Copepod crustaceans from burrows of *Parastacus defossus* Faxon, 1898 in southern Brazil

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Abstract

We report the results of a survey of copepods in burrows of *Parastacus defossus,* near Lami, Porto Alegre, Rio Grande do Sul, Brazil, conducted during the rainy seasons of 2003 and 2004. Copepods were also collected from surface water in nearby ephemeral pools. Twelve species of copepods (6 cyclopoids and 6 harpacticoids) were found either consistently or occasionally in the burrows (several of these also in the surface pools); 3 additional species appeared only in surface waters. None of the species found in the burrows has previously been reported from this subhabitat. In this region, a distinctive crayfish-burrow fauna (*pholeteros*), defined herein as species that occurred more often in the burrows than in surface water and were present in the burrows during 3 or more sampling months in both years, consists of *Diacyclops uruguayensis, Mesocyclops annulatus,* and *Attheyella fuhrmanni. Paracyclops chiltoni* and *Elaphoidella bidens* appeared equally often in both burrows and surface waters. *Microcyclops anceps* and *Tropocyclops prasinus meridionalis* were frequent in surface waters but much less often in burrows; whereas *Acanthocyclops smithae, Metacyclops* cf. *denticulatus,* and *Microcyclops ceibaensis* were found only in surface waters. *Attheyella* cf. *godeti* appeared consistently in the burrows in 2003, but not in 2004. The burrows may serve as a refuge for conserving the species pool in cyclically drying riverine floodplain habitats. These collections provided several new geographical records: from South America for *Acanthocyclops smithae,* from Brazil for *Metacyclops* cf. *denticulatus* and *Attheyella subdola,* and from the state of Rio Grande do Sul for *Diacyclops uruguayensis* and *Microcyclops ceibaensis.*

Key words: Crayfish, *Parastacus defossus,* Copepoda, *Pholeteros,* Brazil.

Introduction

Many kinds of aquatic invertebrates have been found in the burrows of crayfish or land crabs, but the microcrustaceans that are often present in these burrows have seldom been investigated. The species of copepods reported from crayfish burrows in Europe, North America, Australia, and Tasmania, and from the burrows of land crabs on several islands in the Pacific Ocean were reviewed by Reid (2001). In North America, the canthocamptid harpacticoids *Attheyella pilosa* and *Attheyella carolinensis* are facultative associates of several species of crayfish (Prins, 1964; Bowman *et al.,* 1968). In Europe, several other species of canthocamptids, *Attheyella crassa, Attheyella dentata, Attheyella trispinosa, Bryocamptus minutus, Canthocamptus staphylinus,* and *Nitocrella hibernica* have been found in the burrows and also on the gills of crayfish, but they may be only accidentals (Chappuis, 1926; Gurney, 1930). One species, *Nitocrella divaricata,* is an obligate crayfish associate or commensal, occurring only on the carapace or gills of three species of *Astacus* and of *Austropotamobius torrentium* in

Europe (reviewed by Reid, 2001; see for example Defaye, 1996).

The associated fauna in the burrows of South American crayfishes has never before been studied. The burrowing crayfish *Parastacus defossus* Faxon, 1898 occurs only in Brazil (state of Rio Grande do Sul) and in Uruguay. In Rio Grande do Sul, these crayfish are common in the clay soils of the floodplain near Guaiba Lake (Buckup and Rossi, 1980; Buckup, 1993, 1999). They construct subterranean burrows that can reach over 2 meters deep. The burrows are sloping, branched tunnels that extend from the groundwater level to the soil surface, mostly with several openings, each opening encircled by a muddy chimney of pellets. In the research area, during the four seasons, the mean density of burrow openings was about 230 in an area of 100 m^2. The air temperature varied from 15.4°C (August) to 24.3°C (December) and the water temperature in the burrows varied from 15.6°C to 24°C. The dissolved oxygen of the burrow water remained at very low levels throughout the study period: the mean concentration (1.6 mg/L) indicated nearly anaerobic conditions in the burrows. In the course of a general study of the biology and ecological relationships of this crayfish species by C. K. Noro, we investigated the possibility of the occurrence of copepod associates.

In this region, the demarcation between the small surface waterbodies and the water contained in the crayfish burrows is erased during the wet season. During that period (the austral winter, June through August), the level of the water table rises to the surface, forming small pools or puddles that may flood the burrow mouths. A dry season during the austral summer (December through February) is typical in the region; the dry season varies in intensity, but usually there is very little rainfall. During this period, the water table drops to more than 2 m below the soil surface (measured with a piezometer, C. K. Noro and L. Buckup, unpublished data). In the summer of 2003-2004, during an unusually long drought, the crayfish-burrow water became isolated from any remaining surface waterbodies. When the rains returned in the autumn, the burrows became flooded from the surface and probably the animals present in surface waterbodies were transported together with this water into the burrows. The question became, then, to determine which, if any, of the local species of copepods consistently remain in the burrows and may therefore be truly exploiting this microhabitat.

To answer this question, collections were made from several burrows and nearby small surface waterbodies, approximately monthly from July through December 2003 and again from May through November 2004. These periods included the end of the winter/wet season, through the spring and the beginning of the summer/dry season. These are the first collections of copepod crustaceans made from crayfish burrows in South America. We list the species, most of which could be attributed to previously described taxa, and their local subhabitat preferences. We also briefly discuss the known geographical distribution and habitats of the identifiable species.

Material and Methods

The specimens were collected by C. K. Noro from the water contained in burrows of *Parastacus defossus,* located near Lami in the Municipality of Porto Alegre, Rio Grande do Sul (30°11'41"S, 51°06'00"W), approximately monthly from July through December 2003 and May through November 2004. Each month, a 50 ml water sample was taken from each of three to five burrows, and a 160 ml sample of surface water was collected in nearby pools or puddles. The burrow-water samples were taken with the aid of a length of narrow plastic tubing fitted with a squeeze bulb to provide suction. The water in the puddles was collected by direct sampling with a bottle.

In the laboratory, adult and copepodid juvenile copepods were sorted from the sediment and preserved in 70% ethanol. Most of the burrows contained adults and juveniles. Numerous copepod nauplii were also present, but were not identified further. The adults and copepodids were identified to species level, where possible, by J. W. Reid. In a few samples, only young copepodids or adult males were present, and could be identified with confidence only to genus level. The adult and copepodid specimens will be deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Results

A total of 15 distinguishable taxa of copepods appeared in one or more of the samples (Table I). Twelve species of copepods (6 cyclopoids and 6 harpacticoids) were found either consistently or occasionally in the burrows. Three additional species appeared only in the surface waters. Four species, *Diacyclops uruguayensis, Mesocyclops annulatus, Attheyella fuhrmanni,* and *Attheyella godeti,* occurred more often in the burrows than in the surface water, and were present in the burrows during 3 or more sampling months. *Paracyclops chiltoni* and *Elaphoidella bidens* appeared equally often in burrows and surface waters. *Microcyclops anceps* and *Tropocyclops prasinus meridionalis* were frequent in surface waters but occurred much less often in burrows. *Acanthocyclops smithae* and *Microcyclops ceibaensis* were found only in surface waters. Infrequent, occasional species were *Metacyclops* cf. *denticulatus, Microcyclops* sp., *Attheyella subdola, Attheyella* sp., and *Epactophanes* sp.

Discussion

The geographical distribution, range of habitats, and taxonomic considerations pertaining to each individual species are summarized in the following paragraphs.

Acanthocyclops smithae appeared only in the samples from 2004. This recently described species is a member of the taxonomically confusing *vernalis-robustus*-complex. It is so far known from small surface pools in Honduras, the Yucatan Peninsula of Mexico, and possibly Cuba (Reid and Suárez-Morales, 1999). This is the first record from South America. The specimens from Rio Grande do Sul are fully congruent with the Honduran and Mexican populations, except for having slightly longer caudal rami (about 4 times longer than wide) that are sparsely covered by shagreen-like scales.

Diacyclops uruguayensis was described by Kiefer (1935) from southern Uruguay, where it was collected in drains and a temporary pool. Brehm (1935) provided additional records from Uruguay: a small stream pool at Pajas Blancas, and a house drain and ditches at Tarjan. Reid (1998) redescribed *D. uruguayensis,* partly from specimens obtained by C. E. F. Rocha in cultures of leaf litter taken from a coastal dune forest (Portuguese, mata de restinga) at Piçarras in Santa Catarina, Brazil. All these records are from fresh water.

Specimens with slightly different morphological characteristics were found in dug wells in Fortaleza, Ceará, and were initially attributed by Reid (1998) to *D. uruguayensis*. One of the Ceará morphotypes was later included in a new taxon *D. pilosus* by Fiers and Ghenne in Fiers *et al.* (2000), who also defined a second new taxon in this group. The *uruguayensis*-group now includes four named species: *D. uruguayensis* Kiefer, 1935 (Uruguay; southern Brazil, states of Santa Catarina and, now, Rio Grande do Sul), *D. hispidus* Reid, 1988 (western Colombia), *D. pilosus* Fiers and Ghenne in Fiers *et al.,* 2000 (Mexico, state of Quintana Roo, Yucatán Peninsula, and northeastern Brazil, state of Ceará), and *D. ecabensis* Fiers and Ghenne in Fiers *et al.,* 2000 (Mexico, state of Quintana Roo, Yucatán Peninsula).

The specimens from Rio Grande do Sul closely resemble the population found in Santa Catarina, as well as the illustrations of the type material of *D. uruguayensis* provided by Fiers *et al.* (2000). This apparent morphological stability of mutually distant populations reinforces the decision of Fiers and Ghenne (in Fiers *et al.,* 2000) to erect distinct taxa for subtly different morphotypes in the *uruguayensis*-group.

Little is known of the ecological relationships of these species, except for limited inferences from the collection data. All of them were found in temporary or groundwater-related habitats. Most of the records are from fresh water, except the pool in western Colombia where *D. hispidus* was found, which contained a mixture of fresh- and brackish-water species of copepods (Reid, 1988).

Mesocyclops annulatus was originally described from Argentina (Wierzejski, 1892), and has been recorded also from Uruguay, Paraguay, Bolivia, Chile, and Peru (Rocha and Botelho, 1998; Holyrska *et al.,* 2003). A subspecies *M. annulatus diversus* was described by Herbst (1962) from the Brazilian Amazon; however, *M. a. diversus* differs in several respects from the nominate taxon and may be separable above the subspecific level (Holyrska *et al.,* 2003). Montú (1980) reported *M. annulatus* s.l. from plankton of the Lagoa dos Patos in Rio Grande do Sul.

Table I. Species of copepods collected from burrows of *Parastacus defossus* or from nearby surface pools, during the rainy seasons in 2003 and 2004, in Lami, Porto Alegre, Brazil. Several burrows and pools were sampled on each date; water samples from the surface pools were combined. F, adult female. M, adult male. C, copepodid juvenile. The total numbers of individuals collected from each sub habitat are given.

A. June-December 2003

		Sampling date						
No. burrows sampled (no. with copepods)	Micro-habitat	24 Jun 2003 1 (1)	29 Jul 2003 5 (5)	29 Aug 2003 4 (3)	24 Sep 2003 4 (3)	22 Oct 2003 4 (4)	25 Nov 2003 4 (4)	18 Dec 2003 4 (4)
Order Cyclopoida								
Diacyclops uruguayensis	Burrows					2F 2M C	3F 1M 48C	2F 2C
Kiefer, 1935	Surface				2F 2M C			7F 4C
Mesocyclops annulatus	Burrows	2M 3C	2F 4M 4C	4M 3C	3F 1M 3C	5F 4M 7C	2F 3M 12C	10F11M25C
(Wierzejski, 1892)	Surface							2M 8C
Microcyclops anceps	Burrows						1M	
(Richard, 1897)	Surface		3F 3M 5C	2M 4C	1F 5C			1F 2C
Microcyclops ceibaensis	Burrows							
(Marsh, 1919)	Surface		1F 1C					2F 3C
Microcyclops sp.	Burrows					1M 2C		
	Surface							
Paracyclops chiltoni	Burrows	1F		1M		1F 2M 2C	3F 1M	
(Thomson, 1882)	Surface				1F 2C	1F	1M	
Tropocyclops prasinus meridionalis	Burrows		1C			1F 2C	1F	
(Kiefer, 1931)	Surface		1C		5F 3M 1C	10F 5M	15F 1M 19C	
Order Harpacticoida								
Attheyella (Chappuisiella)	Burrows		1F	1F	1F	1F 1M	2F 1M	8F 3M 1C
fuhrmanni (Thiébaud, 1912)	Surface							2F
Attheyella (Chappuisiella)	Burrows			1F 1C		1F 1M	2F	
cf. *godeti* (Delachaux, 1918)	Surface							
Attheyella (Chappuisiella) sp.	Burrows					1C		
	Surface							
Elaphoidella bidens	Burrows	2F	1F		1F	1C		
(Schmeil, 1894)	Surface		1F	1F			1F	1F

B. May-November 2004

		Sampling date						
No. burrows sampled (no. with copepods)	Micro-habitat	12 May 2004 4 (2)	14 Jun 2004 4 (3)	19 Jul 2004 4 (0)	13 Aug 2004 4 (3)	13 Sep 2004 4 (4)	14 Oct 2004 4 (4)	17 Nov 2004 4 (4)
Order Cyclopoida								
Acanthocyclops smithae	Burrows							
Reid & Suárez-Morales, 1999	Surface		1C			2C	1F	4F 1M 68C
Diacyclops uruguayensis	Burrows	3F 1M 1C	1F 1M		8F 3M 2C	2F 1M 8C	1F 2M 36C	2F 2M 1C
Kiefer, 1935	Surface		2F					
Mesocyclops annulatus	Burrows		1F 1C		3F 3M 1C	12F 4M 25C	2F 4M 7C	8F 9M 45C
(Wierzejski, 1892)	Surface		2C					
Metacyclops cf. *denticulatus*	Burrows							
Dussart & Frutos, 1986	Surface		1C					
Microcyclops anceps	Burrows	1C					41C	3C
(Richard, 1897)	Surface	1F	2F 1C	2F 5M 3C	1M 4C	5F 9M 0C	2F 2M 7C	
Microcyclops ceibaensis	Burrows							
(Marsh, 1919)	Surface		3F 4M 4C				4F 4M	
Paracyclops chiltoni	Burrows					54F 2M 2C	12F	6F 4M
(Thomson, 1882)	Surface						2F 5M	1F
Tropocyclops prasinus	Burrows					20C	2F	1F
meridionalis (Kiefer, 1931)	Surface						6F 12M 19C	3M
Order Harpacticoida								
Attheyella (Chappuisiella)	Burrows					4F	28F 36M 9C	1F 1M
fuhrmanni (Thiébaud, 1912)	Surface				1F 1M	1C		1C
Attheyella (Chappuisiella)	Burrows					1M		
subdola (Brian, 1927)	Surface					1M		
Elaphoidella bidens	Burrows							1C
(Schmeil, 1894)	Surface							
Epactophanes sp.	Burrows					1F		
	Surface							

The species has been found in the littoral zone of lakes and reservoirs, the Paraná River (e.g., Menu Marque, 2001) and is a common inhabitant of temporary pools in northern Argentina. Individuals held in laboratory cultures remain at the bottom of their containers most of the time (Micieli *et al.,* 2002). Adults will prey upon larvae of *Aedes aegypti* and *Culex pipiens* if alternative food (such as algae and protozoans) is unavailable (Micieli *et al.,* 2002).

A copepodid referable to *Metacyclops denticulatus* occurred in one surface sample. This small, well-sclerotized species was described from the basin of the Middle Paraná River in Argentina by Dussart and Frutos (1986).

Microcyclops anceps is one of the commonest members of its genus in the neotropics. It ranges from Mexico to Argentina, and has been recorded from several states in Brazil, including Rio Grande do Sul (Rocha and Botelho, 1998). Eurytopic, inhabiting the plankton but more usually the littoral zone of lakes, marshes, and sometimes ephemeral waters. There are no previous records from groundwaters.

Microcyclops ceibaensis, like *M. anceps,* is a common and widely distributed neotropical species, found from Mexico to Uruguay, and previously recorded in Brazil from the Distrito Federal, Mato Grosso do Sul, and São Paulo (Rocha and Botelho, 1998).

As regards the individuals listed as *Microcyclops* sp., because only males and copepodid juveniles were present in the sample, the specimens could not be identified to species level with certainty. The free segment of leg 5 has a tiny spinule on its medial surface, which is congruent with the *M. ceibaensis* found in other samples.

Paracyclops chiltoni is one of the few members of its genus which is probably truly cosmopolitan (Karaytug, 1999). Because of incomplete morphological knowledge prior to Karaytug's review of the genus, *P. chiltoni* was easily confused with *P. fimbriatus* and possibly other congeners. Both taxa have been recorded widely in South America, including several states of Brazil (Reid, 1985; Karaytug, 1999). Members of *Paracyclops* are usually benthic, and occur in all kinds of surface waters and occasionally in subterranean waters as well, i.e., they are stygophilic.

Tropocyclops prasinus meridionalis is the most common member of the genus in South America. Although it has been recorded mostly from the plankton of lakes, reservoirs, and ponds (Menu Marque, 2001; Rocha and Botelho, 1998), it may also occur in shallower waterbodies such as marshes.

Two members of the canthocamptid harpacticoid genus *Attheyella,* and its widely distributed and species-rich neotropical subgenus *Chappuisiella* occurred regularly in the burrows. Members of this group are epibenthic in all kinds of surface waters and occasionally occur in subterranean waters. *Attheyella* (*Chappuisiella*) *fuhrmanni* is the most widespread of all, ranging from Mexico to Argentina, and has been found in a wide range of perennial and ephemeral surface waters.

The species rather tentatively identified as *Attheyella* (*Chappuisiella*) cf. *godeti* is, unfortunately, a good example of the still-cryptic state of taxonomic understanding of many South American canthocamptid harpacticoids. In 1918, Delachaux described *Canthocamptus godeti,* a species with distinctive bottle-shaped caudal rami, from Lake Huaron at an altitude of 5140 m in the Peruvian Andes. Although Delachaux' description was thorough by contemporary standards, he did not illustrate most of the pereiopod rami or any of the anterior appendages that are so useful in distinguishing closely related taxa. Since then, no population attributed to *C.* (now *Attheyella*) *godeti* has been discovered. The females from Rio Grande do Sul are congruent with *A.* (*Ch.*) *godeti* in respect to every point of its description, in particular the long, strongly tapered bottle-shaped caudal ramus, its high dorsal crest ending in a sharp point, and the placement of the caudal setae. Unfortunately, the single male in the sample is much damaged and is missing most of legs 1-4. In 1986, Menu Marque and Bosnia redescribed a closely similar species *Attheyella* (*Ch.*) *crenulata* (Mrázek, 1901), and proposed that two other taxa are junior synonyms of it. These authors noted several kinds of morphological variation and pronounced sexual dimorphism in the population that they examined and those recorded in prior literature; these features apparently contributed to previous confusions regarding this species. According to Menu Marque and Bosnia (1986), *A.* (*Ch.*) *crenulata* has been reported (under several aliases) from Valparaíso and Lake Quillehue (Chile),

Tierra del Fuego, and the Embalse Ezequiel Ramos Mexía in Neuquén Province (Argentina). A second species, *Attheyella* (*Ch.*) *vivianii,* with a somewhat shorter but still strongly tapered caudal ramus and identical chaetotaxy of legs 1-5 to *A.* (*Ch.*) *crenulata,* was described from two locations in Quebrada de la Plata in the coastal range of central Chile, altitude 650 m, by Ebert and Noodt (1975).

Whether or not the population in Rio Grande do Sul is conspecific with *A.* (*Ch.*) *godeti,* it is without doubt part of a group whose other members occur at much higher altitudes and more southern latitudes, mostly in the southern Andes. The occurrence of a member of this group near the Atlantic coast in southern Brazil is surprising, but not unprecedented. Members of the subgenus *Attheyella* (*Delachauxiella*) show a similar distribution, being common in the Andes and extending eastward into eastern Argentina and northward as far as central Brazil (Reid, 1994).

The find of *Attheyella* (*Chappuisiella*) *subdola* was equally unexpected. Only the male is known, from near Buenos Aires (Brian, 1927). To our knowledge, this is only the second record of this species. The strongly modified leg 4 exopodite is distinctive. Unfortunately, only a single male appeared in our samples.

The canthocamptid harpacticoid taxon *Elaphoidella bidens* includes several named subspecies, of which the morph known as *E. bidens coronata* (G. O. Sars, 1904) is widely distributed in the Americas (Canada to Argentina). For detailed discussion of the subspecies see Lang (1948). *Elaphoidella bidens* is a weed species, typical of eutrophic waters and disturbed areas. In the Americas, it has nearly always been found in places where humans lived or had once lived. Like other canthocamptids it is primarily epibenthic. It is usually found in surface waters, but there are a few records from subterranean habitats; i.e., it is a stygophile. It normally reproduces parthenogenetically, and males are extremely rare.

The single specimen identified as *Epactophanes* sp. differs from the nearly cosmopolitan *E. richardi* in having no dentition on the anal operculum. This morph is widely distributed in central and southeastern Brazil (J. W. Reid, unpublished data).

The sparse information available from investigations on other continents seems to indicate that canthocamptid harpacticoid copepods tend to predominate over the other orders found in crayfish burrows; and that the particular species are, as might be expected, normally benthic or epibenthic in epigean waters, rather than true stygobionts. In Europe, eight species of harpacticoids (genera *Attheyella, Bryocamptus, Canthocamptus, Halectinosoma,* and *Nitocrella*) and one cyclopoid (*Paracyclops affinis*) have been found in burrows. In North America, three species of harpacticoids (genus *Attheyella*), one species of cyclopoid (*Acanthocyclops vernalis*), and one species of calanoid (*Osphranticum labronectum*)*;* and in Australia and Tasmania, two species of cyclopoids (*Acanthocyclops* sp. and *Diacyclops cryonastes*) occur in these microhabitats. Most of these harpacticoids and cyclopoids are benthic or epibenthic; a few are stygophile. The single exception is the calanoid *Osphranticum labronectum,* which is normally planktonic in small permanent or ephemeral ponds and sloughs.

In contrast to this pattern, cyclopoids predominated in both species and numbers in the burrows of *P. defossus*. The high proportion of cyclopoids, rather than harpacticoids, was surprising in view of the usual predilection of canthocamptid harpacticoids for epibenthic or even hypogean habitats. Also unexpected was the high proportion of individuals of *Mesocyclops annulatus,* which is normally planktonic in ponds. *Diacyclops uruguayensis* apparently prefers groundwater habitats, and *P. chiltoni* and the six canthocamptid species are more representative of the kind of species which might be expected to easily invade these burrows. None of the species found is known to be an associate of any other invertebrate.

The appearance of *Acanthocyclops smithae* in substantial numbers in surface waters in the second sampling year was startling. *Acanthocyclops robustus* has been reported from the plankton of an artificial lake in the city of Rio Grande, Rio Grande do Sul by Gloeden and Amaral (1990), but because of the unresolved taxonomic conundrums posed by this group, the record can be taken to refer to some member of the vernalis-robustus complex.

As is usual in collections from little-investigated habitats, this sample, although very limited, resulted in valuable new biogeographical and ecological information. The range of *M. annulatus* was extended somewhat northwards. A second locality record in

Brazil was established for *D. uruguayensis*. These are of course new habitat records for all the species.

Lake (1977) and Lake and Coleman (1977) coined the term "pholeteros" (from the Greek for "one who lurks in a hole"), to describe the faunal assemblage in crayfish burrows. This term has not been much used, probably because the burrow fauna in general appears to be some subset of the local aquatic community, rather than a distinctive group of animals. We may define a pholeteros as consisting of species that occur more often in the burrows than in surface water and are consistently present in the burrows (in the case of these samples, during 3 or more months). Using these criteria, in this region a distinctive crayfish-burrow fauna does exist, and consists of *Diacyclops uruguayensis, Mesocyclops annulatus, Attheyella fuhrmanni,* and *Attheyella godeti*.

The remaining species cannot be considered as part of a pholeteros; that is, they showed no predilection for the burrows or did not appear in them at all. This group includes *Paracyclops chiltoni* and *Elaphoidella bidens,* which occurred equally in the burrows and in surface waters; and *Microcyclops anceps* and *Tropocyclops prasinus meridionalis,* which were frequent in surface waters but were found much less often in burrows. *Acanthocyclops smithae* and *Microcyclops ceibaensis* were found only in surface waters. This distribution pattern is congruent with the known habits of all the species: both *P. chiltoni* and *E. bidens* are normally epibenthic creepers and poor swimmers, whereas *M. anceps*, *M. ceibaensis,* and especially *T. p. meridionalis* usually occur in the littoral and pelagic zones of ponds and lakes.

It is likely that the copepods and crayfish do not interact significantly. Remains of copepods have occasionally been found in the gut contents of *P. defossus* (C. K. Noro and L. Buckup, unpublished data). It is likely that these individuals are ingested accidentally together with organic detritus and plant matter eaten by the crayfish, rather than being actively preyed upon. Many species of cyclopoids and harpacticoids will scavenge decaying animal matter, and may simply be attracted to the same food particles as the crayfish.

Robinson *et al.* (2003: 664) observed that "amazingly little is known of the ecology of special habitats associated with intact flood plains." The interplay among elements of the land-water continuum is only beginning to be understood. It may well be that in certain systems, especially in dynamic, seasonally cyclic riverine floodplains, cryptic microhabitats such as crayfish burrows provide refuges for some proportion of the aquatic invertebrate fauna and thereby help to maintain its diversity. In this respect, the concept of pholeteros might be applicable to those species which are able actually to use these burrows as refuges during periods of drought or thermal stress — as active individuals, rather than as resting stages (eggs or diapausing individuals). Moreover, some copepod species may be able to reproduce successfully within the burrows, as evidenced by the large number of nauplii and the high proportion of copepodid juveniles found in the present collection. The burrow habitat may function as much more than an accidental or unusual situation. The ecological role of these subhabitats certainly deserves closer investigation.

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