

# Colonization and persistence of *Crangonyx pseudogracilis* (Bousfield 1958) in temporary pools

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**Abstract:** Crangonyctid amphipods occupy temporary habitats across northeastern North America, but they are mostly known as permanent-water species. *Crangonyx pseudogracilis* (Bousfield 1958) is found at high densities in temporary pools in western New York, but the means by which it persists are not well understood. Our objectives were to: 1) assess the dispersal abilities of *C. pseudogracilis*, 2) explore its ability to descend through inundated porous substrates, 3) assess whether its life cycle and brood releases are related to survival through the dry season, and 4) find their dry-season refugia and measure the period for which they can survive desiccation. During periods of inundation, *C. pseudogracilis* was found in the top 15 cm of soil in holes <10 m from pools. After pools dried in mid-June or early July, *C. pseudogracilis* was not found in the soil to a depth of 45 cm, even when rains temporarily refilled the pools. In the laboratory, small *C. pseudogracilis* descended easily through substrates with  $\geq 0.7$ -mm pore radii but large ( $\geq 7$  mm) and ovigerous *C. pseudogracilis* were unable to descend. In the field, ovigerous females were found from mid-March until late May. The previous year's generation of large and ovigerous individuals began dying in May and was gone by the end June. In the laboratory, *C. pseudogracilis* survived in damp soil (51% average free moisture content) for 15 wk. *Crangonyx pseudogracilis* lacks specialized strategies for survival in temporary waters (e.g., resting eggs, dormant juvenile stages, active burrowing), but has ecological traits well suited for temporary pools and similar environments.

**Key words:** amphipod, *Crangonyx pseudogracilis* (Bousfield 1958), temporary pools, life history, desiccation, underground dispersal

*Crangonyx* spp. (Malacostraca:Amphipoda:Gammaridea:Crangonyctidae) are commonly found in permanent waters (Bousfield 1958, Holsinger 1972, Batzer and Sion 1999) and have few adaptations for drought resistance (Magee et al. 1999). *Crangonyx pseudogracilis* (Bousfield 1958) is found throughout eastern North America in rivers, lakes, sloughs, quarry pools, reservoirs, and other fresh waters that tend to be turbid and warm in the summer (Bousfield 1958). *Crangonyx* spp. also occur in vernal and autumnal pools across North America, including western New York State (Batzer and Sion 1999, Harris et al. 2002). In her review of vernal pool invertebrate communities in North America, Colburn (2004) placed *C. pseudogracilis* in the long-cycle (late summer drying–autumn flood) hydrologic class, woodland-pool setting, and litter-bottom category.

Many aquatic invertebrates inhabiting temporary waters have specialized strategies for survival and reproduction, such as drought resistance, resting eggs, or a dormant juvenile stage (Kenk 1949, Wiggins et al. 1980, Williams 1987, Dietz 2001), but amphipods do not possess these characteristics (Kenk 1949, Wiggins et al. 1980, Batzer and Sion

1999, Magee et al. 1999, Taylor et al. 1999), and the means by which *Crangonyx* spp. persist in temporary pools is an enigma (Higgins and Merritt 1999). We conducted an observational and experimental investigation of the ecology of the freshwater amphipod *C. pseudogracilis* with the goal of understanding its occurrence in temporary pools and its ability to persist in them without a known desiccation-resistant life-history stage.

*Crangonyx pseudogracilis* is sexually dimorphic, and females are ~3 mm longer than males (Henry and Tarter 1997). Ovigerous females occur from November until May (Henry and Tarter 1997), and females produce several broods per year (Bousfield 1958, 1973, Henry and Tarter 1997). The incubation period for amphipod eggs generally ranges from 1 to 3 wk and depends on variations in molting time caused by temperature and age (Bousfield 1973, Pennak 1989), but the incubation period for *C. pseudogracilis* eggs has not been reported. Bousfield (1973) and Henry and Tarter (1997) agreed that *C. pseudogracilis* has an annual life cycle. Adults begin to die in May and are gone before July, but they disagreed on when mating oc-

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curs and when ovigerous females are found in permanent water populations.

*Crangonyx* spp. have been studied in temporary pools, but where they go when the pools dry is not known (Hubricht and Mackin 1940, Holsinger and Dickson 1977, Jass and Klausmeier 2003). Kenk (1949) reported that *C. gracilis* (Smith 1871; probably *C. pseudogracilis* according to Wiggins et al. 1980) first appeared in early winter when pools were frozen and gradually increased in number to peak in April, after which the number of mature animals decreased rapidly during May and June until shortly before the pools dried, when only small specimens from new broods were seen. Kenk (1949) reported that the vast majority of the population in a temporary pool just before they entered sediments in the summer consisted of the smallest size class of *C. gracilis*. Clifford (1966) made a similar observation for *Crangonyx forbesi* (Hubricht and Mackin 1940) in an ephemeral stream in Indiana. Kenk (1949) recovered 2 small specimens from a soil sample long after a pool had dried, and Clifford (1966) found *C. forbesi* living in soil pore spaces during the dry season. Creaser (1931 in Kenk 1949 and Wiggins et al. 1980) reported that *Crangonyx* sp. survived in crayfish burrows during the dry season. Batzer and Sion (1999) concluded that, after a pool dries, amphipods must stay in close proximity to the pool basin because they reappear rapidly when the pool fills again.

Harris et al. (2002) showed that *C. pseudogracilis* and other invertebrates have the ability to disperse underground to isolated depressions or holes, and hypothesized that this ability was a means for colonizing temporary waters. They did not test whether the underground movements were a result of passive mechanisms, possibly aided by flow of ground water, or of active movement through interstitial pore spaces.

We used field and laboratory studies to address unresolved questions related to long-term persistence of *C. pseudogracilis* populations in temporary pools. Our objectives were to: 1) assess the ability of *C. pseudogracilis* to disperse through soil, 2) explore its ability to descend through water-inundated porous substrates, 3) assess whether its life cycle and brood releases are related to survival through the dry season, and 4) measure the period during which they can survive desiccation.

## METHODS

### Study areas

We chose 2 sites with temporary pools, 16 and 24 km west of Rochester, New York (USA), for field studies (State University of New York Brockport campus: lat 43.20755°N, long 77.96207°W; Northampton Park: lat 43.18730°N, long 77.87370°W). Both sites are ~16 km south of central Lake Ontario on the Erie–Ontario Plain, a subzone of the Great Lakes Plain (Roosa 2002), and

have temporary pools for virtually the same amount of time each year. Poorly drained soils, a high water table, and low relief characterize the region and contribute to an abundance of temporary pools that persist for similar periods at both sites (see DiSalvo 2006 for details about soils, topography, vegetation, and other conditions at the study sites).

### Underground dispersal through soil

We dug ten ~45 × 45 × 45-cm holes near the pool at the Brockport site and 6 near the pool at the Northampton site between 19 December 2002 and 2 June 2003. We dug the holes 2 to 10 m from the perimeters of the pools to avoid flooding of the holes after rain (flooding was observed on only 3 of 339 occasions). To prevent 1<sup>st</sup> instar *C. pseudogracilis* (2.5 mm) from entering holes from the surface, we covered the holes with plastic lids, each with a patch of 1.2-mm mesh to admit air and light to the hole. The edges of the lids were weighted down with 1.5 to 2 kg of rocks.

We monitored holes biweekly and after precipitation events between 23 December 2002 and 12 June 2003. We used a visual inspection method to eliminate the need for nets that might have served as dispersal agents to other holes. BCD inspected holes for *C. pseudogracilis* by placing his head at ground level above the hole, lighting the interior of the hole with a flashlight, and stirring and sorting the contents of the hole with a stick. Turbidity, freezing, drying, and flooding prevented inspection of all holes on all dates, including the days they were dug.

We used a 2-tailed runs up and down test (Zar 1999) to assess whether underground dispersal through soil into and out of holes was random, and linear regression to examine the relationship between the percentage of observations with *C. pseudogracilis* in holes and distance of holes from the pool edge.

### Vertical movement through substrate

We collected *C. pseudogracilis* from the Brockport site and tested their ability to disperse through sediment composed of 1 of 4 grain sizes (0.3, 0.5, 0.7, 1.3 mm) in the laboratory. We used plastic, 20-L waste baskets (28 × 20 × 36 cm) to hold sediment (36 cm deep). We inserted a 28-cm-wide sheet of plastic 35 cm into each container to divide it into 2 unequal sections from top to bottom (1 : 2 ratio) parallel to the long axis of the rectangular opening and fastened the sheet in place with silicone sealant. We filled 1/3 of the container with sediment and 2/3 with water. The 1-cm opening at bottom of the divider allowed amphipods to cross from the sediment to the water side (see DiSalvo 2006 for a diagram).

We filled the containers with deionized water to the height of the sediment and placed 10 amphipods in each of 3 size classes (small: <3 mm, medium: 3–7 mm, large:

>7 mm) on the sediment surface. We monitored the containers for 2 h and counted individuals as they crossed under the divider to the water-only side of the apparatus. After completing a replicate, we rinsed the sediment with boiling water to kill the animals not counted. We tested amphipod vertical movements 6 times in each of the 2 smallest pore radii (0.3 and 0.5 mm). None passed through these sediment sizes, so no further tests were conducted. We replicated vertical movement tests 44 times for each of the 2 largest pore radii (0.7 and 1.3 mm). We used Mann–Whitney and Kruskal–Wallis tests to identify differences in the abilities of large, medium, and small amphipods to descend through the 0.7- and 1.3-mm pore sizes.

### Growth and reproduction

We arranged five 1-m<sup>2</sup> quadrats diagonally from northwest to southeast in the Brockport pool. We sampled each quadrat weekly between 23 March and 12 June 2003 by collecting 1 dip net of sediment from 10 places in each quadrat. We removed all amphipods from the samples in the laboratory and counted total amphipods and ovigerous females before preserving them in 95% ethanol. We measured amphipods with the aid of an ocular micrometer on a compound microscope at 40× magnification. Amphipods tend to curl when preserved, so instead of total length, we measured from the base of antenna 1 to the posterior edge of the 2<sup>nd</sup> segment behind the carapace because this part of the body remained straight.

We used 1-way analysis of variance (ANOVA) to compare amphipod lengths before and after the midpoint of the sampling season. We used a *G*-test of independence to test for a relationship between the abundance of brood-bearing females and date from first to last appearance in the holes.

### Dry-season ecology

**Soil sampling** We collected soil samples (~45 × 45 × 45 cm) from the Brockport pool between July 2002 and July 2004. We took samples across the dry pool basin in 2002 and at locations <15 cm from the pool's edge during the period of inundation in spring 2003. In 2004, we tested whether amphipods were following the pool edge or staying in damp soil at their previous locations by collecting samples on transects as the pool receded. We took the 1<sup>st</sup> soil sample <15 cm from the northwestern edge of the pool. On each subsequent sampling day, we collected samples <15 cm from the new pool edge and at the previous pool edge until the pool dried.

In the laboratory, we divided each soil sample vertically into three 15-cm layers, pressed each layer on a tray to a depth of ~1 cm, and flooded it with deionized water. Samples stood at room temperature while soil particles settled (usually within 48–72 h). We then counted amphipods visually, sometimes with the aid of a flashlight.

Occasionally, we found *C. pseudogracilis* in a hole with water on one day, and on the next day the hole was dry with no amphipods. On these occasions (15 dates between 17 July and 26 November 2002 and 11 April to 30 June 2003), we dug an additional 45 × 45 × 45-cm hole ~30 cm toward the pond's edge from the original hole to check for amphipods dispersing in the direction of moisture then searched the sample for amphipods in the laboratory.

**Soil-moisture experiment** We filled thirty 710-mL plastic containers with soil collected near the Brockport pool. We cut a 1-cm<sup>2</sup> hole in the bottom of each container and inserted a 40 × 8-cm strip of nylon stocking through the hole to serve as a wick. We placed the containers atop an inverted glassware drying rack so that the wicks hung through the rack into a tray of deionized water.

We filled the experimental containers partially with soil and monitored them for 1 wk to ensure that the wicks were distributing water to the soil (we did this by touching the soil to check for moisture). We added 14 amphipods (5 small: 1<sup>st</sup> instar, <3 mm; 5 medium: 3–7 mm; 4 large: >7 mm) to each of 18 containers and gently placed more soil over the amphipods. Twelve containers had soil only to assess soil-moisture content. We placed 1 container with soil from the SUNY Brockport campus woods covering the bottom and amphipods of varying sizes in an overlying layer of deionized water next to the experimental setup to provide a control for mortality that might have occurred from leaving amphipods at room temperature. We refilled the trays of deionized water as needed. At 2, 4, 6, 8, 11, and 15 wk, we sampled 3 containers with amphipods and 2 with only soil. We placed soil with amphipods in a flat pan, flooded the pan with deionized water, and counted amphipods after ~24 h. We weighed the containers with only soil, dried the soil by evaporation in a fume hood, and weighed the containers again to estimate free moisture content. We evaluated survival rates with a  $\chi^2$  goodness of fit test.

## RESULTS

### Underground dispersal through soil

At the Brockport pool, we dug 5 holes on 19 December 2002, 2 holes on 20 April 2003, 2 holes on 27 April, and 1 hole on 23 May. The 5 holes dug in December contained water but no amphipods through the end of February 2003 and froze from the beginning of March through 8 April. *Crangonyx pseudogracilis* was present in 1 of 7 holes on 23 April. That hole subsequently dried, and amphipods did not return to it until 16 May. *Crangonyx pseudogracilis* appeared in another hole on 1 May and remained there (except for May 20) until 12 June. Except on 14 May, *C. pseudogracilis* was found in 2 to 8 holes from 6 May through 12 June, after which holes dried and amphipods disappeared (Fig. 1). At the Northampton Park pool, we dug 3 holes on 6 April 2003 and 1 hole each on

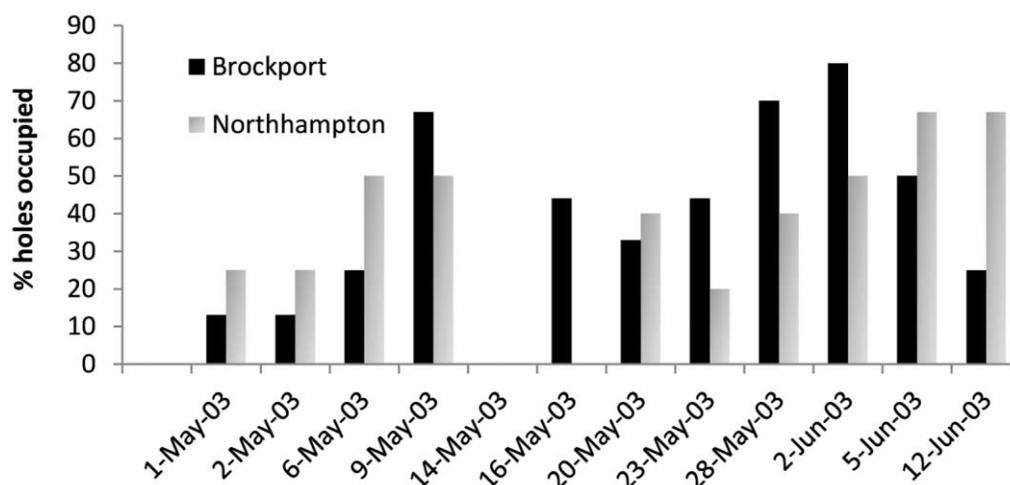


Figure 1. Percent presence of *Crangonyx pseudogracilis* in dug holes on days they were not dug, too turbid, frozen, flooded, or dry. No amphipods were observed from 31 Dec 2002 through 27 Apr 2003, and all holes were dry on 15 June 2003.

27 April, 16 May, and 2 June. Except on 14 May, *C. pseudogracilis* was found in 1 to 4 holes from 1 May through 12 June (Fig. 1).

Fourteen of the 16 holes at the 2 sites were colonized by *C. pseudogracilis* at some point during the field season, and 8 of 14 holes (2 occupied holes dried earlier in the season) were still occupied by *C. pseudogracilis* when the pools dried up in June (Fig. 1). Amphipod movements into and out of holes were not random in 10 of the 11 holes with  $\geq 10$  observations ( $p < 0.05$ ; Table 1), and the slope of the relationship between the percentage of observations with *C. pseudogracilis* in holes and distance of holes from pool edge was not significant ( $R^2 = 0.033$ ,  $p = 0.501$ ).

#### Vertical movement through substrate

The abilities of large, medium, and small amphipods to descend through 1.3-mm and 0.7-mm pores differed significantly ( $df = 2$ ,  $H = 89.862$ ,  $p < 0.001$ ;  $df = 2$ ,  $H = 91.872$ ,  $p < 0.001$ , respectively). Large amphipods were significantly less able to descend through both pore sizes than small or medium amphipods, but small and medium amphipods did not differ in their ability to descend through both pore sizes ( $p < 0.001$ ; Table 2). The ability of small amphipods to descend did not differ between the 0.7- and 1.3-mm pore sizes ( $df = 1$ ,  $W = 2005.5$ ,  $p = 0.682$ ). Medium ( $df = 1$ ,  $W = 2204.0$ ,  $p = 0.034$ ) and large amphipods ( $df = 1$ ,  $W = 2821.0$ ,  $p < 0.001$ ) were better

Table 1. Movements of *Crangonyx pseudogracilis* into and out of holes analyzed for randomness using data from holes that had  $\geq 10$  observations ( $n$ ). Number of changes is the number of times amphipods changed from present to absent or vice versa for that hole. – = holes that had only absences for the duration of the experiment.

Hole	$n$	Number of changes	Amphipods present	Significance ( $p < 0.05$ )
Brockport 1	10	4	Yes	No
Brockport 2	12	0	No	–
Brockport 3	16	6	Yes	Yes
Brockport 4	14	2	Yes	Yes
Brockport 5	17	3	Yes	Yes
Brockport 6	14	2	Yes	Yes
Brockport 7	14	4	Yes	Yes
Brockport 8	11	2	Yes	Yes
Brockport 9	10	1	Yes	Yes
Northampton 1	16	1	Yes	Yes
Northampton 2	15	3	Yes	Yes
Northampton 3	17	0	No	–
Northampton 4	12	2	Yes	Yes

Table 2. Percentage of large (>7 mm), medium (3–7mm), and small (<3 mm) *Crangonyx pseudogracilis* that passed through sediments with pore size = 1.3 mm or 0.7 mm.  $n = 44$  replicates with 10 individuals of each amphipod size class/replicate.

Pore size	Large	Medium	Small	Result	$p$
1.3 mm	29	87	88	L < S = M	<0.001
0.7 mm	6	82	87	L < S = M	<0.001

able to descend through the 1.3-mm pores than through the 0.7-mm pores.

### Growth and reproduction

Mean amphipod length was 1.4 mm upon thawing of the Brockport pool on 23 March 2003 and was 0.8 mm until the pool dried up on 15 June. Amphipods collected on or before 9 May (7 sampling dates,  $n = 437$ ) were significantly larger than those taken on or after 16 May (5 sampling dates,  $n = 467$ ) ( $F = 111.54$ ,  $df = 11$ ,  $p < 0.001$ ). Brood-bearing females were collected from 23 March until 28 May 2003, and the greatest numbers were collected in mid to late April. The presence of brood-bearing females was related to date of sampling ( $df = 15$ ,  $G/q = 94.95$ ,  $p < 0.001$ ). As average size decreased consequent to reproduction, the proportion of brood-bearing females also decreased. In addition, the frequency of large amphipods decreased as the field season progressed. By late spring, samples contained few to no late-instar animals.

### Dry season ecology

**Soil sampling** Three of 8 soil samples taken during the period of inundation in 2003 contained early-instar *C. pseudogracilis*. None were found on 30 June 2003, the day after surface water disappeared from the entire pool. Early-instar amphipods were collected from 11 May to 13 June 2004, and surface water disappeared after 4 July 2004. *Crangonyx pseudogracilis* were found only in the upper 15-cm layer of soil, and none were found in samples taken from a previous pool edge ( $n = 7$ ). After heavy rains, the pool filled on 6 July 2004, dried, filled again 27 July, and new transects were started. In total, twenty-seven 45-cm-deep samples were collected at the pool's edges after 4 July 2004, and none contained *C. pseudogracilis*.

**Soil-moisture experiment** Mean % soil moisture in the containers during the 15-wk experiment was  $51 \pm 2.6$  (SE), with a range of 42 to 58%. No large *C. pseudogracilis* survived after 2 wk. After 11 wk, 50% of the small and 20% of the medium-sized *C. pseudogracilis* survived (Table 3). One 1<sup>st</sup>-instar amphipod survived 18 wk. Survival rates of the small and medium size classes differed ( $\chi^2 = 25.09$ ,  $df = 4$ ,  $p = 0.0001$ ).

## DISCUSSION

Our experiments elucidated several aspects of the dispersal and desiccation ecology of *C. pseudogracilis*. *Crangonyx pseudogracilis* can disperse underground as moisture conditions in soils near temporary pools change, but where they go after pools dry in summer remains unknown. In the laboratory, early instars, but not ovigerous females, were able to migrate vertically in soils with pore radii as small as 0.7 mm and survived in soils with 42 to 58% moisture for up to 15 wk.

### Underground dispersal through soil

How amphipods colonize temporary pools is poorly understood. They have been collected occasionally from the feet and feathers of ducks and the fur of a dog (Wiggins et al. 1980, Swanson 1984 and references therein), but no transport of crangonyctids by birds and mammals has been reported. Moreover, the hundreds of *C. pseudogracilis* found in holes near our study pools were too abundant for hitchhiking to be the source, and any such dispersal was prevented by lids on the holes.

*Crangonyx pseudogracilis* moved to holes near both pools in a nonrandom fashion, which suggests active movement rather than passive transfer by hydrostatic pressure gradients (Wiggins et al. 1980). They left holes that dried within a day, and they were not found within 45 cm adjacent to or below the hole they had abandoned, a result suggesting the ability to move >45 cm/d horizontally or vertically.

Our results suggest that *C. pseudogracilis* colonizes temporary waters by moving through soil. Exploratory behavior would be advantageous for an animal living in a highly variable environment, such as a temporary pool. Colonization of holes was not random, so it is likely that amphipods were using their ability for more than seasonal migratory purposes, e.g., for daily activities, such as feeding. MacNeil et al. (1999) proposed another possibility. Where they co-exist, *Gammarus* preys on *Crangonyx*.

Table 3. Percent survival of *Crangonyx pseudogracilis* in the soil-moisture experiment. Five small (1<sup>st</sup> instar, <3 mm), 5 medium (3–7 mm), and 4 large (>7 mm) amphipods were placed into each of 18 containers on 6 June 2004. Three containers were examined on each sampling date.

Sampling date	Time in situ (wk)	Small	Medium	Large
20 June	2	53	33	0
4 July	4	50	13	0
18 July	6	47	47	0
1 August	8	60	33	0
22 August	11	50	20	0
21 October	15	7	0	0

*Crangonyx* might use its ability to move rapidly through sediment pore spaces (see below) to escape predators.

### Vertical movement through substrate

Pore radius limited the size of amphipods that could pass through substrates in the laboratory. The smallest *C. pseudogracilis* were most able to move vertically, especially in sediment with the smallest pore radius that allowed passage (0.7 mm). Large amphipods had the greatest difficulty moving downward and often remained at the surface for the duration of a test, a result similar to that of Clifford (1966), who reported that moist leaf litter (a habitat not available in our experiments) served as the final 'oasis' for the largest, often ovigerous, *C. forbesi* as pools dried. Sniffen (1981) found that young *C. gracilis*, *C. obliquus* (Hubricht and Makin 1940), *C. serratus* (Embody 1911), and an undescribed species of *Stygobromus* survived the dry season by migrating vertically and remaining in moist or wet subterranean habitats in a North Carolina flood plain. Given the annual life history of amphipods (Henry and Tarter 1997), only individuals of the newest generation are able, by virtue of size, to descend into sediments of temporary pools and survive the dry season (Kenk 1949, Clifford 1966). The oldest, largest individuals from the previous generation perish with the onset of each dry season.

*Crangonyx pseudogracilis* clearly has the ability to move through sediments in the laboratory and in the field. Our laboratory observations indicate that the beating action of its appendages is sufficient to allow passage through sediments with enough water. Whether the results of our laboratory study (movement through uniform pore spaces) are directly transferable to field soils with variable sediment sizes and moisture content, as well as rocks and roots, is uncertain.

### Growth and reproduction

Brood-bearing females were found in the Brockport pool from late March to late May, a shorter time than the early November to early May period reported by Henry and Tarter (1997) in warmer West Virginia. Our first samples with ovigerous females were collected immediately after ice-out, a result indicating that breeding was occurring under the ice during the winter. The decrease in the average size of *C. pseudogracilis* after early May corresponded with the decline of ovigerous females.

### Dry-season ecology

**Soil sampling** We consistently found *C. pseudogracilis* in the upper 15 cm of saturated soil at the pool's edge until it dried up in mid June 2003, after which we did not find *C. pseudogracilis* within the top 45 cm of the sediments. In addition, it did not reappear in the top 45 cm of moist soil after the pool refilled twice in July 2004, a finding consistent with those of Kenk (1949), Clifford (1966), Batzer and

Sion (1999), and Harris et al. (2002). Populations in permanent water descend to deeper water in June (Henry and Tarter 1997), and both permanent and temporary populations return to the surface (shallow water for permanent populations, pool/saturated soil ecotone for temporary populations) in November.

Where does *C. pseudogracilis* go during the dry season? Harris et al. (2002) proposed that they are more closely associated with the water table than with overlying soil. This suggestion seemed to be true before the end of June. Given its demonstrated ability to move rapidly through sediments in the field and laboratory, the only place *C. pseudogracilis* can be during the dry season must be soil deeper than 45 cm—the only habitat not sampled in 2003–2004.

In October 2007, we collected 15 core samples at various locations on the dry Brockport campus pool site (JMH, unpublished data). Because of bedrock and loose rocks, 1 core penetrated to only 35 cm, 7 cores penetrated 36 to 50 cm, and 7 cores penetrated >50 cm. Six of the 15 cores had invertebrates, all in moist soil <50 cm deep. Clifford (1966) reported *C. forbesi* at 60 cm, but none of our cores contained *C. pseudogracilis*. Henry and Danielopol (1999) also found no *C. pseudogracilis* in moist soils below dry temporary pools. Where they go remains unknown.

**Soil-moisture experiment** Amphipods lack adaptations for surviving desiccation, such as resting eggs, but do persist in moist substrates (Taylor et al. 1999, Colburn 2004). Soil moisture during our 18-wk experiment ranged from 42 to 58%, levels between the dry (28–39%) and wet season (76–83%) values measured in a floodplain (Sniffen 1981). Survival in moist soil during the dry season appears to be restricted to small individuals (Clifford 1966, Sniffen 1981). First-instar amphipods are poorly sclerotized, and softer and thinner exoskeletons enable easier gas exchange in soil spaces (Pennak 1989). Crangonyctids survived up to 21 d in water-saturated air in laboratory experiments (Clifford 1966, Batzer and Sion 1999). Thus, pore water and soil are not absolutely required for short-term amphipod survival. In our study, many small- and medium-sized *C. pseudogracilis* survived for 15 wk in water-saturated air in soil spaces. Our results and those of Clifford (1966), Sniffen (1981), and Batzer and Sion (1999) show that amphipods can live for weeks without free water. This ability is important for survival during the dry season and in years of low pool recharge when amphipods must still be active to complete their life cycle and may explain how *C. pseudogracilis* is able to colonize and survive in temporary pools.

### Summary and conclusion

During periods of temporary pool inundation, *C. pseudogracilis* moved in (when wet) and out (when dry) of

holes in a nonrandom way, suggesting a capacity for rapid movement toward favorable and away from unfavorable conditions. Small *C. pseudogracilis* were adept at descending through porous, inundated substrates to a depth of 36 cm in the laboratory. However, large instars or adults were unable to penetrate sediments when temporary waters dried, so by late spring, our samples contained few to no late-instar or ovigerous animals. *Crangonyx pseudogracilis* survived reasonably well in soil with an average soil-moisture content of 51% for up to 15 wk in the laboratory. During the dry season, amphipods presumably reside in soil at depths >45 cm, but we could not verify this supposition. The Brockport pool was nearly permanent during summer and autumn 2004, but amphipods were not present in soil <45 cm deep from July until November, nor were they found in soils 45 to 100 cm deep in October 2007.

Our research dispels the notion that *C. pseudogracilis* has few adaptations for drought resistance (Batzer and Sion 1999). Underground dispersal abilities, an annual life cycle, tolerance for low amounts of O<sub>2</sub> (Dick 1999, MacNeil et al. 2000), and the ability to survive for up to 5 mo in the field (15 wk in the laboratory without free water) allow *C. pseudogracilis* to thrive in temporary habitats.

Several questions remain. How deep does *C. pseudogracilis* go into the sediment during the July–October period? How do sediment pore radii in the field (if they can be measured) compare to those we used in the laboratory in terms of how *C. pseudogracilis* moves horizontally and vertically through sediments? Why do permanent water populations (Henry and Tarter 1997) and temporary pool populations during years of full inundation still move to deep water and deep sediment, respectively? Do amphipods living in permanent waters descend into bottom sediments? If so, perhaps *C. pseudogracilis* was originally a temporary water species that has adapted to living in permanent water rather than vice versa. This hypothesis is consistent with speculation by Batzer and Sion (1999), who found *C. pseudogracilis* only in temporary pools near permanent waters in the same woodland, that temporary water may be more conducive than permanent water to survival, perhaps because of predator avoidance.

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