

REPRODUCTIVE BIOLOGY OF THE FEMALE DEEP-SEA RED CRAB, *GERYON QUINQUEDENS*, FROM THE CHESAPEAKE BIGHT^{1,2}

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ABSTRACT

Collections of the deep-sea red crab, *Geryon quinquedens*, were made at depths from 270 to 1,300 m in the vicinity of Norfolk Canyon in the northwest Atlantic Ocean in November 1974, September 1975, and January 1976. The gross morphology and histology of ovary development are described. The size range in which relative growth of the abdomen changes is associated with maturation of the vulvae, copulation and insemination, gonad development, and egg extrusion. Females become sexually mature within the intermolt size range 65-75 mm carapace length (80-91 mm carapace width). Most intermolt females ≥ 76 mm carapace length show signs of copulation and insemination, and their ovaries are in intermediate to advanced stages of development. Few females < 75 mm are ovigerous.

Historically the red crab, *Geryon quinquedens* Smith, has been seldom utilized commercially (Schroeder 1959; McRae 1961). Explorations have established that red crabs can readily be captured by pot or trap fishing in many regions along the eastern United States. The commercial potential of this crab has spurred investigations of the general biology and distribution (Le Loeuff et al. 1974; Haefner and Musick 1974; Wigley et al. 1975; Gray⁴; Dias and Machado⁵; Ganz and Herrmann⁶) as well as technological and economic aspects of harvesting and processing (Meade and Gray 1973; Holmsen and McAllister 1974).

The present study was prompted by recognition that biological data on sexual maturity are required for proper management of red crab stocks. This paper presents data on collections from Chesapeake Bight and deals with various aspects of reproductive biology of the female crab: ovary development, size composition of catch, size of

ovigerous individuals, abdomen width-carapace length relationship, development of vulvae, and evidence of copulation and insemination.

METHODS

Red crabs were collected at depths from 270 to 1,300 m in Norfolk Canyon and vicinity (lat. 36°32'-37°10'N; long. 74°10'-74°46'W) in November 1974 (RV *James M. Gilliss* 74-04), September 1975 (RV *James M. Gilliss* 75-08), and January 1976 (RV *James M. Gilliss* 76-01). Based on the recommendations of Gray (see footnote 4), all female crabs were measured for short carapace length (CL, distance from the diastema between the rostral teeth to the posterior edge of the carapace, along the midline); width of the fifth abdominal segment was recorded for 190 crabs. Carapace length may be converted into carapace width (CW) by using the equation $CW = 11.04 + 1.06CL$, $r = 0.98$, based on measurements of 268 female crabs.

Pleopods and vulvae were examined to determine if mating and egg extrusion had occurred. Eggs or egg remnants or their absence on pleopods, variations in the size, shape and physical condition of vulvae, and the relative size of seminal receptacles were noted. Selected samples of the spermathecal fluid were withdrawn directly from incisions in the receptacle and examined microscopically for presence of sperm or spermatozoa.

Ovaries were initially classified to relative size following the scheme used for the rock crab, *Cancer irroratus* (Haefner 1976). The scheme for

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⁴Gray, G. W., Jr. 1969. Investigation of the basic life history of the red crab (*Geryon quinquedens*). R.I. Div. Conserv. P.L. 88-309, Proj. 3-46-R Completion Rep., 36 p.

⁵Dias, C. A., and J. S. Machado. 1974. Preliminary report on the distribution and relative abundance of deep-sea red crab (*Geryon* sp.) off Angola. Sci. Pap. No. 26, 12 p. In Scientific papers presented to the second session of the International Commission for the Southeast Atlantic Fisheries (Madrid, December 1973). Publ. Mimeogr. M. E. Bioceanol. Pescas, Angola 12, 75 p.

⁶Ganz, A. R., and J. F. Herrmann. 1975. Investigations into the southern New England red crab fishery. R.I. Dep. Nat. Resour. Div. Fish. Wildl. Mar. Fish. Sect., 78 p.

red crabs was quantified by measuring ovary volume and deriving gonad indices (Giese and Pearse 1974) for the various stages. Certain ovarian samples were selected on the basis of relative size and color and treated in the following manner. Displacement of ovaries was measured by placing the entire, excised ovary in volumetrically graduated tubes containing a known quantity of seawater. Ovary volume (V_o in milliliters) was used to compute a gonad index: $G_i = (\text{Ovary weight})/(\text{Total body weight}) \times 100$, where weights in grams were calculated as follows. Ovary weight = $1.025 V_o$, assuming ovarian specific gravity equals that of seawater. Total body weight was derived from the following relationship based on measurements of 142 females: $\log \text{ body weight} = -3.134 + 2.8833 \log \text{ length}$, $r = 0.968$.

Portions of the ovaries were then preserved in Davidson's fixative for histological processing and in Gilson's fluid (Bagenal and Braum 1971) for measurement of ova size.

Histological sections were stained in haematoxylin and eosin and mounted in Permount.⁷ Descriptions of developmental stages were made from the resultant slides.

Samples in Gilson's fluid were shaken to release ova which were then observed with a dissecting

microscope. The diameters of 20 spherical ova from each sample were measured with a calibrated ocular micrometer. Misshapen ova were not considered. Similarly, 20 extruded eggs from 11 ovigerous crabs were removed and measured (length and width). A mean diameter was computed for each crab.

RESULTS AND DISCUSSION

The Ovary

The following account of the gross morphology and histology of the red crab ovary is based on examination of the gross anatomy of 255 crabs and on histological preparations from 34 crabs.

The ovary is an H-shaped organ located dorsally just beneath the carapace (Figure 1). Two horns extend anterolaterally from either side of the gastric mill and lie dorsal to the hepatopancreas. At the posterolateral borders of the gastric mill, near the origin of the posterior mandibular muscle bundles, the anterior horns are joined by a commissure. Two posterior horns, which lie ventral to the heart, extend posteriorly on either side of the intestine. The seminal receptacles arise from the midlateral border of the posterior horns and open externally through gonopores (vulvae) on thoracic sternite VI, immediately adjacent to sternite V.

⁷Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

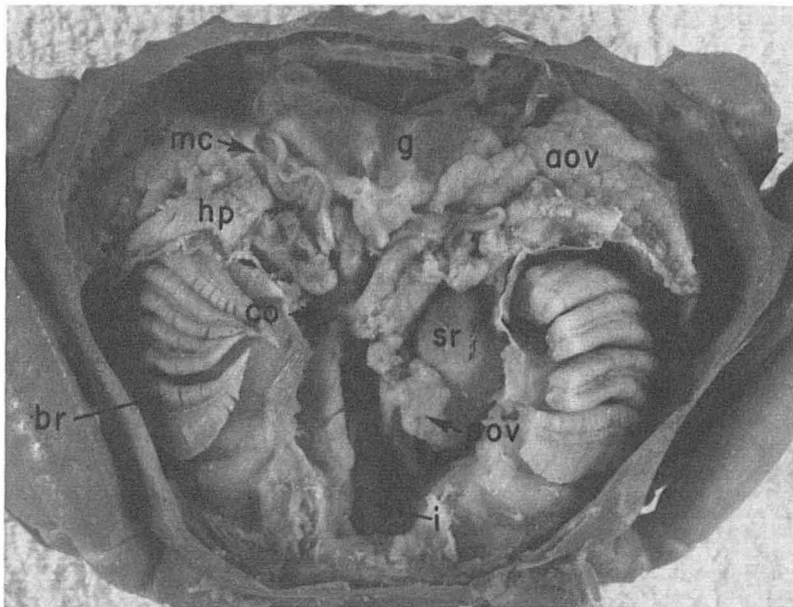


FIGURE 1.—Dorsal dissection of female *Geryon quinquedens*. Heart and medial portion of branchial chamber removed. Anterior (aov), posterior (pov) and commissure (cov) of ovary, gastric mill (g), gill (br), intestine (i), hepatopancreas (hp), seminal receptacle (sr), midgut caeca (mc).

Very Early Development

In very early development (Table 1), the ovary is small (<0.2 ml in volume; horn width 0.5 mm) and colorless. A central lumen is not apparent from gross morphological examination, although the precursor of one is indicated in Figure 2. Lobation is not obvious in this stage. The bulk of the organ consists of fibrous connective tissue, apparently stratified, and blood sinuses (Figure 2A). The outer connective tissue wall of the ovary is not readily distinguishable from the inner connective tissue. Various cell types are present. Most cells contain one oval nucleus (7.2 μm long) while other larger, less numerous cells have a large round nucleus (7.2 μm in diameter). Ova diameters are small (40-172 μm) and confined to germinative areas or strands. In some instances, it is difficult to free the ova from the surrounding tissue even after treatment in Gilson's fluid. The germinal zone consists of columnar cells with (12 μm) elongate nuclei (Figure 2B).

Early Development

White, ivory, light gray, or light yellow ovaries which are small (0.2-2.0 ml volume, 2-6 mm horn width) may exhibit histological development in advance of the previous stage. Most of the organ is filled with ova in various early stages of development (Figure 3A). Connective tissue is still prevalent around the margin, penetrating the ovary in numerous locations to form small lobes which are not readily visible from a gross morphological aspect.

The germinal zone is well defined and branches

throughout the ovary. Cells in an early stage of oogenesis, recognizable by vacuolate nuclei (Figure 3B), are small (14-53 μm) compared with the more advanced ova (74-278 μm) characterized by more compact nuclei and the presence of cytoplasmic yolk granules (Figure 3C, D). They are surrounded by a single layer of follicular cells (Figure 3D) which are spindle shaped with an elongate nucleus (72 μm).

Intermediate Stage

As the ovary progresses to the intermediate stage of development, accumulating yolk, it gradually occupies more space ($G_i = 1.4-2.7$) in the visceral cavity and changes color (Table 1). The ovarian architecture is little changed from that of earlier stages; connective tissue is confined to the margin of the ovary and to the interstices between the now obvious lobes. Germinative zones are present. Ova are larger (112-537 μm) than those in earlier stages.

Mature Stages

A fully mature ovary nearly obscures the hepatopancreas in dorsal view. Only a small portion of the hepatopancreas and the slightly coiled midgut caecae are visible between the ovary and branchial chamber (Figure 1). The high gonad indices (>2.7) attest to the large volume (8-32 ml) of the organ at these stages of development. The color remains variable but is generally darker than that of earlier stages as reddish and brownish hues become evident (Table 1).

The predominant histological feature in a

TABLE 1.—Descriptive stages of *Geryon quinquedens* ovary: color variation, horn size, volume, gonad index, and ova diameter.

Stage of ovary development	Color of ovary	Horn width range (mm)			Ovary volume (ml)			Gonad index			Ova diameter (μm)		
		n	Ant.	Post.	n	\bar{X}	Range	n	\bar{X}	Range	n	\bar{X}	Range
Very early	Colorless, white, ivory	7	0.5-2.2	0.5-1.3	8	<0.2	0.1-0.2	8	0.29	0.09-0.88	3	102	49-172
Early	White, ivory, light gray, light yellow	12	2-6	2-6	15	1.1	0.2-2	15	0.75	0.19-1.75	10	168	74-278
Intermediate	Ivory, white, light yellow, yellow, yellowish orange, light brownish orange	7	8-15	6-10	12	5.2	4.5-7	12	2.05	1.45-2.73	10	289	112-537
Advanced	Yellow, yellowish orange, brownish orange, reddish brown, brownish purple	4	16-23	6-12	6	13.4	8-12	6	4.24	2.74-6.02	6	508	298-666
Mature	Yellowish orange, orange, brownish orange, brownish purple	12	20-32	10-18	10	28.9	21-32	11	8.22	6.00-11.85	9	611	484-788
Redeveloping	Ivory, yellowish orange, light brownish orange, reddish brown, reddish orange, brownish purple	6	8-20	5-7	14	9.0	2.5-21	14	2.67	1.04-7.25	16	347	148-671

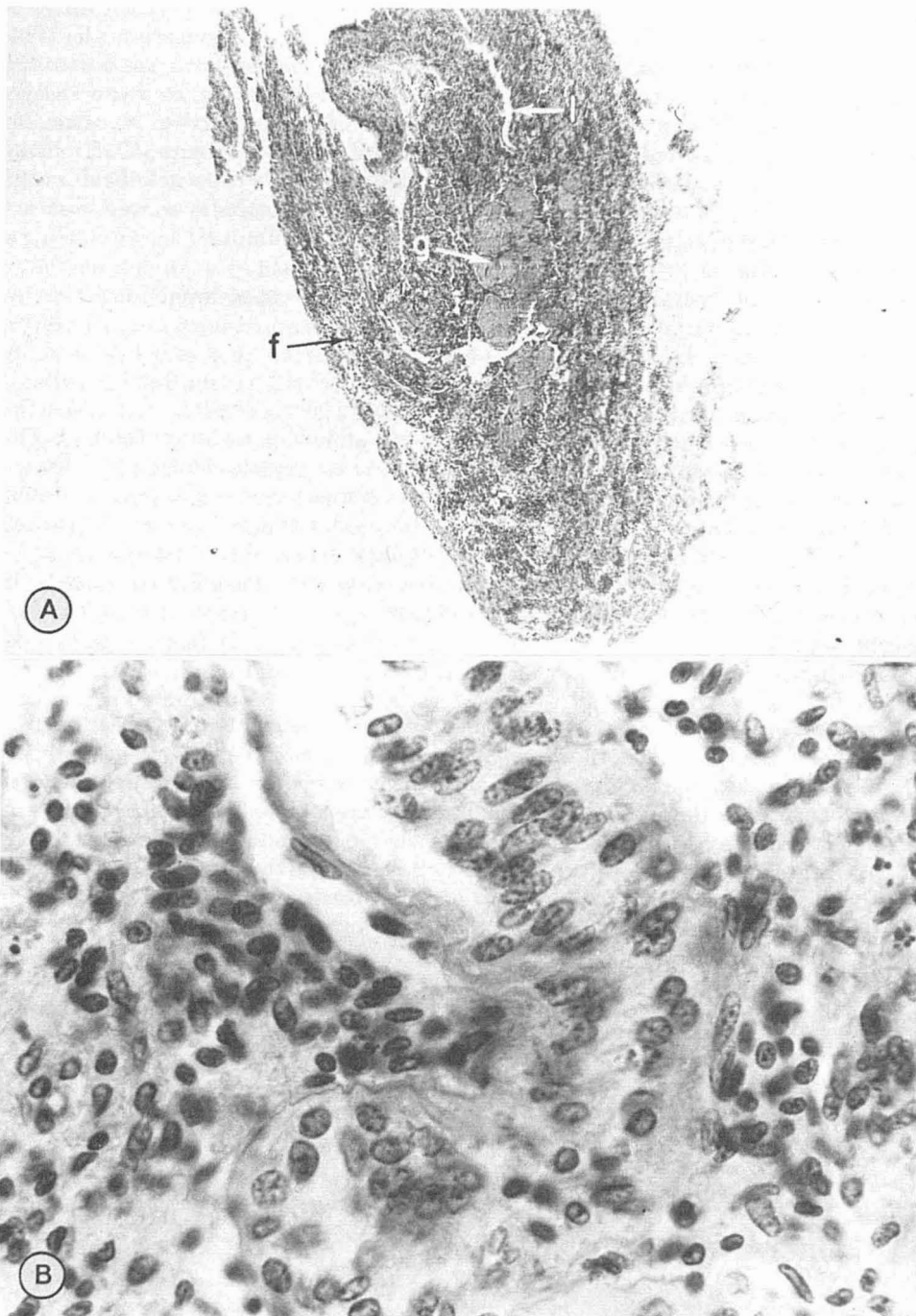
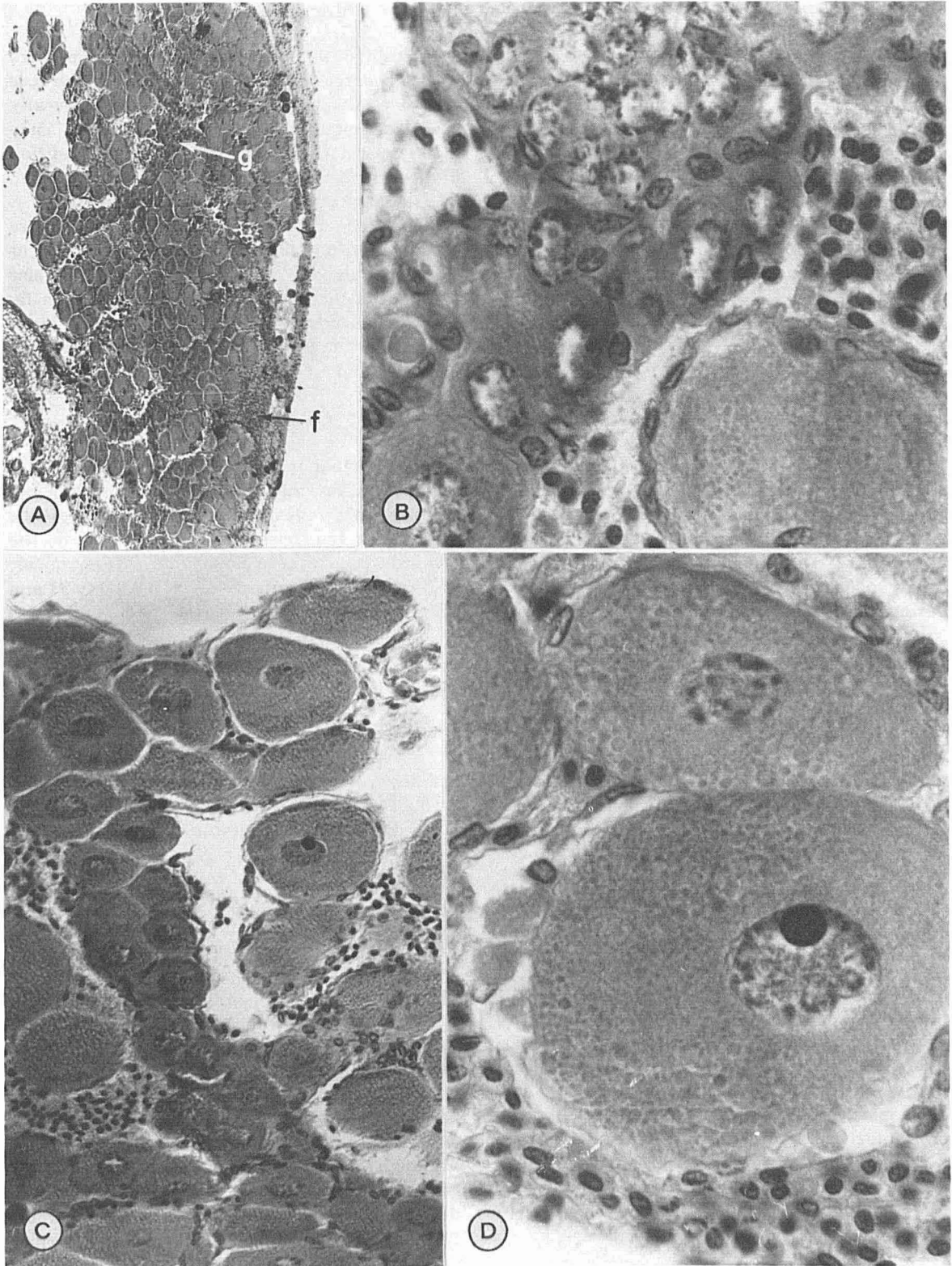


FIGURE 2.—Ovary of *Geryon quinquedens* in very early development stage. A. 25 \times . Fibrous connective tissue (f) predominates. Germinal strand (g) and lumen (l) precursors are present. B. Enlargement (400 \times) of germinal strand region showing columnar cells.

FIGURE 3.—Ovary of *Geryon quinquedens* in early development stage. A. 25 \times . Ova in various stages of development are shown radiating from germinal zone (g). Fibrous connective tissue (f) evident. B. High magnification (400 \times) emphasizing vacuolar nucleate cells in early stages of oogenesis. C. Follicular development (125 \times) in early stage ovary. Yolk granules evident in larger ova. D. High magnification (400 \times) showing yolk granular consistency of cytoplasm in developing ova.



mature ovary, usually brownish orange to brownish purple, is the concentration of large ova (484-788 μm) containing large yolk granules which make sectioning difficult. The size range of these ova overlaps the mean diameter range of extruded eggs (638-817 μm).

The ovary is subdivided into lobes and possesses a central hollow shaft or lumen as described for *Callinectes sapidus* by Cronin (1942) and for *Portunus sanguinolentus* by Ryan (1967). An irregular matrix of compact germinal tissue, surrounded by less compact zones of large ova, borders the lumen.

Redeveloping Ovaries

The presence of developing ova in germinal zones of ovaries suggests that oogenesis continues after ovulation. Such redevelopment is indicated by the range of ovarian developmental stages observed in crabs known to have ovulated. Ovaries from seven ovigerous crabs with egg remnants resembled the early to advanced stages described above. Mean values and ranges of horn width, ovary volume, and gonad index reflect the wide variety of stages of redevelopment (Table 1).

In ovaries from nine ovigerous crabs and seven females with egg remnants on the pleopods, germinative zones were clearly evident (Figure 4A) but the ovary was less compact than that of the mature or ripe ovary as the interstices were filled with connective tissue (Figure 4B). The ova were more variable in size within a given developmental stage. Relatively large ova (388 μm) can be found in an early stage ovary while unusually small ova (168 μm) are numerous in an advanced ovary.

Incidence of Ovarian Development

A relationship exists between size of female and ovarian development (Figure 5). Eighty-eight percent of all crabs ≤ 75 mm CL (91 mm CW) possessed ovaries in early stages of development; 90% of the females > 75 mm were in intermediate to advanced stages of ovarian development. Early developmental stages can occur in large crabs, particularly after recent ovulation. This is evident from the distribution of ovigerous crabs and those with egg remnants on the pleopods. Such ovaries, in redevelopment stages, can recede to early developmental stages.

Size at Sexual Maturity

Hartnoll (1969) regarded a crab as mature "when it enters the intermolt during which it is first able to copulate successfully." It is generally accepted that in brachyurans maturity in some females cannot be determined from the condition of the gonads because development and ovulation often occur a considerable time after mating.

In the case of red crabs, several criteria were examined in an effort to define the size (age) at which females mature. These included the size distribution of ovigerous and nonovigerous females, the incidence of physical indicators of copulation, and changes in the features of the vulvae and abdomen.

Ovigerous Females

The size-frequency distribution of 755 females captured in November 1974, September 1975, and January 1976 reveals the incidence of ovigerous individuals and those with egg remnants on the pleopods (Figure 6). In November and September, 27.3% and 15.7%, respectively, of females ≥ 71 mm CL (97 mm CW) were ovigerous; 9.0% of females ≥ 71 mm in September carried egg remnants. In January, 25.5% of females ≥ 71 mm CL were berried; two of these showed some evidence of egg hatching. Most (94%) of the ovigerous individuals and those with egg remnants were between 71 and 113 mm CL (97-131 mm CW); only four crabs were smaller.

Physical Evidence of Copulation

In numerous species of crabs, recent copulation by the female is indicated by the presence of a hardened mass of spermatozoa and associated secretions protruding from the vulvae (Hartnoll 1969). This so-called sperm plug does not occur in *Geryon quinquedens*.

The exoskeletons of red crabs that have not recently molted are blackened or discolored in abraded or damaged areas and are usually infested with lepadid barnacles *Trilasmis* sp. The association of lepadids and discoloration serves as an indicator of a time lapse since the last molt, although the exact length of time cannot presently be determined. It was reasoned that abrasion and damage of vulval margins due to copulation would result in similar discoloration. This was verified

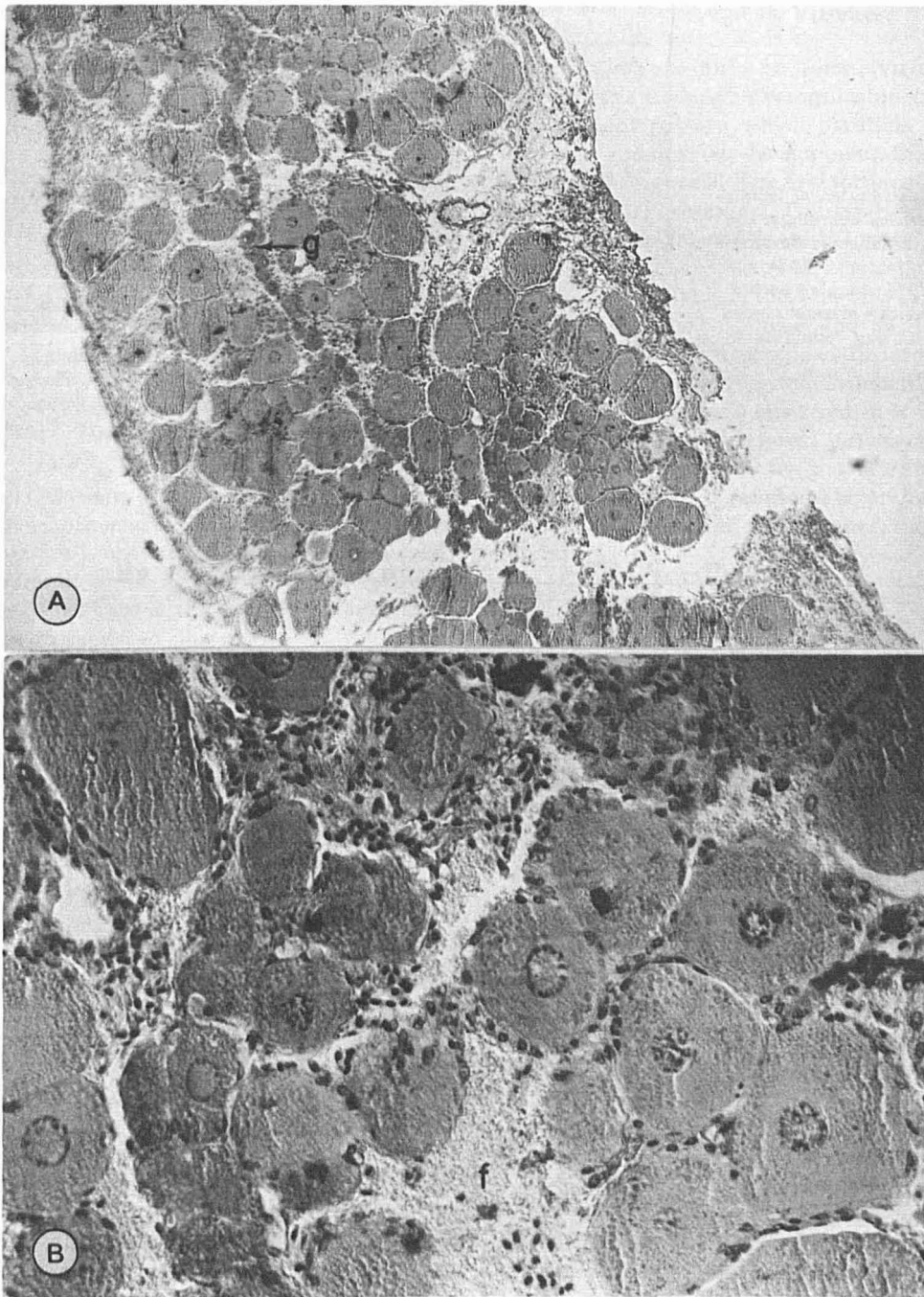


FIGURE 4.—Redeveloping ovary of *Geryon quinquedens* from ovigerous crab. A. 25 \times . Germinative zone (g) and developing ova are evident. B. Higher magnification (125 \times) showing prevalence of fibrous connective tissue (f) among various sizes of developing ova.

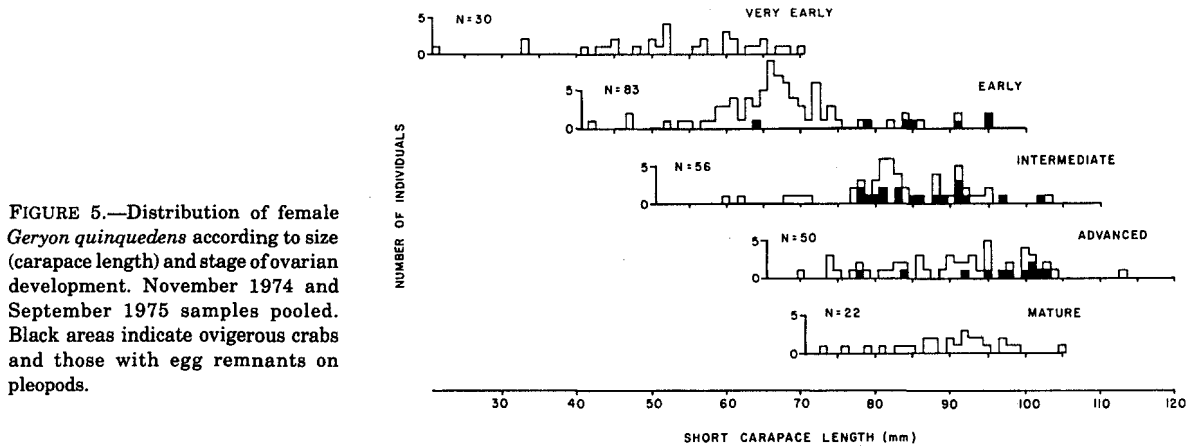


FIGURE 5.—Distribution of female *Geryon quinquedens* according to size (carapace length) and stage of ovarian development. November 1974 and September 1975 samples pooled. Black areas indicate ovigerous crabs and those with egg remnants on pleopods.

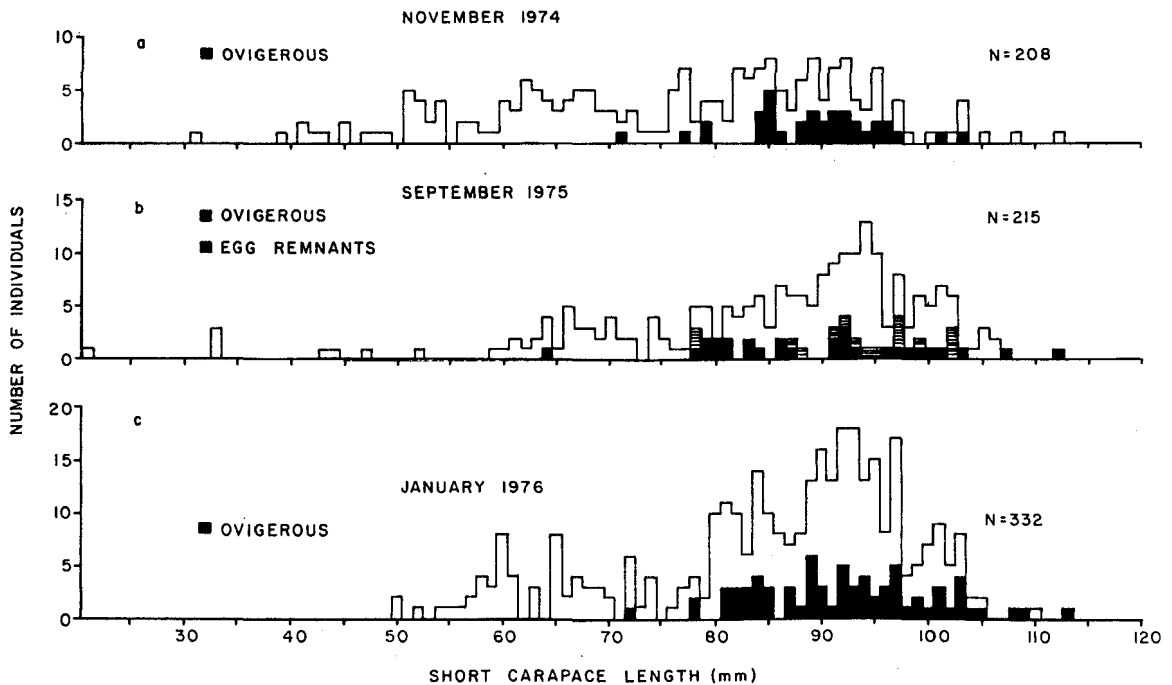


FIGURE 6.—Size-frequency distribution of female *Greyon quinquedens* captured in November 1974 (a), September 1975 (b), and January 1976 (c). Ovigerous individuals are indicated in black; those with egg remnants on pleopods by horizontal stripes.

by examining the spermathecal contents of 67 crabs with discolored vulvae (14 with extruded eggs, egg remnants, or damaged pleopods and 53 with clean, intact pleopods). Eleven (79%) of the recently ovulated females (78-103 mm CL) and 47 (89%) females with clean pleopods (45-105 mm CL) contained sperm (Figure 7). Twenty-one crabs (50-75 mm CL) with immature vulvae were similarly examined; none had sperm in the spermathecae. Another 17 crabs (50-72 mm CL)

with immature vulvae were not examined for the presence of sperm because the spermathecae were undeveloped; only the tubular vagina was present between the ovary and gonopore.

Blackened vulval margins may be used as a criterion to indicate that copulation of the female crab has occurred, if other obvious signs (eggs or remnants) are absent. The 89% incidence among nonovigerous females supports this contention. The 79% incidence among ovulated females is low,

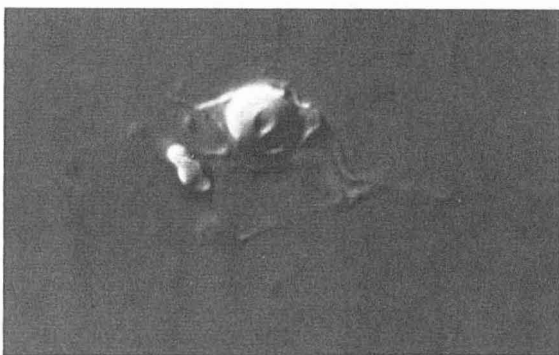


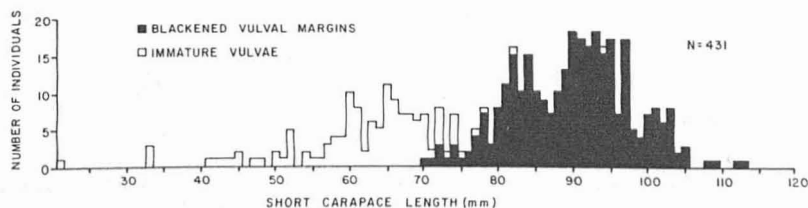
FIGURE 7.—Isolated sperm from spermatheca of 83-mm CL *Geryon quinquedens*. Nonmobile processes extend from nuclear region surrounding a central, refringent structure, most likely the acrosome (Brown 1966). Interference microscopy, 1300 \times .

but expected. None of these crabs had swollen or turgid spermathecae of the type shown in Figure 1. In most cases, only residual quantities of seminal secretions were present in the receptacles, indicating that most of the deposit had been used in past ovulation(s) or absorbed.

The presence of discolored vulval margins among large crabs suggested that they may provide a physical criterion for copulation, similar to those demonstrated for other brachyurans (Veillet 1945; Butler 1960; Hartnoll 1969). Vulval margins of 93.5% of the females ≥ 70 mm CL examined ($n = 328$) were blackened (Figure 8). All females < 70 mm CL had vulvae with intact margins. Not included in Figure 8 are an unusually small inseminated female (47 mm CL) and the ovigerous 64-mm CL specimen included in Figure 6b.

One crab (47 mm CL) with small (1.2 mm long), but open, mature-type vulva was sperm positive. This unusually small crab had obviously mated but the vulval margins were not blackened. It is physically possible for a female this small to mate with a male of similar size. I have observed morphologically functional pleopods, with penis inserted in the first pair, on male crabs as small as 38 mm CL. The size at which males become physiologically mature is not known, but it must be relatively small.

FIGURE 8.—Size-frequency distribution of female *Geryon quinquedens* with immature gonopores (white) and with discolored gonopore margins (black). November 1974, September 1975, and January 1976 collections pooled.



Change in Vulvae

Although variable in form, vulvae of *G. quinquedens* undergo a recognizable growth and development pattern which parallels growth in body size and ovarian development. Six types are recognized (Figure 9). The first form vulvae (a) are slitlike and tightly closed. The observed size range appears to be related to crab length (Table 2). Form (b) vulvae are recurved, closed, and slightly larger than the longest form (a) vulvae. Forms (c) and (d), irregularly shaped and partially open, range from a size comparable to the largest vulvae of type (a) to that of type (e). Unusually large (d) vulvae (2.6 mm) were observed in a 78-mm CL crab. Form (e) vulvae are oval, gaping, and appear to immediately precede the mature vulva. Form (f) is the enlarged (2.4-3.9 mm), gaping, and usually blackened vulvae of the larger, mated crabs.

TABLE 2.—Incidence of vulval type and size range in relation to carapace length of female *Geryon quinquedens*.

Type	n	Carapace length (mm)	n	Vulval length range (mm)
a	4	20-33	4	0.2-0.3
	10	57-66	10	0.6-0.9
b	5	56-60	0	no data
	15	61-74	8	0.7-1.2
c	9	50-60	5	0.5-0.8
	17	61-74	13	0.8-1.5
d	8	61-72	6	0.7-1.3
	1	78	1	2.6
e	3	47-60	3	0.6-1.2
	9	61-72	7	0.8-1.2
f	1	45	1	3.0
	51	70-103	12	2.4-3.9

Change in Abdomen Width

The abdomen width (Y) to carapace length (X) relationship is allometric and is transformed to a straight line by the equation:

$$\log Y = -0.875 + 1.321 \log X, n = 251; r = 0.990$$

The relationship changes in the 60- to 75-mm CL range (Figure 10) so linear regressions were calculated separately for crabs with mature (f) vulvae:

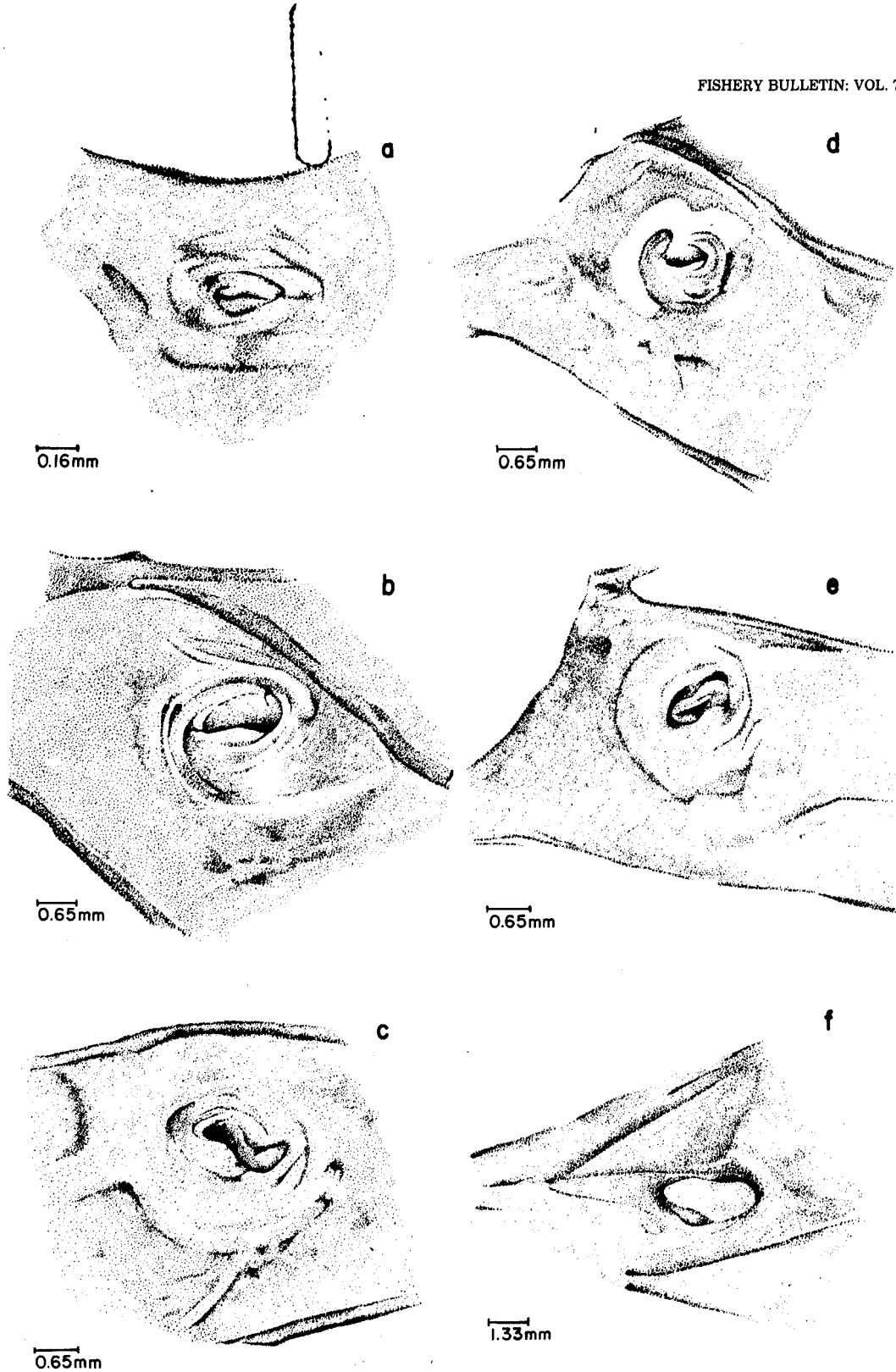


FIGURE 9.—Structural variation in vulvae of female *Geryon quinquedens*. Portions of thoracic sternites V, VI, VII illustrated. a. First form, slitlike, from 20-mm CL crab. b. Recurved, closed, 66 mm CL. c and d. Irregular shape, partially open, 74-mm and 71-mm CL crabs, respectively. e. Oval, gaping, 68 mm CL. f. Oval, enlarged, with blackened margins, 90 mm CL.

$$Y = -8.286 + 0.662X, n = 160; r = 0.943$$

and those with immature vulvae:

$$Y = -8.512 + 0.641X, n = 91; r = 0.971.$$

The size range in which relative growth of the fifth abdominal segment changes is clearly associated with the maturation of the vulvae, copulation and insemination, gonad development, and extrusion of eggs. Females become sexually mature within the intermolt size range 65-75 mm CL (80-91 mm CW). Most intermolt females ≥ 76 mm CL show signs of copulation and insemination, and their ovaries are in intermediate to advanced stages of development. Few females < 75 mm CL are ovigerous.

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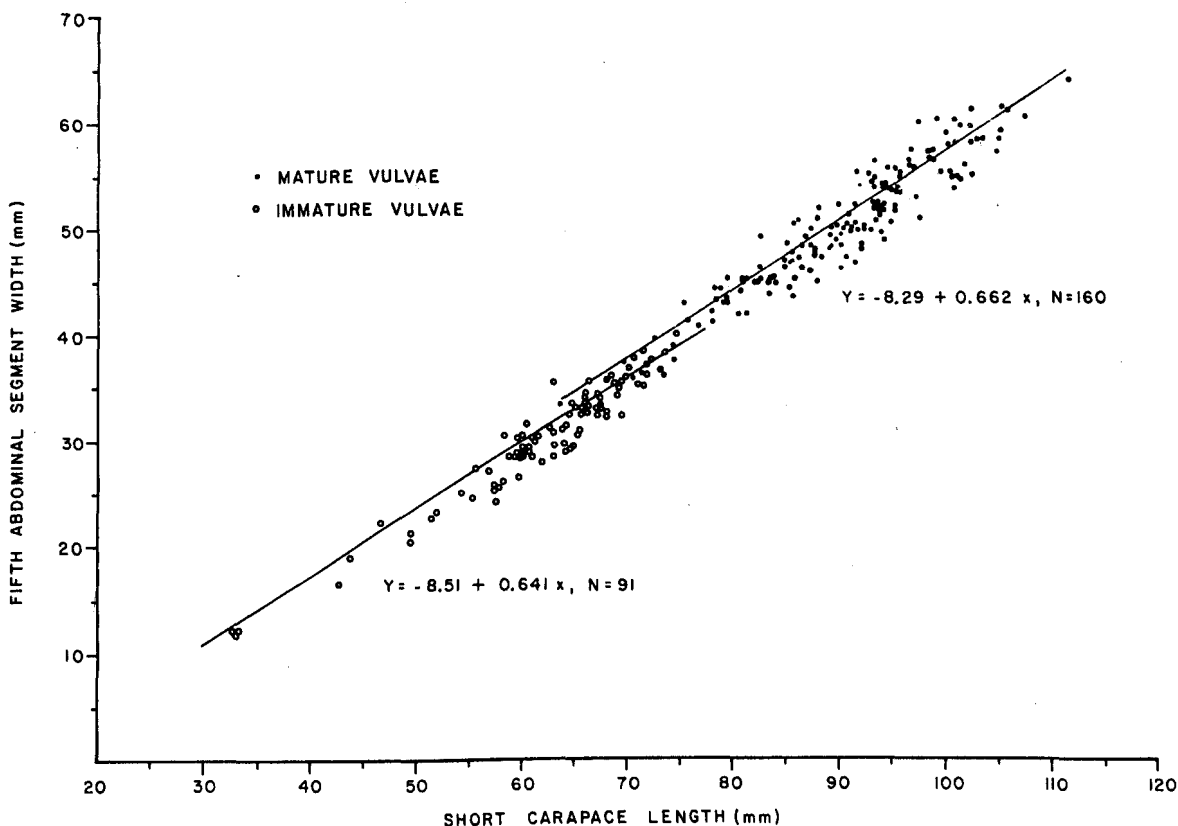


FIGURE 10.—Relationship of width of fifth abdominal segment to short carapace length for *Geryon quinquedens* with mature (dots) and immature vulvae (circles).

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