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CONTENTS

ABSTRACT

Studies on the behavior of the land crab *Gecarcinus lateralis* (Fréminville, 1835) were made on a tract of land at Sabal Point, just north of Boca Raton Inlet, Florida. A portion of this tract is a tropical coastal hammock, one of the few remaining along the east coast of Florida. The thick vegetation of the hammock forms a canopy under which environmental conditions are such as to support a dense population of *G. lateralis*. Here the crabs can be seen outside of their burrows during hours of daylight; such behavior is unusual in this species.

At Sabal Point, information has been gathered on type of vegetation used as food and cover by *G. lateralis* and on activity of this crab. A photographic record of mating has been obtained. Observations indicate that ovigerous females of this species move down the beaches to the ocean to release their young, and young crabs come up these beaches as they begin life on land. Since all stages of growth were available at Sabal Point, we were able to study some parameters of relative growth in *G. lateralis*.

INTRODUCTION

On the southeast coast of Florida a tract of land at Sabal Point, just north of Boca Raton Inlet (figs. 1, 2), supports a dense growth of trees and bushes that screens out direct sunlight and encourages the existence of a large, active population of the land crab *Gecarcinus lateralis* (Fréminville, 1835). This species is found from the Bermuda Islands through the Bahama Islands, the Florida Keys, and the West Indies; along the Atlantic coast of Central America to Colombia, Venezuela, and French Guiana; and to Ascension Island (Rathbun, 1918)—although this last record is being questioned (Fenner A. Chace, Jr., personal commun.). The crab has also been reported from the Gulf Coast of Texas (Ray, 1967; Britton, 1976). For information on the taxonomic status of this species, see Bott (1955), Türkay (1970, 1973), and Klaassen (1975).

During summer in southeastern Florida when rains are frequent, large numbers of *G. lateralis* at Sabal Point can be seen out of their burrows by day, especially in the early morning and at dusk. It is unusual for this species of land crab to be active during the hours of daylight. In Bimini, Bahamas, the crabs restrict their activity almost entirely to hours of twilight and darkness (Bliss and Sprague, 1958; Palmer, 1971). Nighttime activity also characterizes *G. lateralis* on South Padre Island, Texas (Ray, 1967), on the island of Dominica (Chace and Hobbs, 1969), at Rio Buritaca, Colombia (Klaassen, 1975), and on Isla de Salamanca, Colombia (Henning and Klaassen, 1973; Klaassen, 1975). Yet, near Santa Marta, Colombia, there is a daytime-active population of *G. lateralis* living in the shade of bushes and trees at the base of Instituto Colombo-Alemán on the west side of a rocky promontory known as "Punta de Betin" (Henning and Klaassen, 1973; Klaassen, 1975). Nighttime activity is generally characteristic of *G. lateralis* in Bermuda; but on Nonsuch Island, Bermuda, where there is abundant vegetation, these crabs were seen outside of their burrows during the daytime in September (Wolfgang Sterrer and Frank Cantelmo, personal commun.). Recent observations by Lawrence W. Powers (personal commun.) indicate that, during the summer, the activity of *G. lateralis* on Nonsuch Island is mainly nocturnal, although the crabs emerge from their burrows as early as one hour before sunset and remain active outside of their burrows until an hour or so after sunrise. Regardless of the time of day, whenever there is a rain shower, the crabs immediately become active.

At Sabal Point, Boca Raton, Florida, the densely wooded area (fig. 3) is a tropical coastal hammock (also known as a shore hammock or beach hammock), that is, a strip of coastal land covered by a natural plant association (Austin and Weise, 1973). Because a tropical coastal hammock contains some desert-like

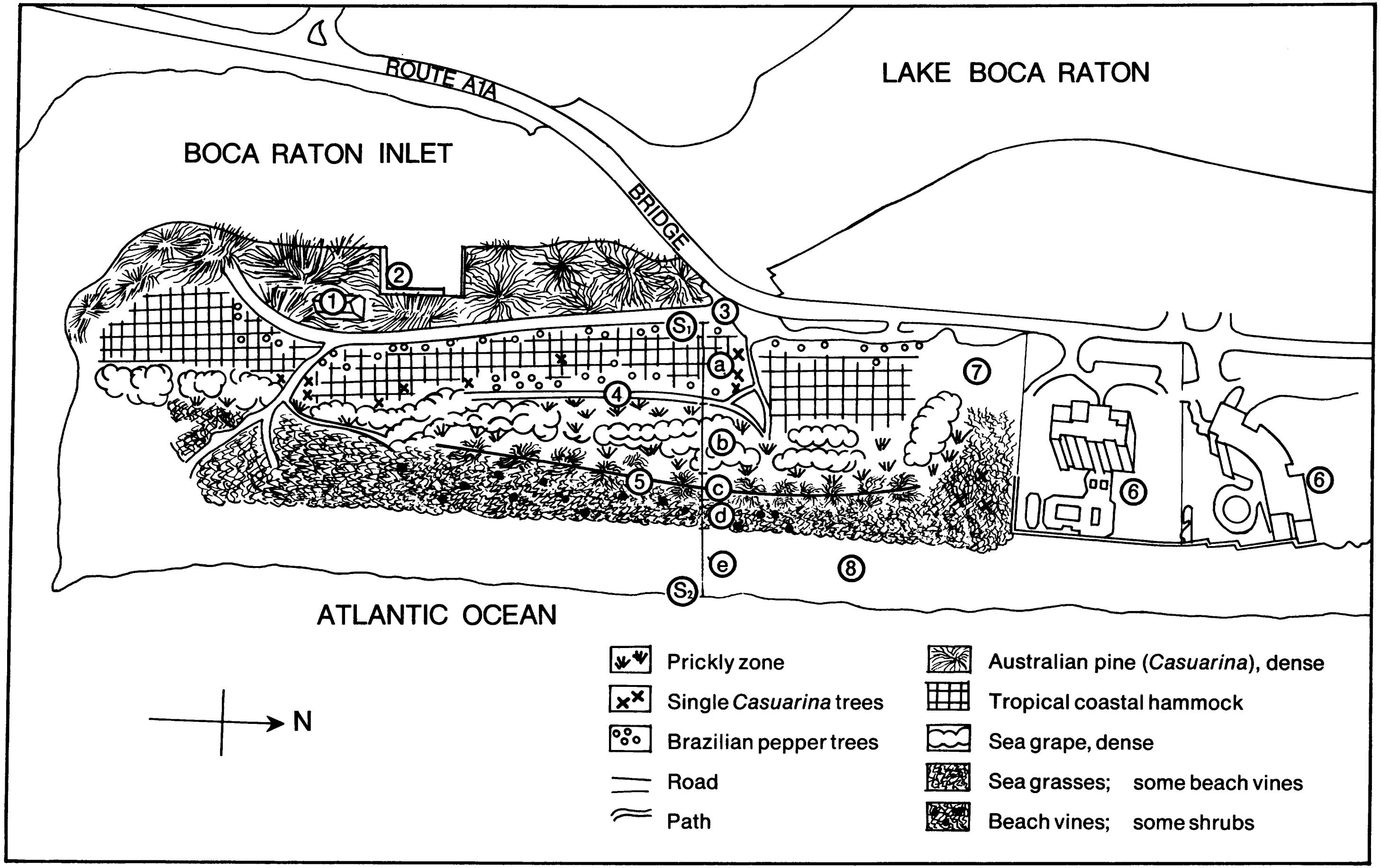

FIG. 1. Map of study area on Sabal Point at Boca Raton Inlet, Florida. Scale, 1-inch = 200 feet. S_1-S_2, cross section shown in figure 2; a-e, see figure 2. 1. U. S. Coast Guard Station. 2. Dock. 3. Entrance to tropical coastal hammock. 4. Path along crest of second dune. 5. Crest of first dune. 6. Condominiums. 7. Disturbed sandy area. 8. Sandy beach.

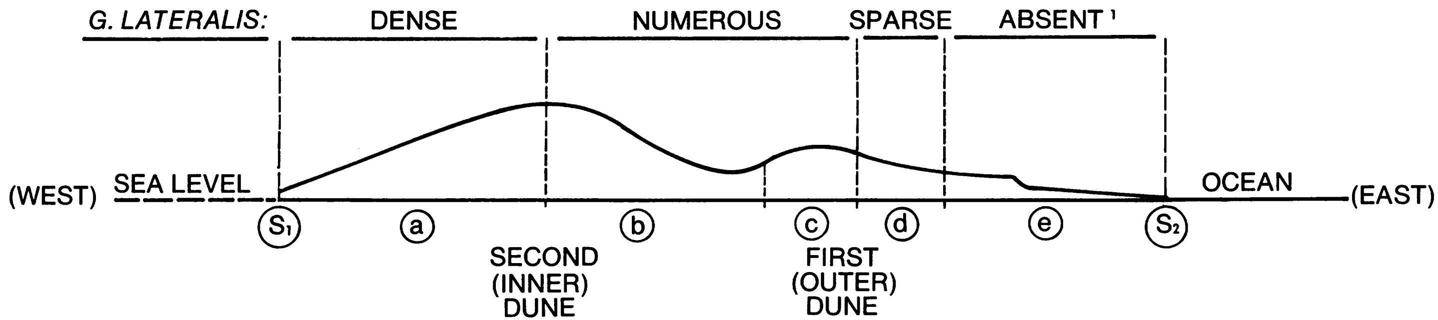

FIG. 2. Cross sectional diagram along section S_1-S_2 of figure 1. Horizontal scale, 1 inch = 77 feet; vertical exaggeration, two times. Height of first dune, about 15 feet; of second dune, about 25 feet. a. Tropical coastal hammock. b. Prickly zone. c. *Casuarina* zone. d. Beach vines, some shrubs. e. Beach.

[1]Except for spawning females, going to or returning from ocean.

vegetation, it is sometimes called a "cactus thicket." Yet, most of the prickly plants (e.g., prickly pear cactus, yucca, century plant) are restricted to the "prickly zone" (fig. 4) on the ocean side of the coastal hammock. From the prickly zone toward the ocean is a beach plant association that is common in subtropical and tropical latitudes of the Western Hemisphere. Inland from the prickly zone is the coastal hammock proper, characterized by such trees as cabbage palm, *Sabal palmetto* (Walt.); gumbo limbo, *Bursera simaruba* (L.) Sarg.; strangler fig, *Ficus aurea* Nutt; mastic, *Mastichodendron feotidissimum* (Jacq.) Cronquist; and sea grape, *Coccoloba uvifera* (L.) L.

The substratum of a tropical coastal hammock consists mostly of sand that is derived from marine bivalves. Thus, it is nonsiliceous and has a high content of calcium. Between the coastal hammock and the shoreline, the substratum takes the form of terraces, which relate to various major high tides. Within the coastal hammock, the substratum consists of old ocean deposits that have been stabilized by the vegetation of the hammock. To quote Austin and Weise (1973, p. 146): "The special xeric conditions of coastal hammocks make them ecologically unique."

Few tropical coastal hammocks remain along the eastern coast of Florida; most have been

FIG. 3. Central portion of tropical coastal hammock looking east-northeast from bridge over Boca Raton Inlet (see fig. 1). Dense vegetation covers west side of second dune. Many observations described here were made just off road in right foreground. September 9, 1974. 1 p.m.

destroyed and replaced by hotels, motels, and condominiums (Austin and Weise, 1973). The tropical coastal hammock north of Boca Raton Inlet may soon be no exception, for it too is in imminent danger of destruction.[1]

For a number of years, the first author had been studying *Gecarcinus lateralis* in the field at Bimini, Bahamas. Yet, on the tract of land north of Boca Raton Inlet, she was able, for the first time, to observe this crab in daylight—and in numbers large enough to study their interactions.

In Bimini even during the summer rainy season, there are periods when rains are infrequent. In the winter dry season, many days pass without any rain at all. During such periods of dryness, dew may be the principal and possibly the only source of moisture (Bliss, 1963, 1968). Thus, in Bimini *G. lateralis* inhabits a particularly dry environment. Furthermore, the vegetation in Bimini is sparse and provides little cover for land crabs. Thus, as stated earlier, the crabs in Bimini are active almost exclusively at twilight and in darkness (Bliss and Sprague, 1958; Palmer, 1971). Study of *G. lateralis* in Bimini has provided much information regarding the adaptations of this species to dryness and sparse cover. But, other than to indicate that the crab is a solitary burrowing form, usually not involved with other members of its species, such study has yielded little understanding of the crab's natural behavior.

The present paper records the existence of the daytime-active population of land crabs at Sabal Point and reports some observations regarding food, cover, activity, reproductive behavior, emergence on land, and relative growth of this species. We wish to note that when this field work at Sabal Point was done, we were not aware of the extensive studies on the reproductive biology of *G. lateralis* in Colombia by Folkert Klaassen. Our paper was virtually complete when Klaassen's account (1975) of his observations appeared in print. Due to the importance of Klaassen's work, we revised this paper to include reference to all of Klaassen's observations pertinent to this study.

[1]We learned, as this paper went to press, that commercial development of the area at Sabal Point had started. In preparation for this, according to Richard Wolf, Chief Environmental Officer of the city of Boca Raton (personal commun.), many thousand individuals of *G. lateralis* have been relocated from Sabal Point to two other promising natural areas nearby. It is hoped that the crabs released in these natural areas will establish themselves in breeding colonies.

ACKNOWLEDGMENTS

The field observations described here were made while the second author was a graduate student at Florida Atlantic University and the third author was associated with the Agriculture Reseach Center, Institute of Food and Agricultural Sciences, Fort Lauderdale, Florida.

We thank Mr. Woodard Miley for his assistance in the field and his identification of the lizard shown in figure 14. We also thank Drs. Frank Cantelmo, Linda H. Mantel, Lawrence W. Powers, Wolfgang Sterrer, Mr. David B. Wingate, and Mr. Richard Wolf for permitting us to cite unpublished field observations; Ms. Stefanie W. Sheehan and Mr. Antony Rudié for technical assistance; Mr. Peter Goldberg of the American Museum's Photography Department for preparation of the photographic prints; members of the American Museum's Department of Exhibition and Graphics for inking the line drawings; Ms. Beatrice Brewster for assistance with translations; Ms. Lynne Judge, Ms. Joan Mey, Ms. Patricia Timlin, and Ms. Parnell Bell for typing different versions of the manuscript; and Mr. Gerald Thurmann for assistance of various sorts.

We are very grateful to Drs. Daniel F. Austin, Fenner A. Chace, Jr., and Linda H. Mantel for their critical reading of the manuscript and their valuable suggestions regarding it. Certain of Dr. Chace's comments are included in the form of a personal communication.

We express appreciation to the Arvida Corporation for granting us permission to study and collect land crabs on their property at Sabal Point; to the Council of the Scientific Staff of the American Museum of Natural History for providing field support for one of us (Bliss); and to the National Science Foundation for a research grant (BMS 74-01546) to Bliss, which has made possible inclusion of the section on relative growth.

Photographs in this paper were taken as follows: figures 10, 11, 13, 16 (upper), 19, 20, 21 (upper left; lower left and right) by Bliss; others by Van Montfrans, except figure 4, which was taken by Mantel.

BEHAVIOR

FEEDING AND PROTECTIVE COVER

A dense canopy is formed by thick upper foliage of trees in the tropical coastal hammock just north of Boca Raton Inlet (fig. 3). This canopy serves a dual function. First it makes available, primarily through leaf fall, a readily accessible and virtually limitless supply of food and protective cover for land crabs living there. In addition to the red, or purple, land crab, *Gecarcinus lateralis*, these include the black land crab, *G. ruricola* (Linnaeus, 1758), which appears to be quite rare; and the land hermit crab *Coenobita clypeatus* (Herbst, 1791) (see fig. 5, also Wilde, 1973), which is abundant.

Second, the canopy serves as an effective screen against the direct rays of the hot sun. The light intensity on the forest floor (fig. 6) is greatly reduced[1] by the thick foliage far above,

[1]The great reduction in light intensity is indicated by the setting required when photographing land crabs there. With Kodak Plus-X Pan film (ASA 125), it was necessary to use a setting of f2 at 1/30 or 1/60 second, rather than f22 as is correct out in the open sunlight. The alternative was to use electronic flash; this was done in many instances.

FIG. 4. Exposed area in prickly zone on west side of first dune. Visible are prickly pear cactus (*Opuntia compressa*), and, in background, saw palmetto (*Serenoa repens*). Note absence of crabs and crab burrows. July 14, 1975. 11 a.m.

particularly in the early morning, when the west side of the second (inner) dune is shaded by the bulk of the dune from the sun lying to the east. The low light intensity may be a principal factor in the high level of activity by land crabs in the early morning (fig. 6, top), compared with that later in the day (fig. 6, bottom). Other factors may be the relative coolness of the air circulating under the canopy and the high humidity. Heavy rain showers greatly enhance activity of land crabs (fig. 7, top), even when the light is relatively strong (fig. 7, bottom).

Among the native species of plants that are most common in the tropical coastal hammock are the sea grape, *Coccoloba uvifera*; cabbage palm, *Sabal palmetto*; strangler fig, *Ficus aurea*; knicker bean, *Caesalpinia bonduc* (L.) Roxb.; and marlberry, *Ardisia escallonioides* Schlecht & Cham. Also widespread in this area is the Brazilian pepper, *Schinus terebinthifolius* Raddi, a species introduced from South America. These plants grow thickly over the landward (west) side of the second (inner) dune, which lies farther from the ocean (figs. 1, 2).

In the tropical coastal hammock, *Gecarcinus lateralis* has been observed eating fallen green and dried leaves of sea grape, leaves of the Brazilian pepper, fruits of the cabbage palm, and other plant material (fig. 8). The crabs have been seen carrying the seed of the knicker bean; but it is unlikely that they can eat this seed, which is very hard. Of the dark, ripe fruits of the cabbage palm, the crabs eat the pulpy outer shell and discard the hard inner part.

The land crabs appear to take some of the leafy food materials with them into their burrow. On excavation of a burrow, at least in the winter months, one may find a "plug" of leaves near its end. Usually a crab can be found just behind the plug. It is likely that in winter the crabs use the plug of leaves as food. In summer, eating is probably done primarily during foraging excursions outside of the burrow.

Trees of the tropical coastal hammock are a direct means of protection and shelter for *Gecarcinus lateralis*. The crabs are excellent climbers, often being found 2 to 6 feet up a tree (figs. 9, 10). One individual was observed at least 18 feet up a strangler fig tree. The crabs appear to have no difficulty gripping the trunk

FIG. 5. Land hermit crabs (*Coenobita clypeatus*) on cabbage palm, *Sabal palmetto* (above), and on tree branch (below). On west slope of second dune. September 10, 1975. 11:15-11:45 a.m. Electronic flash.

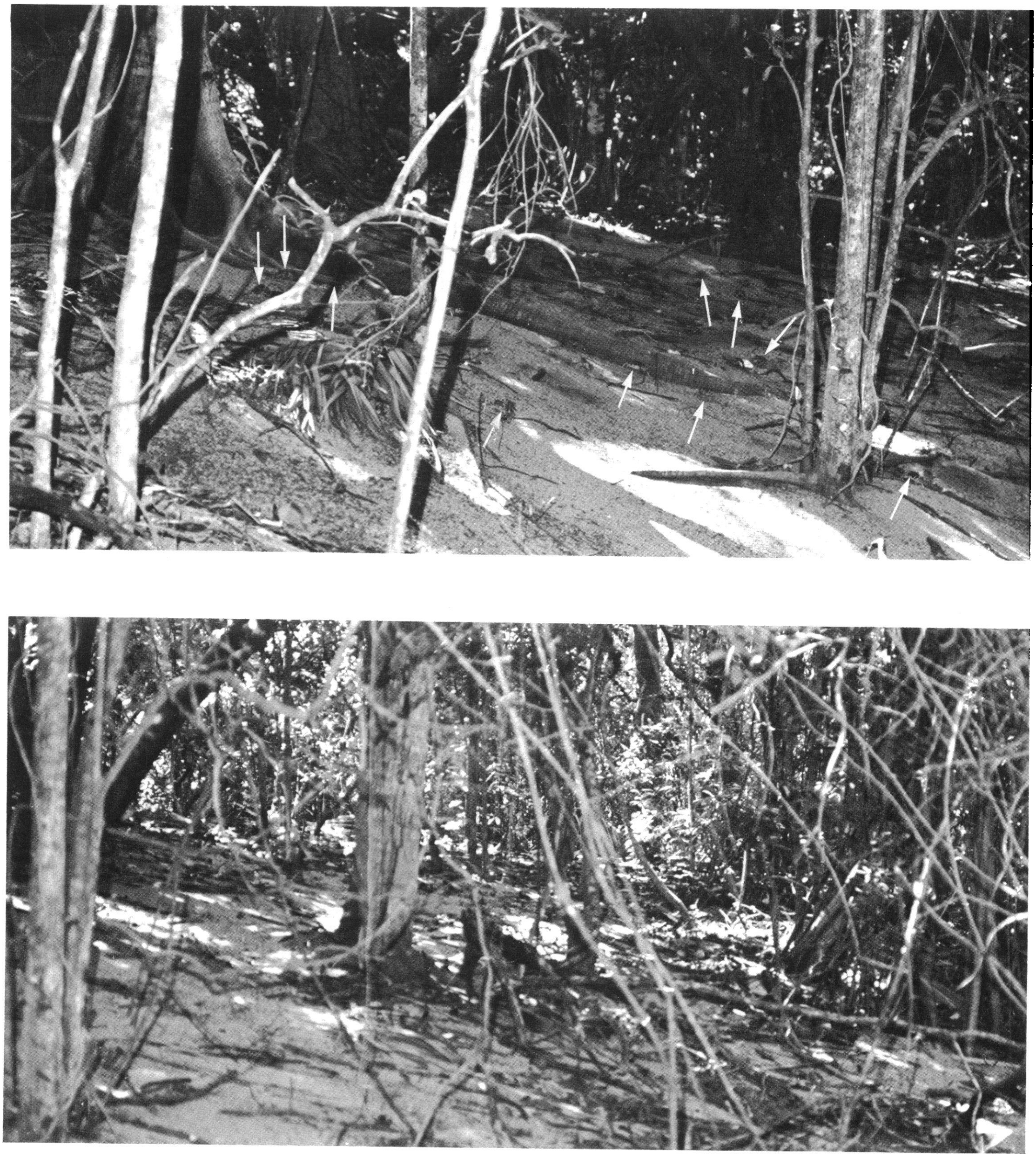

FIG. 6. Within tropical coastal hammock on west side of second dune: at 9:15 a.m. (September 8, 1974), when area is deeply shadowed (above; electronic flash), and at 11:00 a.m. (September 9, 1974), when many patches of sunlight are visible (below). Many crabs (*G. lateralis*; arrows) are active in the dim light of early morning, but few crabs can be seen as noon approaches.

with their sharply pointed walking legs, thereby leaving their claws free for defense (fig. 10) and for seizing and carrying food. Nooks and crannies on the lower part of tree trunks and amongst roots serve as hiding places for crabs (figs. 7, top; 9).

At the upper part of the inner dune, the vegetation of the coastal hammock proper gives way to plants characteristic of the "prickly zone" (fig. 4), such as the saw palmetto, *Serenoa repens* (Bartr.) Small; yucca, *Yucca aloifolia* L; and cactus, *Opuntia compressa*

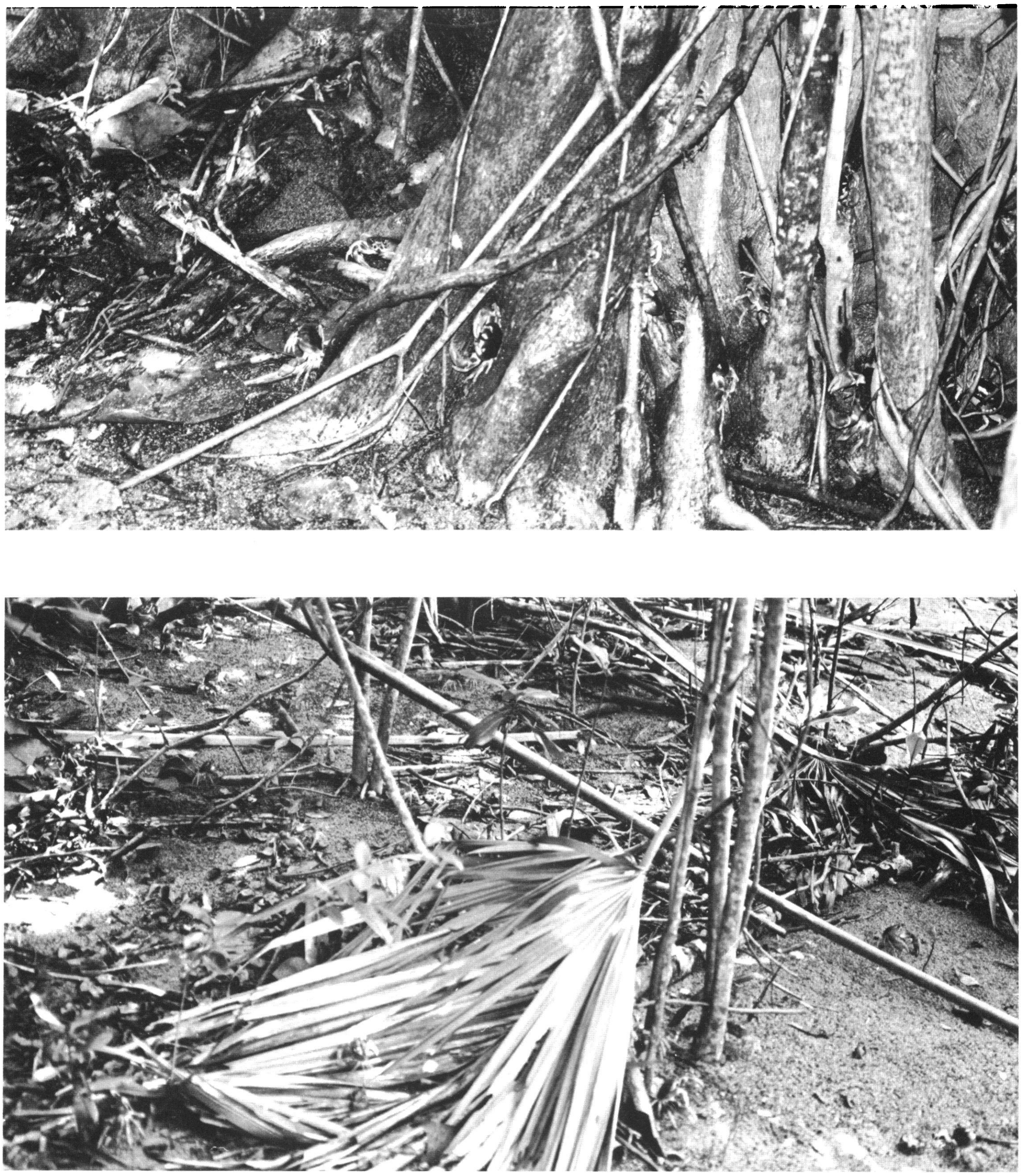

FIG. 7. Heightened activity by *G. lateralis* about two hours after a heavy rain. In each photograph, about 14 crabs are visible. Trees (upper) are strangler fig (*Ficus aurea*). On west slope of second dune. September 10, 1975. 11:40-11:45 a.m. Electronic flash.

FIG. 8. *Gecarcinus lateralis* feeding on partially decayed leaf. On west slope of second dune. September 17, 1975. 10:05 a.m. Electronic flash.

(Salisb.) Macbride. In this zone, nonetheless, dense stands of sea grape still provide abundant shade and groundcover for land crabs. Passing by a sea grape tree from which there has been copious leaf fall (fig. 11), one hears a continuous rustling of the dried leaves as the crabs run about underneath the leaves. Land crabs also use cabbage palm as protective cover, huddling at its base or hiding under fallen fronds.

Near and at the crest of the first (outer) dune, the foliage is much more open than within the hammock, and large patches of sunshine on the floor of the woods are common (fig. 12). The trees found here are *Casuarina equisetifolia* Forst., commonly called the Australian pine but not a true pine. This species was introduced into Florida and has become naturalized there. Dried fallen *Casuarina* needles form thick mats under the trees and sometimes are seen being eaten by *G. lateralis*. During morning hours, the land crabs are active in this area but are less numerous than in the hammock and in heavily shaded portions of the prickly zone.

On the ocean side of the outer dune, the *Casuarina* trees quite abruptly give way to beach shrubs and vines (fig. 12, top). Here one finds the beach morning glory, or railroad vine, *Ipomoea pes-caprae* (L.); the bay bean, *Canavalia maritima* (Aubl.) Thouars; and scattered low-growing sea grape plants (fig. 13, bottom). Here also grow a succulent plant, the marsh elder, *Iva imbricata* Walt., and the beach daisy, *Helianthus debilis* Nutt (fig. 19, bottom). *Gecarcinus lateralis* has been observed eating all these plants. Although crab burrows are numerous in this area, during midday the land crab is seldom seen. It can sometimes be found sheltered from the sun under the broad leaves of the bay bean.

The area of beach shrubs and vines terminates at either end in a dense growth of sea grasses, including sea oats, *Uniola paniculata* L., and an unidentified species of the genus *Panicum* (figs. 1; 13, top). Some beach vines are present among the sea grasses.

Activities of *G. lateralis* are most readily and comfortably studied—and photographed—along the crest of the outer dune (fig. 12, bottom), where the Australian pines provide shade, a sea breeze cools the air, and light is strong enough for the crabs to be easily detected and observed. In this relatively open area, a crab was observed with a portion of the tail and hind legs of a lizard [*Cnemidophorus sexlineatus* (Linnaeus, 1766), the six-lined racerunner] in its claws and mouthparts (fig. 14). Much harassment was required before the crab would drop this morsel. *Gecarcinus lateralis* also eats portions of its own species, when available (fig. 15). These observations confirm those made in the laboratory that, although primarily a vegetarian, *G. lateralis* will eat animal material when it is accessible.

Field studies by other scientists on two other species also have suggested that the genus *Gecarcinus* is omnivorous rather than strictly vegetarian. On the beaches of Clipperton Island in the southeastern North Pacific Ocean, *G. planatus* Stimpson, 1860, eats algae, fishes, and crustaceans left by the high tides. In the interior of the island, the crabs eat leaves of coconut palms and the meat of coconuts, as well as eggs of gannets that have nested on the ground, and very young birds and wounded or dead birds; within a few days, the crabs can reduce to a skeleton any dead animal lying on the ground. At the edge of the lagoon, the crabs eat algae and flowering plants, even immersing themselves in water to do so. In sandy, uninhabited areas, the crabs do not hesitate to eat each other (Ehrhardt and Niaussat, 1970).

On the Brazilian island of Trindade in the western South Atlantic Ocean, *G. lagostoma* H. Milne Edwards, 1837, primarily eats plant life, especially *Ipomoea pes-caprae*, *Waltheria indica* L. (= *W. americana*), and Cyperaceae. Yet the crabs prey on young sea turtles that have emerged from eggs on the beach. The

FIG. 9. Tree-climbing crabs: three individuals of *G. lateralis* on Brazilian pepper tree (*Schinus terebinthifolius*) at left; four individuals of *G. lateralis* on strangler fig tree (*Ficus aurea*) at right. On west slope of second dune. September 8, 1974. 10:30-11:00 a.m. Electronic flash.

FIG. 10. *Gecarcinus lateralis* about 3 feet up an Australian pine (*Casuarina equisetifolia*). On crest of first dune. August 29, 1974. 7:00 p.m.

crabs also eat carrion, feathers, bones, paper, calcareous algae, and plant and animal life of the beach litter. On the upper reaches of the island, the crabs eat algae, mosses, lichens, and organic material in the rich humus soil (Fimpel, 1975).

BURROWS AND ACTIVITY

Near or on the crest of the outer dune at Sabal Point, Boca Raton Inlet, *Gecarcinus lateralis* could often be seen excavating a burrow (figs. 16, 17). In each instance, the crab carried moist sand out of its burrow by cradling the sand in its trailing cheliped, whether left or right. Sometimes a crab did not carry sand out of the burrow but only up to the entrance, placing it there and thereby partially closing the entrance (fig. 19, bottom). A partly plugged burrow of *G. lateralis* is a common sight in winter when the temperature is below 60°F. (15.6°C.), but it is rare in summer.

Occasionally an agonistic encounter between two or more crabs was observed (fig. 18). Sometimes aggressive-defensive behavior is directed toward a human being (fig. 15; 19, top). In such encounters, a crab may assume a position of display that Wright (1968, MS) termed the high-intensity lateral merus (HILM; "Aufbaumreflex" of Bethe, 1897; figs. 15; 18B;

FIG. 11. Fallen dried and green sea grape leaves (*Coccoloba uvifera*). *Gecarcinus lateralis* eats these leaves and uses them as protective cover. Upper photo was taken at 9:45 a.m. on crest of second dune. Lower photo, taken at 11:00 a.m., shows especially thick leaf litter from sea grape trees, also on crest of second dune; note dead *Yucca* plants. August 29, 1974.

FIG. 12. Australian pines (*Casuarina equisetifolia*) on first dune, as seen (above) from the ocean beach (September 9, 1974; 11:30 a.m.) and (below) when looking north along crest of dune (August 30, 1974; 10:30 a.m.).

19, top). According to Wright, the high intensity lateral merus is the display assumed by most species of crabs when danger threatens

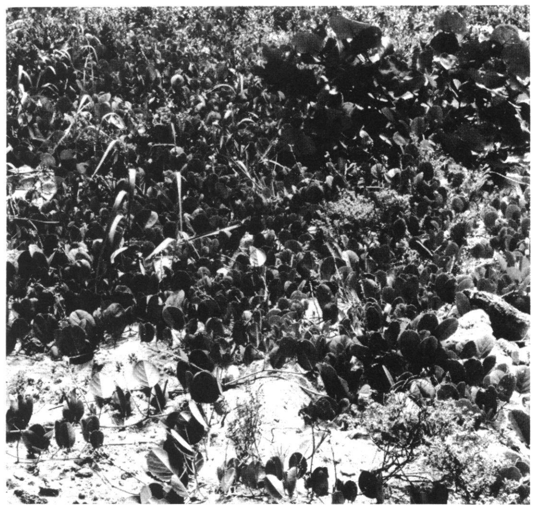

FIG. 13. Atlantic Ocean and beach on eastern side of the study area (above). Condominium in left background is the farther (northern) one of the two shown in figure 1. Visible here is an area south of the condominiums that is densely covered with sea grasses (*Panicum* sp. and *Uniola paniculata*, sea oats), interspersed with some beach vines (see fig. 1). South of the sea grasses lies area of beach vines and shrubs (below). Appearing here is the bushy sea grape (*Coccoloba uvifera*) and a vine known as bay bean (*Canavalia maritima*). During midday, *G. lateralis* is scarce; but some crabs may be found sheltered under broad leaves of the bay bean. August 29, 1974. 11:00 a.m.

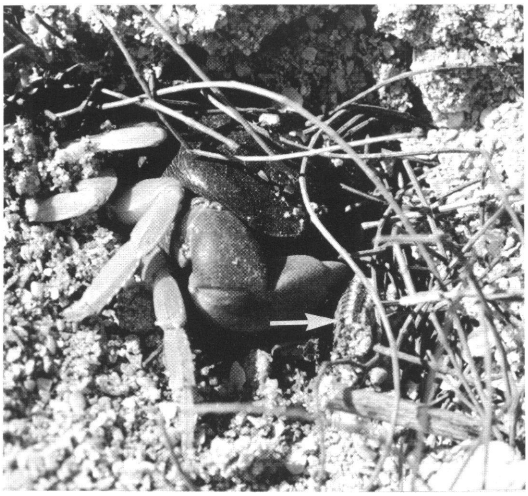

FIG. 14. *Gecarcinus lateralis* with a partially eaten lizard, the six-lined racerunner (*Cnemidophorus sexlineatus*). Only hind legs and base of tail (arrow) of lizard remain. Crab had been intercepted nearby and had retained grip on lizard while seeking refuge at entrance of this burrow. On first dune. August 30, 1974. 10:10 a.m.

and is replaced by mid-intensity and low-intensity lateral merus displays as the danger passes and the crab gradually relaxes.

In the study area at Boca Raton Inlet, the activities of *G. lateralis* outside of its burrow come to a halt with the advent of cold weather, which in the year 1974 occurred on November 12. On this date, the temperature of the air dropped to the mid-forties (°F.) and the crabs went underground. During the ensuing six months, only a few crabs were seen out of their burrow, in warm spells when the temperature of the air rose into the high eighties (°F.) and even into the nineties; a few other crabs were seen at the mouth of their burrow. By late April 1975, the temperature was consistently high, but no crabs were active. Finally, on May 12, 1975, there occurred a heavy rain. Promptly, by the thousands, the crabs emerged, many of them covered with white dust from their long sojourn underground. At once, the crabs began to clean detritus out of their burrow and to feed, some on fruits of the cabbage palm, but most on decayed leaves.

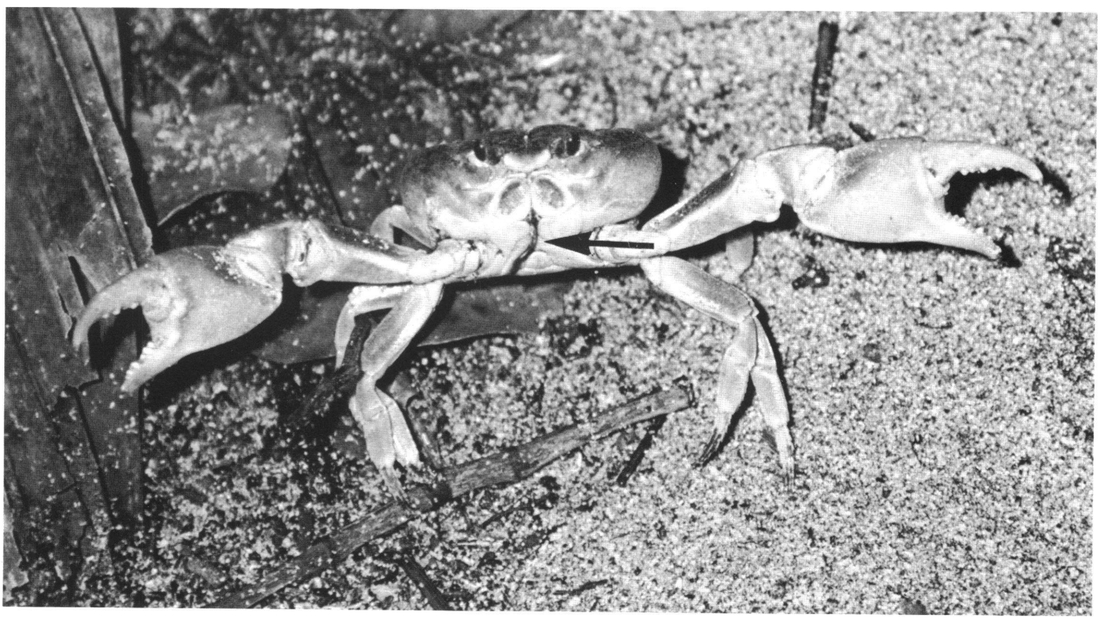

FIG. 15. *Gecarcinus lateralis*. A large specimen, with dactyl of claw (arrow) from another *G. lateralis* in mouth parts. The crab is giving a high intensity lateral merus (HILM) display. On west side of second dune. September 10, 1975. 11:45 a.m. Electronic flash.

In southern Florida, the dry season coincides roughly with the winter months; thus rainfall is lightest in December through March and heaviest in April through June and September through November, with some diminution during July and August (Thomas, 1974). From observations cited in the preceding paragraph, it would appear that in the study area at Boca Raton Inlet *Gecarcinus lateralis* ceases to be active aboveground when the temperature of the air drops below a certain level, as yet undetermined, and fails to resume activity until the temperature is again above that level and, in addition, until rainfall is abundant. Thus, one environmental factor, low temperature, results in cessation of activity; and two environmental factors, favorable temperature and abundant moisture, lead to its onset.

In Bimini, where *G. lateralis* is active at night rather than by day, an air temperature of 18°C. (64.4°F.) is low enough to cause running activity outside of the burrow to cease, although the removal of sand washed or blown into the burrow may continue (Bliss and Sprague, 1958; Bliss, 1968). Weitzman (MS) found no running activity but much burrow-cleaning by *G. lateralis* in Bermuda when the temperature of the air was 17-18°C. (62.6-64.4°F.); and Dustan (1957) reported that the crab remained within its burrow when the air temperature dropped below 18.4°C. (65.1°F.).

David B. Wingate, Conservation Officer, Department of Agriculture, Bermuda, has reported (personal commun.) that in winter, when the temperature of the air drops into the low sixties and fifties (°F.), land crabs (*G. lateralis*) on Nonsuch Island, Bermuda, cease to be active, except to clean out their burrow after a heavy rain. The crabs, nonetheless, show some activity during periods when the temperature rises to the high sixties or low seventies (°F.). At such times, the crabs display an increasing tendency to be active during the day, probably because of milder daytime (as contrasted with lower nighttime) temperatures and greater amount of cloud cover, compared with that existing at other times of the year.

For another species of gecarcinid in southern Florida, *Cardisoma guanhumi* Latreille, 1852,

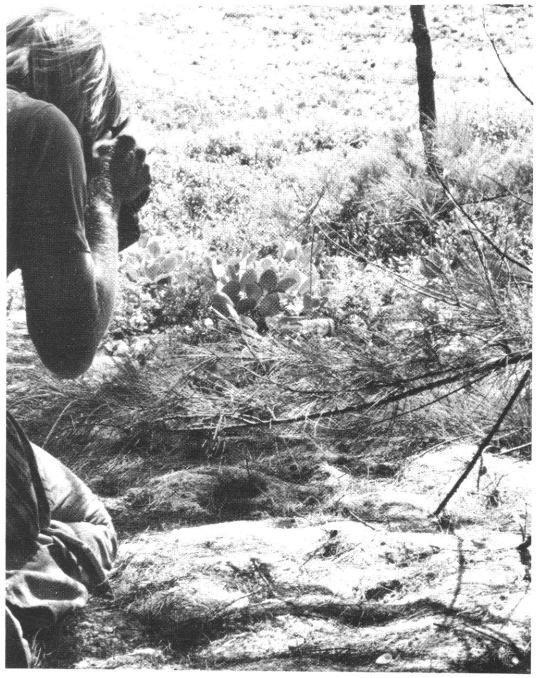

FIG. 16. *Gecarcinus lateralis* being photographed (above) as the crab removes moist sand from burrow. Scene appears below. Crab carries sand with its trailing cheliped. Note mound of damp sand (right center) already removed. Near crest of first dune. August 29, 1974. 10:30 a.m.

FIG. 17. *Gecarcinus lateralis* digging or enlarging a burrow. Crab carries moist sand cradled in trailing cheliped. Out of sight at lower left is mouth of burrow and at upper right is a mound of damp sand previously removed. On crest of first dune. August 30, 1974. 9:45 a.m.

Gifford (1962) has reported that running activity outside of the burrow requires abundant moisture (i.e., it occurs primarily during the rainy season), but he makes no mention of temperature as a critical factor. On Bimini, the running activity of large *C. guanhumi*, a land crab that is primarily nocturnal, is greatly reduced when the temperature of the air falls below 18°C. (Bliss, 1968). Small individuals may be active during the day, provided the air is cool. During heavy rains, even the larger individuals come out of their burrows by day.

In his study of *C. guanhumi* in southern Florida, Gifford (1962) reported that colonies of this land crab situated in exposed areas, such as along the banks of drainage canals, were active at night, whereas one colony of the land crab living in woods was active by day. Herreid (1963) found *C. guanhumi* of southern Florida to be active by daylight in colonies that were shaded from direct sunlight and relatively secluded from the doings of man.

In northern Colombia, at the mouth of Rio Buritaca some 50 miles east of Santa Marta, Henning (1975b) discovered a population of *C. guanhumi*, living in the shade of a hedge, to have two peaks of activity each day. Starting in the afternoon between 2 p.m. and 3 p.m., the crab's activity reached a maximum just before sunset, around 6 p.m.; then it virtually ceased by 8 p.m. The crabs began a second, less intensive period of activity around 5 a.m.; this reached a peak about 7 a.m. and finally terminated by 9 a.m.

In *C. guanhumi*, therefore, the phase of activity seems to be modifiable, in accordance with environmental conditions. Given moderate temperatures and abundant moisture, as well as subdued light, the land crab is not averse to activity outside of its burrow by day. It is likely that *Gecarcinus lateralis* is equally modifiable as to its phase of running activity. In the

FIG. 18. Agonistic behavior in *G. lateralis*. A. Large male crab approaches burrow containing small male. B. Small male emerges and gives HILM display; large male retreats. C. Large male returns and both crabs assume a position with chelipeds overlapping but not gripping. D. Small male abandons burrow, which large male now takes over. In Australian pines on first dune. August 29, 1974. 10:15 a.m.

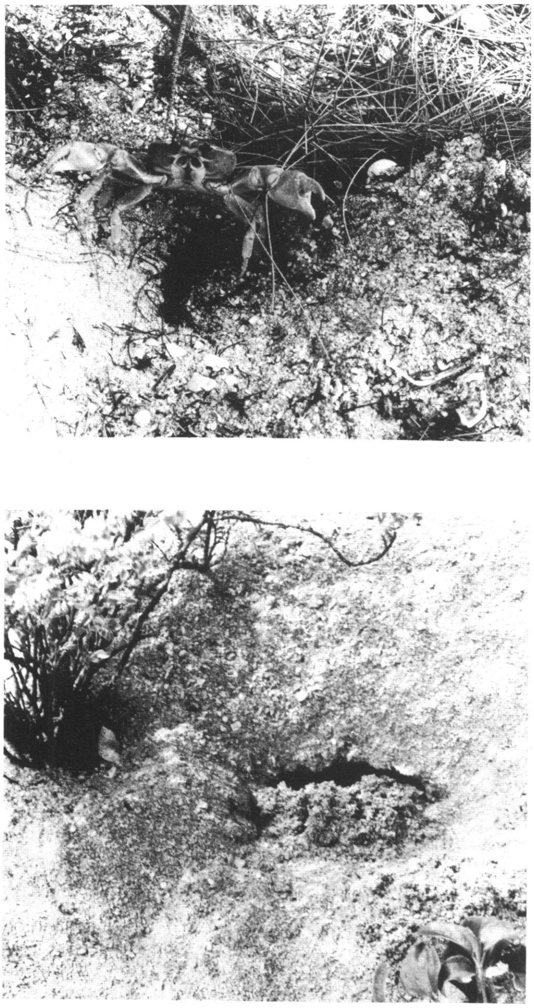

FIG. 19. *Gecarcinus lateralis* (above). A large male standing over entrance to burrow that the crab is cleaning or enlarging. Note pile of excavated soil at extreme right. Crab has assumed HILM display. In Australian pines on crest of first dune. August 29, 1974. 10:00 a.m. Partially plugged burrow of *G. lateralis* (below). On first dune, in area of beach vines and shrubs; beach daisy, *Helianthus debilis* (foreground); shrub *Chamaesyce mesembryanthemifolia* (background). August 29, 1974. 11:00 a.m.

study area at Boca Raton Inlet, where daily summer rains provide abundant moisture and heavy vegetation affords subdued light and protection from a hot sun, the crabs are active by day; in Bimini, where environmental conditions are favorable only at night, the crab is nocturnally active.

At the mouth of Rio Buritaca in northern Colombia, a large population of *Gecarcinus lateralis* inhabits a coconut plantation. Here diverse vegetation, which Klaassen (1975) has classified into seven zones, includes *Ipomoea pes-caprae* just above the sandy beach and bushes and trees some 140 meters inland. During mating time, the *Ipomoea*-zone (zone I) serves as a copulation zone for *G. lateralis* (Klaassen, 1975).

Klaassen observed that in zone I activity of *G. lateralis* usually started after 7 p.m., although in zones II-VII activity generally started about one hour earlier. He attributed this difference to the period of time that is required for the surface layer of exposed zone I to cool, once the sun has set, compared with the time required by the surface layer of less exposed zones. In zone I, a temperature as high as 56°C. could be recorded from the surface layer during the hottest part of the day. In contrast, under the closed vegetation of zone V, the temperature of the surface layer at that time of day was only about 29°C., a favorable level for *G. lateralis*. Klaassen found that, during rainy periods, when the temperature of all zones was about the same, crabs of zone I also became active at about 6 p.m.; and they could be seen in the upper third of their burrow from 4 p.m. on days when the temperature was below 30°C.

Gecarcinus lateralis, according to Klaassen (1973, 1975), possesses a communication system whereby information is transmitted by vibrations traveling through the substrate. This communication system is dependent on temperature. When there is a difference of more than 5°C. in body temperature between two crabs, it is possible that misinformation may be passed between the crab producing vibrations in the substrate and the crab receiving them. It is probable, stated Klaassen, that, despite the onset of twilight or darkness, activity may not start until little difference in temperature exists between a crab on the upper surface of the ground and one in a burrow. Crabs were regularly observed to remain just inside the entrance to their burrow for five to 10 minutes before their first departure from the burrow.

Klaassen interpreted this to indicate that the crab was adjusting its body temperature to that of the upper surface before leaving the burrow.

On Clipperton Island, *Gecarcinus planatus* remains in seclusion during the day, according to Ehrhardt and Niaussat (1970). Large numbers of this species inhabit *Ipomoea*-covered sandy stretches near the lagoon; in these areas, the soil is riddled with their burrows. Within the shade of coconut palms, where fewer than half as many crabs per square meter can be found, the crabs live primarily in crannies in the trunk of trees or between branches. At dusk the crabs leave burrows and crannies to invade open areas and seek the borders of the lagoon to feed. The authors attribute the predominance of crepuscular and nighttime activity to avoidance not of light but of the intense evaporation that would occur during exposure to the sun. Indeed, the authors found that at night the crabs are attracted to electric lights of buildings and will enter if a door is left open. The authors also observed that, if hungry, crabs will come out at high noon to devour a dead animal thrown on the ground.

On the Brazilian island of Trindade, *Gecarcinus lagostoma* occurs most abundantly in fields of *Ipomoea pes-caprae* that cover the low-lying sandy areas near the sea; in addition, some large individuals can be found in mountainous regions, where conditions of temperature, moisture, vegetation, and food are particularly favorable for land crabs. Within both areas, the crabs remain in their burrow during the day, becoming active about the onset of twilight. At the lower altitudes, the crabs wander around the *Ipomoea* zone through the night, seeking shelter in another burrow at dawn; if no burrow is available, the crabs dig one. In mountainous regions, where adequate food is available close by, the crabs remain in the vicinity of their burrow (Fimpel, 1975).

From the observations of Ehrhardt and Niaussat (1970), Fimpel (1975), and Klaassen (1975), added to our own, it would appear that the phase of the 24-hour day in which *Gecarcinus* is active depends upon several environmental factors, namely: intensity of illumination, including the presence of cloud cover; temperature of surface and subsurface layers of the soil, temperature of the air, relative humidity of the air, and availability of protective cover for quick retreat. Regardless of the phase of activity, the degree of activity seems to depend, except at mating time, upon the distance that the crab must travel from burrow or cranny to feeding grounds. *Gecarcinus* seems to be highly modifiable in its behavior. This characteristic undoubtedly explains much of the crab's success in its terrestrial habitat.

MATING

In the study area north of Boca Raton Inlet during the late summer months, one can frequently see mating pairs of *Gecarcinus lateralis*. For example, between 7:20 and 7:50 p.m. on August 29, 1974, we observed and photographed two mating pairs within a few feet of each other and a third pair about 30 feet away. The first two matings occurred on the crest of the first (outer) dune, while the third took place on the ocean side of the dune where trees are replaced by beach shrubs and vines. The light, though fading, was still adequate for taking pictures without flash.

In each mating the female was on top and the male beneath her (figs. 20-23). The female, and the male were in the hard-shelled condition. In two instances, the female was somewhat larger than the male.

One of the three pairs commenced mating outside of a burrow. As we approached, the female was carrying into a burrow the male, who was clasping her from below, and there mating continued (fig. 20). The pair separated after about 15 minutes. Another mating pair, which was picked up to be measured, remained in copulatory position even while being held (fig. 21).

Earlier in the day (8:45 a.m.), a mating pair had been seen on the back (west) side of the second (inner) dune just inside the tropical coastal hammock. Both male and female were in the hard-shelled condition; and the female was above the male. She appeared to be larger than the male, but no measurements were taken. After about 15 minutes, the pair separated. Mating had taken place just outside the mouth of a burrow; once mating was completed, the female ran to another burrow about a foot away and entered it, while the male

FIG. 20. *Gecarcinus lateralis* mating within a burrow. Male is on his back; female is above him. Note that male's claws are flexed. Female was carrying male into burrow when first sighted. Although burrow subsequently was excavated, mating continued for another 15 minutes, after which the pair separated. Carapace width: male, 3.7 cm.; female, 4.2 cm. In area of beach vines and shrubs, on east side of first dune. August 29, 1974. 7:20 p.m. Electronic flash.

moved slowly to still a third burrow and descended into it.

Prior to our observations of mating in *Gecarcinus lateralis*, only one report of it had been known to the authors. Weitzman (MS) remarked on four acts of copulation that had been observed in *G. lateralis* held in community tanks in the laboratory. She said that all four matings occurred either upon arrival of the crabs or shortly thereafter. Both males and females were in hard-shelled condition and apparently in intermolt. In three of the matings, the female was on top and the male beneath her. In the fourth mating, which was observed by one of us (Boyer), the female was beneath the male. Weitzman suggests that this may represent a difference in behavior of crabs from different areas, since the former three pairs came from Bermuda and the latter pair from Bimini.

The first author of the present paper has, however, on one occasion (September 7, 1972) observed mating of *G. lateralis* in Bimini. The male lay beneath the female, and both were in the hard-shelled condition. The position of the two was essentially that pictured here (figs. 21-23) for crabs in Boca Raton. In Bimini, following the mating, the female went down into the burrow at the mouth of which mating had occurred, while the male moved away.

In *G. lateralis* of Boca Raton, during copulation the male lay with one or both claws outstretched on the ground (fig. 21) or, as in one instance (figs. 22, 23), on the trunk of a tree. In close quarters, such as exist when mating occurs within a burrow (fig. 20), the male may keep his claws flexed. According to Klaassen (1975), when the female is restless, especially toward the end of mating, the male may place his claws on the carapace of the female. A male *G. lateralis* is shown in such a position in figure 24. Note that the abdomen (arrow) of the male is not retracted but is pressed loosely against the ventral surface of the thorax. The copulating crabs, when photographed, may have been about to separate, as suggested by Henning (1975a) for a copulating pair of *Cardisoma guanhumi*, the male of which similarly displayed a folded, unretracted abdomen (see Henning's fig. 12).

Many copulations by *G. lateralis* at Rio Buritaca, Colombia, were observed by Klaassen (1975), both in the field and in the laboratory. In every case, the male was beneath the female, clasping her with his walking legs. His first two pairs of legs were always between her claws and her first pair of walking legs. This, too, is the position (figs. 22-24), assumed by *G. lateralis* at Sabal Point, except in one instance (fig. 21, lower left), when the male appeared to have the female's first left walking leg between his first and second walking legs. In the Colombian crabs, as in the crabs of Boca Raton and Bimini, both male and female in every pairing were hard-shelled.

As Bliss (1968; see also Hartnoll, 1969) has pointed out, the emergence of crabs from the sea to take up a terrestrial way of life has been accompanied by two changes in their habits of mating: first, mating tends to occur when both female and male are hard, rather than when the female is soft, as is usual in marine forms;

second, during mating, the female tends to be in topmost position with the male lying beneath her, rather than the reverse, as is usual in marine forms. It is clear that the two changes are related, for on land the topmost position during mating exposes a soft-shelled female to dehydration and mechanical damage, which threaten her survival; once mating has evolved into a state in which the female is hard-shelled, there is no longer this reason why, even though on land, the female should not assume the topmost position.

In the study area at Boca Raton Inlet, mating of *G. lateralis* apparently does not occur uniformly throughout the summer months. In late June and early July of 1975, Linda H. Mantel and the second author saw no mating pairs. Yet, on dissecting some freshly collected

FIG. 21. *Gecarcinus lateralis*. Four views of a mating pair in burrow that has been partially excavated by observer. Small rock has fallen on top of female; she is hard-shelled and lies above the hard-shelled male. Note that abdomen of male no longer lies within groove on thorax. Carapace width, male, 4.2 cm; female, 4.4 cm. On east side of first dune, near north end. August 29, 1974. 7:45 p.m.

FIG. 22. *Gecarcinus lateralis*. A mating pair on strangler fig tree (*Ficus aurea*). Female is uppermost. Note third crab at base of tree. On western slope of second dune. September 10, 1975. 11:30 a.m. Electronic flash.

females of *G. lateralis*, Mantel (personal commun.) found the sperm receptacles to be dark brown in color. This color was probably due to the presence of a "sperm plug," a structure that forms within each sperm receptacle from fluid that is produced, probably by the male, during mating. The color of the sperm plugs differs from species to species. In *Cardisoma gaunhumi*, they are orange (Mantel, personal commun.). In the blue crab, *Callinectes sapidus*, the sperm plugs are pink when first formed but their color gradually fades as they are absorbed (Pyle and Cronin, 1950). In the European edible crab, *Cancer pagurus*, the sperm plugs are white (Edwards, 1966). The function of sperm plugs is unclear; a reasonable possibility is that they prevent the loss of sperms after copulation (Hartnoll, 1969).

At the same time that the sperm receptacles of *G. lateralis* were seen to be dark brown in color, they were also noted to be greatly enlarged (Mantel, personal commun.). These observations constrast with those of Klaassen (1975), who reported that in *G. lateralis* no change in size of the sperm receptacles occurs during maturation of the ovaries. Even in females that had copulated shortly before dissection and were about to ovulate when killed, the sperm receptacles were not enlarged, although they contained great quantities of spermatozoa. According to Klaassen (1975), the sperm receptacles of female *G. lateralis* that have recently laid eggs have enough active spermatozoa for another egg-laying. Thus, twice the number of spermatozoa needed to fertilize eggs released in one ovulation are transmitted from male to female during a single mating. Nonetheless, stated Klaassen, ovulation never occurs except after copulation; and copulation must have taken place during the six hours to nine days that directly precede ovulation, if the eggs are to be fertilized and are to develop normally.

The brown color of the sperm receptacles of female *G. lateralis* observed by Mantel at Sabal Point, and the likelihood that this color was due to the presence of freshly made sperm plugs, strongly suggest that mating had recently occurred. Nonetheless, mating was not occurring at the time in early summer when brown sperm receptacles were observed. On the other hand, late in summer, mating apparently is common. Thus, one can provisionally conclude that a peak of mating takes place in late spring, that this peak is followed by a lull in early summer, and that there is a second peak of mating in late summer.

Our observations of mating in *Gecarcinus lateralis* in Boca Raton did not include any of courting by this crab. But Klaassen (1975) has described courtship by *G. lateralis* of Rio Buritaca, Colombia, as observed in the laboratory: A courting male approaches a female *G. lateralis*, using his claws to generate in the substrate a sequence of pulses that tells the female about his readiness for mating ("die Kopulationsbereitschaft") and, at the same time, stimulates her. By inconspicuous movements of his walking legs on the substrate, the courting male then produces a more rapid sequence of pulses that appeases ("besänftigt") the female and suppresses aggressive reactions ("aggressive Reaktionen unterdrückt"); the male also touches her with his walking legs on the forward side of his body. Sitting sidewise before the female, he produces a sequence of appeasement pulses and a sequence of courting pulses.

The male crab then places himself in front of the female, and with his legs, touches her legs on both sides of her body. At the same time, with his claws he touches her carapace. He now raises his body. If the ovaries of the female are ripe and thus she is ready for copulation (see below), she reacts by raising her body, so that the male can swing under her. Having done so, the male continues to touch her carapace with his claws until the female has lowered her abdomen. The male now inserts his gonopods into her genital openings. As a rule, copulation continues for one and a half to two hours. Subsequent to copulation, a male frequently renews courtship, but the female reacts with threats, driving away the male by drumming with her walking legs.

According to Klaassen (1975), the intensity of courtship in *G. lateralis* is correlated with the nearness of females to ovulation (i.e., release of eggs from the ovaries) and the subsequent deposition (laying) of fertilized eggs. By the fourth or fifth day before ovulation, a female becomes restless and tries to climb out of her container into the light; she also ceases to eat. On the third day before ovulation, the female responds to the stimulation of male courtship by mating. On the second day, she immediately responds to courtship with her

FIG. 23. *Gecarcinus lateralis*. Close-up of mating pair shown in figure 22. September 10, 1975. 11:30 a.m. Electronic flash.

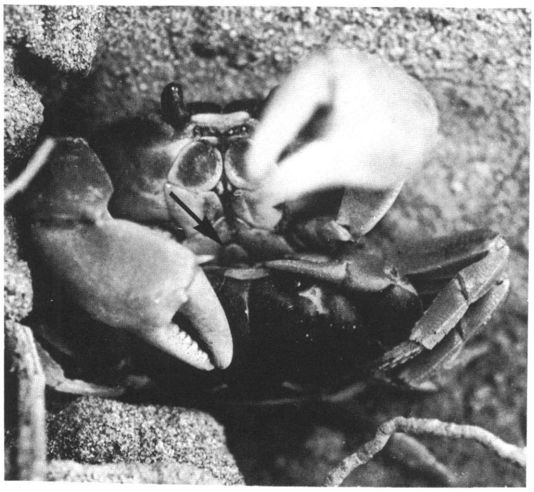

FIG. 24. *Gecarcinus lateralis.* A mating pair at burrow. Male holds abdomen (arrow) loosely against his thorax and maintains a protective position with respect to female. As observer leans over to photograph the pair, male raises claw in defense (above), then covers female with both claws (below). Male is larger than female. Along fence at southwestern boundary of tropical coastal hammock on west side of first dune. September 9, 1974. 10:35 a.m. Electronic flash.

own vigorous courtship of the male, running to him and touching him with her walking legs. On the day before ovulation, the female courts nearby males spontaneously, almost without interruption. Subsequent to ovulation, a female no longer courts males or responds to their courtship by mating. A courting female, stated Klaassen, that is not successful in copulating, or that copulates too late, does not ovulate and lay unfertilized eggs. Instead, the eggs remain within the ovaries and degenerate.

RELEASE OF SPAWN

Until recently, no information had been available regarding the route that is taken by egg-bearing females of *Gecarcinus lateralis* to the sea or their behavior once they arrive there. Then, in 1975 Klaassen published his extensive account of the reproductive behavior of *G. lateralis* in Colombia, including a section on egg-hatching in this crab. In the meantime, we made some observations on release of spawn by *G. lateralis* in Boca Raton, Florida. Our observations, which for the most part support those of Klaassen, are summarized below.

Between midnight and 2 a.m. on August 30, 1974, and again between 10 and 11 p.m. on September 6, 1974, while walking along the ocean beach between Boca Raton Inlet and the condominiums north of the Australian pines, we observed numerous females of *G. lateralis* carrying spawn toward the ocean. Other females of this species were standing in the shallow water of the breaking waves, releasing their spawn. Still others, glistening wet and bubbling froth, were moving back up the beach to the wooded area above (fig. 25, top). The latter, plus some females that we had removed from the shallow water, retained a few eggs on their pleopods (fig. 25, bottom); the main mass of eggs was gone.

On September 7, 1974, at about 1 a.m., one of us (J. von Montfrans) observed a female *G. lateralis*, laden with eggs, move down the ocean beach to the water's edge. Standing on the beach at a level where the waves washed over her, she waited until a wave had just started to recede, then rapidly vibrated her body sideways. Her mass of eggs fell onto the wet sand (fig. 26, top). The following wave,

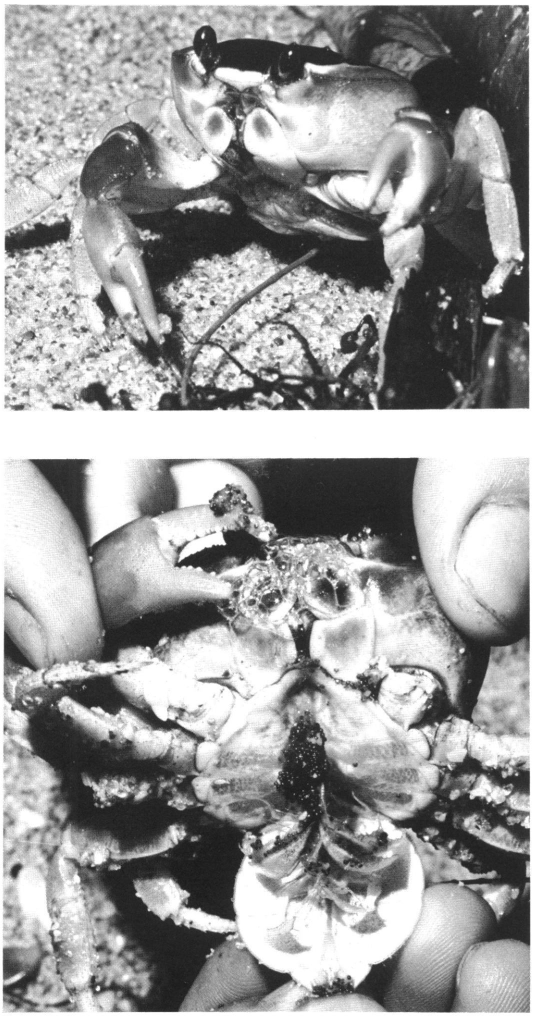

FIG. 25. *Gecarcinus lateralis*. Female (above) on way back up beach after releasing spawn rests beside large mullet washed up on beach. Crab, retaining some unhatched eggs, holds abdomen loosely against thorax. September 6, 1974. 11:00 p.m. Electronic flash. Another individual of *G. lateralis* (below), glistening wet and bubbling froth, retains some eggs after releasing almost all of her spawn in the ocean. September 6, 1974. 10:30 p.m. Electronic flash.

washing over the crab, carried away the eggs that had been lying on the sand (fig. 26, bottom). The crab remained standing until two more waves had washed over her. She vibrated her body at each wave and apparently tried to release any eggs remaining on her pleopods. Then she turned and walked up the beach to the woods.

It is apparently unusual for a female *G. lateralis* to drop her eggs on sand before they are carried away by the waves. Indeed, Klaassen (1975) considered it abnormal for a crab to do so. In the laboratory, stated Klaassen, a female crab deposits her eggs on sand only when no water is available; if forced by lack of water to deposit her eggs on sand, the female later eats them. In our laboratory, we have seen a female *G. lateralis* drop her eggs on sand; subsequently, thousands of zoeas hatched onto the sand (Bliss, 1968). The female *G. lateralis* that was observed to drop her eggs on the beach at Boca Raton after the wave had receded may have been going to release the eggs

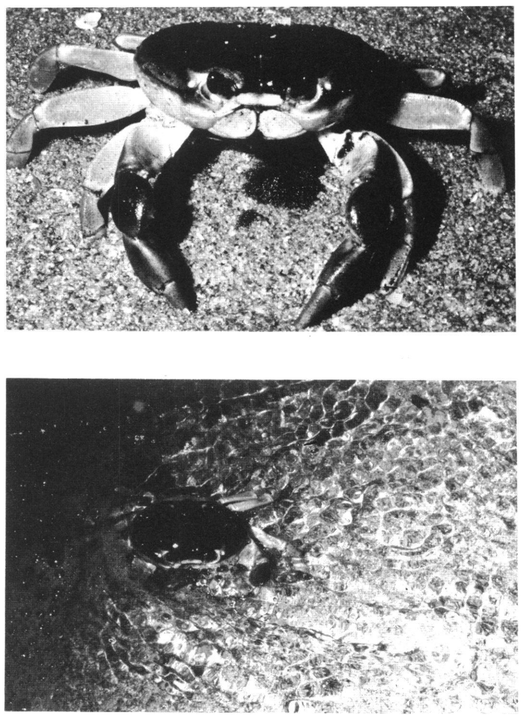

FIG. 26. *Gecarcinus lateralis*. Female (above) just after wave has washed over her. Egg mass, lying on sand, was apparently released too late to be carried away with wave. Same crab (below) as next wave washes away from her, carrying egg mass with it. September 7, 1974. 1:20 a.m. Electronic flash.

as the wave washed over her but failed to do so in time.

As Klaassen (1975) has described behavior of *Gecarcinus lateralis* that is associated with the release of spawn, the following sequence of events occurs: Emerging from their burrow in or near the copulation zone, the females first remain for up to an hour at the boundary of the vegetation or below it, in the shelter of driftwood; then the crabs move along the front margin of the ridge on the beach, running from one piece of driftwood to another and remaining for a few seconds at each piece. Finally reaching the sloping incline of the beach, the female crabs run sidewise toward the sea, stopping only when they come within 5 to 8 meters of the outwash of the waves. Henceforth, after every second or third wave, which still does not reach them, the crabs run some 30 to 50 cm. farther down the beach. As they approach closer and closer to the waves, the crabs start to travel slowly in a forward, rather than in a sidewise, direction.

Even before an incoming wave finally reaches a female crab, she stands high on her legs, propping herself up on her claws. As soon as she is drenched with water, she quickly raises and retracts her abdomen as she moves her entire body up and down; and thus she shakes her larvae out of the egg cases. She waits until washed by waves two or three more times and then runs back up the beach. In the shelter of driftwood or the first vegetation, she frees herself of the empty egg cases under her abdomen and eats them. Half an hour later, she and the other females returning from the sea have disappeared from the copulation zone.

There exists a discrepancy between our observations and those of Klaassen (1975) as to the form in which release of young occurs. Female *G. lateralis* standing in the waves on the ocean beach at Sabal Point appeared to be shaking loose their eggs. Subsequent examination of the glistening wet females revealed a few eggs still on the pleopods (fig. 25, bottom) but no trace of empty egg cases. Yet, as just indicated, Klaassen (1975) stated that the female crabs shake their larvae out of the egg cases and, after moving up the beach, pick off the empty egg cases and eat them.

Our observations of females shaking loose their eggs were made with a lantern. The light may have distracted and disturbed the crabs and caused them to alter their customary behavior. Possibly they would have shaken their larvae out of the egg cases but for the disturbance, which may have caused the crabs instead to release their entire eggs.

An ovigerous female *G. lateralis* may eat her own eggs, according to Klaassen (1975), at any time during the egg-carrying period, if the eggs are damaged or, for any reason, are not developing. Klaassen observed that eating of eggs constitutes the female's only intake of nourishment during the egg-carrying period. He noted that, by eating damaged, nondeveloping eggs, the female reduces the possibility of damage to neighboring eggs in the egg mass and also prevents fouling of her burrow. We suggest that a female *G. lateralis* may also eat her eggs if she is seriously disturbed, as was, presumably, the ovigerous female shown in figure 27. This female had been found on Route A1A (see fig. 1) and was carried to the ocean beach, where she was released—and photographed.

In the laboratory, females of *G. lateralis* remain within a closed burrow while carrying their developing eggs for the 15 to 16 days that elapse between egg-laying and hatching; during this period, the eggs, which may number from 20,000 to 100,000 according to the size of crab, change in color from dark brown through yellow-brown to lusterless gray (Klaassen, 1975). In the field, according to Klaassen, after mating in the copulation zone (zone I), the females may move a short distance inland to the edge of zone II, where they seclude themselves within a closed burrow. The egg-carrying females are next seen on the evening of the fifteenth or sixteenth day thereafter, when they emerge from their burrow and head for the sea to release their larvae.

In Klaassen's view, a sojourn of ovigerous females within a closed burrow is necessary in order to prevent desiccation of the developing eggs by sun and heat or, at least early in development, their swelling through exposure to rainwater. Our observations at Boca Raton tend indirectly to confirm Klaassen's views,

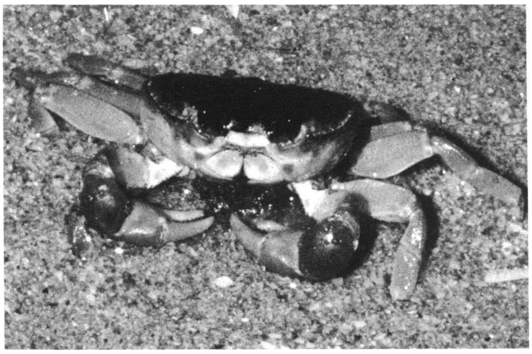

FIG. 27. *Gecarcinus lateralis*. Gravid female found on Route A1A and carried to the ocean beach. When placed on sand, she began removing her eggs and eating them, as shown here. As soon as a wave washed over her, she vibrated her body and released her eggs, which were carried away by the receding wave. September 7, 1974. 1:30 a.m. Electronic flash.

since at Sabal Point ovigerous females were seen outside of their burrow only when they were carrying well-developed eggs and when these females appeared to be moving down the beach to the ocean.

The interval during which larvae can hatch from their egg cases, stated Klaassen (1975), is narrowly defined. Most ovigerous females that emerged from a burrow in or near zone I at about 7 p.m. had released their larvae in the sea by 8:30 p.m. There appeared to be no correlation between the time of larval hatching and that of high tide, although such a correlation has been demonstrated for *Cardisoma gaunhumi* by Henning (1973, as cited by Klaassen, 1975). In captivity, female individuals of *G. lateralis* emerged from their closed burrow within a laboratory container at about 6 p.m. and by midnight had finished releasing their larvae in sea water. If fresh but not sea water was present, the females deposited their larvae in the fresh water, although within 15 minutes the larvae swelled up and died. Klaassen concluded that females of *G. lateralis* must shake off their larvae within eight to 10 hours of leaving their burrow. Klaassen also concluded that such a narrow time span precludes long spawning migrations (i.e., migrations during which the females carry their spawn to the sea for release), such as have been observed in *Cardisoma guanhumi* (Gifford, 1962; Stephens, 1965).

The numbers of ovigerous females that may take part in a spawning migration of land crabs can be impressive. In the Indo-West Pacific, *Gecarcoidea lalandii* Milne Edwards, 1837, may number in the hundreds or thousands, as the females move down to the sea to release their spawn (Johnson, 1965). In southern Florida, migrating, egg-carrying females of *Cardisoma guanhumi* numbered 83 individuals, 296 individuals, and an estimated 8000 individuals on three consecutive nights in October 1961 during a lunar spawning period (Gifford, 1962). Ovigerous females of *Gecarcinus ruricola* in the West Indies have been described as coming down from the hills to the sea in multitudes (Calman, 1911). On Clipperton Island, where the population of *Gecarcinus planatus* is very dense (Ehrhardt and Niaussat, 1970; Niaussat and Ehrhardt, 1971), seaward migration of egg-bearing females in large numbers has been reported (La Faix, 1969, as cited by Klaassen, 1975).

The numbers of *Gecarcinus lateralis* observed by Klaassen (1975) at Rio Buritaca, Colombia, during spawning migrations appear to be far fewer. He mentioned 232 females as about to release their larvae, actually doing so, or having just done so during a period of observation that extended from April to September 1970. He does not state how many such females could be seen at any given time; but, from his total figure, the number could not have been very high.

Similarly, at Boca Raton, at any given time during an evening when ovigerous females of *G. lateralis* were moving down the beach to release their spawn, there was no evidence of mass migration. With some searching, a number of egg-bearing females could be found, but the total was not impressive. On the other hand, each year in late August and early September, when the migration of ovigerous females to the sea reaches its peak, the second author daily found many dead egg-carrying females on Route A1A (see fig. 1), apparently run over by automobiles during the previous night. These females presumably had inhabited the west side of the inner dune (see figs. 1, 3, 6), had mated there, and had burrowed nearby following copulation. On emerging from their burrow, the crabs did not have to approach the highway; they could presumably have moved directly through the woods over the dunes and down onto the beach. Yet this would have involved a somewhat lengthy migration, perhaps too long for the interval allowable between emergence from the burrow and release of spawn (see above). It is quite possible that these migrating ovigerous crabs were attracted by bright lights along the highway. Frequently, egg-bearing females of *G. lateralis* have been seen by the second author clustered at lights along a street or around a condominium.

Certain observations by Klaassen (1975) have an interesting bearing on this point. He stated that egg-carrying females of *G. lateralis* orient themselves by sight and by substrate-vibrations during a spawning migration. In the early part of the migration, visual orientation seems to predominate. Regardless of cloud cover, phase and brightness of the moon, relative humidity, direction and strength of wind, amount of rainfall, and so on, females with spawn invariably run directly toward the sea. But if a source of artificial light is established, the crabs come running to the light from all directions, even away from the sea. Klaassen interprets the crab's behavior as adaptive. At night, the horizon generally is lighter over the sea than over the land; probably for this reason, during the first portion of a spawning migration, the crabs orient toward the sea.

Yet once the ovigerous females of *G. lateralis* come within 5 to 8 meters of the breaking waves, Klaassen has found, they now run toward the water, going down the slope of the beach at an angle to the source of light. He has concluded that, at this part of the spawning migration, the crabs use for orientation the sound of the surf transmitted through the substratum, as well as the brightness of the horizon over the sea. The direction and speed of their movement is, therefore, the resultant of the two vectors.

A casual observation by one of us on a night in September 1971 tends to support the conclusions of Klaassen. While sitting at a campfire on the ocean beach at Sabal Point, the second author saw close to the campfire a number of spawn-carrying females of *G. lateralis* moving past the fire down the beach toward the ocean. These crabs may well have been responding both to the sound of the surf and to the bright light of the campfire in establishing their line of direction to the sea.

EMERGENCE ON LAND

Immature individuals of *Gecarcinus lateralis* are numerous on the eastern (ocean) slope of the first (outer) dune in the study area north of Boca Raton Inlet. If one upturns a large rock (fig. 28), one may find crabs beneath it. Some of these crabs are fully grown adults; others are small juveniles (fig. 29 top); still others represent some of the earliest crab stages, with a carapace width of only a few millimeters (figs. 29, bottom). Frequently, a very small crab is found in the burrow of an adult crab. Since a medium-sized crab is never found in the burrow of an adult, it would appear that a very small juvenile may take advantage of a ready-made burrow, in preference to digging its own, until the juvenile becomes so large that it is no longer tolerated by the adult crab already occupying the burrow.

One may speculate concerning the developmental stage at which *G. lateralis* makes a landfall. The evidence suggests that *Gecarcinus* comes ashore before the first crab stage, since both Klaassen (1975) for *G. lateralis* and La Faix (1969, as cited by Klaassen, 1975) for *G. planatus* stated that the megalopa (postlarva) stage is found on land.

Yet some observations on the fiddler crab *Uca pugilator* (Bosc, 1801-1802) by Herrnkind (1968) suggest another possibility. Raising the larvae of this crab in the laboratory, Herrnkind found that the megalopas swim very actively for the first week, after which they settle on the bottom of the tank, walking with their pereiopods and keeping their abdomen folded under their body. If disturbed, the megalopas swim again briefly. Metamorphosis to the first crab stage occurs at the end of the second week.

When provided with a holding box containing sand as well as sea water, the first two crab stages of *U. pugilator* do not migrate out of the

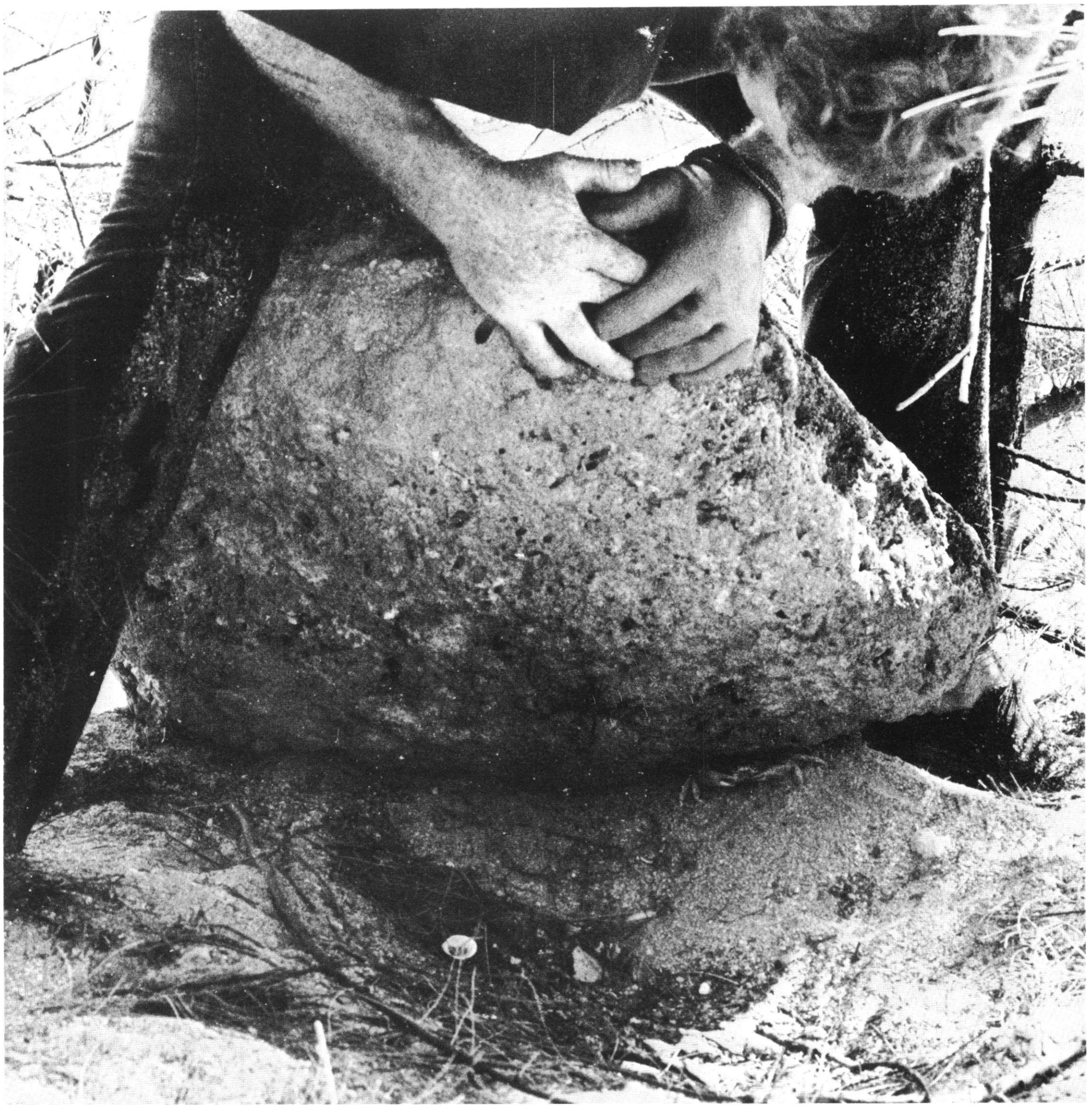

FIG. 28. Large rock on upper east side of first dune, under which very young individuals of *G. lateralis* were found (see fig. 29); one fairly large crab is visible. Amphipods, pill bugs, ants, earwigs, roaches, and centipedes also were found here. Sand and gravel under rock were moist, as was the considerable amount of decaying vegetation, especially needles of Australian pine. Smallest juveniles were hiding under decaying vegetation and in small depressions in sand that they apparently had excavated; they were also in crevices and holes visible on underside of rock. September 8, 1974. 11:15 a.m.

water onto the sand. Isolated third through fifth crab stages do migrate onto the artificial shore, where they dig burrows in the sand similar to those made by adult fiddler crabs.

These observations on *U. pugilator* suggest the alternative possibility that in a land crab such as *Gecarcinus lateralis* metamorphosis from megalopa to young crab may occur in the ocean and that the first few crab stages may remain there, after which the migration to land may take place. It has been pointed out, nonetheless, by Fenner A. Chace, Jr. (personal commun.) that, although the megalopa of *U. pugilator* may be reluctant to leave the sea, this does not necessarily imply that the megalopa of *G. lateralis* is equally so, since the latter has presumably evolved further along the route toward independence of the sea.

The discovery of young *G. lateralis* on the ocean slope of the outer dune is strong evidence that this species of land crab takes a direct route from the ocean up the beaches to protected wooded areas, where they remain. To attain these beaches while a megalopa or in an early crab stage would require some favorable local currents during the larval and postlarval periods. The importance of such currents in repopulating an area with fauna derived from local parental stock has been demonstrated for certain Bermudan invertebrates by Boden (1952) and Boden and Kampa (1953). Also for the island of Barbados, Emery (1972) attributed to a stable eddy system in the downstream wake of the island a restocking of the littoral animal population with offspring of parents that lived on the shores and in the shallows of Barbados. Although no oceanic island exists in the vicinity of Boca Raton, shoreward-directed eddies may play an important role in retention of the local fauna and in recruitment to it from the south.

RELATIVE GROWTH

At Sabal Point, Boca Raton, the tract of land on which *Gecarcinus lateralis* occurs is, in a sense, geographically isolated. The area is hemmed in to the east by the ocean, to the south and southwest by the Inlet, to the west by Route A1A, and to the north by condominiums (see fig. 1). On this 17-acre tract of wooded land lives a dense population of *G. lateralis* that includes all stages of growth from the earliest crab stages to very large, mature individuals. The existence of this sizable population of land crabs, confined within geographical limits that are so precisely defined, has led us to investigate some parameters of relative growth in these crabs. The results of this study are presented here.

The smallest crabs that were collected under rocks on the first dune near Boca Raton Inlet measured 2.65, 3.05, and 3.45 mm., respectively, in carapace width (measured at the widest part). It is to be noted that the difference between these measurements is 0.40 mm. Furthermore, a crab of 6.30 mm. in carapace width molted in the laboratory after arrival, and the increment in carapace width was 0.40 mm. This crab had regenerated all walking legs prior to ecdysis. During experiments conducted in the laboratory, larger individuals of *G. lateralis* that have regenerated many limbs often have displayed an increment in carapace width after ecdysis that is smaller than usual for the size of crab. For the earliest crab stages, nonetheless, it seemed possible that the increment in carapace width after ecdysis might be about 0.40 mm.

It was decided to project for every subsequent hypothetical ecdysis, regardless of the size of crab, an increment in carapace width of 0.40 mm. This projection would certainly be invalid for the larger crabs, which in the laboratory usually undergo increases in size at ecdysis that are much greater than 0.40 mm. It was thought, nonetheless, that the data might fall into groups and that the size of the interval between groups might make possible the calculation of a valid increment(s) in carapace width at ecdysis.

A regression line was drawn that represented an increment of 0.40 mm. in carapace width for every hypothetical ecdysis. On this line, actual data for carapace width of male and female *G. lateralis* collected at Sabal Point in Boca Raton were plotted. Small clusters of data existed at approximately 0.08, 0.32, and 0.70 mm., suggesting increments of 0.24 mm. and 0.38 mm. for these tiny crabs. Otherwise, the data were well dispersed along the regression line. From these data, therefore, it was not possible to conclude what the actual increment(s) in carapace width at ecdysis might be

FIG. 29. *Gecarcinus lateralis* (above). An immature individual from beneath an upturned rock. On east side of first dune. June 14, 1975. 11 a.m. Electronic flash. Tiny individuals of *G. lateralis* (below) found under rock shown in figure 28. At this stage, crabs are brown with light orange legs, and their carapace may be slightly longer than wide. Electronic flash.

for any crabs other than possibly the smallest.

The regression of a skeletal dimension on ecdysis number (or, stated more accurately for the particular case of *G. lateralis*, on increment number, the increment being designated here as 0.40 mm.) can be used to assess certain parameters of relative growth. For *G. lateralis*, data for carapace length (measured along the midline) corresponding to those for carapace width were subjected to linear regression analysis by the least squares method, as were data for abdominal width and length (see fig. 31 for place of measurement). For each of these parameters, the coefficients a and b in the equation $y = a + bx$ were determined (table 1). Regression lines were drawn separately for males and females (fig. 30).

In males of *G. lateralis*, the rate of increase in carapace length, relative to rate of increase in carapace width, declines significantly ($P < 0.001$)[1] after the seventieth increment (fig. 30, ♂ CLb); the same is true of abdominal length ($P < 0.001$) after the fifty-first increment (fig. 30, ♂ ALb). Abdominal width of male *G. lateralis* increases at a constant rate throughout (fig. 30, ♂ AW).

In females, carapace length (fig. 30, ♀ CL) and abdominal length (fig. 30, ♀ AL) increase at a constant rate relative to the rate of increase in carapace width. For abdominal width, the situation is quite different. Onset of maturity is preceded by a brief period of rapid growth (fig. 30, ♀ AWb) that is significantly higher ($P < 0.001$) than during the initial phase of abdominal growth (fig. 30, ♀ AWa). In this brief period, the abdomen becomes rounded in preparation for the carrying of eggs. After the onset of maturity, the rate of increase in abdominal width (fig. 30, ♀ AWc) is different, but not significantly ($P = 0.07$), from that during the initial phase of abdominal growth (note overlapping 99 percent confidence intervals for b in parts a and c under female abdominal width, table 1).

For both sexes, the rate of increase in carapace width (fig. 30, CW) is greater than in carapace length; as a result, the carapace of the crab grows ever wider relative to its length. Youngest stages of both sexes are slightly longer than wide (see fig. 29, bottom). In its

[1]Probability (P) estimated from Student's t, as calculated for the difference between two regression coefficients, according to the method described in Simpson, Roe, and Lewontin (1960), pp. 229, 230.

TABLE 1

Relationship of Carapace Width of *Gecarcinus lateralis* to Carapace Length, Abdominal Width, and Abdominal Length During Growth

	Number in Sample	Calculated Equation for Regression Line (y = a + bx)[a]	99% Confidence Interval for b[b]
Male			
Carapace width			
x = 1-130	65	y = 2.26 + 0.400x	—
Carapace length			
a) x = 1-70	35	y = 2.66 + 0.317x	0.300 – 0.335
b) x = 71-130	30	y = 5.05 + 0.287x	0.273 – 0.301
Abdominal width			
x = 1-130	58	y = 0.770 + 0.107x	0.104 – 0.109
Abdominal length			
a) x = 1-51	28	y = 1.17 + 0.214x	0.203 – 0.225
b) x = 52-130	30	y = 3.59 + 0.171x	0.163 – 0.179
Female			
x = 1-30	36	y = 2.26 + 0.400x	—
Carapace length			
x = 1-130	35	y = 2.70 + 0.317x	0.309 – 0.325
Abdominal width			
a) x = 1-57	12	y = 0.299 + 0.151x	0.133 – 0.169
b) x = 58-76	13	y = −8.84 + 0.320x	0.225 – 0.417
c) x = 77-130	9	y = 4.55 + 0.181x	0.129 – 0.231
Abdominal length			
x = 1-130	33	y = 0.984 + 0.223x	0.215 – 0.232

[a]y = dimension in mm.; x = increment number (see text and fig. 30).
[b]According to method described by Simpson, Roe, and Lewontin (1960), pp. 224-229.

terminal phase of growth, the carapace length (fig. 30, CL) of males increases at a significantly lower rate ($P < 0.001$) than does that of females; in the initial phase, the rate of increase in carapace length of both males and females is the same.

For abdominal length (fig. 30, AL), the rate of increase in females is not significantly different ($P = 0.13$) from that in males prior to the fifty-first increment but is significantly higher ($P < 0.001$) subsequently. In abdominal width (fig. 30, AW), the regression lines for the two sexes are very different, with that of males maintaining a constant slope that is at all times significantly lower ($P < 0.001$) than that of females.

One can visualize changes in abdominal size and shape for male and female *G. lateralis* by reference to figure 31. The sketches in these figures are based upon tracings made on Scotch Magic Tape that was applied to the ventral surface of the crabs. In size, the abdomen of very small females is comparable with that of very small males; but in shape there is already a difference. The terminal half of the abdomen is somewhat broad in very young females, whereas in males this area is attenuated. During subsequent growth, small individual differences in size and shape of the abdomen of male *G. lateralis* are apparent, but the relative dimensions of abdomen and thorax remain fairly constant. In females, the brief period of rapid growth in width of abdomen just before the onset of maturity results in very different relative dimensions of abdomen and thorax in mature crabs.

On specimens of *G. lateralis*, measurements of the abdomen, as of the carapace, were made by means of vernier calipers. When measurements of abdominal width and length are made from the tracings shown in figure 31, the values for abdominal length (but not for abdominal width) are somewhat higher. The discrepancy is due to the increasing convexity of the abdomi-

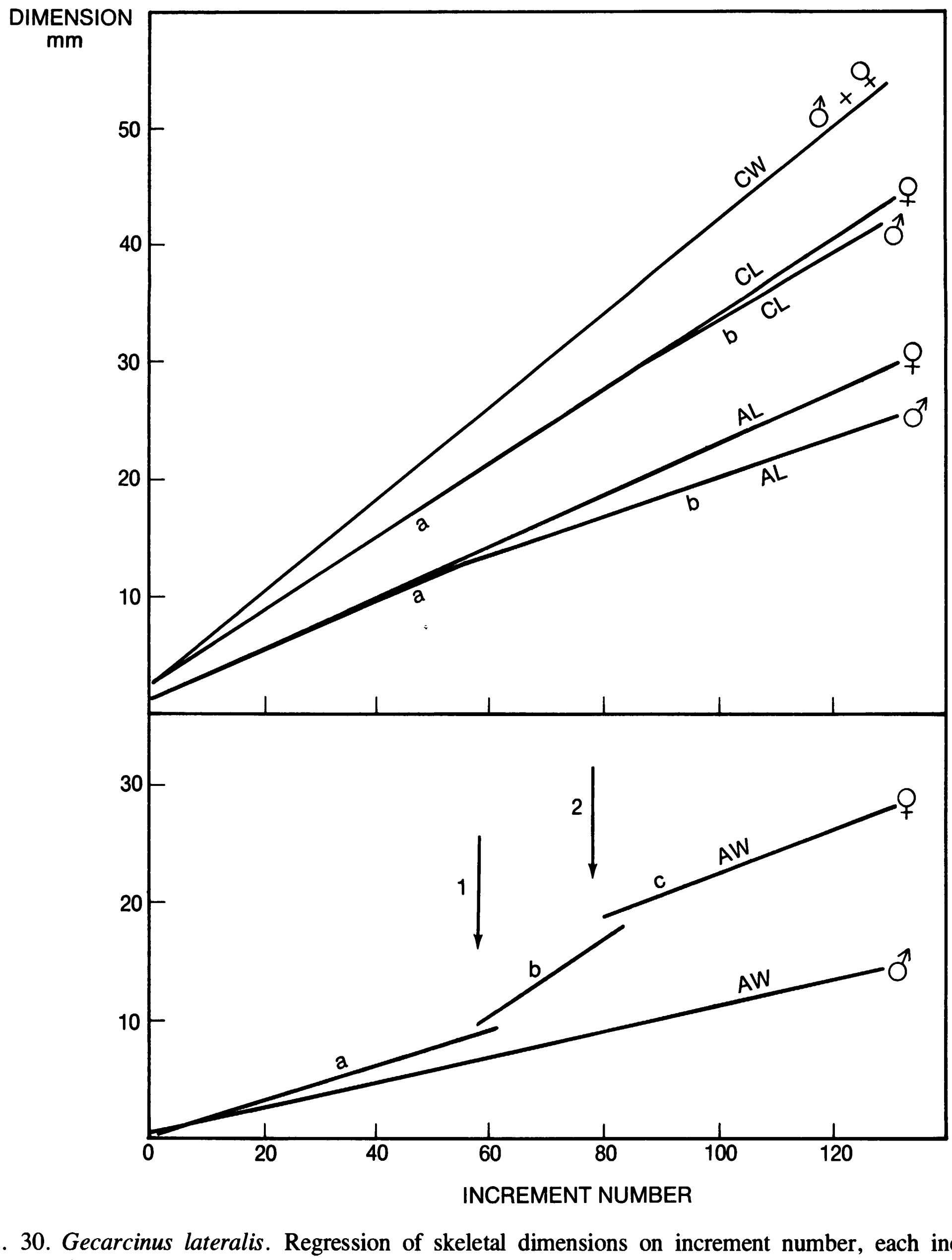

FIG. 30. *Gecarcinus lateralis*. Regression of skeletal dimensions on increment number, each increment in carapace width being 0.4 mm. (see text for explanation). CW, carapace width; CL, carapace length; AL, abdominal length; AW, abdominal width. a, b, c, subsections for which regression equation and other information appear in table 1. Arrows: 1, approximate start of rapid increase in abdominal width in females; 2, approximate onset of maturity in females (see also fig. 31).

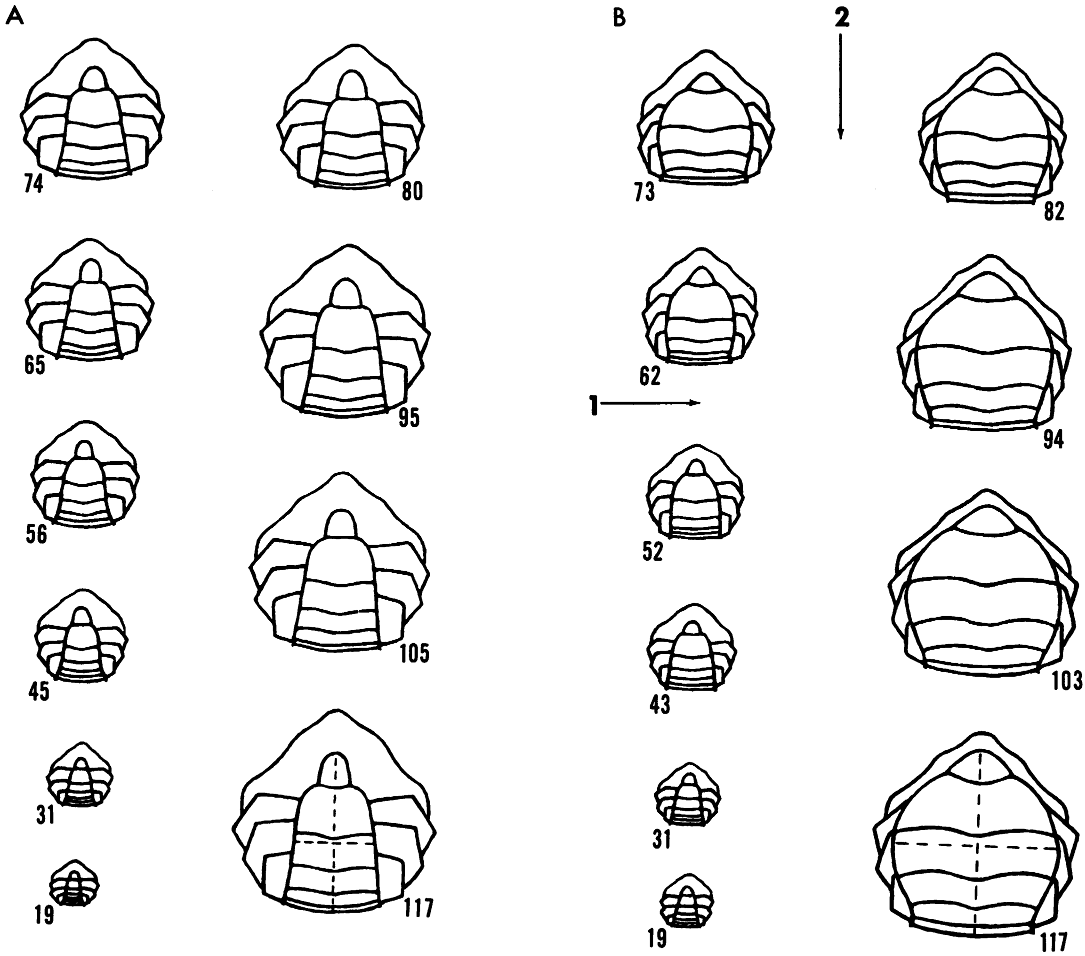

FIG. 31. *Gecarcinus lateralis*. Size and form of the abdomen at various stages of growth. Four-fifths natural size. A. Male. B. Female. Arabic numerals designate increment number (see text and fig. 30). Dotted lines on drawing for increment number 117 designate abdominal measurements used in calculation of regression coefficients (see table 1 and fig. 30). Arrows: 1, start of rapid increase in abdominal width in females; 2, onset of maturity in females (at a carapace width of about 33 mm.).

nal segments close to the posterior margin of the body. The mean ratio of abdominal length as measured by calipers from the specimens to abdominal length as measured by calipers from the tracings is 0.89. This indicates that in figure 31 there is an exaggeration of about 12 percent in length as compared with width.

Data on relative growth in *G. lateralis* that are presented here add to those of numerous early studies (see Teissier, 1960; Kurata, 1962) and of studies more recently reported by Herreid (1967) on the gecarcinid *Cardisoma guanhumi*, Barnes (1968) on 13 species of ocypodid crabs, Hartnoll (1972) on the burrowing crab *Corystes cassivelaunus* (Pennant, 1777), and Hartnoll (1974) on a variety of crabs. In many of these studies, the investigators subjected their data to linear regression analysis.

Recently, Mauchline (1976) has questioned the validity of fitting linear regression lines to data for bodily dimensions of crustaceans, since this procedure assumes that any given growth factor (i.e., percent increase in a bodily dimension at successive ecdyses) is constant. Yet according to Mauchline, Kurata (1962) and numerous other investigators have shown that in decapod and certain other crustaceans growth factors decrease at successive ecdyses, the decrease being logarithmic against bodily dimensions or ecdysis number.

For the relationship between pre-ecdysial and post-ecdysial carapace width in the crab *Pachygrapsus crassipes* Randall, 1839 (data from Hiatt, 1948), Mauchline (1976) found the logarithmic decrease in growth factors to yield two hyperbolae, rather than the three straight lines that constitute the so-called Hiatt growth diagram (see Hiatt, 1948, fig. 9). The three straight lines, according to Hiatt, describe relationships in young crabs, adult males, and adult females; the two hyperbolae, according to Mauchline, depict relationships during the entire life span of males and females. Similar hyperbolae, says Mauchline, can be fitted to data from other crustaceans for which Kurata (1962) has prepared Hiatt growth diagrams.

Fitting a hyperbola to pre-ecdysial and post-ecdysial data for a bodily dimension of a decapod crustacean enables one to obtain an estimate of maximal size—from the asymptote of the hyperbola. Thus, for a given population one can determine limits to growth for individuals within the population.

Mauchline (1976) pointed out that to test the goodness of fit of a hyperbola to experimentally determined pre-ecdysial and post-ecdysial data is cumbersome. Yet, for the relationship of decreasing growth factor derived from such data (or increasing intermolt period) to a bodily dimension or ecdysis number, the log-linear regression equation and its correlation coefficient can readily be determined. The constant describing the slope of the regression line plotted from this equation varies according to species, sex, experimental treatment, and other factors.

The mathematical and statistical treatment of experimental data that is outlined by Mauchline (1976) may provide for future workers a convenient tool for studying growth in decapod crustaceans maintained under various experimental conditions or at different stages of their life cycle. Mauchline's method also may permit one to compare growth in geographically separated populations of a given species.

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