BIOLOGICAL STUDIES ON THE COCONUT CRAB (*BIRGUS LATRO*) IN THE MARIANA ISLANDS

Steven S. Amesbury

Agriculture Experiment Station
College of Agriculture and Life Sciences
University of Guam
Technical Report No. 17

University of Guam
Marine Laboratory
Technical Report No. 66

December 1980
[Reprinted December 2000]

University of Guam Marine Laboratory
Technical Report Reprint Series

Technical reports of the University of Guam Marine Laboratory are printed and distributed in limited numbers on a first-come-first-served basis. Funding for reprinting technical reports is seldom available. Therefore, it is the policy of the Marine Laboratory to produce reprints of its technical report series in electronic format. In producing the electronic reprint versions, no effort has been made to retain the exact pagination for text, figures, or tables because of differences in formatting with fixed-spaced versus proportionally-spaced fonts. Therefore, authors wishing to quote statements from the text should consult a copy of the original printed version for the correct pagination.

—Ed., December 2000

BIOLOGICAL STUDIES
ON THE COCONUT CRAB (*BIRGUS LATRO*)
IN THE MARIANA ISLANDS

by

Steven S. Amesbury

Agriculture Experiment Station
College of Agriculture and Life Sciences
University of Guam
Technical Report No. 17

University of Guam
Marine Laboratory
Technical Report No. 66

December 1980

ABSTRACT

This report reviews the life history, ecology, and culturing potential of the coconut crab (*Birgus latro*). Results of field studies on Guam, on several islands in the northern Marianas archipelago, and on an islet of Kayangel Atoll, Palau, are presented. Observations on the closely related terrestrial hermit crab genus *Coenobita* indicated a close relationship between lunar and tidal phases and larvae-releasing activities. Coconut crabs held in captivity in individual containers underwent ecdysis, but there was no resulting increase in size. Experiments with a large enclosure indicated that coconut crabs could be maintained at higher than natural densities without injuring one another, but no ecdysis or growth occurred. Recommendations for management of natural coconut crab populations are made. It was concluded that commercial cultivation of coconut crabs will require considerable further research, and that culturing of other crustaceans, for which techniques have already been developed, should be given higher priority on Guam.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

This project was funded by the University of Guam Agricultural Experiment Station (Hatch) No. GU00010 and by the Office of Sea Grant, Grant No. 04-5-158-45. I would like to thank Dr. Wilfred P. Leon Guerrero and Dr. Lucius G. Eldredge for their support and encouragement. Mr. Daniel Wooster helped in the coconut crab collection and maintenance on Guam and in the field work in the Northern Mariana Islands. Mrs. Alicia Masterson also assisted in the laboratory maintenance of the crabs. Mr. Frank Cushing was very helpful in field work on Guam and in the Northern Mariana Islands and in the construction of the large coconut crab enclosure; in this latter effort he was assisted by Mr. Ted Tansy and Mr. Pat Beeman. The photographs in Figures 1 and 2 were taken by Mr. Ted Tansy; Mr. Rob Myers took the cover photograph and the photograph in Figure 9; Mr. Vaughan Tyndzik did the photo processing. The final draft was typed by Mrs. Teresita Balajadia and Mrs. Elaine Faria. I would like to make special acknowledgement of Dr. Ernst Reese, of the University of Hawaii, who was instrumental in my initial involvement with the coconut crab.

INTRODUCTION

The coconut crab *Birgus latro* (Linnaeus) belongs to the terrestrial hermit crab family Coenobitidae. It differs from the other members of this family in that it does not inhabit a gastropod shell as an adult. *Birgus latro* is widely distributed throughout the western Pacific and eastern Indian Oceans, occurring almost exclusively on oceanic islands or small offshore islets adjacent to large continental islands. Throughout its range the coconut crab is considered a highly desirable food item among local populations. On islands uninhabited by man, the coconut crab is among the largest of terrestrial animals and is relatively free of predators. On islands with human populations, crabs are harvested for food and are less abundant than on comparable islands where man is not present. On Guam, which supports a large human population and which has been subject to considerable environmental modification, coconut crabs have become scarce.

Because the coconut crab is an esteemed food and is dwindling in abundance on Guam and other population centers in Micronesia, there is a need to better understand its biology so that appropriate stock management measures can be applied to conserve and, if possible, develop this resource. Rearing coconut crabs in captivity may be a useful approach for providing sufficient crabs to meet consumer demands or for restocking areas which have been overharvested. This report presents the results of investigations on the coconut crab carried out at the University of Guam including field surveys of coconut crabs on Guam, the islands of Pagan, Asuncion, and Guguan in the Northern Marianas, and Ngariungs island in Kayangel Atoll, Palau. Other published information on this species is reviewed. Factors important for conserving and managing natural populations of the coconut crab and for rearing them in captivity are discussed.

LIFE HISTORY AND ECOLOGY OF THE COCONUT CRAB

Reproduction

Fertilization is initiated among coconut crabs when the male transfers a packet of sperm, the spermatophore, to the female. On the basis of spermatophore morphology, Matthews (1956) suggested that copulation among coconut crabs occurs in the water, but Helfman (1973) observed a pair of coconut crabs copulating on land at Enewetak in the Marshall Islands. On Guguan, in the Mariana Islands, I encountered a pair of coconut crabs that had apparently just concluded copulation. The female had a white, moist-appearing spermatophore attached to her thorax. These crabs were well away from the water's edge.

The sperm mass is presumably transferred to an internal spermatotheca and fertilization of the eggs occurs internally. Subsequently, the fertilized eggs are extruded from the female's body and carried beneath her abdomen, held in place by three specialized abdominal appendages. Helfman (1973) calculated the number of developing embryos carried by four gravid female coconut crabs in Palau and Enewetak; the number of embryos per female ranged from 51,000 to 138,000.

Female coconut crabs carrying developing embryos have been most commonly observed during the summer months (Helfman, 1973). The single berried female collected on Guam during the present study was found on September 24, 1974. Examination of a small sample of the eggs at this time showed them to be slightly elliptical in longitudinal section, measuring approximately 0.6 by 0.7 mm. The eggs were filled with orange yolk, and no embryos were visible when the eggs were examined with a dissecting scope. By October 7, the eggs were somewhat larger and more elliptical in longitudinal section (approximately 0.7 by 0.95 mm). At this time the orange yolk filled about half the volume of the eggs, and the embryonic eyes, blood vessels, and a beating heart were observable (Figure 1). On October 11, additional eggs were removed and examined. When placed in saltwater, the eggs did not spontaneously hatch, but the embryos inside appeared almost fully formed, and little yolk remained in the eggs. Several embryos were removed from the eggs (Figure 2), but these exhibited no swimming movements. On October 13, the captive gravid female was found to be no longer carrying eggs. No eggs could be found on or in the sandy substrate in the holding container, and the fate of these eggs is unknown. Possibly the female reabsorbed them or ate them.

The berried female crabs observed on Pagan, Asuncion, and Guguan in the Northern Mariana Islands were seen in the summer from July 6 to July 12, 1975; no observations were made on these islands at other times of the year.

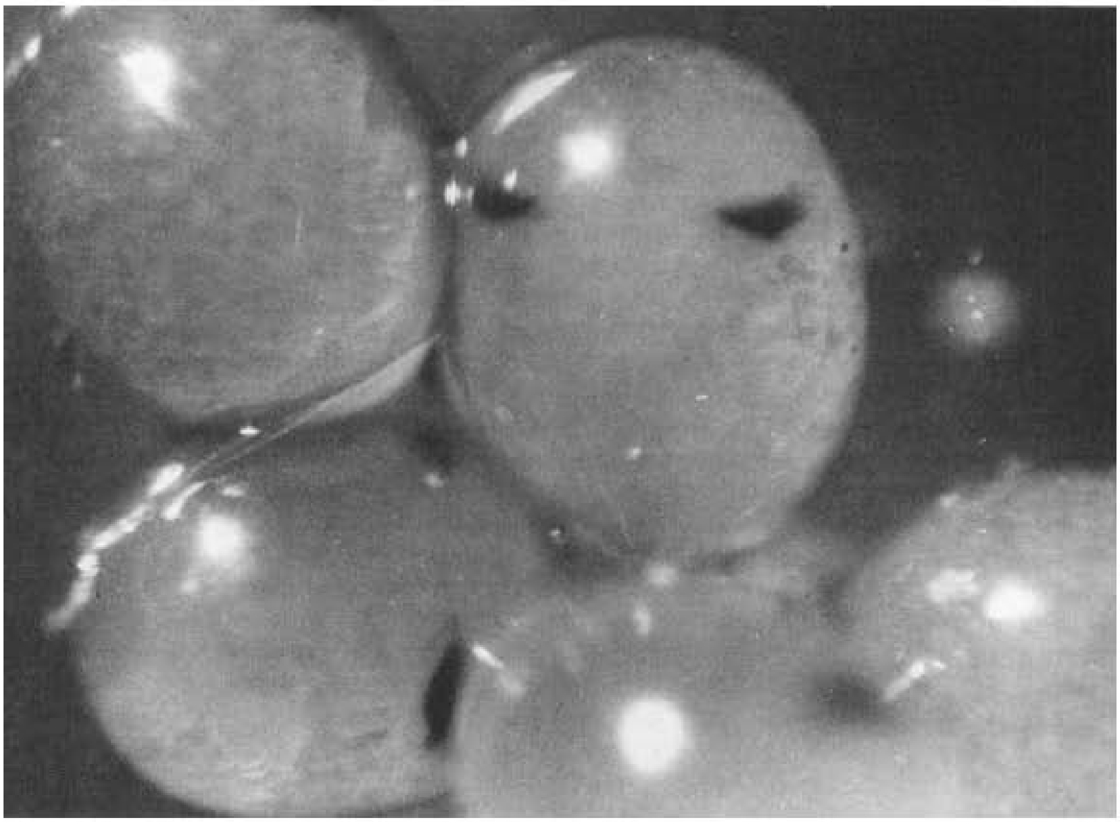

Figure 2. Coconut crab eggs with embryos visible inside. Dark areas are developing eyes. October 7, 1974.

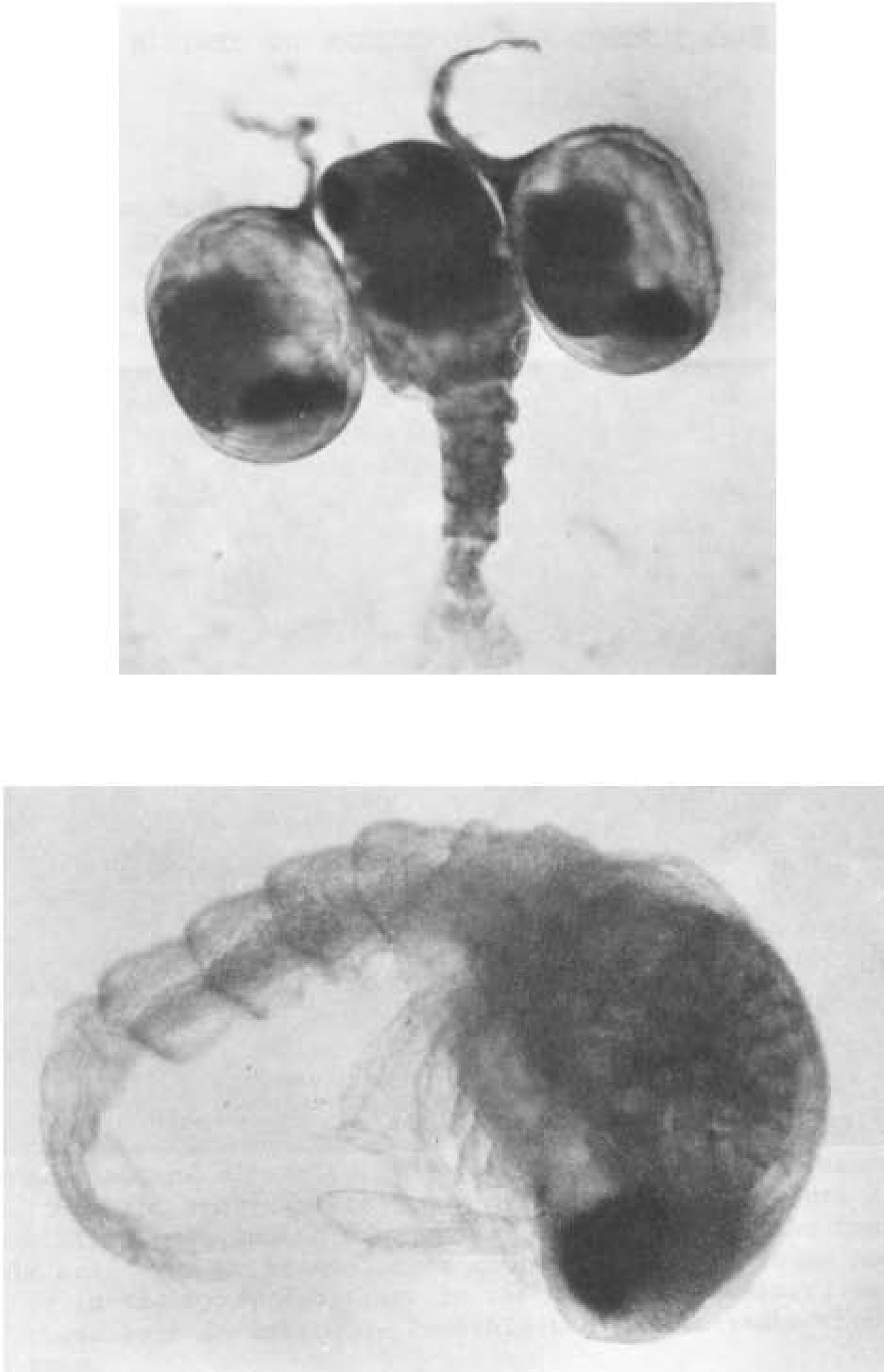

Figure 2. Coconut crab eggs and embryos, October 11, 1974. Upper: Intact eggs and embryo artificially removed from egg. Lower: Lateral view of embryo removed from egg.

Helfman (1973) estimated that 25% of the potentially reproductive female crabs in his Enewetak study site and 8% in his Palau study site were berried. On Guam, only one berried female was found out of 10 females seen with a thoracic length (TL) of 25 mm or greater. On Pagan two female coconut crabs of potentially reproductive size were seen and one was berried. On Asuncion, three potentially reproductive females were seen; of these, two were carrying eggs. On Guguan, 10 potentially reproductive females were observed; three of these were carrying eggs, three were near the ocean and appeared as if they had just released their eggs, and one was carrying a spermatophore. Thus, female crabs in Northern Marianas populations appear to be highly reproductively active, while little reproductive activity has been observed among coconut crab populations on Guam. No berried crabs were seen among the five potentially reproductive females examined on Kayangel Atoll, Palau.

The median size of reproductively active female crabs measure d: in this study was 42.5 mm TL. Berried female crabs measured by Helfman (1973) had a median TL of 27 mm (Ngerkersiul Is., Palau) and 40 mm (Igurin Is., Marshall Islands).

Larval Release

Reese and Kinzie (1968) demonstrated that mature coconut crab embryos will hatch spontaneously when brought into contact with sea water, and they suggested that the berried female crab carries the eggs to the water's edge at an appropriate time to release the larvae into the sea. Helfman (1973) suggested that the larval release is tied to lunar and tidal rhythms, more specifically that larval release predominantly occurs shortly after the new moon. He observed four freshly spent female crabs near the beach at his Enewetak study site on the sixth and seventh days after the new moon. Reese and Kinzie (1968) collected female crabs with mature, ready-to-hatch embryos five days after the full moon and two days after the last quarter moon. During the present study, berried females, with apparently mature embryos, and recently spent female crabs were seen in the Northern Mariana Islands from July 6 to July 12, 1975; the new moon occurred on July 9th. The single berried female collected on Guam was captured on September 24, 1974. The embryos were not mature at this time, but by October 11 had apparently reached maturity, and on October 13 had disappeared. The new moon occurred on October 15.

Within a few days after the new moon (as well as the full moon), tidal ranges typically are at their maximum (spring tides). Water exchange on the reef flat should be at its greatest at this time. It may well be selectively advantageous for an animal such as a coconut crab, which releases its larvae into inshore waters, to do so during spring tides to ensure the greatest opportunity for the eggs to be flushed off the reef flat, where egg predation may be quite severe, out to open ocean waters where predation may be reduced and where a more constant supply of edible phyto- and zooplankton will be available for the developing larvae.

Because of the scarcity of gravid coconut crabs on Guam, it was not possible to investigate their larval release behaviors in any detail. However, four species of the terrestrial hermit crab genus *Coenobita* (*C. brevimana*, *C. rugosa*, *C. cavipes,* and *C. perlata*) occur on Guam in considerably greater numbers than *Birgus latro*. The larval life history of these crabs is presumably very similar to that of the coconut crab, and they are faced with the same problem of ensuring that sufficient larvae survive the immediate post-hatching period to recruit ultimately to their terrestrial populations. The greater availability of these hermit crabs made it possible to investigate the timing of larval release among these species in more detail.

Preliminary observations on a section of beach along Pago Bay, on the east coast of Guam, verified that during the night around the time of the new moon many coenobitid crabs were on the beach releasing eggs into the water. Females belonging to the three larger species of *Coenobita* on Guam (*C. brevimana*, *C. cavipes*, and *C. perlata*) were most frequently seen, and of these, *C. brevimana* predominated. The female crab walked down the beach front until it entered the water or was met by the uprush of a wave. The crab would crouch down and partly, but not completely, pull its body out of the gastropod shell it was carrying. The crab might remain in that position for one or several waves. Then it would return its abdomen into the gastropod shell, walk back up the face of the beach, and disappear into the foliage. No aggressive interactions between crabs were seen at this time. To verify that larval release was actually taking place, I collected several crabs of each of the three species while they were on the beach but before they had reached the water. I took these crabs to the University of Guam Marine Laboratory and held them in aquaria filled with sea water, shaking them gently in the water. Larvae immediately began to pour forth out of the shell and to swim actively around the aquaria. Large aggregations of larvae-releasing hermit crabs were seen on this beach area at night during the new moon period in subsequent months, but no such aggregations were seen during the night at times of the full moon or during the day at either full or new moon.

To delimit more precisely the timing of the larval release activities, a 20-meter stretch of beach on Pago Bay was marked off. At night during new moon periods, this 20-m stretch of beach was censused at 10-minute intervals. A flashlight was used to illuminate the crabs and all crabs in the water or on the beach, presumably going to the water or returning from it, were counted. The results of these censuses are shown in Figs. 3–6.

It is clear that the time of maximum larvae-releasing activity is closely related to the time of highest tide. This supports the hypothesis that the crabs are timing their larval release to maximize the chances of the larvae being carried off the reef into the ocean waters beyond. The lack of larval release activities during the daytime suggests that predation on the larvae may be an important environmental factor shaping this activity. This may also explain the absence of larval release at times of the full moon, when tidal ranges are also high, but when the moon's illumination may increase the vulnerability of the larvae to predators.

The data presented here, though somewhat scanty, indicate the existence of two types of rhythmic activity in these hermit crabs: a cycle of embryonic maturation related to the phase of the moon and a cycle of larvae-releasing activity related both to moon phase and the timing of the tides. This rather complex and precise reproductive chronicity is reminiscent of the spawning

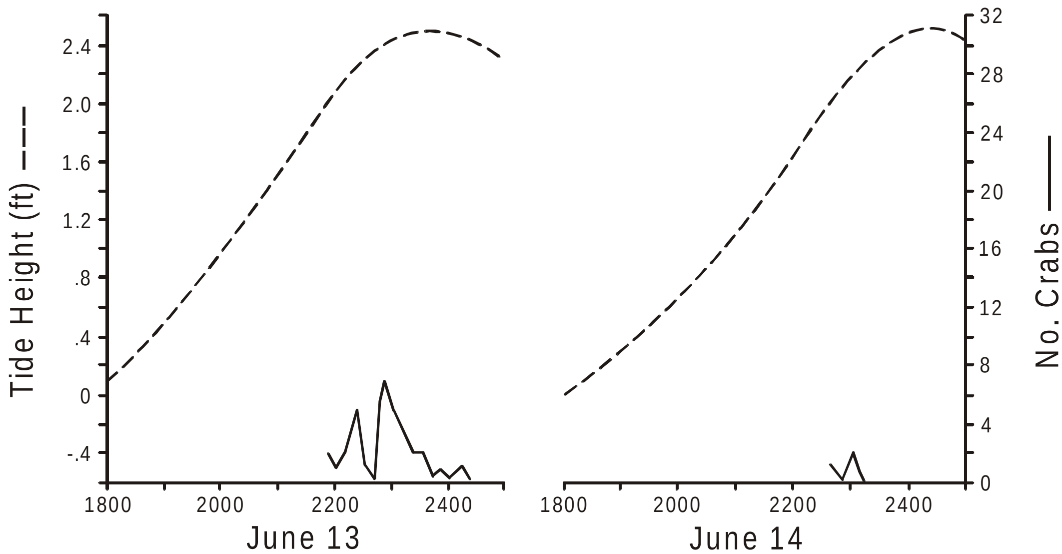

Figure 3. Number of *Coenobita* hermit crabs observed releaseing eggs, at 10-minute intervals, June 13 and 14, 1975. Sinusoidal curve approximates tide height.

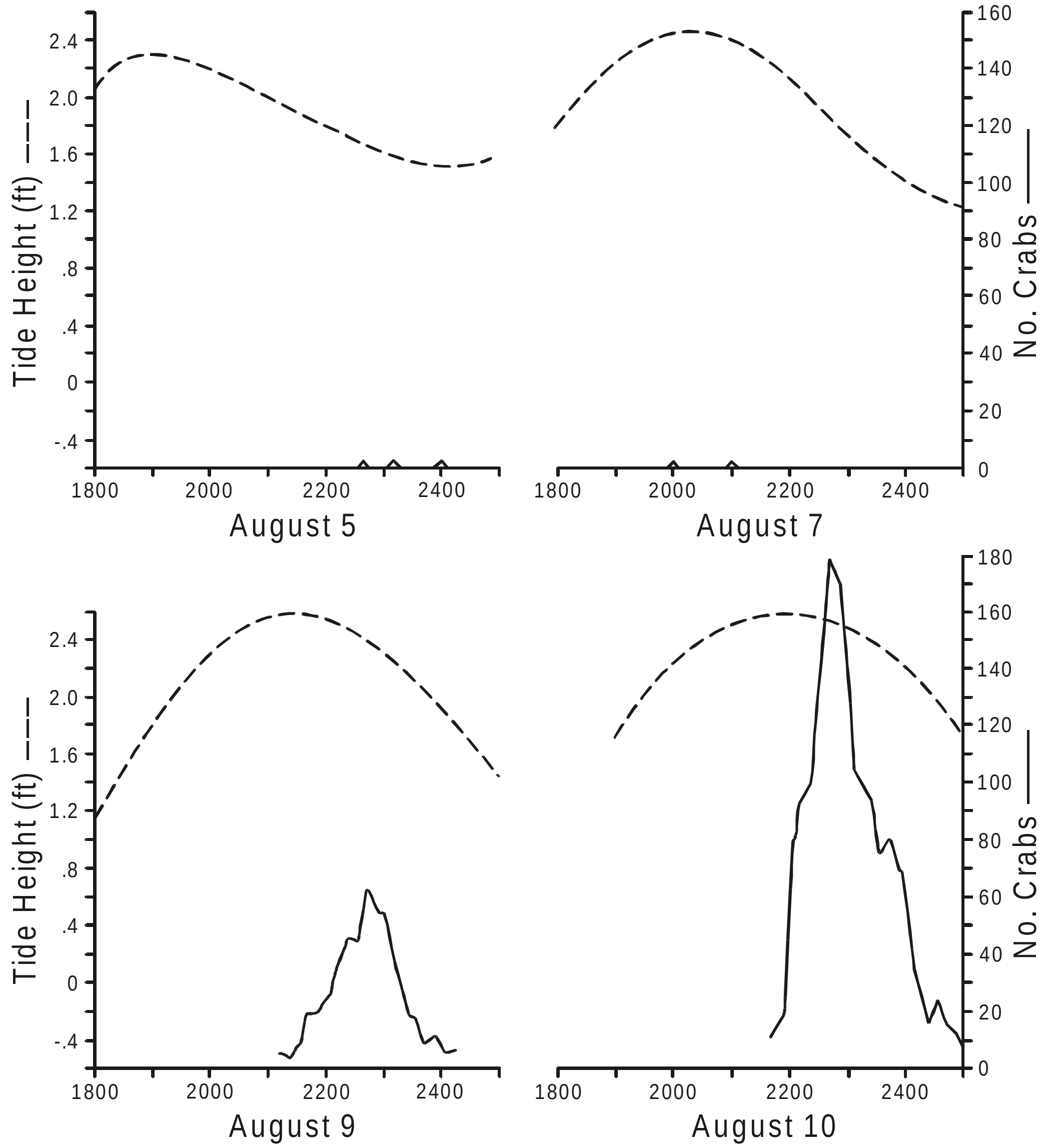

Figure 4. Number of *Coenobita* hermit crabs observed releasing eggs, at 10-minute intervals, August 5, 7, 9, and 10, 1975. Sinusoidal curve approximates tide height.

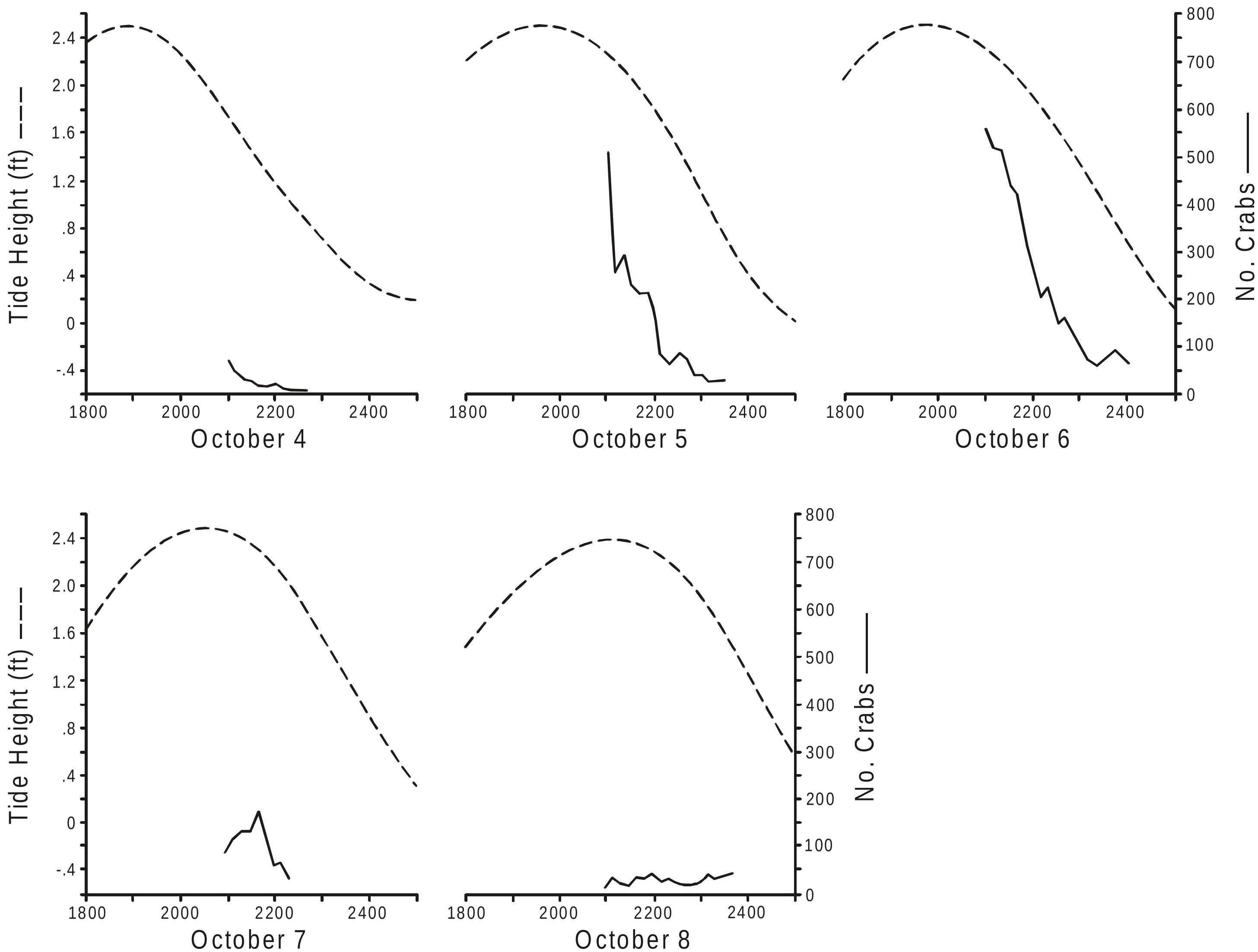

Figure 5. Number *Coenobita* hermit crabs observed releasing eggs, at 10-minute intervals, October 4, 5, 6, 7, and 8, 1975. Sinusoidal curve approximates tide height.

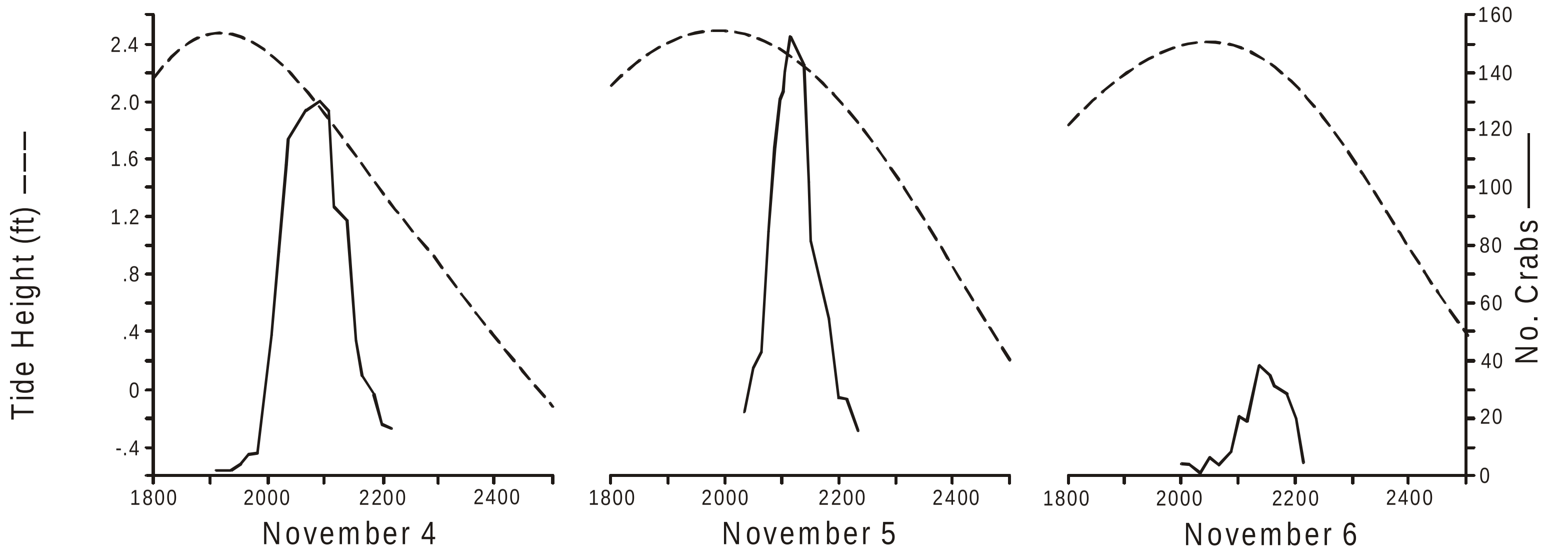

Figure 6. Number of *Coenobita* hermit crabs observed releasing eggs, at 10-minute intervals, November 4, 5, and 6, 1975. Sinusoidal curve approximates tide height.

behavior of the California grunion (although in a reverse way), in which the eggs are shed and fertilized on the beach during a very short and specific period of the lunar and tidal cycles (Frey, 1971). It seems especially remarkable that these crabs can regulate their activity so closely to the tidal phase when they are essentially terrestrial during their adult life.

Although the foregoing observations were made on species of *Coenobita*, and no *Birgus* were ever observed on the beach during these censuses, it seems likely that coconut crabs pattern their larval release in much the same way. Their absence during these censuses probably reflects the scarcity of berried female coconut crabs on Guam.

Larval Development

The pattern of larval development in *Birgus latro* was described by Reese and Kinzie (1968) who reared coconut crab larvae in the laboratory at Enewetak. They described the larval stages, comprising 4 (or sometimes 5) zoeal stages followed by a post-larval glaucothoe stage. The zoeal stages are adapted for a pelagic existence while the glaucothoe is an amphibious stage, during which the young crab, provided the proper circumstances, migrates onto land (Reese, 1968). The pelagic zoeal stages lasted from 17 to 28 days during Reese and Kinzie's (1968) experiments, while the duration of the glaucothoe stage was 21 to 28 days. These observations indicate that larval *Birgus* spend some three to eight weeks in the ocean before migrating onto land.

Successful migration onto land apparently requires that the glaucothoe enter and occupy an empty gastropod shell (Reese, 1968), a behavior indicative of the coconut crab's hermit crab affinities. Once on land, the glaucothoe undergoes a further metamorphosis into a young crab stage (Reese and Kinzie, 1968), becoming morphologically a miniature adult. The young crab maintains residence in an empty gastropod shell for some time, eventually abandoning the shell to become a free-living coconut crab. Reese and Kinzie '(1968) report young coconut crabs which have continued to carry shells for almost 2.5 years in captivity, attaining a carapace length (CL) of 10 to 15 mm [approximate thoracic length 4.8–7.1 mm, based on the conversion factor, TL = CL/2.1, calculated by Helfman (1973)]. Reese and Kinzie (1968) also report that the largest *Birgus* ever found in a shell at Enewetak had a CL of 11.3 mm (TL = 5.4 mm), while the smallest individual ever found without a shell had a CL of 22 mm (TL = 10.5 mm). The smallest coconut crab found on Guam without a gastropod shell had a TL of 4.0 mm (approximate CL = 8.4 mm). Hundreds of small shell-bearing coenobitids have been examined on Guam, but no *Birgus* have been seen; all specimens examined were referrable to species of *Coenobita*. Recruitment of young *Birgus* to Guam may be very low, as suggested by the scarcity of egg-bearing females observed, or the young stages may be occupying some habitat which was not sampled.

The subsequent development of the coconut crab consists of a series of molts during which the crab increases in size but does not appreciably change in morphology.

Length-Weight Relationship

A length-weight relationship was calculated on the basis of 174 crabs measured in the laboratory and in the field from Guam, the northern Marianas (Tinian, Pagan, Guguan, Asuncion, and Maug), and Palau (Kayangel Atoll). Thoracic length is the linear distance between anterior and posterior borders of the thoracic groove (Helfman, 1973). This is the linear measurement least subject to measurement error or to variation caused by damage to the crab (e. g., broken rostrum). The measurement was made with a pair of dividers and a millimeter rule. Weight (W) was total live weight and was measured in the laboratory with an Ohaus Triple-Beam Balance accurate to 0.1 g. Field measurements were made with a set of spring balances (Ohaus and Chatillon) with different ranges of sensitivity: 0–250 g, accurate to 10 g; 0–2000 g, accurate to 25 g; and 0–7500 g, accurate to 100 g.

The regression equation was calculated on log transformed data using Bartlett's Three Group Method (Sokal and Rohlf, 1969). Males and females were combined in the calculation as no consistent differences, other than the narrower range of sizes of the females, were observed between the two sexes. The resulting equation is

$$W = .0077\ TL^{3.0008} \text{ (weight in g, thoracic length in mm);}$$

the plotted points are shown in Fig. 7. The exponent, 3.0008, is very close to 3 and indicates that the crabs are growing isometrically, with no change in shape or specific gravity with increasing size. The weights at the upper end of the distribution tend to be slightly greater than the regression line predictions. This may be a result of weight measurement errors, as all of these points were measured in the field with the least sensitive of the spring balances.

Growth Rates

It was not possible during the course of this study to determine rates of growth in *Birgus latro*. Because increases in size are accompanied by molts in the coconut crab, as in other crustaceans, identifying marks on the exoskeleton are lost at each growth increment, and so measuring of marked individuals in the field was not feasible. In some crustaceans, tags imbedded in the muscles, which are retained through the molting process, can be used to identify individuals through a period of molts (George, 1967). We experimented with this approach on the coconut crab, using lobster tags (Floy Tag Co.) which were inserted between the posterior margin of the carapace and the anterior margin of the first abdominal segment. The muscle bands which pass through this region in the lobster, and in other crustaceans which use their abdomen during swimming, are relatively large, but in *Birgus*, in which the abdomen is curled under the thorax and is not involved in locomotion, these muscles are very slender, and the lobster tags were not retained.

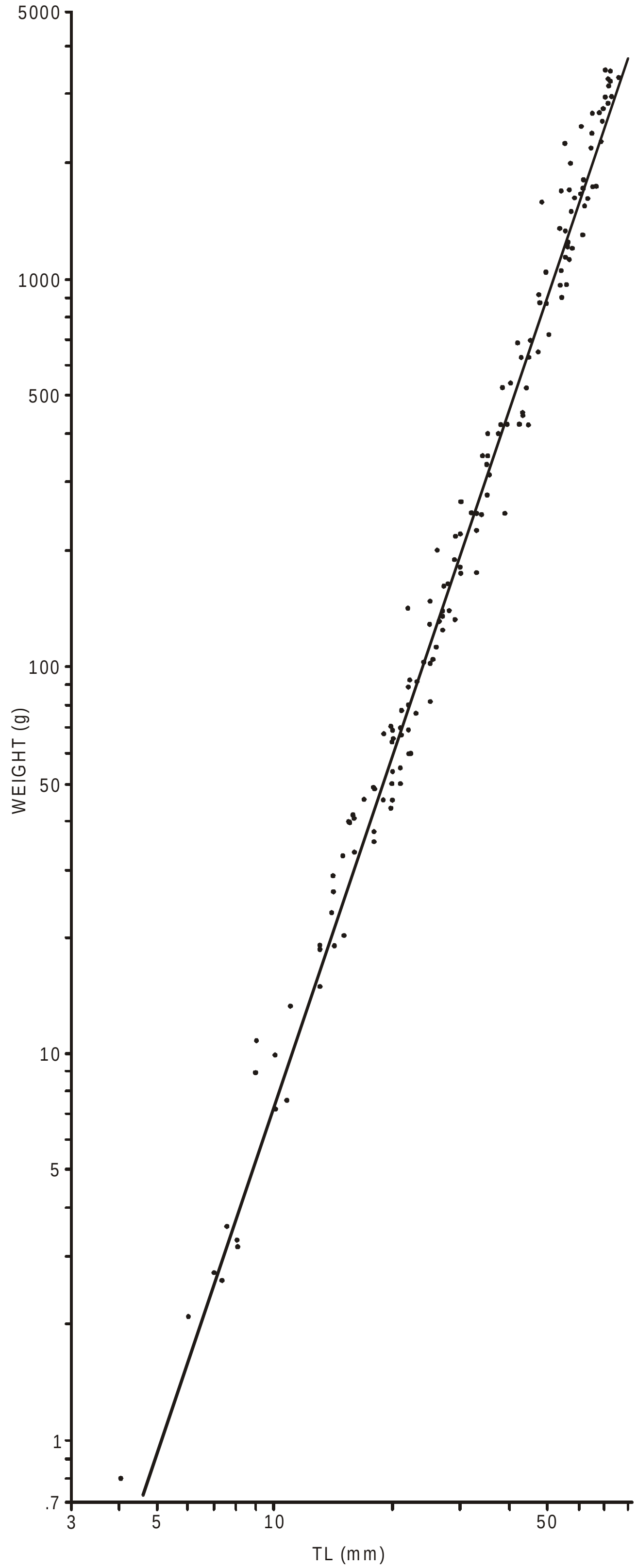

Fig. 7. Coconut crab length-weight relationship.

In a large, seasonally recruiting population, it is sometimes possible to follow growth by documenting the changes in modal year-class sizes over time. This approach was inapplicable on Guam because of the general scarcity of crabs of all sizes.

Growth data obtained from captive crabs is rather suspect when applied to natural populations, because of the different conditions imposed on the crabs by captivity. During the present study, coconut crabs were held under two conditions of captivity, individual containers and mass holding in a large enclosure (described more fully below). We observed several molts among crabs held in individual containers, but these molts resulted in no net increase in size. In the large enclosure, no molts were observed during the two months over which the experiments extended.

Held (1963) described molting in a coconut crab held in a terrarium. Four molts occurred within 463 days of captivity. The four molts resulted in a total increase in cephalothorax length from 20.8 to 30.0 mm and an increase in weight from 6.8 to 20.2 g. The intermolt period ranged from 50 to 83 days while the length of time the crab spent hidden, undergoing ecdysis, ranged from 30 to 39 days.

One indication that the larger coconut crabs in the wild may have quite long intermolt periods is the heavily worn and abraded appearance of the claws and carapace of some of the larger crabs collected. Rates of wear would be dependent on the nature of the habitat and the activity levels of the crabs, but, subjectively, it would seem that the amount of wear observed among some of these crabs would take a considerable period of time to develop.

The smallest berried female crab observed, seen on Pagan Island in the Northern Marianas, had an estimated TL of 27.5 mm. All other berried females seen during this study had TLs in excess of 40 mm (Figure 8). Helfman (1973) found berried females as small as 25 mm TL in Palau and 27 mm TL in Enewetak.

Coconut crabs exhibit sexual dimorphism in the maximum sizes they attain. The largest female measured during the present study reached a TL of 47 mm; the largest male measured 76 mm TL. Helfman (1973) observed the same phenomenon; the largest female he reported had a TL of 52 mm, and the largest male a TL of 74 mm. Helfman (1973) has suggested that successful mating among coconut crabs requires that the female and male partners be of comparable sizes, and so those males larger than any females are reproductively inactive in coconut crab populations.

<u>Habitat</u>

On Guam, coconut crabs are most typically found in the coastal limestone forest habitat. Here they establish burrows within the porous, solution-pitted limestone substrate. They spend the daylight hours in their burrows, and at night emerge to scavenge for food (see below). On Guguan and Asuncion, in the Northern Marianas, coconut crabs occupy burrows dug in the soil

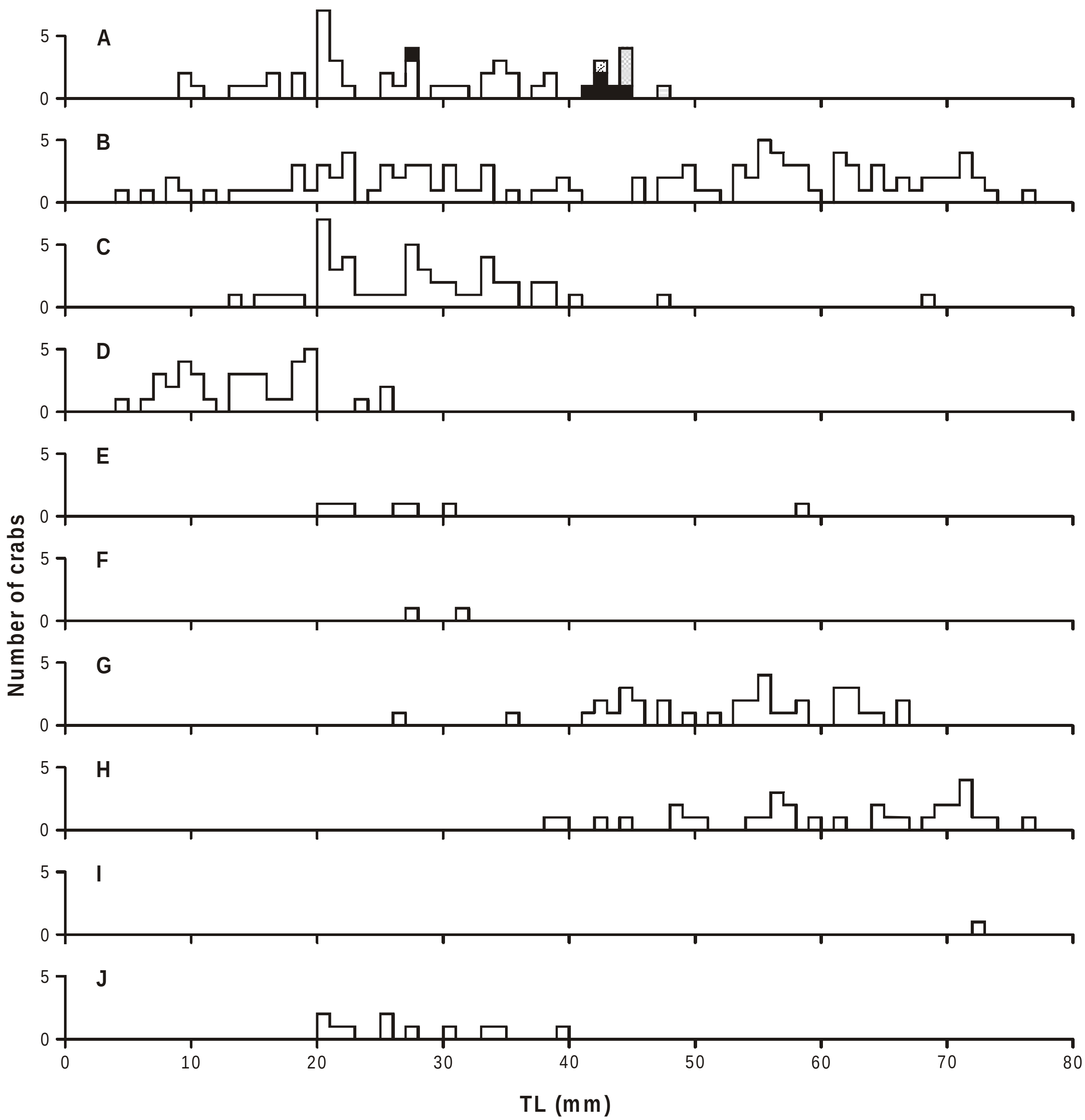

Fig. 8 Size-frequency distribution of coconut crabs. A. All females; black: with eggs; hatched: eggs newly released; stippled: with spermatophore. B. All males. C. All crabs, Guam (omitting Cocos Island). D. All crabs, Cocos Island. E. All crabs, Tinian. F. All crabs, Pagan. G. All crabs, Guguan. H. All crabs, Asuncion. I. All crabs, Maug. J. All crabs, Ngariungs (Kayangel Atoll, Palau).

or in the interstices of the boulder-cobble shorelines. On barrier reef islands such as Cocos Island on the margin of Cocos Lagoon, Guam, and on Kayangel Atoll, Palau, crabs live in shallow burrows in the substrate or hidden among pandanus roots and fallen coconut fronds.

The burrows provide protection for the crab and can be defended against conspecific intruders. Crabs bring large pieces of food (e.g. coconuts, pandanus fruit) to the burrow where they may remain for several days feeding. It is not clear whether individual crabs maintain the same burrow for long periods of time, or whether they just enter any available unoccupied burrow.

It is possible that the burrow may be used as a molting site, but Mr. Frank Gushing of Guam informed me that he has observed specific molting areas on Guam where coconut crabs bury themselves in the soil to molt. These molting sites are completely sealed over with soil so that the crab will not be molested during the time it is undergoing ecdysis and is relatively defenseless. Mr. Gushing led me to one of these areas near the University of Guam Marine Laboratory. We observed several small mounds of loose soil in this area. We dug into several of these mounds and discovered soil-filled chambers beneath them. In one of these chambers we found a 24.8 mm TL male crab with an exceedingly swollen abdomen (Fig. 9) . It is reasonable to assume that this crab was preparing to molt and the swollen abdomen resulted from materials stored in the hepatopancreas to provide energy reserves and perhaps water to sustain the crab during the molt period and to allow it to increase in size before the hardening of its new exoskeleton. The molting site and the condition of the crab accord well with Held's (1963) observations on coconut crab molting in a terrarium.

The occurrence of a pelagic larval stage in the coconut crab dictates that it begins its terrestrial life near the seashore and that reproductively active female crabs remain near enough to the shore to be able to carry the eggs to the water for hatching. Coconut crabs may also go to the beach to drink seawater to maintain their proper salt balance or to scavenge drift material left on the beach by the falling tide. On Guguan several large male crabs were seen at the water's edge at night, possibly drinking. On small barrier reef islands such as Cocos Island (Guam), Ngariungs Island in Kayangel Atoll, and the two islands where Helfman (1973) did his field work, coconut crabs may occur throughout the island. On larger high islands, such as Guam, coconut crabs are rarely found in the interior.

Feeding Habits

The coconut crab is primarily a scavenger, eating a variety of foods. Helfman (1973) observed these crabs feeding on coconuts (husk and meat), decaying wood, the molted exuvia of lobsters and crabs, other crabs, and an intertidal neritid snail. Reyne (1939) reviewed earlier literature on the food of the coconut crab, much of which may be of doubtful validity, and cited reports of coconut crabs feeding on coconuts, *Pandanus* fruits, and carrion. Gibson-Hill (1947) reported that coconut crabs on Christmas Island in the Indian Ocean also fed on coconuts, tropical fruits, and carrion.

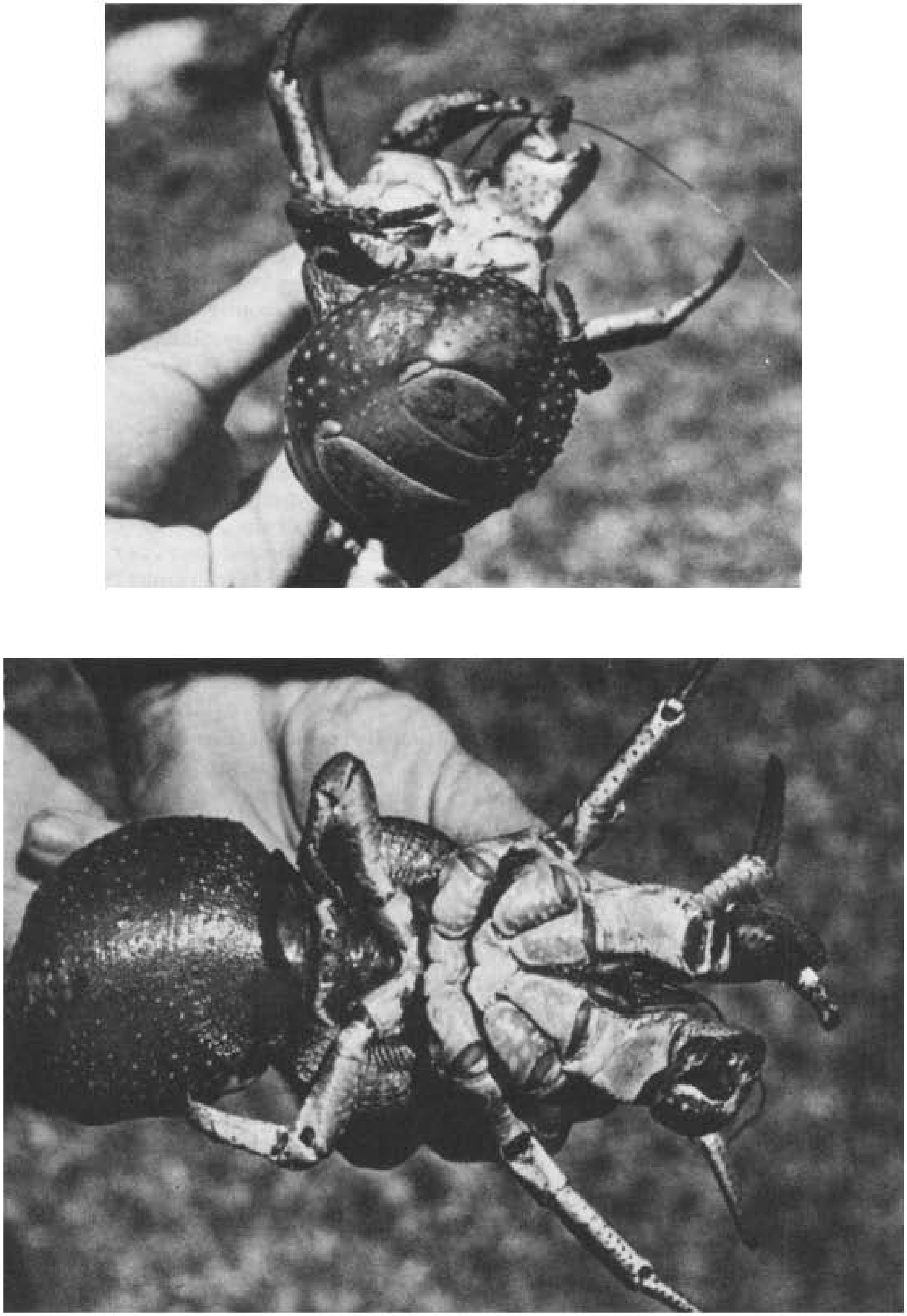

Figure 9. Coconut crab with swollen abdomen in preparation for molting.

Coconut crab burrows on Guguan and Asuncion contained remains of coconuts and *Pandanus* fruit which the crabs had apparently been feeding on.

In captivity, coconut crabs ate a variety of vegetable material (lettuce, cabbage). They also ate giant African snails (*Achatina fulica*), which had been given to them live. Although the crabs ate these snails in captivity, it is not known whether they ever eat them in nature.

Diurnal-Nocturnal Activity

On Guam, under natural conditions, coconut crabs are apparently exclusively nocturnal. The technique of collecting coconut crabs that we used was to make a trail through a limestone forest area during the daytime, setting out coconut baits. The trail was then retraced at night to catch crabs attracted to the baits. No coconut crabs were ever seen during the day while make the trapping trails on Guam. On Asuncion and Guguan, uninhabited islands in the Northern Marianas, crabs were active during daylight hours as well as at night. On Asuncion, approximately 1.45 crabs per man-hour were seen during the day and 3.20 crabs per man-hour at night. On Guguan, 4.36 crabs per man-hour were seen during the day and 4.00 per man-hour at night. Helfman (1973) observed active crabs during both daytime and nighttime on his study islands, with highest levels of activity at night. Helfman noted more injured crabs were seen during the daytime than at night, but this relationship was not observed among the Asuncion and Guguan crabs. Neither was their any difference in the size distribution of crabs seen at night and during the day on these islands.

The differences in the patterns of temporal activity between the crabs on Guam, which are virtually entirely nocturnal, and the crabs on Guguan and Asuncion, which are active both day and night, would seem to be related to human predation on the crabs. The mechanism by which this is brought about, however, is unclear. Conceivably the crabs on Guam have “learned” to confine their activities to the dark nighttime hours to avoid being captured. On the other hand, it may be that certain individuals tend to be active during the day and others at night and those that are active during the day have been harvested out of the population. With regard to the latter hypothesis, it should be noted that a crab on Asuncion and another crab on Guguan were first seen and marked during daylight hours and then were subsequently seen at night, indicating that these individuals did not confine their activities to daytime or nighttime.

Among coconut crabs held captive in a large enclosure on Guam (see below), nocturnal activity also predominated. Those few crabs which were seen active during the day were also observed to be active during the night.

Interspecific Interactions

As discussed above, the coconut crab may interact with other animal species in its habitat by preying on them, although scavenging and herbivory appear to be the most important methods of acquiring food. Other scavengers share the coconut crab's habitat, in particular the terrestrial hermit crabs of the genus *Coenobita*. In areas where *Coenobita* are abundant, these hermit crabs may limit the amount of scavengeable material available to the coconut crab. This competitive interaction is indirect, however, and in confrontations between *Coenobita* and *Birgus*, the *Coenobita* will withdraw, abandoning the sought-after food item to the coconut crab.

The coconut crab apparently has few, if any, predators other than man. According to local lore on Guam, large monitor lizards (*Varanus indicus*) occasionally kill coconut crabs, but this has not been documented. It is likely, although again not documented, that very small coconut crabs are eaten by larger crabs of other species, large toads (*Bufo marinus*), monitor lizards, and perhaps birds. Helfman (1973) suggests that rats and feral pigs may also feed on coconut crabs.

Intraspecific Aggression

Helfman (1973) observed that larger *Birgus* dominate smaller ones, and that smaller crabs will not approach larger ones closer than approximately one meter. Although he never observed a coconut crab attack and kill a conspecific, he did observe a large coconut crab feeding on a smaller one. I observed no incidences of cannibalism among *Birgus* during my field work, although on Asuncion I observed two large males engaging in what was presumably an agonistic encounter. Each had its chelipeds locked with those of the other crab in an arrangement reminiscent of a minuet. Neither, however, was otherwise struggling, and the two crabs remained in this locked cheliped position for some 15–20 minutes, at which time I ceased to observe them.

On Guguan, I observed 5 large male crabs within an area of approximately 10 m^2 among large boulders at the ocean water's edge. Whether they were drinking or feeding was not apparent, but the crabs moved past one another with no display of agonistic behavior.

On Guam, coconut crabs of various sizes were stocked inside a 6.4 m x 6.4 m enclose to a density of 1 crab/1.5–1.8 m^2. There was no evidence of cannibalism or aggressive behavior resulting in injury among these crabs over a two month period (see below).

As coconut crabs encounter one another in nature, they apparently establish dominance-submission relationships based on size. A considerable part of their behavioral repertoire consists of signals used in establishing this relationship (Helfman, 1973), and so actual combat is seldom necessary. Although fighting and cannibalism may occur in coconut crab populations, it is probably a rare event.

REARING EXPERIMENTS

Individual Holding Containers

In our initial attempts to rear coconut crabs in captivity, small containers (from 25 x 30 x 12 cm to 60 x 60 x 45 cm, depending upon the size of the crab) were used to house crabs individually in order to prevent aggressive interactions. Each holding container was provided with approximately 5–10 cm of sand or soil substrate and a jar of fresh water for drinking. Crabs were fed a mixed variety of foods including vegetables (primarily lettuce and cabbage), dried pet food, and coconut. Containers were set up as crabs became available. From June 14, 1973, to January 2, 1975, 29 molts occurred (Table 1). In none of these cases did the crabs exhibit any measurable growth during ecdysis.

On January 7, 1975, the rearing experiments were modified to determine the influence of various diets on the molting and growth of the coconut crabs. Four different diets were tested: 1) vegetables, 2) coconut, 3) dried pet food, and 4) giant African snail (*Achatina fulica*) .

Food was supplied in weighed amounts in excess of the amount which the crabs would be expected to eat. Food uneaten after two or three days was removed and weighed. The difference in the two weights was assumed to be the weight of food consumed by the crab.

It became apparent after a short time, however, that this technique was not providing an accurate measure of food consumed because of the difficulty in recovering all the uneaten scraps which were mixed into the substrate, the loss of weight of food residue through dehydration (or loss of body fluids in the case of the snails) and the irrecoverability of the dried pet food once it had been broken up and moistened by the crab's drinking water. Realizing that quantification of the diet was not practical under these conditions, we continued the feeding experiments to determine whether there would be differences in growth rate related to the types of food provided. During the period of these feeding experiments (January 7 to July 17, 1975) only four molts occurred among the captive crabs, and all of these molts were in February, near the beginning of the experiments. Two of the crabs which molted had been fed diets of giant African snails and lettuce; one had dried pet food and lettuce; and the fourth was fed only lettuce. No measurable increase in size accompanied the molts.

The low rate of molting may be attributable to a variety of factors: the frequent disturbance of the crabs when food was introduced and retrieved, the unsuitability of the small containers for crabs to carry on their normal behaviors, diet inadequacies, etc. Our general feeling was that the small containers were not appropriate for rearing coconut crabs because of their limited size and the unnatural constraints they placed on the crabs' behavior.

Table 1. Molting in coconut crabs held in individual containers, June 14, 1973-January 2, 1975. Crabs which escaped or died before January 2, 1975, are noted in the last column.

ID No.	Starting Date	Dates of Molting	Dates of Escape (E) or Death (D)
1	14 Jun. 73	29 Oct. 73	10 Nov. 73 (E)
2	14 Jun. 73		16 Oct. 73 (D)
3	14 Jun. 73	9 Oct. 73	10 Nov. 73 (D)
4	14 Jun. 73		15 Nov. 73 (E)
5	14 Jun. 73	26 Nov. 73, 7 Mar. 74; 17 May 74	
6	14 Jun. 73	26 Nov. 73	
7	14 Jun. 73	29 Oct. 73; 26 Dec. 73; 9 May 74	2 Jul. 74 (E)
8	14 Jun. 73	29 Nov. 73; 11 Apr. 74; 20 Oct. 74	
9	20 Nov. 73	15 Apr. 74	26 Apr. 74 (D)
10	20 Nov. 73	25 Jun. 74	
11	20 Nov. 73	20 Mar. 74; 19 Jun. 74	1 Jul. 74 (D)
12	20 Nov. 73	24 Mar. 74; 1 Aug. 74	
13	20 Nov. 73	25 Mar. 74	20 Aug. 74 (D)
14	20 Nov. 73	22 Mar. 74; 3 Jun. 74	
15	20 Nov. 73		
16	20 Nov. 73		
17	20 Nov. 73		
18	6 Jan. 74	25 Jun. 74	
19	6 Jan. 74	23 Jul. 74	
20	7 Jan. 74		
21	7 Jan. 74	24 Aug. 74	
22	7 Jan. 74	23 Jun. 74	
23	7 Jan. 74	30 Jul. 74	
24	28 Jan. 74	6 Jun. 74	17 Jul. 74 (E)
25	28 Jan. 74		25 Jun. 74 (D)
26	30 Jan. 74	2 Aug. 74	
27	10 Feb. 74		
28	10 Apr. 74	9 Nov. 74	
29	10 Apr. 74		
30	10 Apr. 74		
31	10 Apr. 74		
32	10 APr. 74		29 Apr. 74 (D)
33	10 Apr. 74		
34	10 Apr. 74		
35	10 Apr. 74		
36	10 Apr. 74		
37	17 Sept. 74		15 Nov. 74 (D)
38	17 Sept. 74		
39	5 Oct. 74		20 Nov. 74 (D)
40	2 Nov. 74		
41	6 Nov. 74		
42	10 Nov. 74		
43	10 Nov. 74		
44	20 Nov. 74		
45	20 Nov. 74		
46	20 Nov. 74		
47	2 Dec. 74		
48	29 Dec. 74		

Large Enclosure

A relatively large (6.4 m x 6.4 m) enclosure of chain link fencing was constructed in an area of semi-natural limestone forest vegetation adjacent to the University of Guam Marine Laboratory. To prevent crabs from burrowing under the fence, a concrete footing extending to a depth of 0.6 m surrounded the entire enclosure, and the fencing was set into this. A strip of sheet metal 1 m high surrounded the inner perimeter of the fence at ground level. This prevented the crabs from climbing out over the fence as they could not cling to the sheet metal. (A crab placed within the enclosure before the sheet metal was installed quickly climbed out over the 2.5 m high fence.) Vegetation was removed from a 1-meter wide strip around the inside perimeter of the enclosure so that crabs could not climb out by crawling along overhanging branches. Within the enclosure, two shallow, cement-lined pools were sunk into the ground, one for fresh water and one for seawater. Ripe coconuts were split and distributed around the interior of the enclosure. Periodically, the coconuts were removed and replaced by new ones.

Coconut crabs placed in the enclosure were measured, weighed, sexed, and marked with an identification number (Table 2). The marking was done by scratching the identification number on the crab's carapace with a metal scriber. Crabs in the enclosure were censused periodically (primarily at night). The identification numbers of all crabs seen were recorded. The enclosure observations were terminated on May 21, 1976 by Typhoon Pamela.

Survival—During the two-month period of enclosure observations only one crab died. It was found dead five days after it had been placed in the enclosure and apparently had been stepped on by a visitor in the enclosure. No parts of its body were missing or mutilated and there was no evidence that its death was caused by another crab. The density of coconut crabs within the enclosure was very high, between 1 crab/1.78 m^2 and 1 crab/1.52 m^2 over the period of time between March 16 and May 11, 1976. By comparison, Helfman (1973) estimated natural coconut crab densities of 1 crab/15 m^2 and 1 crab/68–74 m^2 on small islands in Palau and Enewetak. That these crabs could be held in captivity at such high densities without damaging or cannibalizing one another suggests that it may be possible to raise them under these conditions or to stock them in high densities in preserves. The duration of the enclosure observations was only 2 months during the spring, however, and there may be certain times of the year when intraspecific aggression is more pronounced.

Activity Levels—Nineteen censuses of the crabs were made during the period of the enclosure observations, 16 at night and 3 during daylight hours (Table 2). Twelve of the nighttime censuses were pairs of census made 212 to 3 hours apart on six separate nights. An average of 47% of the captive crabs were seen during the nighttime censuses (range: 35–74%). In the paired nighttime censuses, some crabs were seen during one census which were not seen on the other, and the average percentage of crabs seen when the paired censuses for a given night are combined is 64% (range: 50–78%). Many fewer crabs were seen during the three daytime censuses; an average of 12% (4–17%) of the crabs in the pen were seen during a given daytime

Table 2. Results of large enclosure censuses, March 18 to May 11, 1976. + a crab observed during census; 0 = crab in enclosure but not observed during census.

Crab ID No,	1	2	3	4	5	6	7	8	9	10	11	12	13	1.4	15	l6	17	1.5	19	20	11	22	23	24	25	26	27	28	Total	Total
Sex	F	F	F	M	M	M	M	M	M	M	F	M	F	M	M	M	M	M	F	M	M	M	F	M	F	M	F	F	Crabs in	Seen in
Date stocked	3/9	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	3/16	5/16	3/18	3/19	3/24	4/27	4/27	4/28	Enclosure	Census
Census Date and time																														
3/ 18–2030	+	0	0	0	+	+	+	+	+	0	+	0	+	0	+	0	0	0	+	+	+	0	+						23	13
1/18–2300	+	0	+	+	0	+	+	+	+	0	0	0	+	0	+	+	0	0	+	0	0	0	0						23	11
3/21–2000	+	0	+	+	+	+	+	+	+	dead	+	0	+	+	+	+	+	0	+	+	0	0	0	+					23	17
3/21--2315	+	0	0	+	+	+	+	0	0		0	0	0	+	+	0	0	0	+	+	+	0	0	+					23	11
3/24--2045	0	0	0	0	+	+	+	+	+		+	0	0	+	0	0	+	+	0	+	0	0	+	+	+				24	13
3/24--2330	0	0	0	0	+	+	0	+	0		0	0	0	+	+	+	0	+	0	+	+	0	0	+	+				24	11
3/26--2100	+	0	+	0	+	+	0	0	0		+	+	+	+	+	0	+	0	0	0	+	+	+	+	0				24	14
3/26--2330	+	0	+	0	+	0	0	0	0		0	0	0	0	+	+	0	0	0	0	+	+	+	+	0				24	5
3/28--0930	0	0	0	0	0	0	0	+	0		0	0	0	0	+	0	0	0	0	0	0	0	0	+	+				24	4
3/31--2110	+	0	+	0	+	0	0	0	+		+	0	0	+	0	0	0	+	0	0	+	0	+	+	+				24	11
3/31--2320	0	0	+	0	+	+	0	+	+		+	0	0	0	0	+	0	+	0	0	+	0	+	+	0				24	11
4/ 4–2020	0	+	0	0	+	0	+	0	+		0	0	+	+	0	0	+	0	0	+	+	0	0	+	0				24	10
4/ 4–2330	0	0	+	0	+	0	+	0	0		0	0	+	0	0	+	+	0	0	+	+	0	0	+	0				24	5
4/17--2110	+	0	+	+	+	0	0	+	0		0	+	0	+	+	+	0	0	0	+	0	0	+	0	0				24	11
4/27--2300	0	0	0	+	0	0	0	0	0		+	0	0	+	0	0	0	0	+	+	0	0	+	0	+	+	+		26	9
4/28--1400	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	27	1
4/30--1000	0	0	+	0	0	0	0	0	0		0	0	0	0	0	0	0	0	+	0	0	0	+	0	0	0	0	+	27	4
5/ 3–2115	+	0	0	0	0	0	0	0	+		+	+	0	+	+	0	0	0	+	0	+	0	+	0	0	0	+	+	27	11
5/11--2360	0	0	0	0	0	0	0	+	+		0	0	0	0	+	+	0	0	+	+	+	0	+	0	0	+	+	+	27	11

census. The preponderance of activity among the crabs was clearly at night as it is among natural populations. Those crabs not seen during a census had presumably withdrawn into a burrow.

Molting and Growth—No molts were observed during the enclosure experiment. At the end of the experiment, four crabs had not been seen for over a month, and they may have been withdrawn into a burrow to molt, but several crabs had not been observed for periods of more than a month and had then reappeared without having molted. This could be determined because of the identification numbers scratched on the carapace which were still in evidence. Five unmarked crabs appeared in the enclosure during the study, but, on the basis of sex, size, and the pattern of disappearance and appearance of the stocked crabs, these were determined to be wild crabs which had climbed into the enclosure and then were unable to escape. The lack of molting activity during the 2-month period is not encouraging for the use of such enclosures for rearing coconut crabs. Possibly molting is seasonal and the timing of the study did not coincide with the natural molting cycle of the crabs. Perhaps the high density of crabs in the enclosure had an inhibiting effect on the molting behavior of the crabs. This could be a population-regulating phenomenon or a response to the fact that crabs are quite defenseless and vulnerable to predation or cannibalism while molting. Or it may have been that the environment within the enclosure lacked some factor necessary for molting such as proper soil type.

Reproduction—The sex ratio of the crabs during the enclosure observations ranged from 2.5 males: 1 female to 1.6 males: 1 female. With the exception of one very small female and one very large male, comparably-sized individuals of both sexes were present in the enclosure. No evidence of reproductive activities among the crabs was seen during the course of the observations, i.e., no mating behavior, no females with spermatophores, and no females bearing eggs. Because of the rather short duration of the enclosure experiment, the lack of observed reproductive behavior can not be considered sufficient evidence that no mating occurred. Helfman (1973) describes the mating behavior of the coconut crab as a very short process. The spermatophore mass remained on the exterior of the female crab for about a month, however, after copulation. Some female crabs were not seen for as much as a month or more inside the enclosure and it is possible that they may have mated prior to their temporary disappearance.

Evaluation of the Large Enclosure for Culturing—The survival success of the coconut crabs within the enclosure was encouraging in that it demonstrated that crabs could be held at much higher densities than they exhibit in nature without damaging or killing one another. The apparent absence of molting and growth, however, was rather discouraging from the point of view of culturing the crabs in captivity. Further investigations on the utility of the large enclosures, testing different stocking densities and different substrate types carried out over a longer period of time, might suggest possible culturing strategies for these crabs.

DISCUSSION

Life History Model

A simplified diagrammatic model of the life history of a *Birgus latro* population is presented in Figure 10. Five stages in the life history are recognized: 1) pelagic larvae, 2) glaucothoe [transitional to land], 3) immature terrestrial crabs, 4) sexually mature terrestrial crabs of both sexes [from size at first maturity to maximum female size], and 5) large males [sizes larger than maximum female size]. Each stage is more or less distinct from the others in its habitat, its susceptibility to various types of mortality, its contribution to the reproductive activities of the population, and/or its liability to human harvesting.

Pelagic Larval Stage—The quantity of larval *Birgus* in the vicinity of a given island will depend on the density and reproductive success of the mature adult crabs in the island population and may additionally by supplemented by input of larvae released from other nearby islands. Mortality among the larvae as a result of starvation, predation, unfavorable oceanographic conditions, and possibly disease is probably high. Patterns of ocean currents may carry larvae away from the island preventing them from recruiting to the parent population. The duration of this stage is approximately 17 to 28 days (Reese and Kinzie, 1968).

Glaucothoe Stage—Those zoeal stage larvae which survive, return to the island, and successfully metamorphose into the glaucothoe stage will be potential recruits to the terrestrial *Birgus* population. During the glaucothoe stage, which lasts 21 to 28 days, the crabs are subject to mortality from predation by reef and beach animals, inhospitable conditions of the inshore waters, dessication once they have left the water, and possibly starvation and disease. An important limiting factor during this stage may be the availability of very small gastropod shells in the beach environment (Reese, 1968). On islands with very large *Coenobita* populations, such as Guam, there may be considerable competition for these small shells between *Birgus* glaucothoe and *Coenobita* glaucothoe.

Immature Terrestrial Recruits—During the young crab stage, up to 25 mm thoracic length, the coconut crab is subject to mortality from predation by larger terrestrial forms, disease, starvation, and possibly cannibalism by larger *Birgus*. Although they are small, crabs of this size may be harvested by man (on Guam, although it is illegal, small coconut crabs are sometimes collected, preserved, and mounted to sell as tourist sourvenirs). Because of the absence of growth rate information, the duration of this stage is unknown.

Mature Crabs of Moderate Size—This stage includes the crabs with TL between approximately 25 mm (the onset of sexual maturity) and approximately 52 mm (the maximum female size). Crabs within this stage are the source of the eggs and larvae which allow the

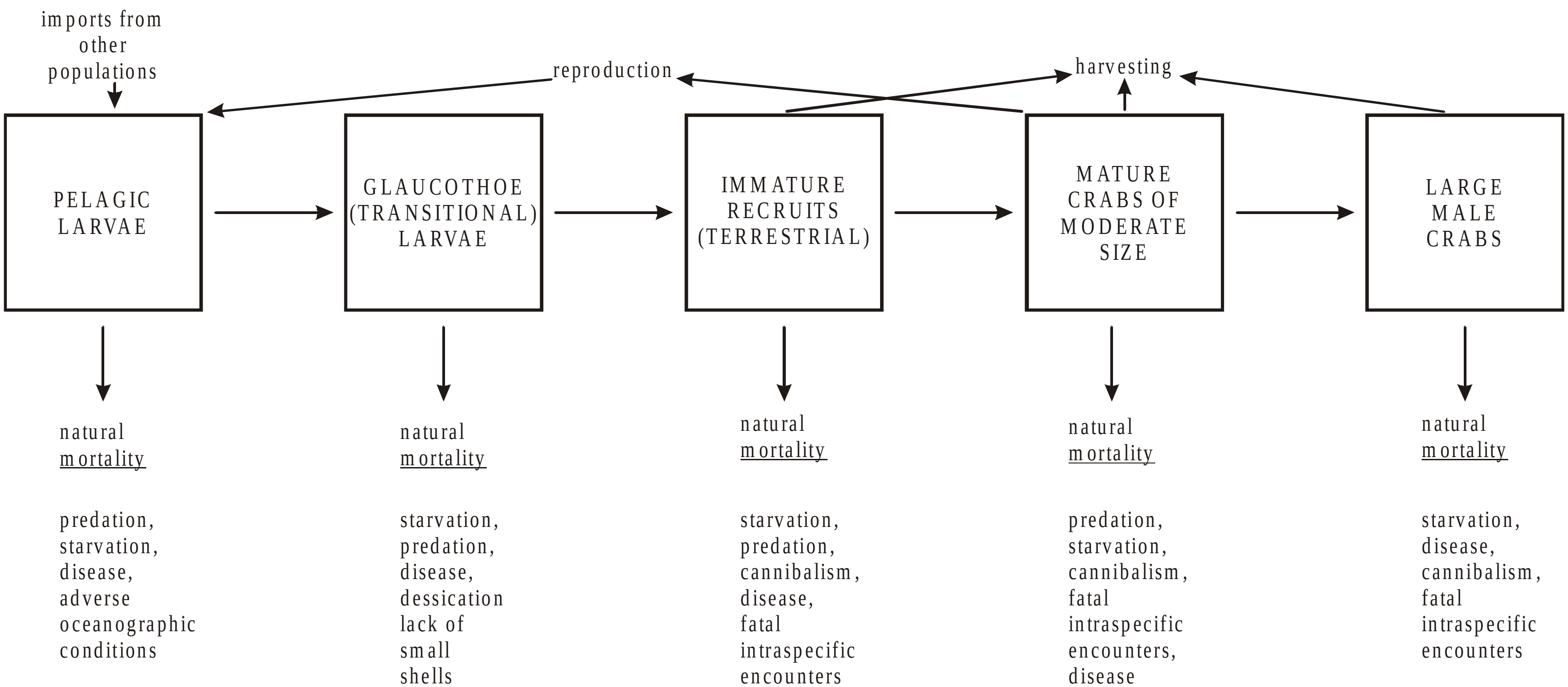

Figure 10. Coconut crab life history model.

population to reproduce itself. The rate of reproduction during this stage is presumably influenced by food availability, sex ratios, crab density, and access to the ocean. Possible sources of mortality during this stage are starvation, disease, predation (which is probably less severe during this stage than during the previous stage when crabs are smaller), cannibalism and fatal intraspecific encounters (which may be high if density is high and food or appropriate burrow sites are limited), and human harvesting. The duration of this stage is not known.

Large Male Crabs—Large males in excess of 52 mm TL may not be reproductively active in natural coconut crab populations (Helfman, 1973). Because of their large size, they are probably not subject to natural predation. Mortality is most likely caused by disease, starvation, fatal intraspecific encounters, and human harvesting. These large crabs are the most sought-after crabs for food. Helfman (1973) has suggested that these large male crabs may inhibit the crabs of reproductive size, excluding them from potential burrow sites, competing with them for food, and attacking and killing them. This has not been clearly demonstrated, however, and on Asuncion and Guguan, which had the highest density of large male crabs seen during this study, the proportion of reproductively active females observed was also very high.

Interspecific Competition—Larger coconut crabs can dominate most other terrestrial animals found in their habitat. However, it is possible that other scavengers can consume potential food items before the food is discovered by a coconut crab. On Guam the principal scavengers which share the coconut crab's habitat are the *Coenobita* hermit crabs. *Coenobita* are very numerous on Guam, and this high density appears to be attributable to the great number of available giant African snail (*Achatina fulica*) shells which they can occupy. Of the four species of *Coenobita* on Guam, *C. brevimana*, *C. rugosa*, and *C. cavipes* are found almost exclusively in *Achatina* shells. Only *C. perlata*, the least abundant of the four species, does not normally inhabit *Achatina* shells, and instead uses shells of *Turbo* spp. preferentially. As *Achatina fulica* was introduced to Guam during the years of World War II, *Coenobita* on Guam must have undergone an explosive, though undocumented, increase in abundance within the last four decades. It is not inconceivable that *Coenobita* are outcompeting *Birgus* for food on Guam. Additionally, this increase in abundance of adult *Coenobita* no doubt has led to an increase in abundance of *Coenobita* larvae in nearshore waters, and an increase in *Coenobita* glaucothoe migrating onto land. The *Coenobita* glaucothoe may be putting heavy pressure on the availability of small gastropod shells and making them less available to *Birgus* glaucothoe.

Habitat Modification—The development of the coastal zone on Guam during recent years has modified or destroyed much of the preferred habitat of the coconut crab. Areas which are presently most densely populated with coconut crabs are those areas of relatively unmodified habitats within the various military installations on Guam. Destruction of favorable coastline habitats has a three-fold impact on the successful reproduction of the species: 1) it reduces the total availability of coconut crab habitats and so reduces the number of breeding individuals, 2) it reduces the gravid female crabs' access to the ocean and so reduces larval release, and 3) it reduces the extent of coastline favorable for the recolonization of the island by the glaucothoe stage crabs.

Harvesting Pressure—The technique of harvesting coconut crabs on Guam involves setting out a number of opened coconuts for bait, waiting until nightfall, and then visiting each of the baits, collecting the crabs which have been attracted to it. Coconut crabs of all sizes are attracted to the baits and so the crab hunter can collect crabs of various sizes, leaving behind only those which are too small. The largest sizes of crabs are probably overrepresented at the baits because, being larger, they can move around more rapidly and encounter baits at a greater distance from their initial location than can smaller crabs, and because larger crabs tend to drive smaller crabs away from baits (Helfman, 1973). Therefore, the harvesting pressure on the larger crabs is probably heavier with respect to their proportional representation in the population than it is on smaller crabs.

On Asuncion and Guguan, baits were not used. Daytime and nighttime forays were made in appropriate habitats, and the crabs seen were sitting at the mouths of their burrows or walking abound in the forest. Almost all crabs seen on these two islands had TL greater than 40 mm. Unless smaller crabs are truly very scarce on these islands, it appears that large coconut crabs are much more likely to be out in exposed locations than are smaller crabs. Thus, in areas such as these, harvesting pressure will fall heavily on the larger crabs.

Heavy harvesting pressure, then, is identifiable in two ways: loss or reduction of the largest sizes and general decline in crab density. The very small crabs, less than 25 mm TL, are probably not ordinarily collected for food, but, as has been noted previously, they are sometime collected on Guam for sale as tourist souvenirs.

Status of Stocks

In general, stocks of coconut crabs are low on Guam. No specific attempts were made to quantify crab density on Guam, but during the course of trying to collect crabs for rearing experiments, it was apparent that the areas of highest crab densities were on military reservations where it is difficult for civilians to get permission to hunt for crabs. At Orote Point, on U. S. Navy property, 21 crabs were collected in a night's hunting. At Pati Point, on Andersen Air Force Base, approximately 8–10 crabs were seen during an evening's search. Elsewhere crabs were rarer. Near the Marine Laboratory on Pago Bay, several evening searches, using bait, were made and no crabs were seen, although 4 were seen on one evening. Several daytime searches were made on Cocos Island and some 38 crabs were collected in total.

The size-frequency distribution of Guam crabs (Figure 8) points up the scarcity of large coconut crabs in this population. The preponderance of crabs collected on Guam have a TL less than 40 mm; on Cocos Island crab sizes are even smaller with TL less than or equal to 25 mm. Clearly, coconut crabs on Guam have been subjected to heavy harvesting pressures.

On Guam at the present time, there is a continued but rather specialized demand for coconut crabs as a luxury food item, served at parties and fiestas. Coconut crabs are occasionally featured as a special dish at restaurants. However, the crab population on Guam cannot satisfy the local demand, and crabs are imported from the Northern Mariana Islands where these crabs are still reasonably abundant and where large crabs are not as rare as they are on Guam. Recent efforts to protect the populations of crabs in the Northern Mariana Islands (J. Villagomez, pers. comm.; see below) will no doubt reduce the availability of these imported crabs and possibly will result in increased pressures on the already scarce local stocks.

On the uninhabited islands of Guguan and Asuncion in the Northern Mariana Islands, coconut crab densities are much higher. On Asuncion we observed 3.20 crabs per man-hour at night and 1.45 crabs per man-hour during the day. On Guguan we observed 4.00 crabs per man-hour at night and 4.36 crabs per man-hour during the day. The coconut crabs seen on these islands were mostly large ones, greater than 40 mm TL (Figure 8). On Asuncion a significant number of large males with TL greater than 68 mm were seen; on Guguan the largest seen had TLs of 68 mm. These islands are occasionally visited by passing boats, and coconut crabs may be collected from time to time, but it is apparent that at the present time harvesting pressure is low, resulting in a higher density of crabs and a greater abundance of the largest sizes.

On the island of Ngariungs in Kayangel Atoll (Palau) we collected, with the help of several people from the nearby island of Ngajangel, 11 crabs in a two hour period. These crabs were comparable in size to crabs from Guam, with TL lying between 20 and 40 mm (Figure 8). Although uninhabited, Ngariungs is very close to Ngajangel islands, and we were told that people often come there to collect coconut crabs. The size-frequency distribution indicates that larger-sized crabs are scarce or absent.

Management of Natural Populations

Before an effective strategy for the management of natural stocks of coconut crabs can be proposed it is necessary that the objectives of the stock management be determined. Two possible objectives would be the following:

1) maximizing sustainable yields of coconut crabs as a food source, and

2) preservation of insular coconut crab populations for aesthetic, cultural, and scientific reasons.

Although historical documentation is lacking, it seems reasonable to suppose that stocks of crabs on Guam have become significantly reduced in size and in the proportion of larger animals in the population. Any management strategy designed to achieve a maximum sustainable yield would need, first of all, to establish a moratorium on crab harvesting until crab populations could build themselves up and larger-sized crabs could become more common. In the absence of any reliable data on growth rates among coconut crabs, the duration of such a moratorium cannot be calculated. In light of the direction of Guam's socio-economic development, however, it is likely that coastal zone development will continue to reduce the extent of favorable coconut crab habitats on the island and reduce the likelihood of successful larval recruitment to natural populations. There seems to be no reasonable probability that Guam's coconut crab stocks can be managed to maximize sustainable yields to the point where local stocks can satisfy local demands.

The management objective most appropriate for Guam would be the second of two listed above, preservation of natural stocks for their aesthetic, cultural, and scientific value. The most important step in achieving this goal is the establishment of sanctuaries for coconut crabs, where the natural coastal environment, including access to the ocean, is left undisturbed, and where human harvesting is eliminated or kept to a minimum. Additional conservation measures would be the proing crabs smaller than the median size of female reproductive activity (TL approximately 43 mm), and the prohibition of the sale of mounted coconut crabs as souvenirs. As these souvenirs often command prices in excess of those which people are willing to pay for coconut crabs as food, there is an economic stimulus for coconut crab hunters to continue to harvest in areas which already have very reduced populations. The use of crabs for souvenirs directly competes with the use of crabs for food as it is not possible to extract the crab meat without damaging the exoskeleton. Because island people have been eating coconut crabs for centuries, and because among Chamorros, in particular, coconut crabs, like fruit bats, are a traditional fiesta food, cultural considerations (not to mention enforcement difficulties)-.make a complete ban on coconut crab harvesting on Guam unrealistic. A ban on the sale of mounted coconut crab souvenirs would not run counter to local cultural traditions and would also be reasonably easy to enforce.

Coconut crab sanctuaries already exist on Guam to some extent in the form of the large military installations which control tracts of relatively undisturbed natural crab habitat. Few military personnel are interested in hunting for coconut crabs and the military's policy of limiting civilian access to the bases keeps harvesting pressures rather low on these stocks. The Guam Comprehensive Development Plan (Guam Bureau of Planning, 1978) designates rather extensive areas on Guam as Conservation Area. However, many of these conservation areas are not useful as coconut crab sanctuaries because they are too far inland, out of the natural habitat of the crabs; they do not provide free access to the ocean; or they are designated for low density residential and agricultural use. Conservation Areas most appropriate as coconut crab sanctuaries are the proposed Seashore Park and Wildlife Reserves near Umatac, the Open Space areas on the southeast coasts of Guam, and the Open Space and Wildlife Reserve near Yigo. If harvesting is discouraged in these areas, natural populations of coconut crabs could maintain themselves there. If preservation of natural crab stocks is the objective of stock management on Guam, annual surveys should be made to determine stock densities and size distributions of crabs in various areas on Guam. Analysis of this census data would measure the success of the management program and would indicate whether additional conservation measures need be instituted.

In the islands of the Commonwealth of the Northern Mariana Islands (CNMI), several measures have been enacted to protect the coconut crab. Saipan Municipal Ordinance No. 25-22-1974 prohibits sale of coconut crabs for any purpose except for human consumption, prohibits collection coconut crabs with carapace widths less than 3 inches, and prohibits collecting coconut crabs of any size during the summer months (June 1 to September 30) on the island of Saipan. The purpose of these regulations is to provide the coconut crabs opportunity to reproduce themselves, as crabs less than 3 inches in carapace width are primarily pre-reproductive, and the summer months (according to Helfman, 1973) are the times of greatest reproductive activity.

Public Law No. 1-18, signed by the Governor of the CNMI on December 22, 1978, prohibits the collecting of coconut crabs from the island of Aguiguan (Goat Island) for three years, and, after that, allows coconut crabs to be collected as authorized by the mayor of Tinian, if it is determined that their stocks are large enough to justify harvesting.

Public Law No. 5-21, passed by the Fifth Northern Mariana Island Legislature and signed by the Resident Commissioner on September 9, 1977, established a one-year moratorium on the harvesting of coconut crabs from the islands north of Saipan, after which harvesting crabs is permitted during the months of August through October, providing that no male crabs with smaller than 3 inch carapace width can be taken. The rationale for the selection of the open season is not clear, as this does allow crab collection during part of the summer months. Also the law affords no protection to pre-reproductive (less than 3 inch carapace width) female crabs.

Although data is insufficient to assess the status of coconut crab stocks on most of the islands of the Northern Marianas, some comments can be made on management strategies for the islands of Asuncion and Guguan. The data presented earlier indicates that coconut crab populations on these two islands are flourishing, no doubt because the islands are not inhabited by people and the only access to them is by boat. These islands have the potential of providing commercial yields of crabs which could be sold on Saipan or Guam. However, it is not possible, without reasonably accurate data on coconut crab growth rate and more detailed information on the distribution of crab stocks on these islands, to estimate the level of harvesting that could be sustained on Asuncion and Guguan without substantially reducing stock densities. Because of the possible competitive interaction between *Birgus* and *Coenobita* spp., appropriate efforts should be made to prevent the introduction of the giant African snail *Achatina fulica* to those islands of the Marianas which presently are free from this pest. The shells of these snails allow populations of *Coenobita* spp., heretofore limited by shell availability, to increase tremendously as has presumably occurred on Guam.

Rearing Strategies

The culturing of crustaceans and other organisms may be approached in various ways depending upon the biology of the organisms and the objectives which are to be achieved by culturing. If the objective is to rear the animals to a size appropriate for human consumption, the ideal strategy would be to culture the organism throughout its entire life cycle in order to maintain greatest control over culturing productivity. Among some cultured species, however, the earlier stages of the life cycle are not amenable to artificial rearing; in these cases culturing has depended upon capture of younger stages in nature and using these wild-caught young to stock managed “grow-out” facilities. For other species, culturing has concentrated on hatchery operations to produce large numbers of young which are then released in the wild to enhance natural stocks or transferred grow-out facilities for subsequent rearing to harvestable size.

Our lack of success in the rearing of the terrestrial stages of the coconut crab’s life, while not precluding the possibility of future breakthroughs, indicates that much further work needs be done before raising coconut crabs to a harvestable size is routinely feasible. However, an operation based strictly on the growing out of young crabs collected in nature, should future work lead to the development of appropriate techniques, will be limited by the availability of young crabs in the wild. And unless such a grow-out operation succeeds in achieving a mortality rate significantly lower than the natural mortality rate of wild crabs, there would be no net gain in culturing the terrestrial stages over allowing them to remain in their natural habitat subject to traditional harvesting.

Culturing coconut crabs can only be economically and ecologically sound if culturing begins with the initial larval stages. It is certainly during the aquatic phase of its life cycle, from zoeal release to the terrestrial emergence of the glaucothoe, that coconut crabs suffer their greatest rates of mortality. Successful mass rearing of coconut crab larvae offers the possibility of actually increasing the stocks of coconut crabs available for grow-out operation or for enhancing natural stocks of terrestrial stage coconut crabs.

Reese and Kinzie (1968) have demonstrated the feasibility of rearing coconut crab larvae throughout their aquatic larval stages; the next appropriate step is to develop methods for raising large numbers of larval *Birgus*. Because of the scarcity of berried female coconut crabs, it would be most feasible to undertake this research using *Coenobita* spp. larvae, which are much more readily available and which have much the same larval life history as does *Birgus latro*. Once mass rearing techniques for *Coenobita* larvae have been developed, these same methods could be applied, with such modifications as may be necessary, to coconut crab larvae. Mass rearing of larval *Birgus* is a requirement for any rational culturing program for coconut crabs and would provide opportunities for restocking wild populations should this be necessary for maintenance of natural stocks of these crabs.

CONCLUSIONS AND RECOMMENDATIONS

The coconut crab is a unique and fascinating component of the biota of Guam, the Marianas, and Micronesia. The coconut crab plays a meaningful role in the Chamorro culture in the Marianas, and its popularity as a tourist souvenir indicates that this crab can capture the imagination of people everywhere. Clearly the coconut crab deserves recognition as a resource worthy of conservation and management. The recommendations presented below are designed primarily for Guam and the Commonwealth of the Northern Mariana Islands, but some of the suggestions may also be appropriate for other Pacific areas where coconut crabs are found.

A. Preservation and Management

1. A decision must be made by the appropriate governmental agency as to the objectives to be achieved by management of coconut crab populations.

    a) For Guam, the most feasible management objective would be the preservation of natural populations for aesthetic, cultural, and scientific reasons.

    b) For the CNMI, where human population density is rather low compared to Guam, it may be possible to manage coconut crab populations to provide-sustainable harvests sufficient to meet local demands for the crabs for food.

2. In much the same way that various states have State Birds and State Flowers, it might be useful to declare the coconut crab a Territorial or Commonwealth Crustacean. Although this suggestion may seem frivolous, such recognition would help to establish an official policy of preservation of coconut crabs and would bring public attention to the need for management of this resource.

3. Fundamental to the preservation of coconut crab populations is the establishment of sanctuaries where harvesting crabs is prohibited. Such refugia should be reasonably large and should have broad access to the ocean to permit larval release and return. Limestone forest and coconut-dominated habitat should be present in the refugia. In the CNMI, various of the uninhabited northern islands, notably Guguan and Asuncion, should be established as coconut crab (and other wildlife) sanctuaries.

4. Periodic censuring of sanctuaries, as well as areas where harvesting is permitted, should be undertaken to monitor coconut crab population size and the relative proportions of different-sized crabs in the populations.

5. Efforts should be undertaken to prevent giant African snails from becoming established on those Northern Mariana Islands which are presently free of these snails. On Guam, Saipan, Tinian, Rota and Pagan, which are already infested with the snails, efforts should be made to eradicate them and to destroy the empty shells. This would stop the increasing supply of snail shells which are used by *Coenobita* spp. (and would also benefit farmers in areas where snails are pests).

6. An effort needs to be made to prevent harvesting of small coconut crabs less than 90 mm (3.5 inches) carapace length [43 mm (1.75 inches) thoracic length] and female crabs with eggs.

7. Collecting coconut crabs on beaches should be prohibited within two days prior to and six days after the new moon. This may be a difficult regulation to enforce, but would allow female coconut crabs to release their eggs into the ocean undisturbed. This is necessary to ensure future generations of crabs.

8. Sale of mounted coconut crab should be prohibited or restricted to crabs with carapace length greater than 90 mm (3.5 inches) [thoracic length greater than 43 mm (1.75 inches)]. It is necessary to regulate sale of mounted coconut crabs separately from size regulations on harvesting since vendors can claim that undersized souvenir crabs have been brought in from off-island and so are not in violation of local harvesting regulations.

9. Because of the ease in transporting crabs between Guam and the CNMI, size regulations should be uniform between the two jurisdictions.

B. <u>Research</u>

1. One of the most important parameters of the coconut crab's biology, both for stock management and for culturing of the animals, is its natural growth rate. Our attempts to measure growth rates were unsuccessful, as described above. Perhaps further experiments with tagging methods would lead to the development of a tag or mark that would be retained through successive molts. Future research on the coconut crab should concentrate on the solving of this problem.

2. If commercial culturing of the coconut crab is to be achieved techniques for mass culture of the larval stages must be developed. In areas where coconut crabs are scarce and *Coenobita* are abundant, initial studies could be carried out on the rearing of *Coenobita* larvae. Once appropriate methods have been developed with these larvae, attention could then be given to the larvae of the coconut crab and such modification as become necessary could be developed. Young crabs raised from the larvae could be used to stock natural areas or could be transferred to a grow-out facility for further rearing.

3. Rearing of the terrestrial stages can best be done in a large area wherein a variety of natural conditions are available. A small islet or a large, enclosed area would be appropriate if escape of the crabs and poaching can be prevented.

Although commercial rearing of coconut crabs may be ultimately feasible, the amount of research needed to develop appropriate techniques appears to be considerable. Culturing of other crustaceans, such as Malaysian prawns or others for which culturing techniques have been developed or are being developed, would be more likely to offer economic payoffs in the short run than would efforts to develop coconut crab culturing.

LITERATURE CITED

Frey, H. W., ed. 1971. California's living marine resources and their utilization. State of California Department of Fish and Game. 148 p.

George, M. J. 1967. Mark-recovery experiments in crustaceans. Mar. Biol. Assn. India, Symposium on Crustacea 4:1284–1295.

Gibson-Hill, C. A. 1947. Field notes on the terrestrial crabs. Bull. Raffles Mus. 18:43–52.

Guam Bureau of Planning. 1978. Guam Comprehensive Development Plan. Guam Bureau of Planning. 206 p.

Held, E. E. 1963. Moulting behaviour of *Birgus latro*. Nature 200(4908):799–800.

Helfman, G. S. 1973. Ecology and behavior of the coconut crab, *Birgus latro* (L.). Master’s Thesis, Univ. of Hawaii. 158 p.

Matthews, D. C. 1956. The probable method of fertilization in terrestrial hermit crabs based on a comparative study of spermatophores. Pacif. Sci. 10:303–309.

Reese, E. S. 1968. Shell use: an adaptation for emigration from the sea by the coconut crab. Science 161:385–386.

Reese, E. S., and R. A. Kinzie III. 1968. The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridea). Crustaceana, suppl. 2:117–144.

Reyne, A. 1939. On the food habits of the coconut crab (*Birgus latro* L.), with notes on its distribution. Arch. Neerl. Zool. 3:283–320.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 p.

Aspects of this work were carried out under the auspices of research sponsored by NOAA Office of Sea Grant, Department of Commerce, under Grant No. 04–5–158–45 through an award to the University of Guam. The U. S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.