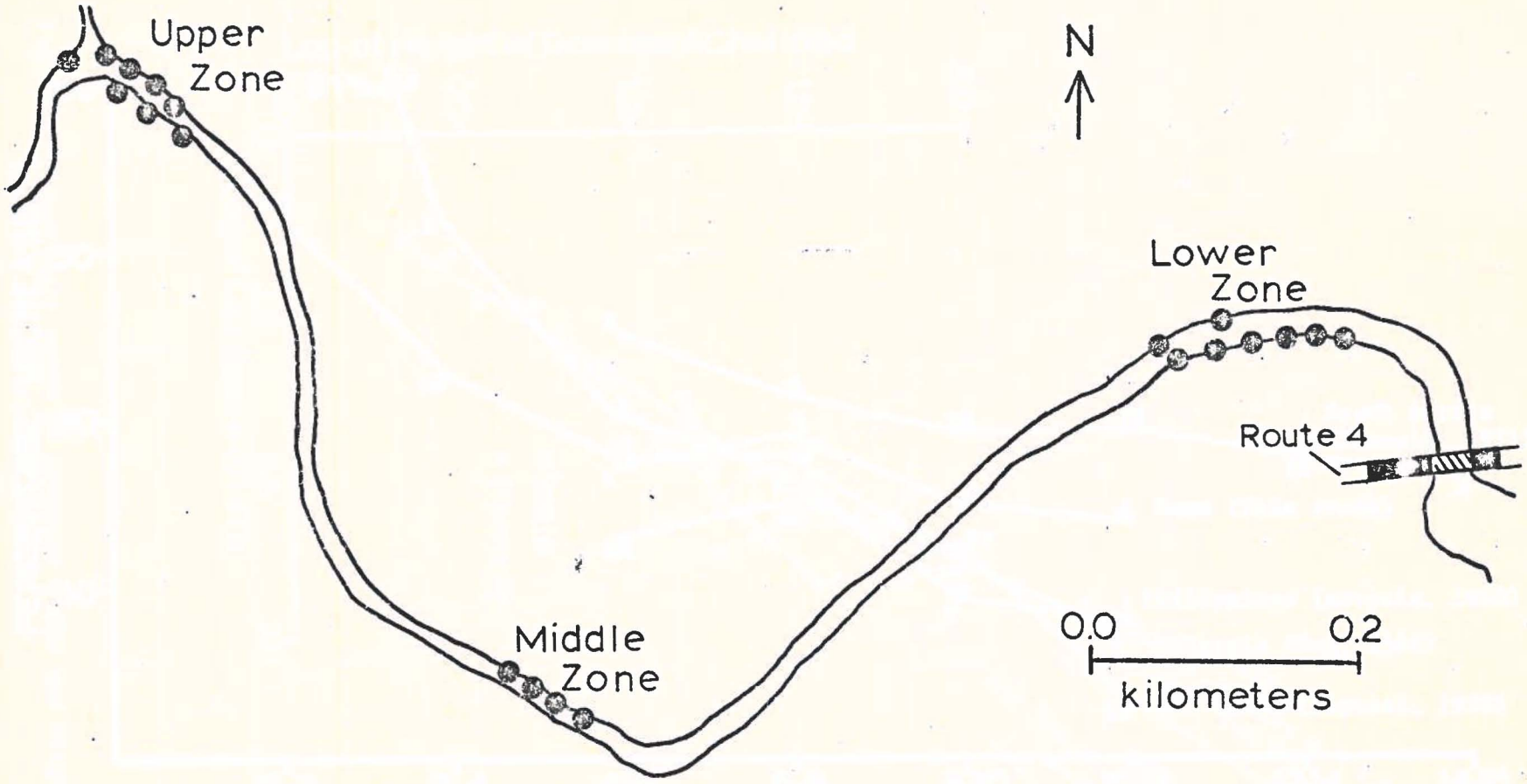

Fig. 8. Trapping stations and zones in Talofofo River at Guam. Each dot represents one station.

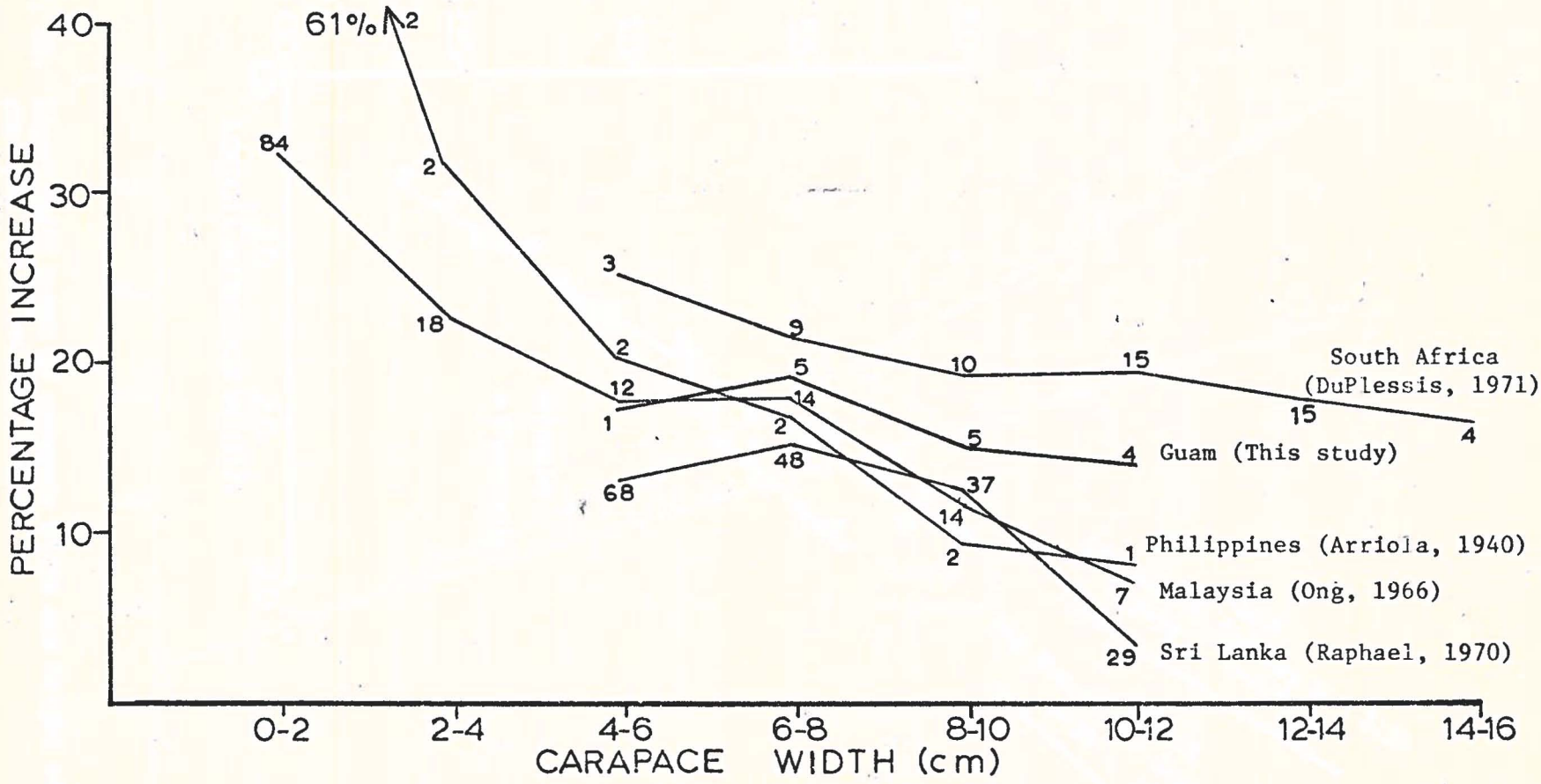

Fig. 9. The percentage increase in crab carapace width after molting. Crab carapace widths are grouped in 2.0 cm intervals along the horizontal axis. The vertical axis is the mean percent increase in width after molting for the respective group. The number at each data point is the number of observations from which the increases were computed. Example: Five crabs from Guam with premolt carapace width between 6.0 and 8.0 cm had a mean percentage increase in width of 19%.

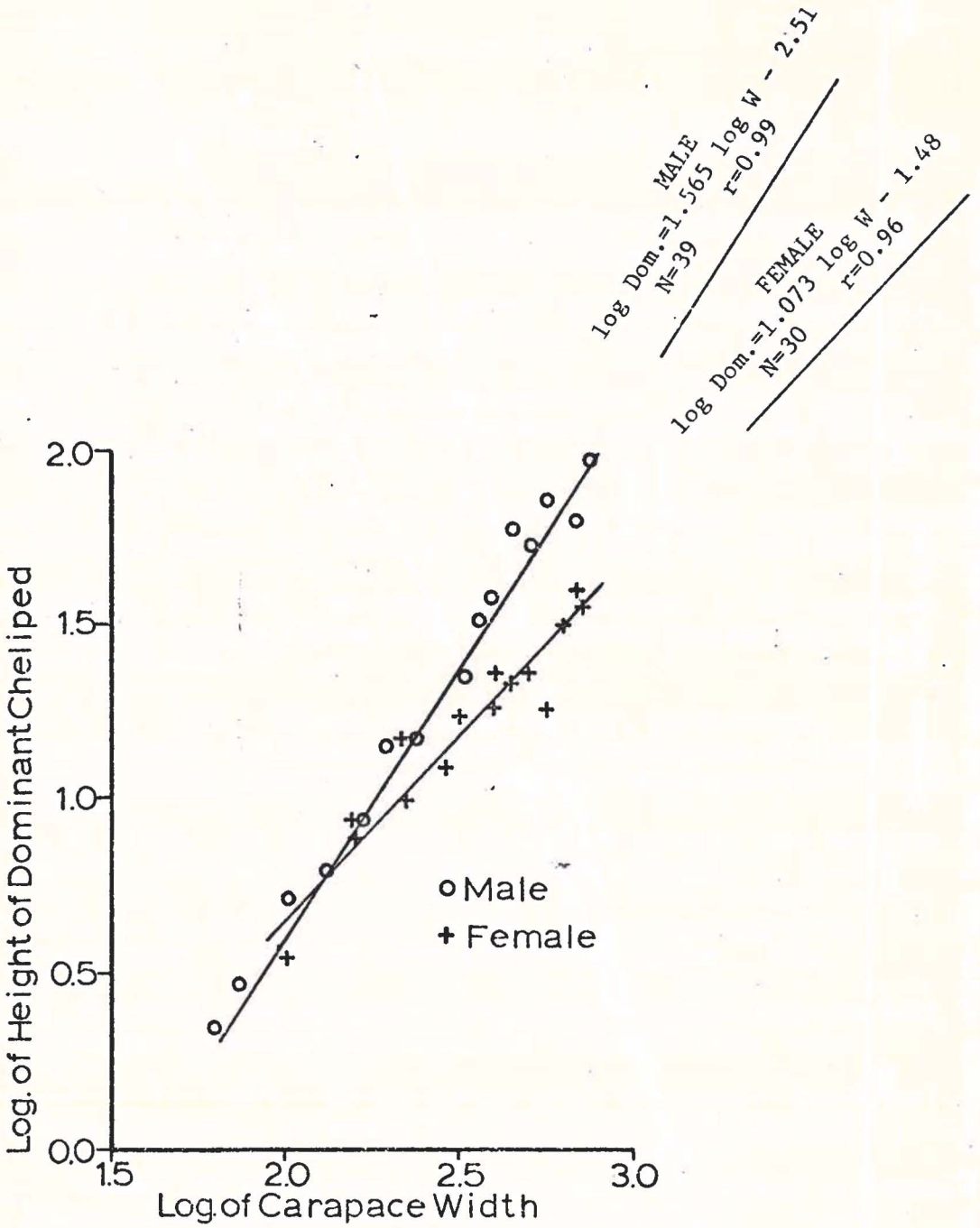

Fig. 10. Logarithmic graph of carapace width and height of dominant cheliped for males and females.

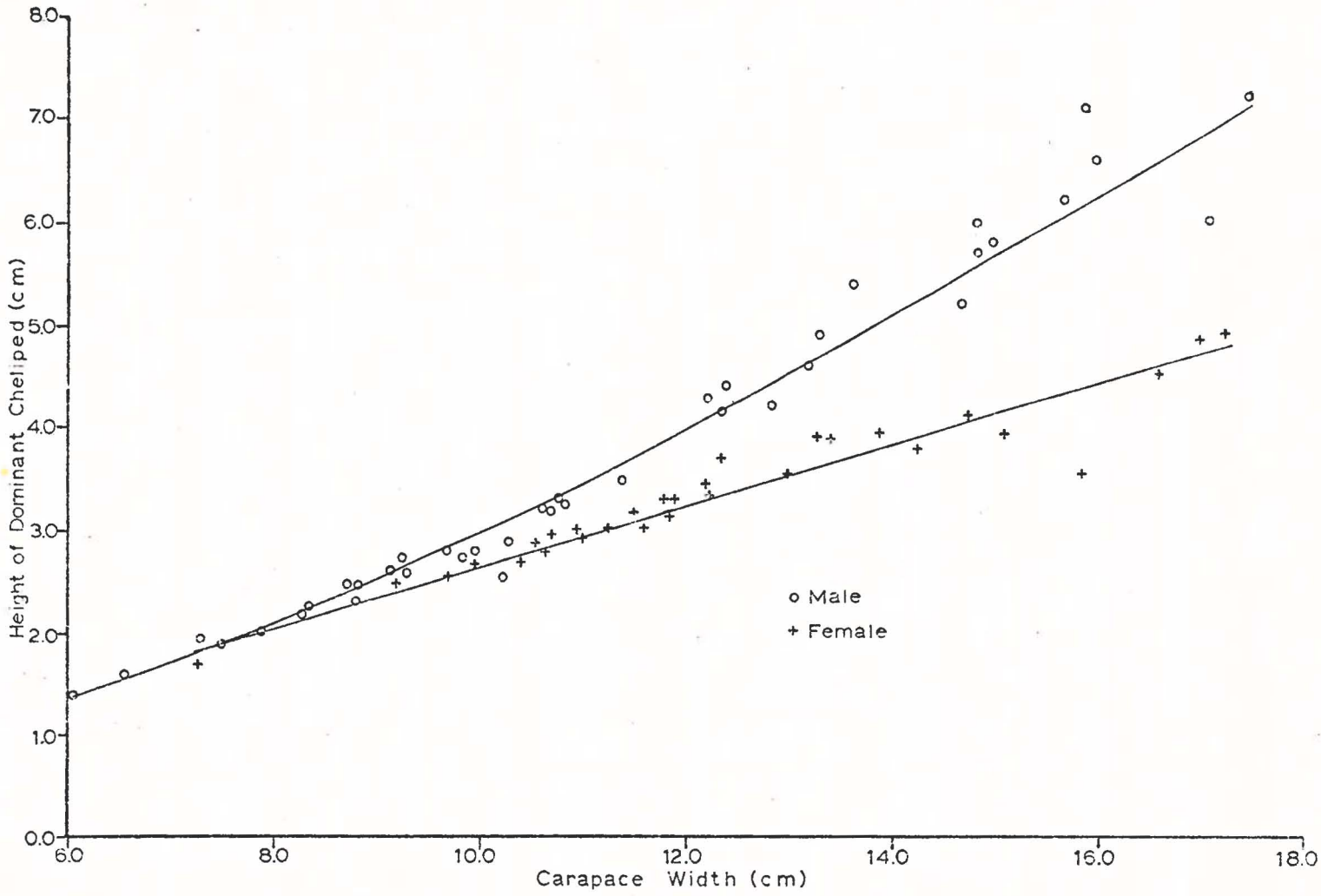

Fig. 11. Graph of carapace width and height of dominant cheliped for males and females.

Literature Cited

Airan, J., and A. Karat. 1953. Aminoacids in Scylla. Sci. Culture 19(2):92-93.

Arriola, F. J. 1940. A preliminary study of the life history of Scylla serrata. Phil. J. Sci. 73(4):437-456.

Bablet, J., and O. Cayet (eds.). 1972. Le monde vivant des atolls. Société des Océanistes, No. 28. Paris. 148p.

Baneriji, S. 1932. Vital staining experiments in Scylla serrata (Forsk). Bull. Acad. Sci. United Prov. Agra and Oudh, Allahabad, India 1:76-79.

Barnard, K. H. 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). Ann. S. Afr. Mus. 38:1-837.

Bhattacharya, D. 1931. On cytoplasmic inclusions in the oogenesis of Scylla serrata (Forsk). Allahabad Univ. Studies 8(2, Sci. Sect.):63-103.

Brick, R. W. 1974. Effects of water quality, antibiotics, phytoplankton and food on survival and development of larvae of Scylla serrata (Crustaces: Portunidae). Aquaculture 3:231-244.

Brock, V. 1960. The introduction of aquatic animals into Hawaiian waters. Int. Rev. Ges. Hydrobiol. 45(4):463-480.

Carlisle, D. B., and F. Knowles. 1959. Endocrine control in crustaceans. Cambridge University Press, London. 120p.

Chandy, M. 1973. New records of brachyuran decapods from the Gulf of Kutch. J. Bombay Nat. Hist. Soc. 72(2):401-402.

Chhapgar, B. F. 1957a. On the marine crabs (Decapoda: Brachyura) of Bombay State. J. Bombay Nat. Hist. Soc. 54(2):399-439.

_____. 1957b. On the marine crabs (Decapoda: Brachyura) of Bombay State. J. Bombay Nat. Hist. Soc. 54(3):503-549.

Churchill, E. P., Jr. 1919. Life history of the blue crab. Bull. U.S. Bureau Fish. 36(Doc. 860):91-128.

Crosnier, A. 1962. Crustacés décapodes Portunidae. Faune de Madagascar 16:1-154.

Day, J. H. 1969. A guide to marine life on South African shores. A.A. Balkema, Cape Town. 300p.

Deshmukh, R., and P. Rangneker. 1965. Some observations on the neurosecretory system of the marine crab Scylla serrata (Forskal). J. Biol. Chem. 8(1):16-23.

_____. 1966. Some observations on the hormonal control of chromatophores in the crab Scylla serrata (Forskal). J. Biol. Sci. 9(112):25-29.

_____. 1973. A study on the control of blood sugar regulation in the marine crab Scylla serrata. J. Anim. Morph. Physiol. 20(1-2): 139-149.

Ekman, S. 1953. Zoogeography of the sea. Sidgwick and Jackson Ltd., London. 417p.

Escritor, G. L. 1972. Observations on the culture of the mud crab, Scylla serrata. Pages 355-361 in T. V. R. Pillay, ed. Coastal aquaculture in the Indo-Pacific region. F.A.O., Rome.

Estampador, E. P. 1949a. Studies on Scylla (Crustacea: Portunidae), I. Revision of the genus. Phil. J. Sci. 78(1):95-109.

_____. 1949b. Scylla (Crustacea: Portunidae) II. Comparative studies on spermatogenesis and oogenesis. Phil. J. Sci. 78(3):301-353.

Fraser, P. 1976a. Free hook hair and thread hair input to fibre 5 in the mud crab, Scylla serrata, during antennule rotation. J. Comp. Physiol., A. Sens. Neural Behav. Physiol., 103(3):291-313.

_____. 1976b. Three classes of input to a semicircular canal interneuron in the crab, Scylla serrata, and a possible output. J. Comp. Physiol., A. Sens. Neural Behav. Physiol., 104(3):261-271.

Fraser, P., and D. Sandeman. 1975. Effects of angular and linear accerlerations on semicircular canal interneurons of the crab Scylla serrata. J. Comp. Physiol., A. Sens. Neural Behav. Physiol., 96(3):205-222.

Gangal, S., and N. Magar. 1967a. Biological evaluation of crab meat (Scylla serrata) in the rat. Brit. J. Nutr. 21(1):1-15.

_____. 1967b. Canning and storage of crab meat. Food Technol. 21(3 A Suppl):79-82.

Gibson-Hill, C. 1948. The island of North Keeling. Roy. Asiatic Soc. Malayan Br. J. 21(1):68-103.

Guinot, D. 1966. Les espèces comestibles de crabes dans l'Océan Indien occidental et la mer rouge. Mem. Inst. Fond. Afrique Noire 77:355-390.

_____. 1967. Les crabes comestibles de l'Indo-Pacifique. Paris, Editions de la Fondation Singer-Polignac. 145p.

Hackman, R. H. 1974. The soluble cuticular proteins from three anthropod species: Scylla serrata (Decapoda: Portunidae), Boophilus microplus (Acarina: Ixodidae) and Agrianome spinicollis (Coleoptera: cerambycidae). Comp. Biochem. Physiol., B. Comp. Biochem., 49(3):457-464.

_____. 1975. Light scattering and infrared-spectrophotometric studies of chitin and chitin derivatives. Carbohydr. Res. 38:35-46.

Hashmi, S., and S. Zaidi. 1965. Incidence of Lepas infestation on the gills of Scylla serrata (Forskal) in Karachi Waters. Agr. Pakistan 16(1):117-118.

Hepburn, H. R., I. Joffe, N. Green, and K. J. Nelson. 1975. Mechanical properties of a crab shell. Comp. Biochem. Physiol. 50A:551-554.

Hepburn, H., and H. Chandler. 1976. Material properties of arthropod cuticles and the arthrodial membranes. J. Comp. Physiol., B. Metab. Transp. Funct., 109(2):177-198.

Hiatt, R. 1944. Food-chains and the food cycle in Hawaiian fish ponds. Part II. Biotic interaction. Trans Amer. Fish. Soc. 74:262-280.

Hill, B. J. 1974. Salinity and temperature tolerance of the portunid crab Scylla serrata. Mar. Biol. 25(1):21-24.

_____. 1975. Abundance breeding, and growth of the crab Scylla serrata in two South African estuaries. Mar. Biol. 32(2):119-126.

_____. 1976. Natural food, foregut clearance-rate, and activity of the crab, Scylla serrata. Mar. Biol. 34(2):109-116.

Jones, S., and K. H. Sujansingani. 1952. Notes on the crab fishery of the Chilka Lake. J. Bombay Nat. Hist. Soc. 51(1):128-134.

Kinne, O. 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. Oceanogr. Mar. Biol. Ann. Rev. 2:281-339.

Kleinholz, L. H. 1967. Problems in crustacean endocrinology. Symp. Crustacea, Mar. Biol. Assoc. India 3:1029-1037.

Krishnamurthy, K., T. Ramprasad, and T. Venkateswarlu. 1967. Free amino acids in the blood of Ocypoda platytarsis and Scylla Serrata. Symp. Crustacea, Mar. Biol. Assoc. India 3:1026-1028.

Krishnamoorthy, R., and A. Venkatramiah. 1969. Myosin ATP-ase activity in an estuarine decapod crustacean, Scylla serrata, as a function of salinity adaptation. Mar. Biol. 4(4):345-348.

_____. 1971. Kinetic changes in flexor myosin ATP-ase of Scylla serrata adapted to different salinities. Mar. Biol. 8(1):30-34.

Lee, S., and T. Lim. 1973. Electrophoretic serum protein patterns in some penaeid prawns Crustacea Decapoda. Malays. Agr. J. 49(1):11-15.

MacNae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. Adv. Mar. Biol. 6:73-270.

MacNae, W. and M. Kalk., ed. 1958. A natural history of Inhaca Island, Mocambique. Witwatersrand University Press, Johannesburg, South Africa. 163pp.

Maguire, G., and D. Fielder. 1975. Disc electrophoresis of the haemolymph proteins of some portunid crabs (Decapoda: Portunidae): II. Physiological and taxonomic aspects. Comp. Biochem. Physiol., A. Comp. Physiol., 52(1):43-48.

Menon, K., and P. Sivadas. 1967. Blood sugar regulation in the crab Scylla serrata. I. Effect of injection of eye-stalk extract. Indian J. Exp. Biol. 5:175-178.

_____. 1968. The hormonal control of blood calcium and sugar levels in the estuarine crab Scylla serrata (Forskal). Proc. Indian Acad. Sci., Sect. B., 67(3):132-140.

Miller, J. N. 1975. Ecological studies of the biota of the Ala Wai Canal. Haw. Inst. Mar. Biol. Tech. Rep. 32:1-37.

Momin, M., and P. Rangneker. 1974. Histochemical localization of acid and alkaline phosphatases and glucose-6-phosphatase of the hepatopancreas of the crab, Scylla serrata (Forskal). J. Exp. Mar. Biol. Eco. 14(1):1-16.

_____. 1975a. Histochemical patterns of lipolytic enzymes of the hepatopancreas of Scylla serrata and their possible relation to eye-stalk factor(s). Zool. J. Linn. Soc. 57(1):75-84.

_____. 1975b. Variants in the histochemical patterns of lipids in the hepatopancreas of Scylla serrata (Forskal) (Brachyura, Decapoda). Z. Mikrosk. Anat. Forsch. 89(1):170-182.

_____. 1976. Histochemical localization of oxidative enzymes in the hepatopancreas of Scylla serrata (Forskal) (Brachyura: Decapoda). J. Exp. Mar. Biol. Ecol. 20(3):249-264.

Musgrave, A. 1929. Life in a mangrove swamp. Austral. Mus. Mag. 3(10):341-345.

Nagabhushaman, R., and K. Rango Rao. 1968. Neurosecretory system of portunid crab, Scylla serrata. J. Anat. Soc. India 15(3):138-144.

Niiyama, H. 1942. Chromosomes of four species of crabs (Brachyura, Decapoda). Zool. Mag. (Tokyo) 54(8):302-306.

Okajima, A., and D. Sandeman. 1972. Statocyst-induced eye movements in the crab Scylla serrata. I. The sensory input from the statocyst. J. Exp. Biol. 57(1):1-19.

Ong, K. S. 1964. The early developmental stages of Scylla serrata Forskal (Crustacea Portunidae), reared in the laboratory. Proc. I.P.F.C., 11th Session, Document/C64/Tech:135-146.

_____. 1966. Observations on the post-larval life history of Scylla serrata Forskal, reared in the laboratory. Malays. Agr. J. 45(4):429-443.

Pagactipunan, R. 1972. Observations on the culture of alimango, Scylla serrata at Camarines Norte (Philippines). Pages 362-365 in T. V. R. Pillay, ed. Coastal aquaculture in the Indo-Pacific region. F.A.O., Rome.

Passano, L. M. 1960. Molting and its control. Pages 473-536 in T. H. Waterman, ed. The physiology of Crustacea. Academic Press, New York and London.

Patel, B., Mulay, C., and A. Ganguly. 1975. Radioecology of Bombay Harbor: A tidal estuary. Estuarine Coastal Mar. Sci. 3(1):13-42.

Pearse, A. 1932. Observations on the ecology of certain fishes and crustaceans along the bank of the Matla River at Port Canning. Rec. Ind. Mus. 34:289-298.

_____. 1933. Parasites of Siamese fishes and crustaceans. J. Siam Soc. Nat. Hist. Suppl. 9(2):179-191.

Pillay, T. 1954. The ecology of a brackish water bheri with special reference to the fish cultural practices and the biotic interaction. Proc. Nat. Inst. India 20(4):399-427.

Prasad, R. R., and P. R. S. Tampi. 1953. A contribution to the biology of the blue swimming crab Neptunus pelagicus (Linnaeus) with a note on the zoea of Thalamita crenata Latreille. J. Bombay Nat. Hist. Soc. 51(3):674-698.

Raja Bai Naidu, K. G. 1955. The early development of Scylla serrata (Forsk.) De Haan and Neptunus sanguinolentus (Herbst). Indian J. Fish. 2(1):67-76.

Randall, R. H. 1974. Talofofo Bay Coastal Survey. Univ. Guam Mar. Lab. Tech. Rep. 13:1-77.

Rangneker, P. 1954. Comparative study of the blood volume in the crustaceans Scylla serrata, Panulirus polyphagus and Paratelphusa guerini. J. Anim. Morph. Physiol. 1(1):62-64.

_____. 1955. A comparative study of the blood plasma of some crustaceans and molluscs. J. Anim. Morph. Physiol. 1(2):42-47.

Rangneker, P., and R. Deshmukh. 1969. Effect of eyestalk removal on the ovarian growth of the marine crab, Scylla serrata (Forskal). J. Anim. Morph. Physiol. 15(1-2):116-126.

Rangneker, P., and M. Madhyastha. 1969. Effect of eye-stalk removal on the rate of oxygen consumption in the crab, Scylla serrata (Forskal). J. Anim. Morph. Physiol. 16(1):84-88.

Rangneker, P., M., Madhyastha, and A. Latey. 1971. Hormonal control or reproduction in the male crab, Scylla serrata. J. Anim. Morph. Physiol. 18(1):17-29.

Rangneker, P., and M. Momin. 1975a. Histochemical studies on the distribution and hormonal regulation of carbohydrates in the hepatopancreas of the crab Scylla serrata (Forskal). Z. Mikrosk. Anat. Forsch. 88(5):871-883.

_____. 1975b. Histochemical localization of oxidative enzymes in the hepatopancreas of Scylla serrata (Forskal) (Brachyura: Decapoda). J. Exp. Mar. Biol. Eco. 20(3):249-264.

Rangneker, P., P. Vyankoji, and M. Momin. 1975. Histochemical observations on the occurrence of glycolytic and pentose phosphate cycle enzymes in the hepatopancreas and their possible relation to eyestalk factor(s) in the crab Scylla serrata (Forskal). Z. Mikrosk. Anat. Forsch. 89(1):128-142.

Raphael, Y. I. 1970. A preliminary report on brackish water pond culture of Scylla serrata Forskal in Ceylon. Proc. I.P.F.C., 14th Session, Document/C70/21:1-10.

Saha, N., and D. Raychaudhuri. 1973. Protease activity in the gut of the crab Scylla serrata Crustacea Decapoda. Proc. Zool. Soc. (Calcutta) 26(2):113-119.

Sakai, T. 1976. Crabs of Japan and the adjacent seas. Kodansha Ltd., Tokyo. 773p.

Samuel, N. 1945. Some aspects of the morphology and physiology of the antennary glands of three decapod crustaceans. J. Univ. Bombay 14(3):29-41.

Sandeman, D. 1971. The excitation and electrical coupling of four identified motoneurons in the brain of the Australian mud crab, Scylla serrata. Z. Vergl. Physiol. 72(2):111-130.

_____. 1975. Dynamic receptors in the statocysts of crabs. In H. Schoene (ed.). Forsch. Zool. 23(1):185-191.

Sandeman, D., and C. Mendum. 1971. The fine structure of the central synaptic contacts on an identified crustacean motoneuron. Z. Zellforsch. Mikrosk. Anat. 119(4):515-525.

Sandeman, D., and A. Okajima. 1973a. Statocyst induced eye movements in the crab Scylla serrata. Part II. The responses of the eye muscles. J. Exp. Biol. 58(1):197-212.

_____. 1973b. Statocyst induced eye movements in the crab Scylla serrata. Part III. The anatomical projections of sensory and motor neurons and the responses of the motor neurons. J. Exp. Biol. 59(1):17-38.

Serene, R. 1951. Les espèces du genre Scylla à Nhatrang (Vietnam). Proc. I.P.F.C., Sect. II, pp. 133-137.

Silvey, G. 1974. Integration at a sensory motor synapse in the oculomotor system of the crab Scylla serrata. Am. Zool. 14(4):1273.

Silvey, G., and D. Sandeman. 1976a. Integration between statocyst sensory neurons and oculomotor neurons in the crab Scylla serrata: I. Horizontal compensatory eye movements. J. Comp. Physiol., A. Sens. Neural Behav. Physiol., 108(1):35-44.

_____. 1976b. Integration between statocyst sensory neurons and oculomotor neurons in the crab Scylla serrata: III. The sensory to motor synapse. J. Comp. Physiol., A. Sens. Neural Behav. Physiol., 108(1):53-56.

_____. 1976c. Integration between statocyst sensory neurons and oculomotor neurons in the crab Scylla serrata: IV. Integration phase lags and conjugate eye movements. J. Comp. Physiol., A Sens. Neural Behav. Physiol., 108(1):67-74.

Silvey, G., P. Dunn, and D. Sandeman. 1976. Integration between statocyst sensory neurons and oculomotor neurons in the crab Scylla serrata: II. The thread hair receptors. J. Comp. Physiol., A. Sens. Neural Behav. Physiol., 108(1):45-52.

Steinacker, A. 1975. Perfusion of the central nervous system of decapod crustaceans. Comp. Biochem. Physiol., A. Comp. Physiol., 52(1):103-104.

Stephenson, W., and B. Campbell. 1960. Australian portunids (Crustacea: Portunidae). IV. Remaining genera. Austral. J. Mar. Freshw. Res. 11(1):73-112.

Stephenson, W. 1972. An annotated check list and key to the Indo-West Pacific swimming crabs (Crustacea: Decapods: Portunidae). Roy. Soc. N. Z. 10:1-64p.

Strickland, J., and T. Parsons. 1968. A practical handbook of seawater analysis. Fish. Res. Brd. Canada. Bull. 167. 311p.

Tamura, T. 1966. Marine aquaculture, n.p.[Transl. from Japanese, Nat. Tech. Info. Serv.].

Thia-eng, C. 1974. An ecological study of the Ponggol Estuary in Singapore. Hydrobiologia 43(3-4):505-533.

Thomas, A. J. 1972. Crab fishery of the Pulicat Lake. J. Mar. Biol. Assoc. India 13(1-2):278-280.

Tinker, S. 1965. Pacific Crustacea. Charles E. Tuttle Co., Inc., Tokyo. 134p.

Varikul, V., S., Phumiphol, and M. Hongpromyart. 1972. Preliminary experiments on pond rearing and some biological studies of Scylla serrata (Forskal). Pages 366-374 in T. V. R. Pillay, ed. Coastal aquaculture in the Indo-Pacific region. F.A.O., Rome.

Veerannan, K. M. 1972. Respiratory metabolism of crabs from marine and estuarine habitats. I. Scylla serrata. Mar. Biol. 17(4):284-290.

_____. 1974. Respiratory metabolism of crabs from marine and estuarine habitats: an interspecific comparison. Mar. Biol. 26(1):35-43.

Verwey, J. 1930. Einiges uber die biologie Ost-Indischer mangrovekrabben. Treubia 12(2):167-261.

Wilder, M. J. 1976. Estuarine and mangrove shorelines. Pages 157-189 in R. H. Randall and L. G. Eldredge, Atlas of the reefs and beaches of Guam. Coastal Zone Management Section, Bureau of Planning, Guam.