TULANE STUDIES IN ZOOLOGY

Volume 1, Number 7 October 23, 1953

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Price for this number: $0.50.

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THE LIFE HISTORY OF THE CRAWFISH *ORCONECTES (FAXONELLA) CLYPEATUS* (HAY)

(DECAPODA, ASTACIDAE)

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The details of the life histories of comparatively few species of crawfishes in the United States have been studied, however the life history of at least one species in each of the four major genera is fairly well known. Within the genus *Orconectes* two species of the subgenus *Orconectes* have been well studied: *O. propinquus propinquus* (Girard) by Creaser (1933a) in Michigan, and by Van Deventer (1937) and Bovbjerg (1952) in Illinois; and *O. immunis immunis* (Hagen) by Tack (1941) in New York. The subject of the present study, *O. clypeatus,* a member of the subgenus *Faxonella,* has a somewhat distinctive life cycle which might prove to be characteristic of this subgenus alone.

When this study was begun practically nothing had been published concerning either the ecology or life cycle of the species. The entire literature may be summarized in a few sentences. Hay (1899) described it as *Cambarus clypeatus* on the basis of a single female collected from a skiff at Bay St. Louis, Hancock County, Mississippi. From the date of this inauspicious first scientific recognition, *clypeatus* remained a species of questionable affinities (*c.f.* Faxon, 1914) until Creaser (1933b) described the first and second-form males and redescribed the female from two series of specimens collected in Louisiana and Alabama. He also included brief notes describing the "pools along the roadside" and "pools in a bog or swamp" respectively in which it was collected and included the statement that "many burrows were found along the edge of these pools . . . no doubt this species is a burrower, for the pools certainly dry at certain seasons of the year." Later the same year, Creaser and Ortenburger (1933) recorded *O. clypeatus* from Oklahoma and repeated Creaser's notes on its ecology. Lyle (1938) recorded it from Mississippi without comment. Hobbs (1942) recorded it from Florida, Georgia, Alabama and Arkansas and described its burrows along the sides of a roadside ditch in Jackson County, Florida as "marked by small, neatly constructed chimneys, simple, and ranging in depth from six inches to a foot." Penn (1942) recorded the species as abundant in a "pine barren pond" in Louisiana. Finally, Penn (1952) published a compilation of the data of the distribution and ecology of the species in Louisiana.

Within the boundaries of Louisiana *O. clypeatus* is one of the commonest species of crawfishes, and occurs in the following variety of habitats as listed by Penn (1952); temporary situations (58%), including roadside ditches, pineland sloughs, puddles and borrow pits, potholes in dry creek beds, and burrows; permanent situations (42%),

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including ponds, creeks, rivers, swamps and swamp ponds. Within the state it occupies these habitats in all physiographic regions except the recent alluvial lands and coastal marshes. The overall distribution of the species as presently known includes the Coastal Plain from southeastern Oklahoma to northeastern Arkansas and Georgia.

THE STUDY AREA

The life history of *O. clypeatus* was studied from October 1949 through January 1951 by means of field observations and statistical analyses of periodic samples of a natural population. The population which was studied and from which the samples were collected was located in a pineland ditch 2.4 miles south of Hickory, St. Tammany Parish, Louisiana. The ditch itself lay to the south side of an unused logging road which formed a retaining levee for an extensive, permanently inundated slough on its north side. The ditch was about 200 feet long, from one to two-and-one-half feet deep, and from three to five feet wide. On the bottom and along the sides, the ditch was covered with a thick carpet of *Juncus repens* Michx. throughout the entire year, and at least some parts of the ditch were shaded throughout each day.

Drought conditions, characterized by the complete absence of standing water anywhere in the ditch, and wet conditions characterized by the presence of standing water throughout the ditch, both occurred periodically during the study period (Table 1). During the wet periods the water level fluctuated with the amount of local rainfall, occasionally overflowing the banks. Usually either one or the other situation obtained when sampling was done, but an intermediate condition existed in which the deeper parts of the ditch were wet and the shallower parts dry. At such times separate samples were collected from each situation. Other crawfishes present in the ditch were numerous *Cambarellus shufeldtii* (Faxon) and occasional *Procambarus blandingii acutus* (Girard).

METHODS OF STUDY

The primary approach to the study was the analysis of periodic samples removed from the population. Collections of samples were originally planned for four week intervals over a period of sixteen months, but it was not practical to adhere strictly to this schedule. A total of sixteen samples on fourteen dates was collected; however, samples for six of the sixteen months are not represented (Table 1). During November and December 1949, drought conditions prevailed and, although field trips were made, the burrowing population was not found. During the other four months, January, March, August and November 1950, no field trips were made because of transportation difficulties.

The samples were collected by dipnet during the wet periods and by digging during the dry periods. Both methods were used along the sides of and in the middle of the ditch for each collection. From one-fourth to one-third of the length of the ditch was sampled when the ditch was wet, but during drought conditions the slower and more

TABLE 1.

BASIC DATA FOR HICKORY, LA. SAMPLES OF *Orconectes clypeatus*.

Lot Number	Date of Collection	Condition of Ditch	Type of Sample: Water	Type of Sample: Burrows	Maximum Water Depth (in inches)	Number (and percentages) of Specimens in Sample: ♂ I	♂ II	♀	Total
1583	1949: Oct. 16	Wet	X		15	3 (4.4)	48 (70.5)	17 (25.1)	68
——	Nov. 25	Dry		X	0	0	0	0	0
——	Dec. 6	Dry		X	0	0	0	0	0
1799	1950: Feb. 24	Wet	X		12	28 (3.6)	343 (44.2)	405 (52.2)	776
1885	Apr. 9	Wet	X		10	46 (10.2)	194 (42.8)	213 (47.8)	453
1946	May 12	Intermediate		X	6	5 (2.7)	102 (53.1)	85 (44.2)	192
1972	June 2	Dry		X	0	4 (2.9)	83 (60.6)	50 (36.5)	137
1980	June 13	Wet	X		12	16 (4.9)	158 (47.9)	156 (47.2)	330
2017	July 12	Dry		X	0	5 (8.5)	22 (37.3)	32 (54.2)	59
2022	July 15	Intermediate	X		3	37 (22.0)	58 (34.5)	7[illegible] (43.5)	168
2207	Sep. 29	Intermediate	X		6	88 (67.1)	7 (5.4)	36 (27.5)	131
2208	"	"		X	6	1	1	2	4
2218	Oct. 16	Dry		X	0	0	3	1	4
2229	Oct. 27	Dry		X	0	13 (86.6)	1 (6.7)	1 (6.7)	15
2246	Dec. 1	Dry		X	0	1 (7.0)	2 (10.7)	14 (82.3)	17
2255	Dec. 29	Wet	X		12	7 (1.7)	163 (47.3)	177 (51.0)	347
2261	1951: Jan. 24	Wet	X		12	18 (1.9)	422 (44.2)	515 (53.9)	955

laborious digging was restricted to from one-sixteenth to one-eighth of the length of the ditch.

The first sample made from burrows was taken in the second dry period (May 1950) after the study was begun. The burrows were found over the bottom and along the sides of the ditch and each was marked only by an inconspicuous entrance hole, usually less than three-fourths of an inch in diameter; chimneys were never seen. Below the entrance each burrow branched off into several tunnels, which eventually led to individual pockets or "cells" from eight to fifteen inches beneath the surface. Each pocket was occupied by one crawfish only.

Although this collection established the fact that the population burrowed during dry periods, the possibility that a portion of it might migrate during such times remained to be determined. Accordingly, each time a visit was made to Hickory, the slough across the road was checked with a dipnet for a migrating part of the population. Only six individuals of *O. clypeatus* were found in the slough and these only during wet periods following times when the ditch could have overflowed and flooded the road. If drought is a necessary factor for the completion of the life cycle of this species then the facts that the road was seldom flooded and that the unpopulated slough always contained water explains the scarcity of this species in collections from the slough. It was felt therefore that the absence of *O. clypeatus* from collections during the October-November 1949 drought was a result of faulty technic in sampling, not of an absence of the burrowing population.

The majority of the samples was preserved in alcohol either in the field or immediately upon return to the laboratory. Some first-form males, collected December 1, 1950, and some ovigerous females, collected between September and December 1950, were kept alive for observation in the laboratory.

In the laboratory the length of the cephalothorax was measured on all specimens. This measurement was taken on an observed mid-dorsal line from the tip of the rostrum to the end of the cephalothorax. All measurements were made with an ocular micrometer calibrated for a stereoscopic microscope. Each measurement was estimated to the nearest part of a micrometer unit but was converted for recording only to the nearest one-tenth (0.1) of a millimeter. As it was measured and recorded each specimen was assigned a sub-lot number and kept in an individual vial until the entire lot (*i.e.*, sample) had been completely studied.

A series of females was selected for the study of ovarian egg growth and production. After an ovary had been removed, the eggs were teased from it in a dish of water. Eggs were measured along their longest diameters and recorded to the nearest hundredth of a millimeter (0.01). Total ovarian egg count was recorded for only a few of the females so analysed.

A few specimens, in addition to certain samples, were collected separately and kept alive for observation in the laboratory. Such individuals were placed each in separate bowls or small aquaria containing rain water, sand, and usually some vegetation. All were fed Pablum.

STATISTICAL ANALYSES

A detailed discussion of the statistical analyses used in this study is not included in this paper. However, since the conclusions and interpretations of the life cycle are based largely on statistical methods, a brief summary of the methods employed and the steps of the various analyses is included here.

Methods used in the statistical analyses were modeled closely on those given by Peatman (1947) and Cazier and Bacon (1949). The measurement of cephalothorax length was taken as the criterion of age, but sexual maturity was based on other well-established biological criteria, *i.e.,* attainment of first form in the males, and maturation of ovarian eggs or the ovigerous condition in the females.

Since it was anticipated that each sample would give a clue to the stage of development of the entire population during a given time fragment in its annual cycle, it was necessary first to determine the homogeneity or extent of heterogeneity of the apparent age components (*i.e.,* size groups) of each sample. This was done following the grouping of measurements according to the following criteria: (1) each sample was kept separate according to time and place (*i.e.,* either aquatic or burrowing); (2) females, first-form males, second-form males, and unsexed young were separated into sub-groups respectively whenever they occurred in any one sample. At this point the sub-groups of the samples were each considered to be homogeneous on the fundamentals of location, time, and sex, but not on age.

Determination of homogeneity of age of these groups was based on three hypotheses: (1) that the frequency distribution of the cephalothorax length describes the form of the normal curve when the group is homogeneous; (2) that those groups which do not fit the normal curve, do not because of the presence of more than one age group within the group tested, and vice versa, those groups that do, do so because of the presence of only one age group; and, (3) that the heterogeneous groups (according to age only) can be resolved into their homogeneous components under certain conditions.

Grouped data were used throughout the study for all calculations of mean, standard deviation, and for those other statistics that were based upon the mean or standard deviation. The criteria for class groupings of the samples were: one-tenth millimeter (the very youngest crawfishes); two-tenths millimeter (the maturing groups), and five-tenths millimeter (the adult groups).

The first hypothesis was proved by using a set of young crawfish removed from the pleopods of their mother, thus of a known uniform (or homogeneous) age (Table 2, Dec. 1, group "j"). The second and third hypotheses, dependent on the proof of the first, were resolved by applying the chi-square Test of Significance to the separate frequency distributions of each of the sub-groups already known to be homogeneous except for age. The results (chi-square probabilities)

TABLE 2.

BASIC STATISTICS FOR GROUPS OF FEMALES AND UNSEXED JUVENILES

Date	Group	Number of Specimens	Cephalothorax Length in Millimeters		P
			Actual Range	Mean	
1949:					
Oct. 16	Q	1	18.8	—	—
	R	16	13.4 — 16.1	14.9	.50
1950:					
Feb. 24	a	5	5.2 — 5.8	—*	—*
	A	333	6.0 — 10.0	8.0	.02
	I	17	10.3 — 12.7	11.0	.50
	S	46	13.8 — 18.6	15.7	.99
Apr. 9	b	6	7.8 — 8.8	—	—
	B	141	8.9 — 12.3	10.6	.30
	II	39	13.0 — 16.9	15.1	.50
	T	30	15.5 — 18.2	16.7	.50
	W	3	19.0 — 19.6	—	—
May 12	c	1	8.1	—	—
	C	80	9.8 — 13.3	11.5	.90
	III	8	13.6 — 14.6	—	—
June 2	D	50	10.6 — 13.3	12.0	.90
June 13	d	4	8.6 — 10.2	—	—
	E	148	10.5 — 13.8	12.2	.10
	IV	8	14.1 — 16.5	—	—
July 12	F	32	10.9 — 13.8	12.4	.50
July 15	G	73	9.6 — 14.4	12.4	.10
Sep. 29	H	36	12.3 — 15.4	13.7	.50
Oct. 15	g	6	4.8 — 5.2	—	—
	J	1	14.7	—	—
Oct. 27	h	3**	2.1 — 2.3	—	—
	K	1	14.8	—	—
Dec. 1	j	50**#	2.4 — 2.8	2.6	.20
	k	44**	2.0 — 3.2	2.7	.50
	m	2**	3.8 — 4.2	—	—
	e	1	11.2	—	—
	M	12	13.1 — 15.2	—	—
Dec. 29	n	6	2.8 — 3.4	—	—
	o	148	3.5 — 4.7	4.2	.50
	N	23	11.5 — 18.0	14.2	.50
1951:					
Jan. 24	p	30	3.0 — 3.4	3.2	.90
	q	155	3.7 — 4.6	4.1	.30
	r	174	4.5 — 5.8	5.2	.50
	s	119	5.6 — 6.6	6.1	.50
	t	5	6.7 — 7.6	—	—
	f	4	10.8 — 11.7	—	—
	P	52	13.8 — 19.0	16.7	.02

* Mean and chi-square probability not calculated for groups of less than 15 specimens. A chi-square probability of 0.10 (10%) and above estimates with confidence that the groups are homogeneous.

** Unsexed juveniles.

\# Attached to pleopods of mother.

gave estimates only of the occurrence of significant deviations or the lack of deviations of any of the distributions from the normal distribution. A significant deviation was interpreted as the result of the inclusion of more than one age group within a distribution. Accordingly, the frequency distributions of the thus-established heterogeneous age groups were re-observed and subdivided into apparent smaller homogeneous groups (*i.e.,* at apparent modal breaks, or de-

TABLE 3.

Basic Statistics for Groups of Males

Date	Group ♂ II	Group ♂ I	Number of Specimens	Cephalothorax Length in Millimeters: Actual Range	Cephalothorax Length in Millimeters: Mean	P
1949: Oct. 16	R		48	11.9 — 16.6	14.4	.50
		1	2	13.7 — 13.9	—*	—*
		Q	1	19.2	—	—
1950: Feb. 24	a		6	3.7 — 5.8	—	—
	A		310	6.0 — 10.2	8.1	.50
	I		27	10.4 — 14.8	12.4	.20
		S	28	12.6 — 17.3	14.8	.09
Apr. 9	b		5	7.2 — 8.5	—	—
	B		168	8.9 — 12.4	10.4	.50
	II		20	12.5 — 15.4	13.6	.50
	T		2	16.1 — 16.4	—	—
		2	36	11.9 — 14.8	13.6	.50
		W	10	15.1 — 17.5	—	—
May 12	c		1	8.7	—	—
	C		99	9.5 — 13.4	11.5	.50
	III		2	14.2 — 14.7	—	—
		3	5	11.5 — 13.8	—	—
June 2	D		83	9.8 — 13.8	11.6	.20
		4	4	12.0 — 13.6	—	—
June 13	d		3	8.4 — 9.8	—	—
	E		153	10.0 — 13.2	11.7	.50
	IV		3	13.7 — 14.5	—	—
	V		1	16.1	—	—
		5	16	11.8 — 13.6	12.8	.20
July 12	F		22	11.1 — 13.1	12.1	.50
		6	5	11.3 — 13.6	—	—
July 15	e		1	9.2	—	—
	G		56	10.4 — 14.2	12.1	.50
	VI		1	15.3	—	—
		7	37	11.0 — 14.2	12.5	.10
		8	1	18.2	—	—
Sep. 29	H		7	12.8 — 14.6	—	—
		9	88	10.8 — 15.3	12.9	.50
		10	1	16.4	—	—
Oct. 15	J		3	13.0 — 13.8	—	—
Oct. 27	K		1	14.0	—	—
		11	12	11.9 — 14.1	—	—
		12	1	16.4	—	—
Dec. 1	M		2	12.9 — 13.3	—	—
		13	1	13.5	—	—
Dec. 29	n		6	3.3 — 3.6	—	—
	o		140	3.7 — 4.6	4.2	.50
	N		17	10.7 — 15.8	13.3	.50
		14	6	11.8 — 14.5	—	—
		15	1	16.6	—	—
1951: Jan. 24	p		30	3.0 — 3.6	3.4	.90
	q		146	3.6 — 4.4	4.0	.50
	r		81	4.5 — 5.1	5.0	.95
	s		121	5.2 — 6.1	5.7	.30
	t		47	6.1 — 6.8	6.4	.50
	f		10	13.4 — 13.9	—	—
	P		23	14.0 — 18.4	15.8	.90
		16	18	11.6 — 18.5	14.2	.50

* Mean and chi-square probability not calculated for groups of less than 15 specimens. A chi-square probability of 0.10 (10%) and above estimates with confidence that the groups are homogeneous.

pressions in the frequency distributions) and the chi-square test applied to each new sub-group. In the majority of cases the heterogeneous age groups could be subdivided by this procedure into homogeneous age groups with an acceptable degree of confidence.

When all lots had been subdivided into their component homogeneous age groups (Tables 2 and 3), the data were plotted as bars (actual ranges and means) on time graphs and the major facts of the annual cycle of this species were ready for interpretation. Reference to these graphs (figs. 1 and 2) will be made repeatedly in connection with the elaboration of the life cycle which follows.

THE LIFE CYCLE

Females.—The maturing females (fig. 1, series A, B, C . . . P) increased significantly in size from February to early June at which time they reached a growth plateau that was maintained through July. Between July and September another significant increase in growth was evident. Since ovigerous females were first seen in September this last increase in size is interpreted as representing the "maturity molt" of the spawning population of females and probably compares to the male maturity molt (*i.e.,* transformation from second- to first-form) which must occur prior to copulation. From September to December the mature females did not show any additional significant change in size.

The December adult females (group "N") appeared to have increased again in January forming part of group "P", indicating that at least one molt had taken place. That females molt after the young leave them was substantiated by laboratory observations. In terms of the life history this molt may be interpreted as marking the end of the active reproductive season. Tack (1941) with *Orconectes immunis* and Penn (1943) with *Procambarus clarkii* both found that females molted after their young had left, although not immediately.

Group I (fig. 1, series I-IV) is assumed to have been a continuation of a 1949 group comparable to group "f" of January 1951, and was probably about a year old. Although not represented by large numbers, this series was definitely represented in the samples through June, but by September seemed to have disappeared, reappearing presumably in December and January to form the upper ranges of groups "N" and "P".

In view of the facts that representatives of Series I-IV were not in the samples from July to December and that several large females were collected in September showing signs of having already completed spawning (*i.e.,* with remains of hatchlings' exuviae on their pleopods) it is thought that other individuals also had been ovigerous before September and had been overlooked because they were already in burrows.

Individuals of the series "Q" through "W" were not evident in the samples from April on, and it is assumed that they had died by this date. It is assumed that group "P", representing the terminus of two combined series (A-P and I-IV) which were one and two years old

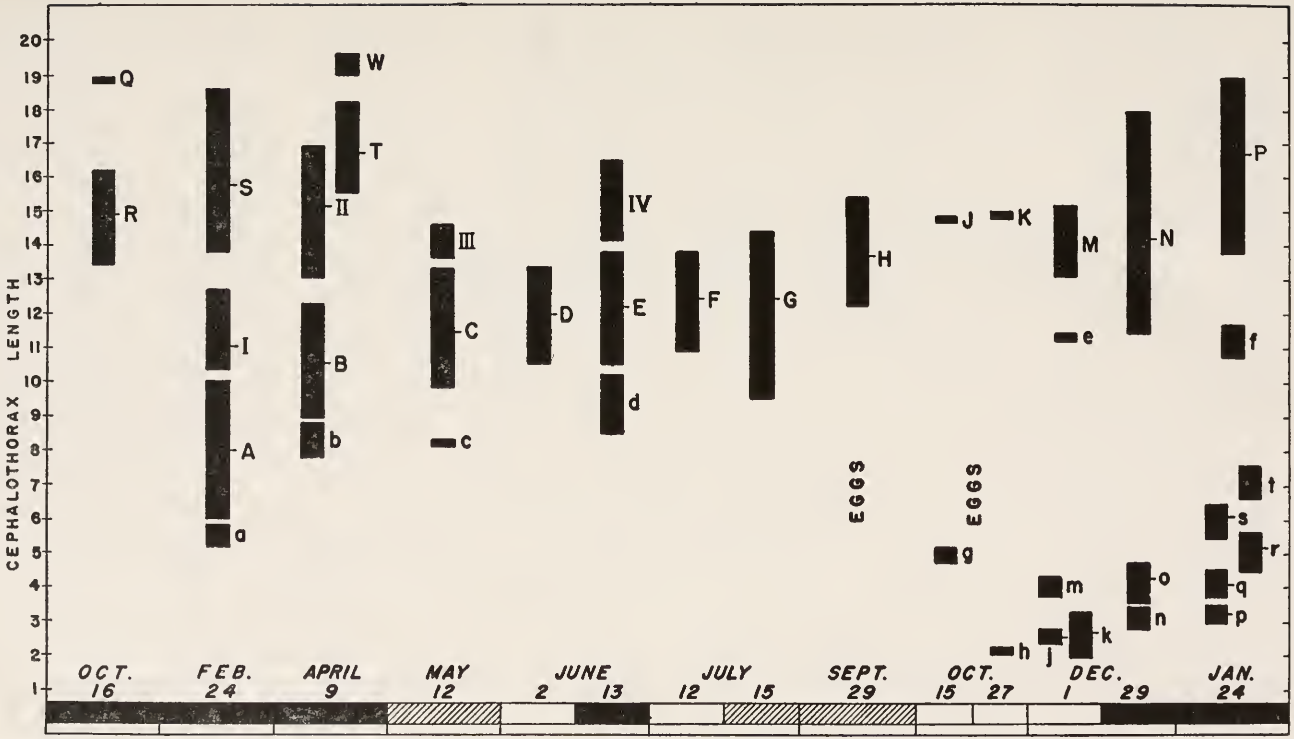

Figure 1. Females. Vertical bars represent age groups, horizontal lines represent the means of the groups. Those groups for which the means are not given contain less than fifteen individuals. Horizontal bar at bottom of graph indicates the condition of the ditch: solid=wet; cross-hatched=intermediate; open=dry.

respectively, followed the same trends as groups "Q" thru "W" and died in the spring of 1951.

The presence of various groups of juveniles (fig. 1, series a, b, c . . . f) from October through January indicates that egg maturation and embryonic development of the entire population was spread over a period of several months. The growth trends of each of these groups cannot be clearly understood from the analyses. The latest juveniles added to the free-swimming population (group "p") probably represented the offspring of the few late-spawning females found in December with young still attached to their pleopods. It is assumed that the January juvenile groups eventually gave rise to groups comparable to groups "a" and "A" of February 1950.

Males.—As might be expected the growth of the male population as a whole paralleled that of the females in most respects, but the interpretation is complicated by the shifts in groupings accompanying the maturation molt from second- to first-form. The maturing second-form males (fig. 2, series A, B, C . . . P) increased significantly from February to May; from May through July they endured a growth plateau as did the maturing females of the same time period. Sometime between May and July some of the larger second-form males apparently matured and molted to first-form, and there is evidence that the greater percentage actually transformed by May. The period from February to May was characterized by significant growth increases, and, if the male population exactly paralleled the female a maturity molt should not have occurred during this time. However, with the advent of the summer growth plateau and because of the overlap of size groups of second- and first-form males in May and June (fig. 2, groups "C" with "3", and "D" with "4") it is inferred that some of the larger second-form males had molted into first-form by May (fig. 2, group 3), and that others molted and became parts of the groups "4", "5" and "6", and most of the groups "7" and "9" when the climax of breeding was reached in September.

The majority of group "9" is thought to have continued as first-form males to December. Groups "H" through "M" represent either second-form males that had already molted back to first-form (*i.e.,* from group "3" through "7") and/or those which would molt to first-form later in January. From the statistics comparing these groups the latter assumption seems most justified.

Groups "11", "13" and "14" represent, at least in part, a continuation of group "9". By December and January, individuals of these groups molted back to the second-form and constituted the upper parts of groups "N" and "P". Those individuals of groups "N" and "P" which had not yet molted to first-form apparently did so in January and constituted the upper part of group "16".

The fact that first-form males molt back to second-form was established by laboratory observations of first-form males of the December sample, most of which had molted back to second-form by January 27th.

Group "e" (fig. 2, series a, b, c . . . e) appears to have developed by December into the lower part of group "N". By January the lower part of group "N" is thought to have molted into first-form and

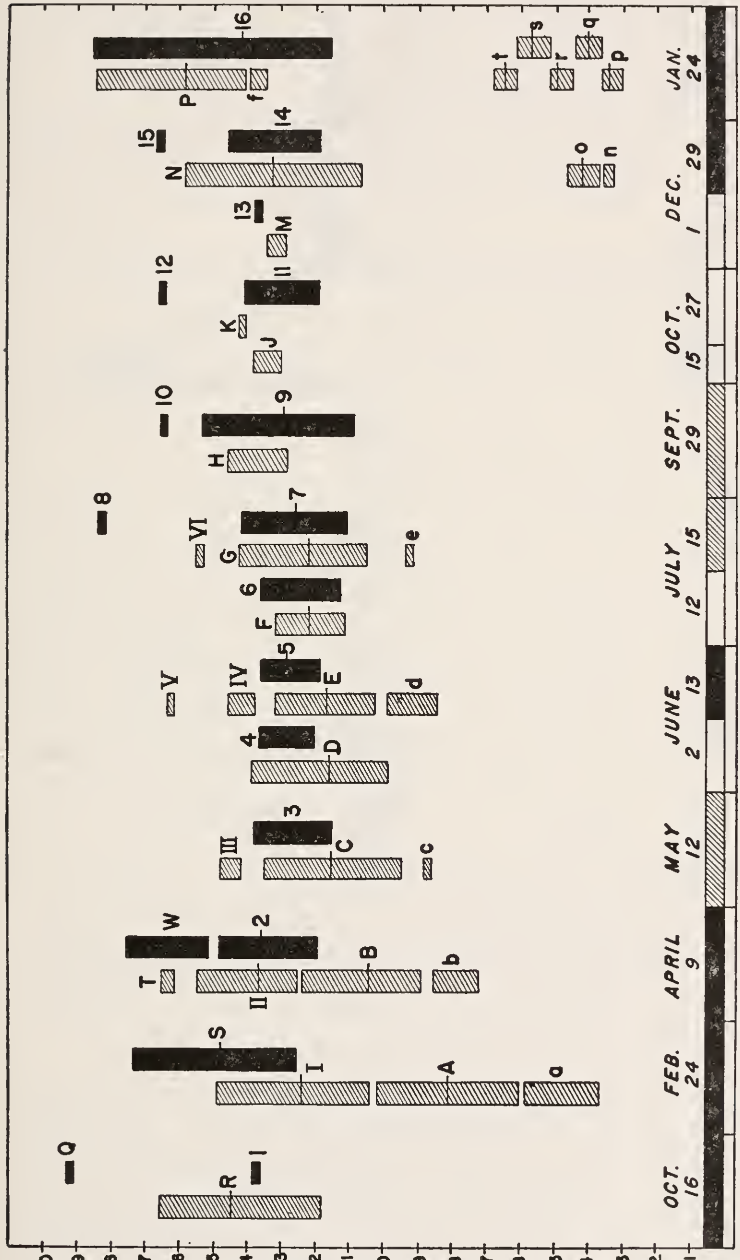

Figure 2. Males. Second-form males represented by cross-hatched bars, first-form males by solid bars. Vertical bars represent age groups, horizontal lines represent the means of the group. Those groups for which means are not given contain less than fifteen individuals. Horizontal bar at bottom of graph indicates the condition of the ditch: solid = wet; cross-hatched = intermediate; open = dry.

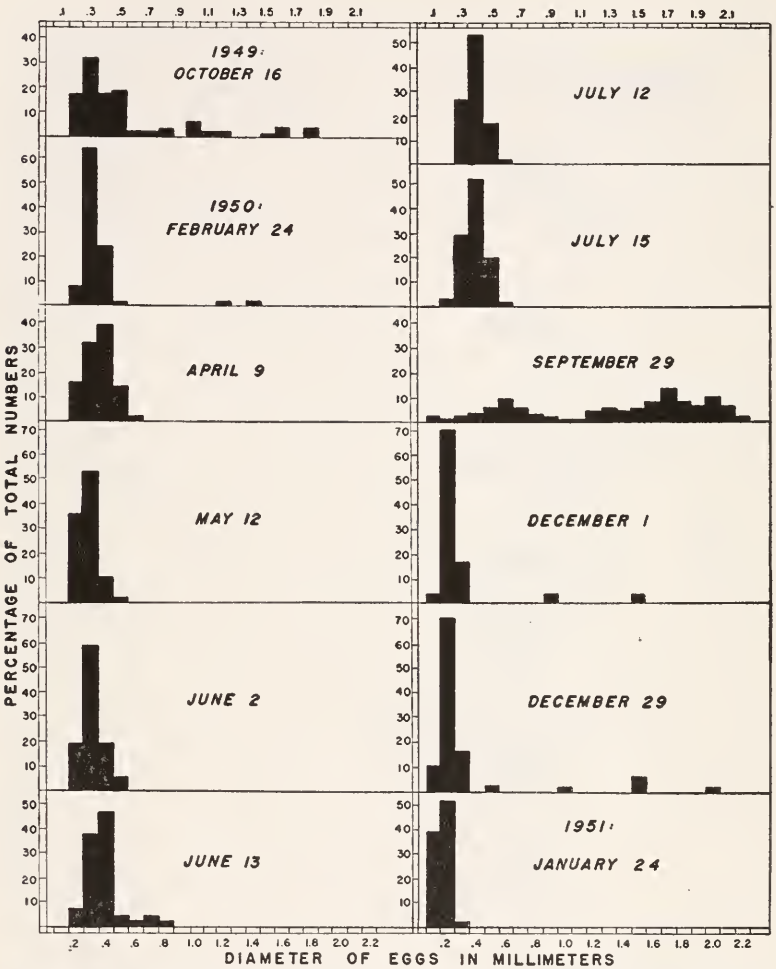

Figure 3. Maturation of ovarian eggs. Each sample is represented by a percentage frequency histogram in which each bar represents the percentage of the total number of individuals within the histogram.

then constituted at least the lower part of group "16".

Group I of February (fig. 2, series I-VI) apparently was constituted of contributions from group "R" (its upper range) and from a group comparable to group "f" of January (its lower range). Representatives of this series were in each sample from February through July 15th. Prior to February some individuals molted to first-form (group "1") and from February through July the majority also molted to first-form contributing to the groups "S" and "2" through "7". From September through December the remaining few molted to first-form and were represented by groups "10", "12" and "15".

Groups "Q" and "W" and the upper part of "S" apparently died in the spring as indicated by the absence of the proper size in the May and June samples. The upper range of group "R" was probably composed of males recently molted from first- to second-form. Group "T" was a continuation of this group which apparently died by May.

From these conclusions the fate of the January adult group may be stated. The upper ranges of groups "P" and "16" should have died first and the remainder of these groups probably died before the next major reproductive period in 1951. Group "f" should have formed a group comparable to group "I" of February and lived to be about two years old.

The growth trends of the male juveniles (fig. 2, series n, o, p . . . t) were assumed to be essentially similar to those of the female juveniles.

Ovarian Egg Development.—The trend of ovarian egg development for the year 1950 was determined quantitatively from a comparative study of percentage frequency histograms (fig. 3) made for each sample, in which the measurements of ovarian eggs were grouped into 0.10 mm size classes.

Prior to July 12th the ovarian eggs seemed to have been static in size and in this stage did not show any tendency toward maturing at different rates as might have been expected from the study of the egg-laying and rates of development of the young.

Except for the samples of February and June 13th the upper ranges of these did not exceed 0.6 mm (fig. 3). Only two percent of the February sample fell within the higher range, and since it was concluded previously that most of the females had already undergone a molt terminating the major reproductive period, it is inferred that these larger eggs in February were eventually resorbed. Penn (1943) for *Procambarus clarkii* gave evidence that a greater number of eggs may be developed in the ovary than are laid, and Stephens (1952) showed that ovarian eggs are readily resorbed by female *Orconectes virilis* under experimental conditions.

By September the majority of the eggs were in the large size group with peaks at 1.3, 1.7 and 2.0 mm. The presence of these large eggs within the ovaries coincided with the presence of eggs on the pleopods. Within the range below 1.0 mm the peak of 0.6 mm occurred. It is thought that these eggs eventually matured and were laid.

In September another small peak was noted at the 0.10 mm size. These are believed to represent recently developed ovarian eggs of females which had already spawned prior to the date of the sample.

In October females carrying eggs were still present in the samples. Although no ovarian study was made for this month, due to the inadequacy of the sample, it is assumed that the results of the October 1949 analysis would roughly apply. Although apparently egg-laying was still in progress, the majority of the mature female population had already spawned, as indicated by the higher percentages of small eggs.

The December samples showed that at least ninety percent of the population had already laid eggs prior to this date. The large eggs still present in the ovaries represented either those that were eventually resorbed, or that were eventually laid at the individual erratic spawning times. In general composition this sample compared with that of February 1950.

By January 1951 the ovarian eggs of the females were all immature, indicating that the reproductive period for the population as a whole had definitely terminated.

The reproductive potential was determined from a total count of the ovarian eggs of all mature non-ovigerous females (nineteen) of the September sample. The average of these counts is 14.2 eggs per female within the relatively wide extremes of 9 and 21 (Table 4).

Sex Ratio and Burrowing Responses.—Although burrowing during drought was adequately confirmed by field observation, these activities could not be observed directly during the wet periods and an analysis of the sex ratio of these collections was relied on to furnish these data. It was assumed that if the water samples, which were apparently representative of the water population, did not contain the expected sex ratio, then a significant absence or predominance of one or the other sex for any particular sample would indicate a burrowing component.

The "theoretical sex ratio" was based on the actual sex ratio of the younger male and female homogeneous groups of the February 1950 sample (figs. 1 and 2, groups "A"). The sex ratio for this group was females/males=333/310 or 1.07. This group was chosen because the specimens were large enough to sex easily and all of the young population was assumed to be in the water at this time of the year. To determine the chance differences and real differences between this ratio and the sex ratio of any other group or sample, the limits of a continuum of likely hypothesis (differences due to chance) and the limits marking off two continua of unlikely hypothesis (real differences) were established from the percentage of males to females in the young February groups.

The results of the comparison (Table 5) show that the females were not significantly different from the theoretical sex ratio during the months of February and December 1950 and January 1951, and possibly April 1950. For these months either both sexes were burrowing or both were not and the fact that both sexes were responding alike obscures the issue. However, since all these samples were large in numbers and taken from the ditch during decidedly wet periods (Table 1) it is assumed that most of the population was probably in the water.

Those collections in which the percentages of females were significantly less than the theoretical ratio were the samples of October 1949 and June 13, July 15 and September 1950. Since the females were not in the water samples it is assumed that they were burrowing. Since burrowing coincided in September with the presence of large eggs in the ovaries (fig. 3) or the presence of eggs on the pleopods, it is concluded that the egg-laying activity was a stimulus to burrowing. This conclusion lends corroboration to the possibility of erratic or pre-seasonal reproductive activities of the June 13 and July 15 samples as already indicated (fig. 3) from the study of ovarian eggs.

Analyses of the samples taken from burrows indicates that with one

TABLE 4.

OVARIAN EGG PRODUCTION

Cephalothorax Length (mm)	Number of Eggs of Individual Females	Total Number of Females of Size Class	Total Number of Eggs of Size Class	Average Number Eggs per Female
13.1	11	1	11	11.0
13.3	12, 16	2	28	14.0
13.5	10, 11, 12	3	33	11.0
13.7	9, 12, 16, 20, 21	5	78	15.6
13.9	15, 15, 18	3	48	16.0
14.1	13, 14	2	27	13.5
14.3	12, 15, 18	3	45	15.0
		—	—	—
	GRAND TOTAL	19	270	14.2

exception (July 12) there was a significant absence of females in each of the dry samples. Since it has been established that the entire population burrowed during drought there is no logical reason why the females should not have been collected except that the technic of dry sampling was inadequate. The only other conclusion would be that of a mass death of only the females during drought times and this is biologically unacceptable.

SUMMARY AND DISCUSSION OF LIFE CYCLE

During the dry periods the crawfishes burrowed along the sides of and in the bottom of the ditch instead of migrating to the adjacent slough, a permanent body of water. There was no evidence during the course of this study to indicate that the crawfish ever migrated over dry land; however, dispersal was possible and evidences of it were observed during periods of flooding rains. Ovigerous females were found in burrows regardless of the conditions in the ditch. Indeed, the first ovigerous females collected were dug from burrows alongside the flooded ditch in September. It may be significant that immediately following this observation a drought period ensued and the remainder of the population was forced to burrow. The females carrying the vulnerable eggs were thus, by natural instincts, already in protected burrows when the drought conditions began. It would seem that an ovigerous female could not be so agile or successful a burrower as one unencumbered by eggs. However, it is not known whether spawning females burrowed before or after laying their eggs.

The eggs of *O. clypeatus* are surprisingly large in comparison to the relatively small size of the females carrying them. This certainly is correlated with the low average of 14.2 eggs per female, and perhaps the whole concept is correlated with the burrow habitat of the ovigerous females. It is interesting, and possibly significant, that a very low reproductive potential also obtains in *Procambarus hagenianus* (Faxon) in which the females similarly shun free-water when ovigerous (Lyle, 1938).

Ovigerous females were collected on September 29 and October 15, 1950. No collections at all were made in November, but females collected on December 1st were carrying young still clinging to their pleopods. Although the length of time between oviposition and hatching, and the time that females normally carry their young was not determined it is assumed that both time periods were of short duration since free-living young first appeared in the population in the October 15th sample, about two weeks after the first ovigerous females were collected.

The juveniles of January 1951 were represented by five overlapping age groups. Three groups comparable to the three larger groups of this sample probably participated in the major spawning period (September-October) of 1950. Groups comparable to the two younger groups of January 1951 may have given rise to groups that spawned erratically (*i.e.,* post-seasonal: November-December) during 1950.

As a group the maturing females increased significantly in size from February to early June. From this date until July 15th they

TABLE 5.

SEX RATIOS

Date	Range	Total Crawfish	Males	Females	Percent of Females
1949:					
Oct. 16	All	68	51	17	25
1950:					
Feb. 24	Adults	122	55	67	55
	Juveniles	654	316	338	52
Apr. 9	All	453	240	213	47
May 12	All	192	107	85	44
June 2	All	137	87	50	36
June 13	All	340 .	184	156	46
July 12	All	59	27	32	54
July 15	All	169	96	73	43
Sep. 29	All	131	95	36	27
Dec. 29	Adults	47	24	23	49
	Juveniles	300	146	154	51
1951:					
Jan. 24	Adults	107	51	56	52
	Juveniles	848	389	459	54

remained nearly static in size, but between mid-July and September they again increased significantly in size, presumably undergoing a maturity molt. Another molting period ensued during December and January marking the termination of the active reproductive period for the majority of the mature females. Apparently most of these females lived about a year and a half, dying before the next major spawning period. The females that were already a year old in early 1950 probably constituted an erratic pre-seasonal (July-August) spawning group in 1950 and died in the first months of 1951 at an age of about two years.

As a group the males were similar to the females in growth patterns. The maturing second-form males increased significantly in size until May at which time the growth plateau was reached. During May a few of this group molted into first-form males. By September the majority of them molted into first-form except the very youngest. These latter apparently transformed towards the end of December and formed an erratic post-seasonal spawning group among the males. Many of the first-form males molted back to second-form during December and January. The participants of the major spawning group lived to be about one year old, while the participants of the post-seasonal spawning period lived to be about two years old.

ACKNOWLEDGEMENTS

The writer is deeply indebted to Dr. George Henry Penn under whose direction this study was made. She is particularly grateful for his help on many of the field trips and especially for the collections of June and July which he made; for his many helpful suggestions during the laboratory exploration, and for his guidance and encouragement in the presentation of this paper. She is also indebted to Prof. Joseph A. Ewan, of the Department of Botany of Tulane University, for the identification of the plants in the ditch, and to Messrs. Lothar E. Hornuff, Jr. and Edward N. Lambremont for their assistance on several field trips.

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