

NOTE

CYST FORMATION IN TUBIFICIDAE (NAIDINAE) AND OPISTOCYSTIDAE (ANNELIDA, OLIGOCHAETA) AS AN ADAPTIVE STRATEGY FOR DROUGHT TOLERANCE IN FLUVIAL WETLANDS OF THE PARANÁ RIVER, ARGENTINA

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Abstract: During a broad study of invertebrate colonization in marginal fluvial wetlands of the Middle Paraná River in Argentina, cyst formation was observed in two of the 26 species of aquatic oligochaetes identified from the study—*Dero multibranchiata* Steiren, 1892 (Tubificidae, Naidinae), and *Trieminentia corderoi* (Harman, 1969) (Opisthocystidae). All specimens of the two species in which cyst formation was observed had been collected after drying conditions ranging from 14 to 28 days. A clitellum was not observed in any of the specimens collected. Lengths of specimens ranged from 0.88 mm to 2.84 mm in *Dero multibranchiata* and 2.25 mm to 2.40 mm in *Trieminentia corderoi*. The development of protective cysts by *Dero multibranchiata* and *Trieminentia corderoi*, and perhaps many other species of aquatic oligochaetes, appears to be an adaptive strategy enabling them to survive drought in temporary wetlands, recolonize freshwater habitats upon inundation, and disperse both laterally and downstream with rising water levels in wetlands and streams.

Key Words: Annelida, Oligochaeta, Naidinae, Opisthocystidae, cyst formation, drought resistance, floodplain habitats, Paraná River, Argentina

INTRODUCTION

Large river-floodplain systems are subjected to a wide range of environmental conditions, resulting in periodic and often significant changes in community structure and, in particular, multiple interactions between the terrestrial and the aquatic phases in associated floodplain habitats, referred to as the Aquatic Terrestrial Transition Zone (ATTZ) by Junk et al. (1989) and Junk (1997). Floodplain habitats are situated along a gradient of permanently aquatic to permanently terrestrial conditions, with the interactions between the channel and the floodplain controlled by seasonal fluctuations in water levels and occasional floods. The hydrosedimentological pulse includes both a flood-phase (potamophase) and a dry-phase (limnophase) (Neiff 1990, 1996). Periodic flooding and drying, along with sediment deposition and erosion, often leads to a permanent temporal and spatial renewal of habitats and communities of plants and animals (Junk and Weber 1996).

During these flood pulses, the bankline changes dramatically as the edge of the rising water body encroaches onto the wetland habitats of the ATTZ; ben-

thic invertebrates are carried and thus dispersed by the spreading water body, providing an opportunity for them to colonize the ATTZ during flooding events (Reiss 1977, Irmiler 1989, Montalto unpubl.). When water levels recede, the ATTZ dries out, often completely, resulting in the replacement of the aquatic invertebrates by terrestrial invertebrates. A variety of responses and survival strategies have evolved in aquatic invertebrates, allowing them to survive desiccation, including physiological resistance, resting, eggs, and great mobility, as well as life-cycle adaptations (Casey and Ladle 1976, Ladle and Bass 1981, Junk 1997, Schellenberg et al. 2001).

The behavioural adaptations and survival strategies of terrestrial invertebrates in flooding habitats, as well as the interaction between the surface and hyporheic zone, are well-documented (Adis and Righi 1989, Adis 1992, Marmonier et al. 1992, Stanford and Ward 1993, Clinton et al. 1996, Brunke and Gonser 1999, del Rosario and Resh 2000, Schellenberg et al. 2001), yet the strategies of aquatic invertebrates and their responses to drying habitats are relatively unknown. Some oligochaetes are able to form cysts to survive dehydration or freezing of the sediment. The formation

of resistant cysts has been observed in *Tubifex tubifex* (Müller, 1774) by Cernosvitov (1927), Semernoi (1971), Kaster and Bushnell (1981a), and Anlauf (1990), in *Lamprodrilus mrazeki* (Hrabê, 1929) by Hrabê (1929), and in *Lumbriculus variegatus* (Müller, 1774) by Cook (1969), but has not yet been reported for species in Naidinae [Naididae was proposed as a subfamily within Tubificidae by Erséus and Källersjö (2004)] and Opisthocystidae. In another paper, Kaster and Bushnell (1981b) noted the formation of tests in *Tubifex tubifex*, providing temporary refugium and protection from predation by chironomids, rather than as an adaptation to avoid desiccation, like cyst formation.

We present here our observations on formation of dehydration-resistant cysts by *Dero multibranchiata* Steiren, 1892 (Naidinae) and *Trieminentia corderoi* (Harman, 1969) (Opisthocystidae). The observations and data presented in this paper are part of a broader study focusing on colonization of the ATTZ by freshwater invertebrates during floods and other periods of high water and the impact of drying at the end of flood pulses.

The hydrosedimentological dynamics of the Paraná River create a large amount of habitat heterogeneity to be colonized by worms, but there have been only few studies on oligochaetes in limited areas of this river (Marchese and Ezcurra de Drago 1992, Marchese et al. 2002). Eighty one species of oligochaetes are reported from the Paraná River basin (Di Persia 1980, Righi and Varela 1983, Varela 1984, 1990, Brinkhurst and Marchese 1987, Marchese 1987, 1995, Takeda 1999, Montanholi-Martins and Takeda 1999, Marchese and Paggi 2004); nevertheless, there have been no studies of oligochaetes occurring in fluvial marginal wetlands.

STUDY SITE

The study area in which this research was conducted, designated by several names (vis, the ATTZ (Junk et al. 1989), riparian wetland (Mitsch 1996), or marginal fluvial wetlands (Neiff et al. 1994)), is located in the Middle Paraná River (31° 40'S – 60° 30'W) in Argentina.

The hydrosedimentological cycle in the Paraná River in Argentina is rather predictable in spite of considerable annual fluctuation in amplitude, with maximum peaks in March–April and a minimum flow in September–October; thus, our study area is periodically inundated by the Tiradero River (a secondary channel of the Paraná River) when the Paraná River rises above 13.29 m a.s.l. (as measured at the Paraná Harbour staff gauge). The study area remained flooded from February 10 through April 2, 2001, when the water began

to recede until complete dry out was reached on June 27.

The plant taxa present in the study area were *Tesaria integrifolia* Ruiz et Pavon, *Salix humboldtiana* Willdenow, *Sesbania virgata* (Cavanilles) Persoon, *Thalia multiflora* Horkel, *Panicum elephantipes* Nees, *Panicum prionitis* Nees, *Paspalum repens* Bergius, *Echinochloa polystachya* (Humboldt, Bonpland et Kunth) Hitchcock, *Polygonum acuminatum* Kunth, *Eleocharis* spp., *Eichhornia crassipes* (Martius) Solms, *Salvinia herzogii* de la Sota, *Azolla caroliniana* Willdenow, and *Pistia stratiotes* Linné.

METHODS

Samples were collected along a transect at 10-m (station 1) and 30-m (station 2) distance onto the temporary wetland from the right (North) bank of the Tiradero River. Five replicate sediment samples were taken at each station using a 10-cm-diameter coring tube; each sediment core sample was taken at a depth of 15 cm. This sampling procedure was repeated every two weeks in winter (June–July 2001) for as long as the area remained dry. Samples were preserved in 10% formaldehyde and filtered through a 100- μ m sieve. Cysts were sorted from sediment samples under a stereoscopic microscope at 4 \times magnification, stored in 90% alcohol, and measured under the microscope. The environmental variables analyzed were air temperature ($^{\circ}$ C), relative humidity (%), granulometry, and organic matter content of the sediment (CPOM: > 1 mm; FPOM: 250–1000 μ m; UFPOM: 63–250 μ m) by ignition at 500 $^{\circ}$ C for two hours. The water content of the sediment was measured as weight loss after 24 h at 105 $^{\circ}$ C.

The oligochaetes were identified using the keys by Brinkhurst and Jamieson (1971), Harman and Loden (1978), and Brinkhurst and Marchese (1992).

RESULTS

In total, twenty-six species of oligochaetes were identified in samples collected during this study; however, we observed that only *D. multibranchiata* and *T. corderoi* had the physiological capacity to form resistant cysts (Table 1).

The formation of resistant cysts by these two species was observed in samples collected after 14 days of drying in sandy sediments (vis, 3.88 to 26.96% of organic matter content with atmospheric relative humidity ranging from 37 to 100% [\bar{x} = 79, CV = 10.5%] and a mean temperature of 13 $^{\circ}$ C [CV = 30.9%]) (Table 2). The water content of the sediments at the sampling area was reduced from 100 % in June to 40–50 % in July.

Table 1. Oligochaeta species collected and identified from drying sediments samples taken on 11 and 25 July 2001. S1 = station 1, 10-m, and S2 = station 2, 30-m; distance from the right bank of the Tiradero River onto the temporary wetland.

	Ind/m ²			
	July-11		July-25	
	S1	S2	S1	S2
Oligochaeta				
Opistocystidae				
<i>Trieminentia corderoi</i> * (Harman, 1969)	51			102
<i>Opistocysta serrata</i> Cordero, 1948	51			
Tubificidae				
<i>Pristina leidy</i> Smith, 1896	204	917		255
<i>Pristina aequiseta</i> Bourne, 1891		51		
<i>Pristina macrochaeta</i> Stephenson, 1931	51			
<i>Pristina americana</i> Cernosvitov, 1937	3209	102	153	
<i>Pristina menoni</i> (Aiyer, 1929)		51		
<i>Pristina osborni</i> (Walton, 1906)				51
<i>Dero multibranchiata</i> * Steiren, 1892	1019	7130	356	611
<i>Dero pectinata</i> Aiyer, 1929		102		
<i>Dero digitata</i> (Müller, 1773)	51			
<i>Dero obtusa</i> d'Udekem, 1885		102	153	102
<i>Dero sawayai</i> Marcus, 1943	153	255		
<i>Dero nivea</i> Aiyer, 1929		51		
<i>Dero righii</i> (Varela, 1990)		51		
<i>Dero furcatus</i> (Müller, 1773)	51			
<i>Dero tonkinensis</i> (Vejdovsky, 1894)			51	
<i>Dero costatus</i> (Marcus, 1944)			51	51
<i>Dero vagus</i> (Leidy, 1880)	102	255		102
<i>Slavina evelinae</i> (Marcus, 1942)	102	51	153	
<i>Nais communis</i> Pigué, 1906	102		102	51
<i>Limnodrilus hoffmeisteri</i> Claparede, 1862	458	306	51	102
<i>Limnodrilus udekemianus</i> Claparede, 1862	51			
<i>Aulodrilus pigueti</i> Kowalewski, 1914	255	356	611	662
<i>Bothrioneurum americanum</i> Beddard, 1894	204	356		611
Lumbricidae				
<i>Eiseniella tetraedra</i> Savigny, 1867			51	51

* Total number of individuals (encysted and without cysts).

Table 2. Granulometry and organic matter of sediments in wet (June) and dry period (July). S1 = station 1, 10-m, and S2 = station 2, 30-m; distance from the right bank of the Tiradero River onto the temporary wetland.

	June-27		July-11		July-25	
	S1 (0-2 cm)	S2 (15 cm)	S1 (dry)	S2 (dry)	S1 (dry)	S2 (dry)
Granulometry (%)						
Sand	88.57	85.01	75.71	78.82	51.34	69.02
Silt	5.23	5.60	15.23	9.02	28.41	16.42
Clay	6.20	9.39	9.06	12.16	20.25	14.56
Organic matter (%)						
CPOM (>1mm)	19.41	5.65	6.14	2.48	12.11	23.93
FPOM (>250-1000 μ m)	0.32	0.30	0.28	0.18	0.98	0.48
UFPM (>63-250 μ m)	0.84	1.47	1.29	1.22	2.80	2.55

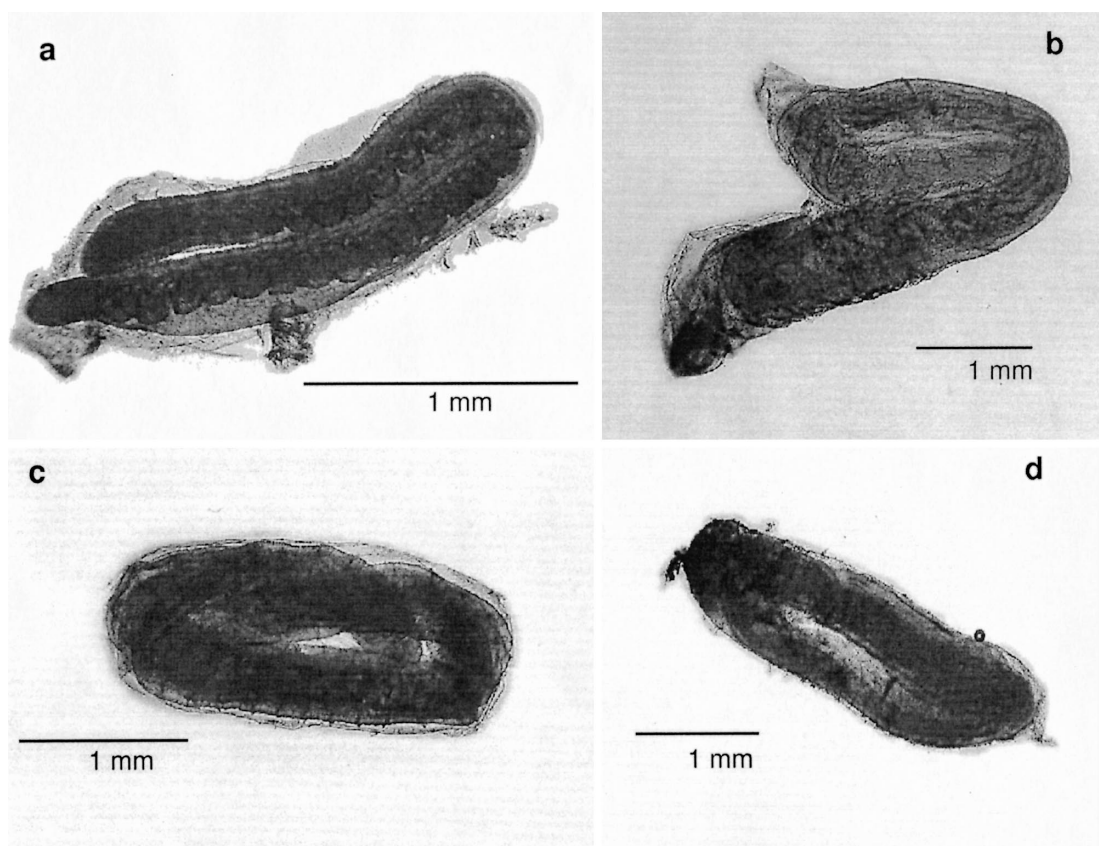


Figure 1. (a) Initial encystment of *Dero multibranchiata* with the cephalic segments bound to the posterior segments by a thin layer of mucus. (b) The cephalic and posterior segments bound to segments nearer the media region by a thin mucous layer. (c) The worm retracted into the forming cyst. (d) The completed cyst showing the sealed protective capsule and the transparent filament.

Cyst formation in *D. multibranchiata* began with the cephalic segments binding to segments nearer the posterior region by a thin layer of mucus, and the retraction and reduction of branchial fossa. This latter process occurred when the worm was tightly coiled and immobile within a hardened coat of mucus. When the worm was completely retracted, the apertures were sealed with additional secretions, resulting in a cyst forming a transparent filament. The encysted worm was covered with sediment material adhering to the mucous secretion. The length of these cysts ranged from 0.88 mm to 2.84 mm (Figure 1 a–d). Density of encysted worms ranged from 102 to 560/m² (density was inversely proportional to the water content in the sediments); the density of worms that had not encysted ranged from 51 to 611/m² (Figure 2).

Cyst formation in *T. corderoi* began with the cephalic and posterior segments binding to segments nearer the media region by a thin layer of mucus and retraction of proboscis. As in *D. multibranchiata*, *T. corderoi* cysts were covered with additional secretions and the apertures were sealed (Figure 3). The length of these cysts ranged from 2.25 to 2.40 mm; the den-

sity of encysted worms ranged from 0 to 102/m², while the density of worms without cysts ranged from 0 to 204/m² (Figure 2).

DISCUSSION

Migration is one of the most important escape mechanisms for both aquatic and terrestrial animals during phases of the hydrosedimentological cycle. These movements may follow the water line along the banks, or terrestrial animals may change their habitat from the ground to the branches of the trees (Irmiler 1979, 1989, Adis 1981, 1984). Irmiler (1989) showed that *D. multibranchiata* immigrate along the water line in the Amazon flooded forests and, over a 4–5 month period, may travel distances of 200–300 m. Experimentally, he found that the chemical attraction of leaf litter and glutamic acid suggested that the bacterial decomposition of the leaves during the flood phase attracts the worms. Additionally, the increase in the water pressure resulting from the rising water level might be important, triggering the migration. In a river-floodplain system like the Paraná River, annual flooding is

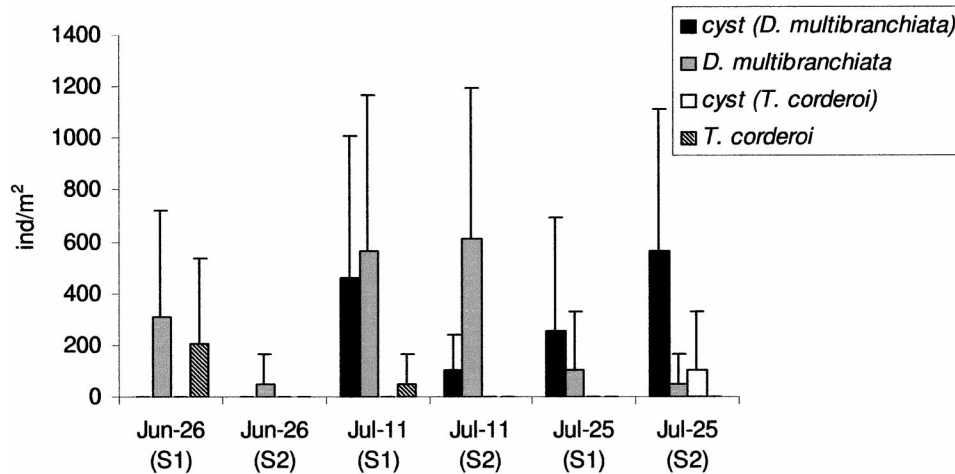


Figure 2. Mean density (ind/m²) of encysted worms and those without cysts: *Dero multibranchiata* and *Trieminentia corderoi*. Bars represent + 1 SD.

the normal and predictable behaviour of the system, and many oligochaete species commonly occur in habitats associated with both the river bank and the ATTZ, suggesting that migration occurs when water levels begin to rise (Montalto and Marchese unpubl.). The dry phase is a powerful selection factor in the distribution and abundance of aquatic invertebrates in marginal wetlands.

Under favorable conditions, reproduction in Naidinae is normally asexual; sexual reproduction begins to occur when conditions deteriorate (e.g., in response to desiccation (Mehra 1920)). We did not observe mature specimens in samples collected at the time the habitat began to dry; only specimens that were reproducing asexually and immature *D. multibranchiata* and *T. corderoi* worms capable of cyst formation were observed. These observations are different than those for *Tubifex tubifex*, as reported by Kaster and Bushnell (1981a) where mucous secretions from the clitellum

were necessary for the formation of cysts. On the other hand, Kaster and Bushnell (1981b) noted test formation by *T. tubifex* as another strategy, providing minimal protection from environmental perturbations because the worms maintained open passageways in the tests, remained active within the tests, and often were observed extending their anterior end through the orifice while probing about in an investigative manner.

Species of *Nais*, *Dero*, and *Slavina* were reported by Kent (in Wiggins et al. 1980) to occur in flooded soil samples from dry basins of temporary pools in Michigan, USA. During that study, Kent noted that most Naidinae specimens were collected in the Spring but seldomly in Winter, suggesting that they remain dormant in autumnal pools and thus are subjected to some stimulus other than flooding. Anlauf (1990) suggested that encystment by worms can be stimulated by limiting food supply.

Williams and Hynes (1976) found a few active *T. tubifex* in samples taken from the moist substrates of temporary streams in Canada; they noted that some of the tubificids, probably *T. tubifex* had secreted mucus envelopes around themselves, to which sand grains had become attached.

Encystment of worms appears to be associated with the drying conditions of wetlands and perhaps other aquatic habitats and could be regarded as an adaptive strategy for survival and recolonization. No evidence, however, was observed during this study of specimen survival during an extended dry phase.

During this study, we observed cysts of *D. multibranchiata* and *T. corderoi* in sediment samples collected after periods of drought ranging in length from 14 to 28 days.

In a previous study, Anlauf (1990) reported the presence of *T. tubifex* cysts in field samples taken after

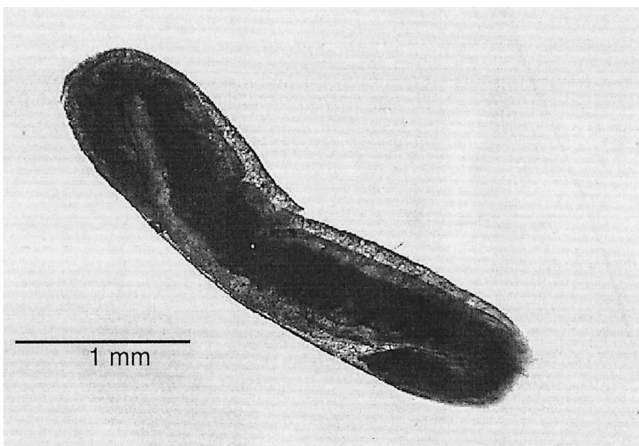


Figure 3. The completed cyst of *Trieminentia corderoi* showing the reduced proboscis.

a five-month drought period. During the laboratory phase of his study using incubated cultures of *T. tubifex*, Anlauf first detected cysts after an eight-week period in cultures that had been aerated but did not detect cysts in unaerated cultures until after a sixty-week period.

It is possible that drying occurs more slowly in nature than in laboratory conditions, thus providing a much longer period for the secretion of the cyst wall (Cook 1969). During this present study, 26 of aquatic oligochaetes were collected and identified in sediment samples collected from areas affected by drought conditions; however, of these 26 species, only *D. multibranchiata* and *T. corderoi* were observed to have formed cysts. It is probable that cysts of Naidinae and Opistocystidae have never been observed prior to this study because of the infrequency of analyses performed on samples collected from wetlands during drought conditions. We conclude that *D. multibranchiata* and *T. corderoi* present an adaptive strategy by developing protective cysts, enabling them the ability to survive drought, colonize temporary wetlands, and disperse into other freshwater habitats.

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