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On the Use of Morphometric Data as a Guide to Reproductive Maturity in the Ghost Crab, *Ocypode ceratophthalmus* (Pallas) (Brachyura, Ocypodidae)[1]

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ABSTRACT: Morphometric data and gonadal histology of the Hawaiian Ghost Crab, *Ocypode ceratophthalmus* (Pallas), were compared in order to define external morphological guides to reproductive maturity. Males begin producing mature spermatozoa at a carapace width of about 27 mm, an eyestalk length of 12 mm, a copulatory pleopod length of about 11 mm, and a chelar shape index (major chelar propodus length/propodus width) of 1.5. Spermatophores are found within the posterior extensions of the testes in all males for whom these first three values exceed 33 mm, 18 mm, and 14 mm, respectively; and the chelar shape index is 1.45.

Females first show evidence of copulation (measured by the presence of spermatozoa in the spermathecae) and initiate vitellogenesis (production of yolk within oöcytes) at carapace widths of about 33 mm and 29 mm, respectively.

THE VALUE of morphometric studies is well established among students of the Crustacea, and relative growth data have been utilized extensively to evaluate stages of crustacean development. In working with the Hawaiian Ghost Crab, *Ocypode ceratophthalmus* (Pallas), I require a reliable technique for recognizing, in the field, the degree of reproductive maturation, without sacrificing animals. To define puberty-related relative growth patterns and to provide a harmless, reliable method for determining gonadal maturity, I have compared morphometric data with the results of histological examinations of the gonads of 161 males and 192 females of this species, these data spanning the entire range of postmetamorphic growth (range of carapace width, 4.2–43.6 mm).

I know of four studies utilizing *O. ceratophthalmus* (Cott 1929, Huxley 1931, Edmondson 1962, and Fellows 1966), and three others involving congeners (Sandon 1937, Crane 1941, and Haley 1969), which were addressed in part to the problem. Only two (Fellows 1966 and Haley 1969) include attempts to relate histological and morphological evidence for the size at puberty; in all other studies this size remains only vaguely defined.

In this study, I have restricted myself to two major endeavors. I attempted to define the relationships between body size and shape, and certain reproductive traits. Also, I have investigated the utility of the isometric and allometric growth equations in describing relative growth in these animals. Two dimensions which maintain a constant ratio of sizes are said to be growing isometrically. If a graph of the logarithmic values for these two dimensions is linear, they are considered to be growing allometrically, as has been described by previous investigators of *Ocypode* (Cott 1929, Huxley 1931, and Sandon 1937).

METHODS

Animals were captured at night along the beach at Kaoio Point, Oahu, Hawaii, over a period of 2 years. Specimens were retained in individual containers overnight and measured the following morning. Only entire, apparently healthy crabs were considered. Following ice-water shock to immobilize them (usually requiring an exposure of 3–5 minutes), the ani-

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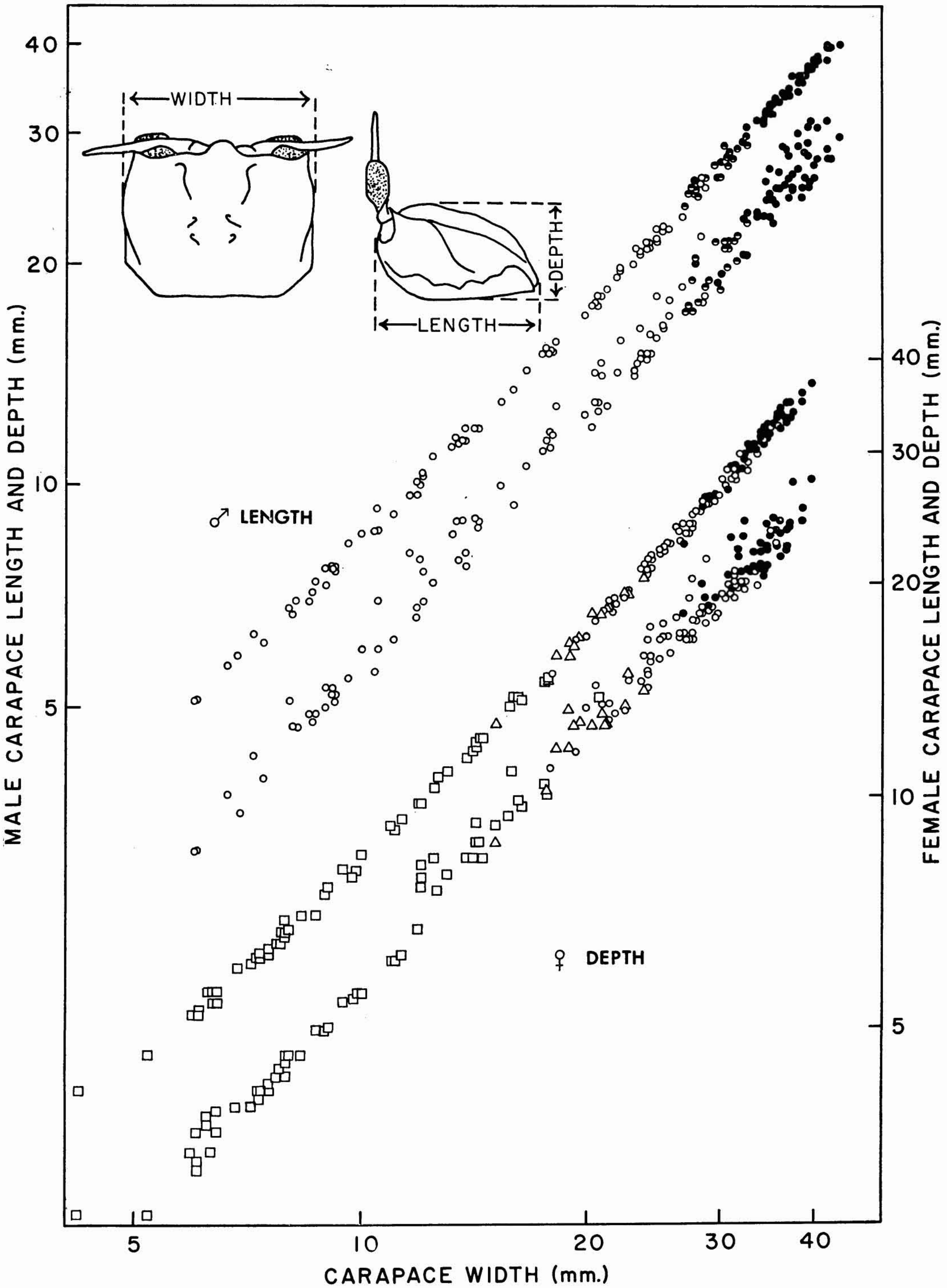


Fig. 1. *Ocypode ceratophthalmus* (Pallas). Relative growth of the carapace. Males: ○ = immature testes; ◓ = maturing testes, with mature spermatozoa present; ● = mature testes, with spermatozoa organized into spermatophores. Females: □ = first abdominal segment widest; △ = third abdominal segment widest; ○ = fourth abdominal segment widest, and virgin; ● = fourth abdominal segment widest, and copulated. N = 161 males, 192 females.

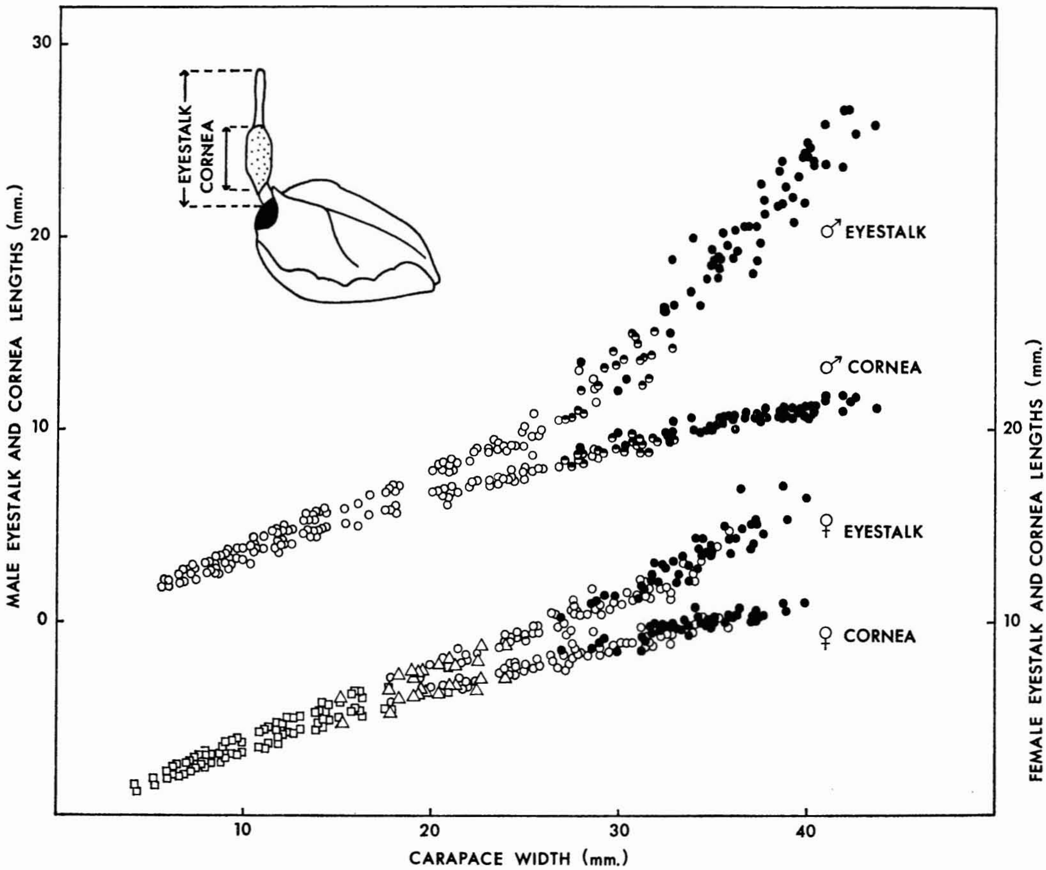


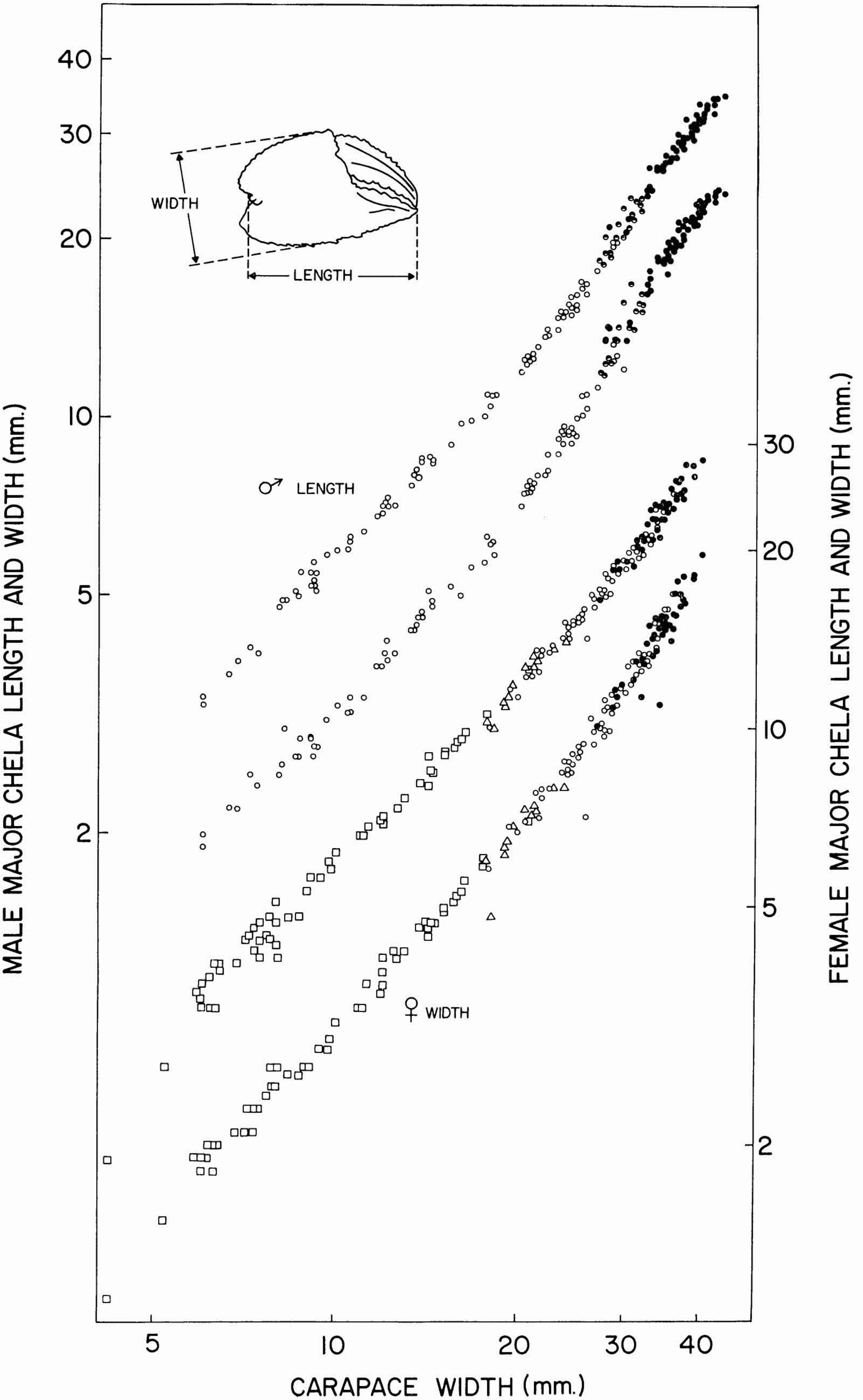
FIG. 2. *Ocypode ceratophthalmus* (Pallas). Relative growth of the eyestalk and cornea. Symbols are as given for Fig. 1. $N = 161$ males, 192 females.

mals were measured along several dimensions with direct-reading metric calipers, and then were dissected to evaluate the condition of the gonads. Some of the dimensions measured are illustrated in Figs. 1–5.

Maximum width of the carapace was chosen as the reference dimension. Total length of the third ambulatory leg was measured from the proximal end of the merus to the distal tip of the dactyl, with the leg maximally extended. All measurements of this appendage were made on the side ipsilateral to the major chela. Length and width measurements of the merus of that appendage were at their maximum spans. The first pleopods in males (the intromittent organs) were measured along a straight line from their distal tips to their points of articulation with the abdomen. All of these measurements are summarized in Tables 1 and 2.

Male crabs were considered to be "maturing" whenever mature spermatozoa could be detected in their testes, and "mature" whenever the lower extremities of their testes contained spermatozoa enclosed within spermatophores (Table 3). Females were considered to be "mature" whenever their spermathecae contained spermatozoa (evidence of copulation), and their gonads evidenced oöcytes undergoing vitellogenesis (Table 4). The relationship between widest abdominal segment and carapace

FIG. 3. *Ocypode ceratophthalmus* (Pallas). Relative growth of the major chelar propodus. Symbols are as given for Fig. 1. $N = 161$ males, 192 females.


WIDTH
LENGTH
♂ LENGTH
♀ WIDTH
40
30
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2
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MALE MAJOR CHELA LENGTH AND WIDTH (mm.)
FEMALE MAJOR CHELA LENGTH AND WIDTH (mm.)
CARAPACE WIDTH (mm.)

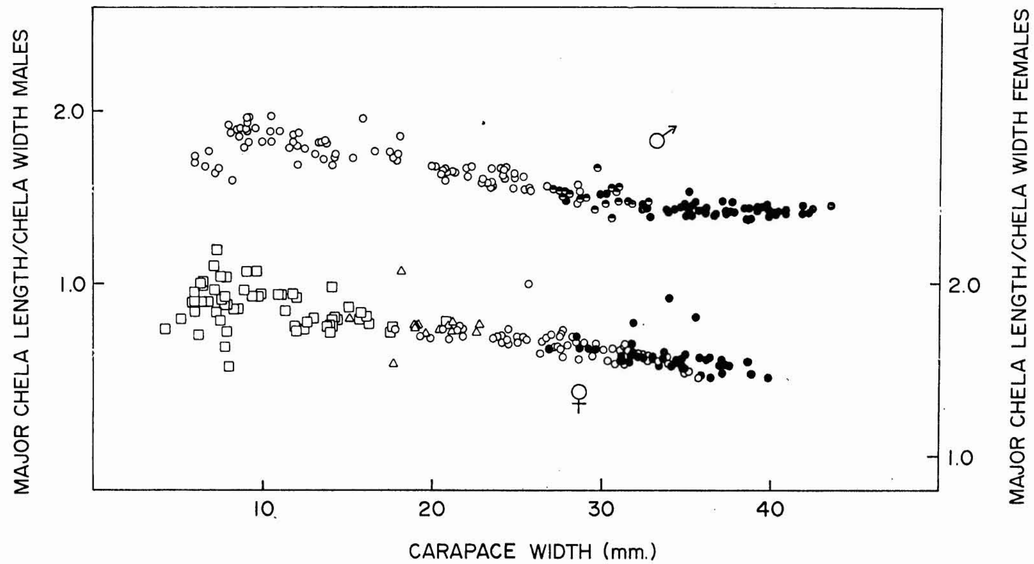

FIG. 4. *Ocypode ceratophthalmus* (Pallas). Puberty related change in growth of the major chelar propodus, as an alteration of chelar shape index. Symbols are as given for Fig. 1. $N = 161$ males, 192 females.

width was determined in order to investigate its possible use as an indicator of puberty, as demonstrated for another species (Haley 1969).

To determine and express the size at which the animals attained reproductive maturity, I grouped them into size classes based upon 2.0-mm intervals of carapace width. Because of the variation in size at which individuals first displayed a particular characteristic, I chose the minimum size class in which $\geqslant 50$ percent of the animals displayed the trait.

The growth of different body parts relative to carapace width was also analyzed to determine whether certain dimensions are reliable indicators of reproductive maturity. These scatter diagrams (Figs. 1–5) are coded to indicate gonadal maturity (♂), or evidence of copulation and widest abdominal segment (♀). The original scatter diagrams which appeared to exhibit an exponential trend were replotted along logarithmic coordinates. Allowing X to represent the reference dimension and Y the variable dimension, equations of the form $Y = a+bX$ were used to express linear relationships, where a is the Y-intercept and b the slope; $Y = aX^b$ expresses the allometric or exponential relation, in which a represents the Y-intercept and b the allometric constant. This latter value is about 1 for isometric exponential growth; a value less than 1 indicates negative allometry, whereas a value greater than unity reflects positive allometric growth. Regressions were fitted by the method of least squares, and testing for linearity was accomplished by analysis of variance (Dixon 1971: BMD no. 05R); the residual sum of squares due to deviations between a simple linear regression and a second-degree polynomial expression were compared, with the mean square due to deviation about the curvilinear regression. My null hypothesis was "H_0: deviations about the linear regression = deviations about the curvilinear regression," and I chose to reject H_0 whenever $P < 0.05$.

None of the dimensions tested illustrated simple isometric or allometric growth over the entire size range. Examination of Figs. 1–5 suggested to me that these complex growth curves might be resolved into isometric or allometric components by considering prepubertal and postpubertal animals separately. As inflections appeared to exist at 27 and 31 mm of carapace width, I considered each sex twice, once by examining the size ranges of < 27.0 mm and $\geqslant 27.0$ mm carapace width, then < 31.0 mm and $\geqslant 31.0$ mm. Within these smaller size ranges, several dimensions do exhibit isometric

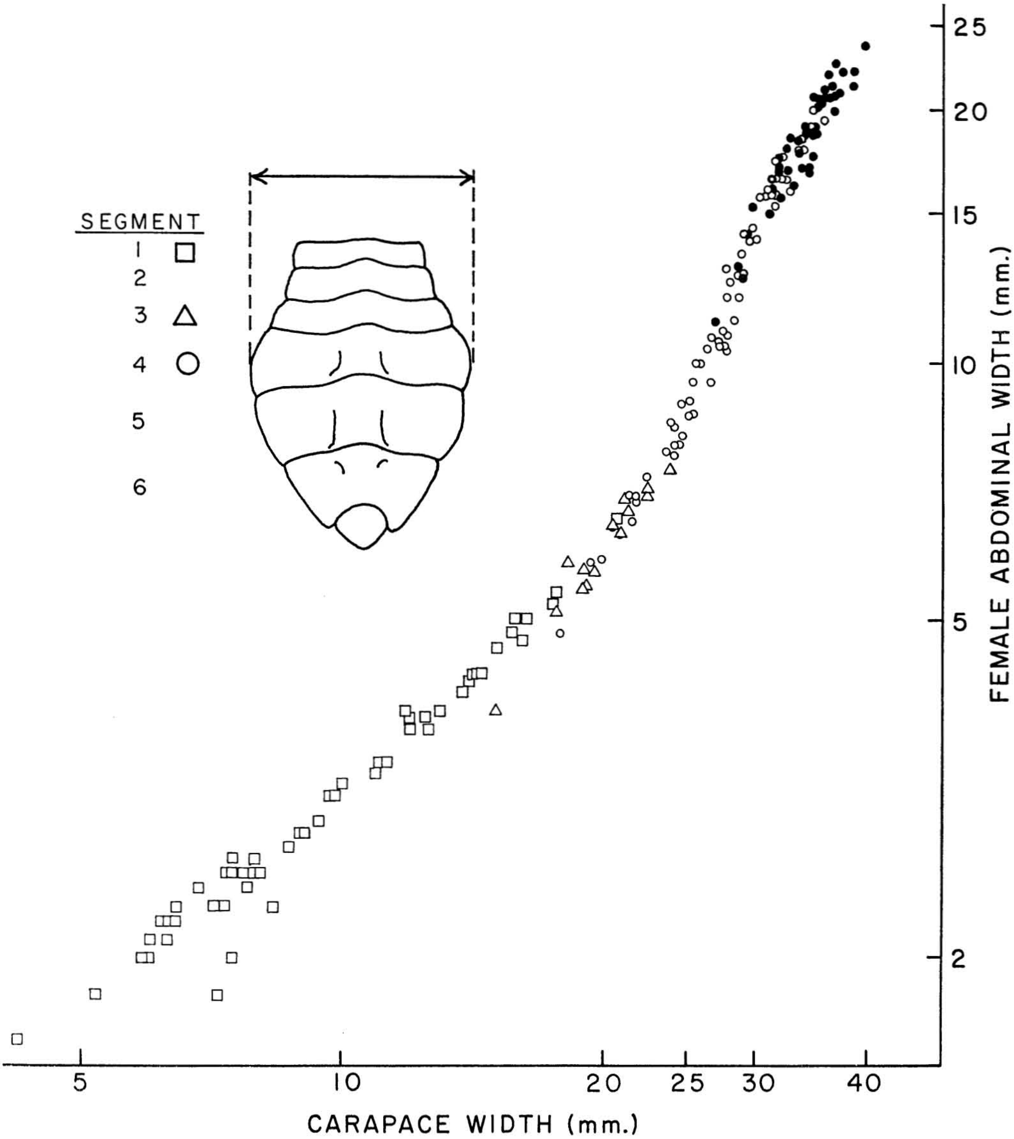

FIG. 5. *Ocypode ceratophthalmus* (Pallas). Relative growth in width of the female abdomen. Symbols are as given for Fig. 1. $N = 192$ females.

or allometric growth when plotted against carapace width. The equations for these regressions and tests of their linearity are given in Table 5.

RESULTS

Examination of Table 3 reveals that onset of reproductive maturation in males occurs at a carapace width of about 28 mm (27.0–28.9), and the process is complete by the time the animals measure 33 mm along this dimension.

Table 4 indicates that 26 mm carapace width was the minimum size for copulation in females, and is also the smallest size at which vitellogenesis was detected in the oöcytes. The minimum size class for copulation is 34 mm (33.0–34.9) for females, whereas the minimum size class for onset of vitellogenesis is 30 mm

TABLE 1

RELATIVE GROWTH MEASUREMENTS FOR MALES OF *Ocypode ceratophthalmus* (Pallas)

CARAPACE WIDTH SIZE CLASSES	CARAPACE			EYESTALK LENGTH	CORNEA LENGTH	PROPODUS OF MAJOR CHELA		THIRD AMBULATORY LEG			FIRST PLEOPOD LENGTH
	WIDTH	LENGTH	DEPTH			LENGTH	WIDTH	TOTAL LENGTH	MERUS LENGTH	MERUS WIDTH	
6.0 (4)	6.4±0.4	5.4±0.4	3.4±0.3	2.4±0.2	2.1±0.1	3.6±0.3	2.1±0.2	12.6±0.8	5.2±0.2	1.6±0.2	0.6±0.2
8.0 (8)	8.1±0.6	6.8±0.4	4.7±0.4	3.2±0.2	2.6±0.2	4.8±0.5	2.7±0.2	16.9±1.6	7.0±0.7	2.1±0.2	0.9±0.3
10.0 (12)	9.6±0.6	8.1±0.6	5.5±0.6	3.8±0.2	3.2±0.2	5.6±0.4	3.0±0.2	20.7±1.3	8.4±0.6	2.6±0.2	1.3±0.3
12.0 (8)	11.9±0.4	10.0±0.5	7.2±0.7	4.8±0.1	4.0±0.2	7.0±0.3	3.9±0.2	25.2±1.4	10.3±0.6	3.3±0.2	2.2±0.4
14.0 (9)	13.8±0.4	11.7±0.3	8.6±0.5	5.5±0.2	4.8±0.1	8.2±0.3	4.7±0.2	28.3±1.2	11.6±0.6	3.9±0.1	3.4±0.6
16.0 (3)	16.0±0.6	13.6±0.6	10.0±0.6	6.3±0.4	5.3±0.4	9.6±0.5	5.3±0.3	32.6±2.0	13.3±0.8	4.7±0.2	4.1±0.4
18.0 (6)	17.8±0.2	15.3±0.2	11.7±0.6	7.0±0.1	5.9±0.1	10.6±0.3	6.0±0.2	37.6±0.9	15.2±0.4	5.3±0.1	5.6±0.5
20.0 (7)	20.6±0.3	17.6±0.4	13.1±1.0	8.0±0.2	6.7±0.3	12.4±0.3	7.5±0.2	41.6±3.3	16.9±1.1	5.8±0.7	6.9±0.5
22.0 (5)	21.8±0.5	19.0±0.7	14.4±1.2	8.6±0.3	7.1±0.2	13.5±0.5	8.1±0.4	45.5±1.9	18.3±0.7	6.6±0.3	7.6±0.7
24.0 (14)	24.0±0.6	21.0±0.6	15.5±1.2	9.3±0.4	7.5±0.3	15.2±0.5	9.4±0.4	51.1±2.2	20.4±0.9	7.3±0.3	8.9±0.4
26.0 (5)	25.8±0.6	22.4±0.4	17.2±1.0	10.1±0.5	8.1±0.3	16.8±0.5	10.7±0.4	52.0±1.4	20.8±0.6	7.1±0.6	10.0±0.1
28.0 (11)	28.1±0.5	25.2±0.7	18.6±1.5	11.8±1.0	8.6±0.3	19.4±0.8	12.8±0.7	59.7±1.2	23.6±0.6	8.6±0.3	11.3±0.4
30.0 (9)	30.1±0.6	27.1±0.8	20.0±1.2	13.5±1.2	9.2±0.4	21.5±1.0	14.3±1.3	63.1±1.6	24.7±0.5	9.1±0.5	12.1±0.6
32.0 (12)	32.0±0.7	28.7±1.0	21.6±1.1	14.9±1.9	9.5±0.4	23.6±1.2	16.0±1.1	66.4±1.2	26.1±0.5	9.6±0.5	12.9±0.6
34.0 (6)	34.4±0.5	31.4±0.5	23.8±1.1	18.2±1.4	10.1±0.2	26.6±0.6	18.4±0.4	72.5±3.4	28.2±1.5	10.4±0.4	13.9±0.4
36.0 (12)	35.8±0.6	33.0±0.7	25.4±2.0	19.4±0.9	10.4±0.3	27.9±1.0	19.4±1.0	73.6±3.5	28.6±1.2	10.8±1.0	14.5±0.4
38.0 (12)	37.9±0.6	34.8±0.8	26.4±1.7	21.4±1.8	10.7±0.2	29.9±1.0	21.0±0.7	77.6±2.4	30.2±1.0	11.4±0.5	15.2±0.4
40.0 (13)	40.0±0.5	36.9±0.7	27.8±2.0	23.7±1.4	11.0±0.3	32.1±0.8	22.5±0.6	81.6±2.1	31.5±0.9	11.9±0.4	16.2±0.5
42.0 (4)	42.1±0.3	39.0±0.8	28.8±1.7	25.6±1.4	11.5±0.4	33.8±0.9	23.6±0.4	85.4±2.5	32.7±0.4	12.1±0.3	16.9±0.8
44.0 (1)	43.6	39.6	26.9	25.8	11.2	34.8	23.8	87.6	33.3	12.0	17.7

NOTE: The number in parentheses represents the number of specimens. Values are expressed as means (mm) with standard deviations. $N = 161$.

TABLE 2

RELATIVE GROWTH MEASUREMENTS FOR FEMALES OF *Ocypode ceratophthalmus* (Pallas)

CARAPACE WIDTH SIZE CLASSES	CARAPACE WIDTH	CARAPACE LENGTH	CARAPACE DEPTH	EYESTALK LENGTH	CORNEA LENGTH	PROPODUS OF MAJOR CHELA LENGTH	PROPODUS OF MAJOR CHELA WIDTH	THIRD AMBULATORY LEG TOTAL LENGTH	THIRD AMBULATORY LEG MERUS LENGTH	THIRD AMBULATORY LEG MERUS WIDTH	ABDOMEN WIDTH
4.0 (1)	4.2	4.1	2.8	1.7	1.5	1.9	1.1	7.8	2.8	0.8	1.6
6.0 (12)	6.1±0.4	5.4±0.3	3.5±0.3	2.5±0.2	2.0±0.1	3.6±0.4	1.9±0.2	12.6±1.2	5.2±0.4	1.5±0.1	2.1±0.2
8.0 (17)	7.8±0.5	6.6±0.4	4.4±0.3	3.1±0.2	2.6±0.2	4.6±0.3	2.4±0.2	16.6±1.0	6.8±0.4	2.0±0.2	2.4±0.2
10.0 (6)	9.8±0.6	8.4±0.6	5.5±0.4	4.0±0.2	3.3±0.2	6.0±0.4	3.0±0.2	21.9±1.7	8.9±0.6	2.7±0.2	3.1±0.2
12.0 (8)	11.9±0.5	10.1±0.5	7.5±0.9	4.8±0.3	4.1±0.3	7.0±0.2	3.8±0.3	24.8±0.8	10.1±0.4	3.4±0.1	3.7±0.2
14.0 (8)	14.0±0.4	11.9±0.4	8.7±0.4	5.6±0.2	4.8±0.2	8.2±0.4	4.6±0.2	28.5±1.5	11.6±0.3	4.0±0.2	4.2±0.2
16.0 (6)	15.7±0.5	13.6±0.5	9.9±0.8	6.3±0.2	5.3±0.3	9.4±0.3	5.2±0.2	33.2±1.6	13.5±0.7	4.6±0.2	4.7±0.4
18.0 (5)	17.8±0.3	15.1±0.5	11.0±0.7	6.8±0.3	5.8±0.2	10.2±0.2	5.8±0.6	36.4±1.6	14.9±0.7	5.2±0.2	5.2±0.4
20.0 (10)	19.8±0.7	17.2±0.8	13.1±0.8	7.7±0.3	6.5±0.3	11.8±0.7	6.8±0.4	41.0±2.2	16.7±0.9	5.8±0.3	6.0±0.4
22.0 (12)	21.8±0.6	18.9±0.4	13.6±0.7	8.3±0.4	6.9±0.2	13.1±0.5	7.6±0.3	45.5±2.8	18.3±1.1	6.2±0.6	6.8±0.3
24.0 (10)	24.1±0.3	21.1±0.4	15.5±1.0	9.1±0.3	7.5±0.2	14.5±0.4	8.5±0.3	49.7±2.2	20.0±0.8	7.0±0.6	8.2±0.4
26.0 (10)	25.9±0.7	22.7±0.6	17.1±0.8	9.9±0.5	8.0±0.3	15.7±0.8	9.2±0.9	54.0±1.7	21.6±0.6	7.8±0.3	9.8±0.8
28.0 (16)	28.0±0.6	24.7±0.9	18.3±1.4	10.7±0.6	8.6±0.5	17.5±0.8	10.6±0.7	57.1±2.2	22.7±0.9	8.1±0.6	11.8±1.1
30.0 (9)	29.9±0.6	26.7±0.9	18.8±0.6	11.2±0.4	8.9±0.2	19.0±0.6	11.8±0.7	61.1±1.3	24.0±0.5	8.9±0.3	14.8±0.8
32.0 (23)	31.8±0.6	28.7±0.8	20.7±1.4	12.1±0.6	9.4±0.4	20.5±1.0	12.8±0.8	64.2±2.3	25.2±0.9	9.4±0.4	16.5±0.8
34.0 (20)	34.1±0.6	31.1±0.8	21.5±1.0	13.2±0.7	10.0±0.3	22.7±0.9	14.5±1.1	68.1±1.2	26.4±0.4	9.8±0.2	18.0±1.1
36.0 (10)	35.7±0.6	32.9±0.8	23.2±0.8	14.6±1.0	10.3±0.3	24.5±1.0	15.8±1.1	72.0±1.5	27.7±0.5	10.3±0.5	20.3±0.9
38.0 (8)	37.6±0.8	34.6±1.2	24.1±1.6	15.1±1.0	10.4±0.3	25.8±1.4	16.9±0.9	74.4±1.8	28.5±0.7	10.5±0.2	21.1±0.9
40.0 (1)	39.9	37.4	27.7	16.5	11.1	28.3	19.4	79.6	30.6	11.8	23.6

NOTE: The number in parentheses represents the number of specimens. Values are expressed as means (mm) with standard deviations. $N = 192$.

TABLE 3

THE RELATION BETWEEN CARAPACE WIDTH AND MATURITY OF THE TESTES IN *Ocypode ceratophthalmus* (Pallas), AS OBSERVED UPON DISSECTION

MAXIMUM WIDTH OF CARAPACE (AVERAGED FOR 2-MM INTERVALS)	NUMBER OF MALES WITH IMMATURE TESTES	MATURING TESTES	MATURE TESTES
6.0	4	–	–
8.0	8	–	–
10.0	12	–	–
12.0	8	–	–
14.0	9	–	–
16.0	3	–	–
18.0	6	–	–
20.0	7	–	–
22.0	5	–	–
24.0	14	–	–
26.0	5	–	–
28.0	3	7	1
30.0	–	6	3
32.0	–	6	6
34.0	–	–	6
36.0	–	–	12
38.0	–	–	12
40.0	–	–	13
42.0	–	–	4
44.0	–	–	1

NOTE: $N = 161$ males. Range of carapace width, 6.0–43.6 mm.

TABLE 4

THE RELATION BETWEEN CARAPACE WIDTH, COPULATION, AND THE PRESENCE OF MATURING OÖCYTES IN THE OVARIES OF FEMALES OF *Ocypode ceratophthalmus* (Pallas)

MAXIMUM WIDTH OF CARAPACE (AVERAGED FOR 2-MM INTERVALS)	NO. VIRGINS	NO. COPULATED	NO. WITH MATURING OÖCYTES
4.0 (1)	1	–	–
6.0 (12)	12	–	–
8.0 (17)	17	–	–
10.0 (6)	6	–	–
12.0 (8)	8	–	–
14.0 (8)	8	–	–
16.0 (6)	6	–	–
18.0 (5)	5	–	–
20.0 (10)	10	–	–
22.0 (12)	12	–	–
24.0 (10)	10	–	–
26.0 (10)	9	1	3
28.0 (16)	13	3	11
30.0 (9)	7	2	9
32.0 (23)	13	10	22
34.0 (20)	5	15	20
36.0 (10)	2	8	9
38.0 (8)	–	8	8
40.0 (1)	–	1	1

NOTE: Copulation determined by examination of spermathecae for stored spermatozoa. The numbers in parentheses represent the numbers of specimens in the size classes. $N = 192$ females. Range of carapace width, 4.2–39.9 mm.

of carapace width. Clearly, copulation is not prerequisite to ovarian maturation.

Data for size at puberty are summarized in Table 6. The values for largest immature specimen and smallest mature specimen suggest a fairly restricted range of size at puberty in males. The greater differences in these values for females probably reflect the limitations of the criteria; e.g., a large "virgin" female (Table 4) may well have copulated previously and discharged her supply of sperm during ovulation or pathologically (if either is possible), or she may indeed be mature in all other respects but has yet to copulate. The determination of onset of vitellogenesis is subjective in that microscopic inspection was employed to detect the presence of yolk materials within the oöcytes. Prior to vitellogenesis, the oöcytes are transparent in saline solution. As yolk is produced, these cells increase in size, appearing opaque white, then yellow and orange.

The mean size of mature specimens (item D in Table 6) suggests a sexual dimorphism in size of mature individuals. The range of postpubertal growth (item E in Table 6) is represented by the carapace width of the largest mature specimen, expressed as a percentage of the smallest. I have not yet determined whether this crab exhibits a distinct "molt of puberty," as discussed by Pérez (1929) for another species. If such a molt exists, it is probably not a terminal molt, as judged by the range of postpubertal growth.

Males and females are of the same relative size for most dimensions considered (Table 7). Sexual dimorphism with advancing age (carapace width) is most apparent for the eyestalk and major chelar propodus.

Fig. 1 illustrates the relative growth of the primary carapace dimensions. Simple size allo-

TABLE 5

Regressions and Tests for Linearity for Dimensions Exhibiting Simple Isometric or Allometric Growth

Carapace Length	♀ $X \geqslant 31.0$ mm	$Y = -4.34 + 1.04X$	$H_0: P \gg 0.20$
Eyestalk Length	♂ $X \geqslant 27.0$ mm	$Y = -17.06 + 1.02X$	$H_0: P \gg 0.20$
	♀ $X \geqslant 31.0$ mm	$Y = -5.57 + 0.55X$	$H_0: P \gg 0.20$
Cornea Length	♀ $X \geqslant 31.0$ mm	$Y = 3.17 + 0.20X$	$H_0: P > 0.05$
Third Ambulatory Leg			
Total Length	♂ $X < 27.0$ mm	$Y = 0.31 + 2.07X$	$H_0: P \gg 0.20$
	♂ $X \geqslant 27.0$ mm	$Y = 8.02 + 1.84X$	$H_0: P \gg 0.20$
	♀ $X < 27.0$ mm	$Y = 0.34 + 2.06X$	$H_0: P \gg 0.20$
Merus Length	♂ $X < 27.0$ mm	$Y = 0.47 + 0.82X$	$H_0: P > 0.20$
	♂ $X \geqslant 27.0$ mm	$Y = 4.98 + 0.66X$	$H_0: P \gg 0.20$
	♀ $X \geqslant 27.0$ mm	$Y = 5.49 + 0.62X$	$H_0: P \gg 0.20$
Merus Width	♂ $X < 27.0$ mm	$Y = -0.32 + 0.31X$	$H_0: P > 0.05$
	♀ $X < 27.0$ mm	$Y = -0.36 + 0.31X$	$H_0: P \gg 0.20$
First Pleopod Length	♂ $X \geqslant 27.0$ mm	$Y = -0.11 + 0.41X$	$H_0: P \gg 0.20$
Abdominal Width	♀ $X \geqslant 31.0$ mm	$Y = -10.88 + 0.86X$	$H_0: P \gg 0.20$
Carapace Depth	♂ $X < 27.0$ mm	$Y = 0.310X^{1.13}$	$H_0: P \gg 0.20$
	♀ $X < 31.0$ mm	$Y = 0.283X^{1.09}$	$H_0: P \gg 0.20$
	♀ $X \geqslant 31.0$ mm	$Y = 0.172X^{0.94}$	$H_0: P \gg 0.20$
Major Chelar Propodus			
Length	♀ $X \geqslant 31.0$ mm	$Y = 0.131X^{1.44}$	$H_0: P \gg 0.20$

Note: X = carapace width; Y = variable dimension; P = probability for a test of the null hypothesis that no significant curvilinear component exists within the regression.

TABLE 6

The Size at Puberty and the Range of Postpubertal Growth of *Ocypode ceratophthalmus* (Pallas) Expressed as a Percent of the Smallest Mature Size

	Maximum width of carapace (mm)			
		Females (192)		
Item	Males (161)	Copulation	Maturing oöcytes	Abdominal width
A. Largest Immature Specimen	28.7	35.8	36.4	23.8
B. Smallest Mature Specimen	27.1	26.9	25.4	17.8
C. Largest Mature Specimen	43.6	39.9	39.9	39.9
D. Mean of Mature Specimens	35.1	33.9	32.5	30.2
E. Range of Postpubertal Growth = (C/B) × 100	160.9	148.3	157.1	224.1

Note: Criteria for puberty for males was the presence in the sperm ducts of mature spermatozoa; for females it was the presence of maturing oöcytes in the ovaries, and the widest abdominal segment.

metry does not describe adequately the relation of carapace length to carapace width in males; the relationship is curvilinear. Carapace length in females with carapace widths $\geqslant 27.0$ mm appears to grow isometrically (Table 5).

Fig. 2 illustrates the value of the eyestalk as a guide to reproductive maturity in males. Growth in length of the eyestalk appears asymptotic in males and females up to a carapace width of about 27 mm and 31 mm, respectively.

TABLE 7

THE RATIOS OF MALE SIZE TO FEMALE SIZE FOR SEVERAL DIMENSIONS IN *Ocypode ceratophthalmus* (Pallas)

Range of Carapace Width (mm)	5.0–8.9	9.0–18.9	19.0–28.9	29.0–38.9	39.0–40.9
Carapace Length	1.00	0.99	1.01	1.02	1.00
Carapace Depth	1.03	0.99	1.01	1.10	0.98
Eyestalk Length	0.99	1.00	1.05	1.34	1.44
Cornea Length	0.99	1.00	1.01	1.04	0.99
Chelar Propodus Length	1.03	1.00	1.07	1.17	1.14
Chelar Propodus Width	1.06	1.02	1.14	1.26	1.18
Length of Third Walking Leg	0.99	1.00	1.02	1.06	1.07
Length of Merus	1.01	1.00	1.01	1.06	1.07
Width of Merus	1.02	0.99	1.03	1.06	1.02
Number of Pairs Tested	12	30	38	45	1

NOTE: $N = 126$ pairs.

At a carapace width of 27 mm, the rate of growth of the male eyestalk alters dramatically. The symbols for gonadal maturity reveal the correlation of histological maturity with the change in external configuration of the eyestalk. No comparable alteration in growth of this structure occurs in females. The growth in length of the cornea in both sexes appears to be asymptotic, although for females with carapace widths $\geqslant 31.0$ mm, it may be argued that isometry (on an arithmetic plot) is a sufficient description. Again, however, the linearity of the regression is marginal (H_o: $P > 0.05$), and the distinction between males and females is not obvious enough to be of value in this study.

Growth of the major chelar propodus is illustrated in Fig. 3. Again, simple allometry is not a satisfactory description of these growth patterns in males, patterns which indicate a constantly changing ratio of geometric rates of increase for both length and width of the propodus. This is true also for females if those with carapace widths $\geqslant 31.0$ mm are excluded; for the latter, propodus length appears to increase by positive allometry.

A chelar propodus index was prepared as the ratio of major chelar propodus length to propodus width, and was plotted against carapace width, the reference dimension (Fig. 4). Major chelar shape in males appears to stabilize at a carapace width of about 31 mm, a figure which correlates well with the stage at which spermatozoa are accumulated into spermatophores within the testes. The female propodus appears to become relatively wider throughout life.

Relative growth of the third ambulatory leg presents no obvious sexual dimorphisms or useful puberty-related distinctions. Isometry adequately describes the growth in total length of this structure, and in merus length, for males with carapace widths of < 27.0 mm, and $\geqslant 27.0$ mm. For females with carapace widths < 27.0 mm, statistical analysis indicates that this leg grows asymptotically to its total length, as does the merus in females with carapace widths $\geqslant 27.0$ mm. However, this difference between males and females is not obvious when one is working with them in the field.

Growth in width of the merus of the third ambulatory leg is asymptotic in both sexes with carapace widths $\geqslant 27.0$ mm. For smaller individuals, isometry is perhaps an adequate description.

For males with carapace widths $\geqslant 27.0$ mm, the copulatory pleopods grow by isometry, whereas for smaller males they grow asymptotically. This is in keeping with their function; continually altering in growth rate prior to puberty, these pleopods stabilize in rate of growth at the onset of reproductive maturity.

In Fig. 5, the graph of maximum abdominal width of females clearly indicates an alteration in growth rate at a carapace width of 31 mm, a width which is associated with onset of copulation and vitellogenesis. Beyond this carapace width, growth in width of the abdomen in females is by linear isometry. Another obvious inflection in the curve is indicated for a carapace width of about 24 mm, a width which is associated with the change to abdominal segment four as being widest. The growth in width of segment four clearly differs for females with carapace widths of 24–31 mm, when compared with those greater than 31 mm.

DISCUSSION

These results permit the use of a few external morphological measurements for the reliable prediction of reproductive maturity in *Ocypode ceratophthalmus* (Pallas) in Hawaii. Males enter puberty at a carapace width of about 27 mm, an eyestalk length of 12 mm, and a copulatory pleopod length of about 11 mm. They are reproductively mature when these values exceed 33 mm, 18 mm, and 14 mm, respectively. The chelar shape index (major chelar propodus length/propodus width) of males continually decreases from its initial value of 1.7 until it stabilizes at 1.45, a carapace width of about 31 mm. Females begin copulation and vitellogenesis at carapace widths of about 33 mm and 29 mm, respectively, and at a maximum abdominal width of about 12 mm.

Mature males produce spermatozoa throughout the year. Mature females carry spermatozoa within their spermathecae and exhibit vitellogenesis also throughout the year. However, the rate of vitellogenesis appears to vary with season, as the frequency of females with large oöcytes was greatest from April through August. Females with spent ovaries (with residual large oöcytes remaining in the ovaries after ovulation) were collected from May through August. Apparently, ovigerous females are secretive and rarely appear on the beach until the larvae have hatched and are ready to be shed into the ocean.

Ratios of cornea length and length of the second ambulatory leg to the length of the carapace in five specimens of *O. ceratophthalmus* (Pallas) influenced Cott (1929) to conclude that juveniles are precocious for both vision and speed of running. An examination of seven specimens of the same species led Huxley (1931) to conclude that growth of the cheliped is practically isometric with that of the carapace. In his sample, however, the largest complete male had a carapace width of but 16 mm, about one-third of the maximum width possible in Hawaii.

The data of this study corroborate Cott's (1929) conclusion regarding growth of the cornea and ambulatory leg. The length of these structures is relatively longer in juveniles than in adults, in that the former grows asymptotically and the latter by linear isometry, with the rate of increase being greatest for animals with carapace widths less than 27.0 mm.

Contrary to Huxley's (1931) report, I did not find the growth of the major cheliped to be isometric with the carapace. Only for females with carapace widths $\geqslant$ 31.0 mm does positive allometry describe the growth in length of the major chelar propodus. With the exception of these larger females, the pattern of growth in length and width of the propodus is not compatible with simple allometry in either sex. The ratio of geometric rates of increase changes constantly for each dimension. Undoubtedly, these results differ from those of Huxley (1931) due to his limited sample.

Edmondson (1962) was correct in suggesting that the appearance of the styliform process of the eyestalks indicates onset of adulthood in *O. ceratophthalmus* (Pallas), the change occurring at a carapace width of 27 mm. To my knowledge, no one has demonstrated the function of this structure. Fellows (1966) examined 32 males and 32 females of this species, within the range of carapace width of 10–43 mm, and concluded that physical maturity (body with adult size and shape) in males and females occurs at carapace widths of 25–28 mm, and 28–30 mm, respectively. Evidence based upon burrow structure led Fellows to suggest that physical and sexual maturity are not attained simultaneously by males. Although he correctly indicated the range of size at puberty, Fellows (1966) reported an average mature size of 33 mm carapace width in females, and 44 mm for males. My findings (Table 7) are in agreement for females only. This discrepancy may be due to sample size, population differences, or to the behavioral criteria which Fellows also employed.

Negative allometry in the growth of the walking legs of 32 specimens of *O. saratan* (Forskål) (as *O. aegyptiaca* Gerstäcker) was reported by Sandon (1937), who noted changes in growth at carapace lengths between 20 and 30 mm. However, he studied only males, and none with carapace widths in the range 24.8–31.0 mm. A study of 64 specimens of *O. gaudichaudii* H. Milne Edwards & Lucas, led Crane (1941) to conclude that the juvenile carapace is relatively broader and shallower than that of an adult. She, too, reported that juveniles are precocious for speed and vision. Anatomical maturity in that species she determined to be in the range 22–24 mm of carapace length.

The difference between my findings and those of Sandon (1937) and Crane (1941), I attribute to species variation. I have never examined specimens of *O. saratan* (Forskål) or *O. gaudichaudii* H. Milne Edwards & Lucas. However, their carapace sizes at maturity closely approximate that of *O. ceratophthalmus* (Pallas). For the latter species, however, carapace shape and third ambulatory leg length are not useful guides to reproductive maturity.

Utilizing 499 specimens of *O. quadrata* (Fabr.), I determined earlier (Haley 1969) that females begin copulation at a carapace width of about 26 mm, the same size at which the abdominal shape stabilizes; and that males produce spermatozoa at carapace widths beyond 24 mm. When compared to those data, the findings of this study demonstrate variability in relative growth within the genus *Ocypode*. Structures which appear to grow isometrically in *O. quadrata* (Fabr.) (e.g., carapace length, carapace depth, eyestalk length) grow by more complex patterns in *O. ceratophthalmus* (Pallas). It is important that one bears this in mind when—as is often done—one attempts to extrapolate conclusions between brachyuran genera.

Barrass (1963) has suggested that the major cheliped of *O. ceratophthalmus* (Pallas) serves as a courting device. This is in keeping with the observed postpubertal sexual dimorphism in size of this structure (Table 7). The propodus of the major cheliped of males is relatively larger overall than that of females after puberty and becomes relatively longer beyond a carapace width of 31 mm.

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