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SOME ASPECTS OF THE LIFE HISTORIES OF THREE CLOSELY RELATED CRAYFISH SPECIES, ORCONECTES OBSCURUS, O. SANBORNI, AND O. PROPINQUUS^{1, 2}

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ABSTRACT

The life histories of three closely related species of crayfish, Orconectes obscurus (Hagen), Orconectes sanborni (Faxon) and Orconectes propinquus (Girard), which occupy separate rivers in northeastern Ohio, were studied and compared. Crayfish were collected from the same location, approximately bi-weekly, from April through October 1967.

Major aspects of life histories of the three species are similar and can be summarized as follows. Mature crayfish mate in August and September; eggs are laid in April and May and young become independent in June. Growth and activity cease during the winter and resume in the spring. First-form males change to second form in the spring and in late summer revert back to first form. Immature individuals molt several times during the summer, each time increasing in carapace length by one mm, or sometimes by two mm or more. Males of Orconectes obscurus and O. sanborni do not attain sexual maturity until their second summer, but many O. propinquus males become sexually mature in their first summer.

Attempts at interspecific mating in the laboratory yielded one successful mating, that between a male *Orconectes propinquus* and a female *O. sanborni*. This female could not be kept, so it is not known whether viable young would have been produced.

The pleura were clipped in different combinations for marking and recapture studies which were conducted during the summer of 1967. Rates of recapture of marked individuals were: Orconectes obscurus, 28%; O. sanborni, 1%; and O. propinquus, 14%.

INTRODUCTION

Although literature on crayfish systematics is extensive, relatively little information is available on life histories, and no one has published a comparative study of the life histories of closely related crayfish species using identical methods. This study compares the life histories of Orconectes obscurus (Hagen, 1870), Orconectes sanborni (Faxon, 1885) and Orconectes propinguus (Girard, 1852).

Fitzpatrick (1967) revised the taxonomy of the Propinquus Group of Orconectes, after statistical and qualitative analyses of several characters, and proposed two subgroups, Sanborni and Propinquus. Orconectes obscurus and O. sanborni are in the Sanborni Subgroup and O. propinquus is in the Propinquus Subgroup.

METHODS

The studies of *Orconectes obscurus* were made in the West Branch of the Mahoning River, a tributary of the Ohio River, in Ravenna Township, Portage County, Ohio (north of Ohio Route 5); those of *O. sanborni* were made in the Cuyahoga River, in Streetsboro Township, Portage County, Ohio (between Ohio Routes 14).

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and 303); and those of *O. propinquus* were made in Morgan Township, Ashtabula County, Ohio (west of Ohio Route 45). Collections were always made at the same sites in each of the rivers; habitat areas in each of the rivers were approximately the same size. Water temperature was taken at each collection; the mean temperatures were 14.9°C for the West Branch, 16.0°C for the Cuyahoga, and 17.8°C for Bronson Creek. Substrate in the West Branch and Cuyahoga areas was cobbles and boulders (65 to 256 mm and up) composed predominantly of sandstone but some shale. The substrate of the Bronson Creek area was shale with some clay and was less firm than was that of the other two sites. The Cuyahoga River area was the only one having submergent vegetation, which consisted of species of *Elodea*, *Vallisneria*, *Potamogeton*, *Myriophyllum*, and *Ceratophyllum*.

Collections were made about bi-weekly; the duration of each period of collecting was approximately one hour. At each collection the following was entered on a data sheet: time, date, specific geographical location, method of capture, collection zone (riffle or pool), type of banks, substrate (type and compaction), flow stability (intermittent or continuous), amount of current, width and depth of water, aquatic vegetation, temperature of the air and water, and general weather conditions. Crayfish were captured by use of a minnow seine (¼-inch mesh, 6-foot length), held downstream from rocks being overturned by foot in order to catch crayfish dislodged from under them. Sometimes the seine was supplemented by a dip net. The carapace length (the distance from the tip of the rostrum to the posterior border of the thoracic region), sex, and form (if male) of each crayfish were recorded and then the crayfish was returned to the water. (No distinction was made between juvenile and second-form males.) Record was made of crayfish that were ovigerous, about to molt, recently molted, or copulating. Age groups were determined from graphs, using the methods of Van Deventer (1937).

From 13 July through 4 September 1967, all crayfish were marked by clipping the pleura in different combinations (Goellner, 1943). For example, in R12 L34, the clipped pleura would be the first and second on the right side and the third and fourth on the left side. In this way, records could be kept as to frequency of recapture, approximate time of molting, and growth per molt for individual crayfish. The scars from the clippings were distinct even after three molts, because regeneration was relatively slow and usually produced deformed pleura (Goellner, 1943).

Mating experiments were conducted in the laboratory, first with members of the same species and then with individuals of two different species together, on 28 August and 31 August 1967, respectively. One or two individuals of each sex, of approximately equal size, were placed in fingerbowls, 20 cm in diameter. Seventeen pairs were used in the intraspecific experiment and eighteen pairs in the interspecific experiment. In the interspecific-mating experiment, all three combinations of species were tried. Pairs were observed every 15 minutes. The presence of a sperm plug was chosen as the criterion for a successful mating. All females were examined for sperm plugs before and after each experiment.

RESULTS

Composition of the Collections

Population sampling was started during the first week of April 1967 and continued through October 1967, when growth for the year had ceased and sizes corresponded to those of individuals caught in April. (Freshly molted individuals of October obscurus and O. sanborni were last observed on 30 September and of O. propinguus on 7 October 1967.)

Several general trends in the population size and composition were noted (figs. 1, 2 and 3). The early-spring and late-fall collections were the smallest, but the summer collections were relatively large, reflecting recruitment of young-of-the-

year. The major periods of form change occurred during May and from the end of June through July and August. In May, most of the first-form males of all three species changed to second form (demonstrated best in fig. 1). During June, no first-form males of *Orconectes obscurus* were captured (fig. 1), but newly molted first-form males of *O. sanborni* were captured beginning on 30 June, and of *O. propinquus* beginning on 24 June, thus identifying the beginning of the time of change to first form in these species (figs. 2 and 3). The first freshly molted first-form males of *O. obscurus* were captured on 9 July.

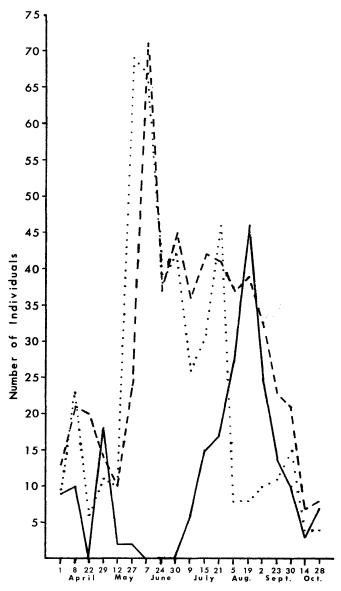
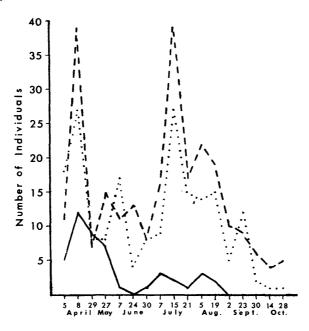


FIGURE 1. The relationship of abundance, form, and season in *Orconectes obscurus*, females; ———= first-form males; • • • • • = second-form males.

Sex ratios of all three species were approximately 1:1 most of the time. The only departures from this ratio were in the fall samples of *Orconectes sanborni* (when the numbers collected were small), and in the collections of all species in April and May, at both times of which the ratio of females to males was 1:2. In the latter case, the difference was probably a result of inadequate sampling at a time when ovigerous females remain hidden.



Ovigerous Females and Appearance of Young

Orconectes obscurus, O. sanborni, and O. propinquus all laid their eggs in the spring. Ovigerous females of O. obscurus were collected on 8, 22, and 29 April, and 27 May; of O. sanborni on 8 and 29 April and 27 May; and of O. propinquus on 27 May. Juveniles of all three species were seen on 24 June, but were too small (approximately 6 mm in carapace length) to be caught in the seine. The young were found in the shallowest places (approximately 3–10 cm deep).

Form Changes in the Males

Both first-form and second-form males of all three species were present in the April collections, but most of the larger males were first form and the smaller ones second form (figs. 4, 11, and 18). During the current study (1967), the crayfish had begun molting by 29 April, because recently molted individuals of both *Orconectes obscurus* and *O. sanborni* were collected on that date. Individuals in a premolt stage were distinguishable because of their soft, debris-laden exoskeletons. As early as 22 April, specimens of *O. obscurus* were taken that were in a premolt stage.

Change of males from first to second form began in May, as can be seen by the decrease of first-form males and increase of large second-form males (figs. 5, 12, and 19). By the end of May, virtually all males of all three species were in the

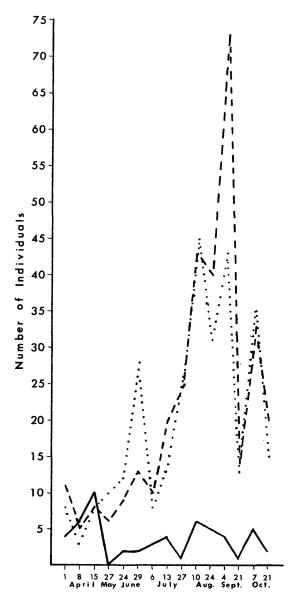
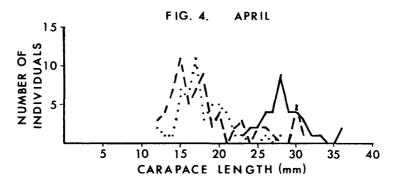
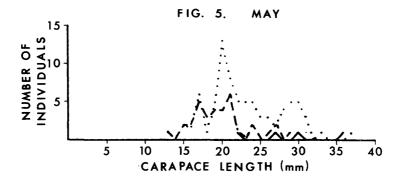


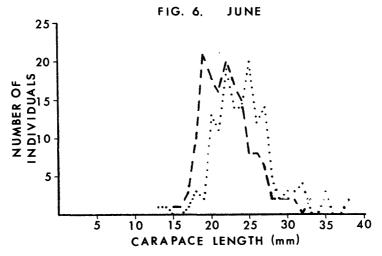
FIGURE 3. The relationsip of abundance, form, and season in *Orconectes propinquus*. ----= females; ----= first-form males; • • • • = second-form males.

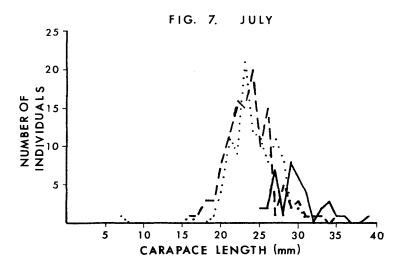
second form. In June, only the following few numbers of first-form males were collected: no *Orconcectes obscurus*, two *O. sanborni*, and four *O. propinquus* (figs. 6, 13, and 20). Of these, one of the specimens of *O. sanborni* and all four of *O. propinquus* had just become first form for the first time in 1967 (as evidenced by their clean exoskeletons).

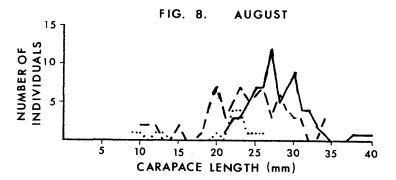
The mid-summer change from second form back to first form began in late June or early July (Figs. 7, 14, and 21). The first capture of *Orconectes obscurus* first-form males was 9 July, but one of *O. sanborni* was taken on 30 June, and two of

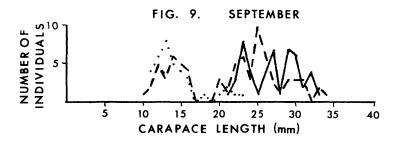


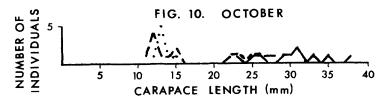




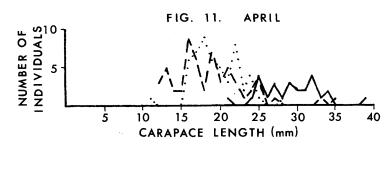


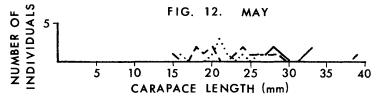


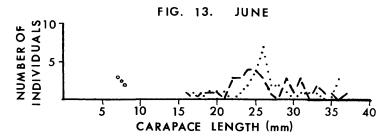




Figures 7-10. Size-frequency distributions of *Orconectes obscurus*. ----=females; ----=f







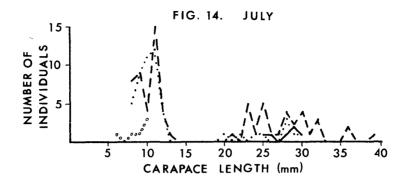
FIGURES 11-13. Size-frequency distributions of *Orconectes sanborni*. ----=females; ---=first-form males; ---=second-form males; o o o o o = juveniles.

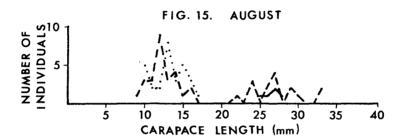
O. propinguus on 24 June. These individuals had clean exoskeletons, indicating that they had molted previously the same year.

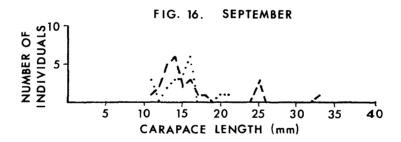
Copulation

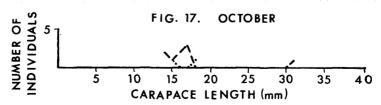
Copulation was observed from the middle of August through September. In one hour on 18 August, nine pairs of Orconectes obscurus were observed copulating; four pairs were observed on 26 August and two pairs on 1 September. Two pairs of O. sanborni were observed copulating, one on 14 August and another on 26 August. In addition, one pair of O. sanborni was observed copulating after being taken into the laboratory on 26 July. One pair of O. propinquus was observed copulating on 24 August in the collecting bucket, after being collected and prior to being released again.

During the laboratory mating experiments, the following successful matings were observed: two matings of *Orconectes sanborni*, one lasting 15 minutes and one 45 minutes, and one mating of *O. propinquus* lasting two hours. Although four interspecific matings were observed, only one was successful. The one successful mating lasting 30 minutes, was between a 24 mm male *O. propinquus* and a 25 mm female *O. sanborni*.

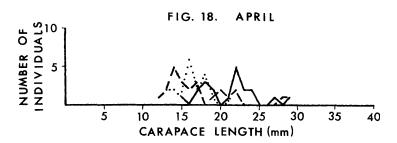


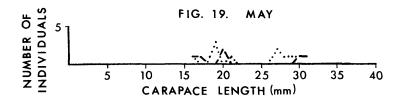


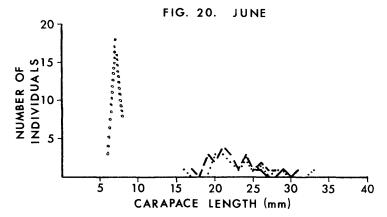




FIGURES 14-17. Size-frequency distributions of *Orconectes sanborni*. ----= females; ---= first-form males; ---= form males; ---= form males; ---= first-form males; ---= females; ---= first-form males; ---= females; ---= females; ---= females; ---= first-form males; ---= first-form males; ---= females; ---= females; ---= females; ---= first-form males; ---= females; ---= first-form males; ---= first-form



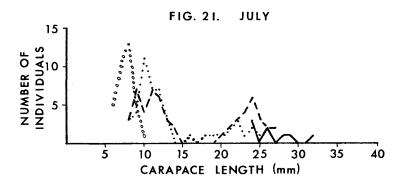


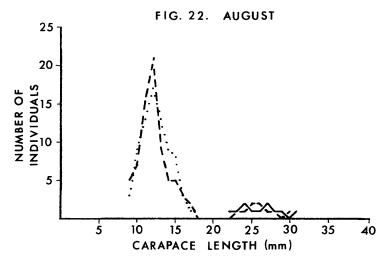


Figures 18-20. Size frequency distributions of Orconectes propinguus. ----=females; ————=first-form males; ••••=second-form males; o o o o o = juveniles.

Growth and Maturity

The smaller, second-form males caught in the spring had over-wintered as second-form males, having been immature the previous fall. The second-form males of all three species molted in the spring, but did not change form at that time (figs. 4, 5, 11, 12, 18, and 19). These males continued growth and became first form by late summer. One instance of a change from second to first form was recorded on 13 July, when one *Orconectes propinquus* male molted in the collection bucket and grew from 20 mm to 22 mm carapace length. Growth does not always accompany a form change. Of the recaptured *O. obscurus* males, thirteen became first form with an increase of one mm, but nine became first form with no additional growth at all. The growth of all marked crayfish (both re-

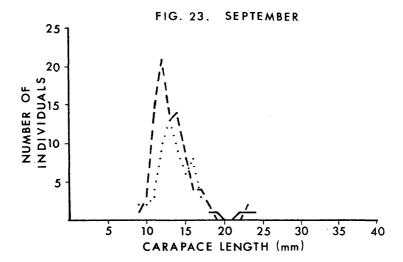


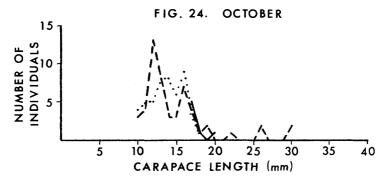


Figures 21-22. Size-frequency distributions of *Orconectes propinquus*. ---- = females; —= first-form males; •••• = second-form males; o o o o o = juveniles.

captured crayfish and laboratory specimens) is shown in Table 1. The most common growth increment was one mm of carapace length per molt, followed by two mm per molt.

Individuals of Orconectes obscurus and O. sanborni apparently did not become sexually mature at the end of their first summer. Inasmuch as the smallest length at which sexual maturity has been observed to be attained in the males of O. obscurus and O. sanborni is 21 mm, it seems probable that the majority, if not all, of the breeding population is derived from the yearlings rather than from the young-of-the-year. Some individuals of O. propinquus appeared to reach maturity their first summer. Small first-form males that were evidently from the young-of-the-year were captured in the late summer and fall of 1967 and were as follows: one 20 mm, one 19 mm, two 18 mm, and five 17 mm. Figure 24 clearly shows that the first-form males caught in October belong to the young-of-the-year and not to the yearling group. No such relationship was apparent in the other two species.





The graphs show the separation of the various age groups and can be used to trace them through the year (demonstrated best in figs. 7, 8, and 9). In Orconectes obscurus in July, there was a wide gap between the size of the young crayfish (7 mm) and of the yearling individuals (16 to 36 mm). The 39-mm male was probably a two-year-old. In August the young ranged from 9 to 15 mm, the yearlings from 18 to 34 mm, and the two-year-olds from 38 to 40 mm. By September the young were 10 to 18 mm, the yearlings were 20 to 34 mm, and most of the two-year-olds were dead. Considering 21 mm as the minimum size for sexual maturity (Ortmann, 1906), only yearlings could have been sexually mature.

In Orconectes sanborni, the size range was very similar to that of O. obscurus (figs. 14, 15, and 16). In July the young were 6 to 13 mm, the yearlings 20 to 36 mm, and the two-year-olds about 39 mm. In August the young ranged from 9 to 17 mm, and the yearlings from 22 to 33 mm. In September the young were 11 to 18 mm, and the yearlings were 20 to 33 mm. In O. sanborni, as in O. obscurus, the majority of individuals seem to mature as yearlings.

Only two age groups could be determined for *Orconectes propinquus* (figs. 21, 22, and 23). In July the young ranged from 6 to 16 mm, and the yearlings from 18 to 32 mm. The young in August were from 9 to 17 mm, and the yearlings from 22 to 31 mm. At least some of the larger males of the season's young (9 to 19 mm) attained first form by September (fig. 23). The yearlings ranged from 22 to 24 mm. Figure 24 shows even more clearly that the first-form males included some individuals from the young-of-the-year.

Table 1

Growth of marked crayfish*
Increase in carapace length

Species	1 mm	$2~\mathrm{mm}$	3 mm	4 mm	$5~\mathrm{mm}$
O. obscurus	36	7	0	1	0
O. sanborni	2	0	1	0	0
O. propinquus	19	13	5	1	1
Total	57	20	6	2	1 = 86
Per cent	66.3	23.2	7.0	2.3	1.2=100

^{*}Both recaptured crayfish and laboratory specimens.

Recapture of Marked Crayfish

The marking period lasted from 13 July through 4 September 1967, although collections continued through October. During this time the best returns were for Orconectes obscurus, because 100 of the 359 marked indviduals were recaptured. Of these, 67% were caught only twice, 21% three times, 9% four times, and 3% five times. Although 204 of O. sanborni were marked, only 3 were recaptured. Of 359 marked individuals of O. propinguus, 52 were recaptured. Most of these were caught only twice (92%), but 6% were caught three times, and 2% four times. (Specific information on individuals may be found in Davis, 1968.)

DISCUSSION

Composition of the Collections

Population sampling was conducted from April 1967 through October 1967. No collecting was done during the winter because of the difficulty of capturing specimens in cold weather and because growth ceases. Creaser (1934) and Van Deventer (1937) found that no molting occurs in winter. The last recently molted specimen of Orconectes propinquus collected by Van Deventer (1937) was obtained on 6 October in Illinois. Creaser (1934) stated that individuals of O. propinquus ceased growing after 24 September in Michigan. The general trends in population size and composition were the same for all three species.

Ovigerous Females and Appearance of Young

Ovigerous females of all three species were collected in the spring. Orconectes obscurus and O. sanborni females had eggs in the collections of 8, 22, and 29 April, and 27 May, and O. propinquus females in the 27 May collection. Although three apparently mature females (defined as 20 mm and over by Van Deventer, 1937) were present in the 15 April collection of O. propinquus, none of these had eggs. Similar collection dates for ovigerous females were recorded by Ortmann (1906) for O. obscurus in Pennsylvania, and by Van Deventer (1937) for O. propinquus in Illinois.

Individuals which had molted in the spring of 1967 were recognized by their clean exoskeletons, as opposed to the algae- and debris-covered exoskeletons of animals which had not molted recently. Such mature females of all three species were caught on 27 May. Because ovigerous females do not molt until after the eggs hatch and the young are shed, the appearance of molted, mature females suggests that some of the young were independent in late May and that, for other females, the period of egg carrying was almost completed. All females of Orconectes obscurus and O. sanborni that were collected on 7 June had molted, thus most of the young were independent. No collection of O. propinquus was made on this date.

No females with young were collected, probably because the young are carried for only a short time while the females remain concealed (Ortmann, 1906; Van Deventer, 1937). Ortmann (1906) caught Orconectes obscurus females with young in Pennsylvania on 30 May and 5 and 6 June; after 15 June he caught no females with either eggs or young. Ortmann (1906) stated that the young of O. obscurus are independent in early June, but his first reported captures of young were 10 and 24 July. On 18 June, Ortmann (1906) collected newly hatched young of O. sanborni which had a carapace length of approximately 6 to 7.5 mm. Van Deventer (1937) found all females of O. propinquus that were captured on 7 June 1933 had molted. Van Deventer (1937) first collected young on 7 June in 1933 and on 13 May in 1934 (Van Deventer attributes this time difference to the fact that 1934 had a much warmer spring than did 1933). In the current study, juveniles of all three species were seen on 24 June (1967).

Form Changes in Males

Two periods of form change in males were found in this study. Males of all three species, which had remained in first form since the previous fall, changed to second form in late April and May. Second-form males then reverted to first form in late June and July. Other investigators have recorded similar dates for these form changes. All male specimens of *Orconectes propinquus* collected by Ortmann (1906) on 7 June were second form. Van Deventer (1937) found the change to second form lasted from 6 to 21 May in 1933 and from 7 to 28 April in 1934. Ortmann (1906) found that males of *O. obscurus* began changing back to first form beginning 11 July and increasing in number through September. Van Deventer (1937) found that this molting period lasted from late June through the middle of July for *O. propinquus*.

Copulation

In the current study (1967), copulation was observed taking place from the middle of August through September. Ortmann (1906) first recorded the copulation of Orconectes obscurus in Pennsylvania on 5 September and observed mating through November. Van Deventer (1937) observed copulation of O. propinquus couples in Illinois in the fall (September through November) and also in March. Other observations of copulation in this species were: in Michigan in September (Turner, 1926) and in October and November (Creaser, 1933); in Wisconsin in August (Turner, 1926); and in New York in July, August, and October (Crocker, 1957). Although Crocker (1957) watched for copulation in March, April, May, and June in New York, none was observed. Van Deventer (1937) concluded that the time and length of the mating season of O. propinquus varied greatly with the latitude, mating occurring only in the fall in the more northern latitudes, but in both the spring and fall in more southern latitudes. My data agree with his interpreted season for the more northern latitudes.

In laboratory mating experiments, there was one successful interspecific mating, that between a male of *Orconectes propinquus* and a female of *O. sanborni*. Unfortunately, the *O. sanborni* female that mated with the *O. propinquus* male could

not be kept (because of loss of research space due to campus construction); thus it is not known if viable young would have been produced. Because these two crayfishes are assigned to different subgroups by Fitzpatrick (1967), it seems doubtful. The only published record of hybridization among these three species is by Crocker (1957), who believes that he has collected hybrids of O. obscurus and O. propinquus in New York. Fitzpatrick (1967), on the other hand, has examined collections from the same area and has sorted the adults by species with no difficulty. In the present study, interspecific mating was tried with all three combinations of species, but there were no attempts at copulation between individuals of O. obscurus and O. propinquus.

Growth and Maturity

According to my data, individuals of Orconectes obscurus and O. sanborni do not attain sexual maturity in their first summer, though some individuals of O. propinguus do. In contrast, Ortmann (1906) believed that most individuals of O. obscurus in Pennsylvania were sexually mature at the end of their first summer. Most individuals of O. propinguus in Illinois were sexually mature by their first fall (Van Deventer, 1937). Creaser (1933) found that some of the males of O. propinguus in Michigan became first form (sexually mature) in their first fall, but that the majority did not (as was also the case for O. propinguus in my study). Van Deventer (1937) attributes this variation in the length of time required to attain sexual maturity in O. propinguus to the length of the growing season; fewer males reach sexual maturity in their first fall where the growing season is short, as it is in Michigan or Ohio. Perhaps temperature differences within an area also affect the time at which sexual maturity is attained. In the current study, the stream in which O. propinguus was collected was consistently warmer than were either of the other two areas, and O. propinguus was the only one of the three species studied in which individuals became sexually mature their first fall.

Recapture of Marked Crayfish

Most of the marked crayfish were not recaptured. Most of those that were recaptured were caught only twice. For Orconectes obscurus, 67% of the recaptured individuals were caught just twice, and for O. propinquus, this value was 92%. Only three of 204 marked O. sanborni individuals were recaptured and these were caught only twice. These data suggest that none of these species have home ranges, or if so, they must be relatively large.

Studies of Other Species

There have been several extensive life history studies on other crayfish species. Two will be discussed here, and their life histories compared with those of the three species studied here.

A very detailed life history for Orconectes immunis, in New York, has been given by Tack (1941). This species is quite different from the three species of the present study because O. immunis prefers mud bottoms, and stagnant or slowly flowing water. In addition, O. immunis burrows and sometimes migrates from pond to pond. Copulation for O. immunis was observed from June through October in New York, while the present study found copulation in O. obscurus, O. sanborni, and O. propinquus to occur in August and September. Although the time of copulation was similar, egg-laying for O. immunis was in late October and early November, as opposed to April and May for O. obscurus, O. sanborni, and O. propinquus.

A study of a Cambarus species has shown it to be quite similar to Orconectes obscurus, O. sanborni, and O. propinquus. This species is Cambarus longulus longulus, which was studied in Virginia by Smart (1962). Cambarus l. longulus occupies a stream habitat similar to that of the species considered in the present

study, except that *C. l. longulus* burrows in the winter. Males occupy the burrows from October through April, and females occupy them from October until the time when the young are independent. Copulation occurs in the burrows from September through April (Smart, 1962). Other than these differences, related to the burrowing habit, the events and dates of events in the life cycles for *C. l. longulus*, and *O. obscurus*, *O. sanborni*, and *O. propinguus* are all very similar.

SUMMARY

Orconectes obscurus, O. sanborni, and O. propinquus copulate primarily in August and September. No known molting occurs during the winter. Mature first-form males remain so until spring. Mature females do not molt until after the young have been shed. Eggs are laid in April and May, and hatch in late May. The young, measuring approximately 6 mm carapace length, become independent in early June.

Growth resumes among the adults and yearlings in the spring, and males that overwintered in first form change to second form. Practically all males are second form in June and most do not begin molting to first form until July. Males overwintering in second form are the smaller ones that were immature the previous fall. Immature males and females continue molting and growing through the summer, becoming mature by the end of their second summer. The growth increment per molt, as determined by field and laboratory studies, is usually one mm of carapace length, though this growth may sometimes be as much as two mm or even more. Growth may or may not accompany a form change.

Orconectes obscurus and O. sanborni in northeastern Ohio usually attain sexual maturity only in their second summer, not in their first summer. These mature males overwinter as first form, molt to second form in the spring of their third year, molt back to first form in late summer, and later, die. Mature females molt after their young have left and also die in their third summer.

The structure of the later-summer population of Orconectes propinquus was strikingly different from those of O. obscurus and O. sanborni in that virtually all of the first-form males were from the young-of-the-year rather than the yearling group. These males were small compared to first-form males of the other two species. In fact, the size range for O. propinquus was less than those of the other two species, and no individuals of O. propinquus larger than 32 mm were captured. In late summer there was a decrease in the numbers of larger individuals of O. propinquus similar to the decreases found in O. obscurus and O. sanborni, but in O. propinquus most of these individuals were probably yearlings. Maturity may come a year early for individuals of O. propinquus, but death apparently comes early also. Perhaps the warmer temperatures of the O. propinquus collecting area influenced the earlier attainment of sexual maturity in this species.

Under the artificial conditions of the laboratory, interspecific mating may occur. A successful mating between a male *Orconectes propinquus* and a female *O. sanborni* was observed.

The life histories of these three crayfish species are quite similar. Since they are closely related, this was to be expected. It is interesting, however, that only in *Orconectes propinquus* do some of the males become first form during their first summer.

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