15 Benthic invertebrates of the Pantanal and its tributaries

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Abstract

This chapter summarizes current information on benthic invertebrate assemblages in different habitat types (rhithral, potamal, floodplain) of the Pantanal wetland in the Upper Paraguay River Basin and its tributaries. Special attention is given to adaptations of selected taxa to the floodpulse, and the use of benthic invertebrates as indicators for physical, toxic, and organic pollution. Comparing species richness in different dimensions, we found that it is much lower along the longitudinal (river channel) compared with the transversal (channel to floodplain) axis. Sandy river bed sediments provide a monotonous habitat with a similar assemblage dominated by the oligochaete *Narapa bonettoi* along the entire channel of the Paraguay River. Rare solid substrates such as rocky outcrops and woody logs represent hotspots for biodiversity and biomass in the river channel, however they also provide stepping stones for the invasive mytilid, *Limnoperna fortunei*. Diversity and biomass estimates for the floodplain habitats vary considerably according to their structural diversity, with floodplain channels being the most important, thus requiring major attention for conservation. Density and diversity of benthic assemblages of floodplain lakes depends strongly on their connectivity to main water bodies, which reduce the terrestrialization process. The benthic fauna reveals interesting adaptations to the floodpulse, including drought resistance, short life cycles, “pond-hopping” etc. to survive the wet-and-dry cycle. Lack of this adaptedness and a large number of vertebrate predators (fish, cayman juveniles and birds) limit success of invasive species to a certain degree, but the naiad fauna (large mussels) of the Pantanal is endangered by the “biofouling” through *L. fortunei* in a similar manner as the naiad fauna of temperate lakes by the zebra mussel.

Junk, W.J., Da Silva, C.J., Nunes da Cunha, C., Wantzen, K.M. (Eds) 2009
The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland, pp. 127-141.

15.1 Introduction

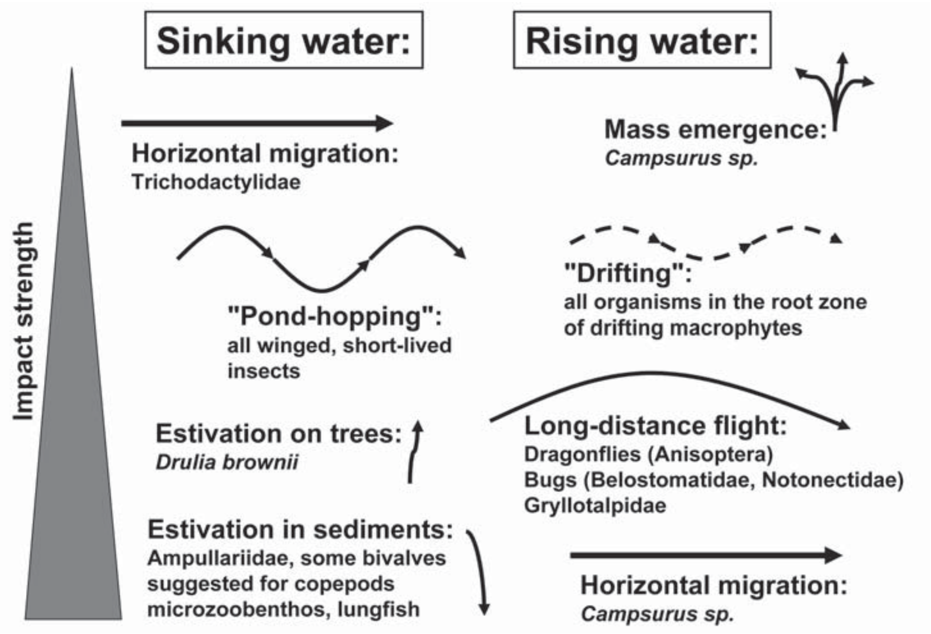
Benthic and epiphytic invertebrates are of great importance for floodplain ecosystems. They are an important member of the floodplain foodweb, conveying energy from living or dead organic matter to vertebrates (mainly fish). The benthic invertebrates also act as ecosystem engineers by influencing sediment characteristics, e.g. by bioturbation (increasing the oxygenation of the sediments) or by tube spinning (consolidating the sediment surface, and reducing the oxygen exchange). Mass emergences of chironomids or mayflies in the Pantanal give us an idea of the enormous productivity of these organisms. Studies of their species traits yield important information on the understanding of ecosystem processes and for biomonitoring. However, benthic invertebrates of Neotropical wetlands have yet received little attention by researchers because sampling and sorting are very time-consuming (see Wantzen & Rueda-Delgado 2009 for a review of study methods in the Neotropics) and because wide gaps in taxonomic knowledge reduce precision of the studies. Recently, there are some attempts to shed light into the taxonomy and biology of South American invertebrates, e.g. the ABLA project (Aquatic Biodiversity in Latin America, with so-far existing volume on fish parasites (Thatcher 2006), blackflies (Coscarón & Coscarón-Arias, 2006), mayflies (Dominguez et al. 2006), ceratopogonids (Borkent & Spinelli 2007), stoneflies (Stark et al. 2008) and the new book by Dominguez & Fernandez (2009). The literature on Pantanal invertebrates, however is yet very scanty. Based on this database, we can not determine yet if an invertebrate species in the Pantanal has to be considered rare or not, however we can identify key taxa and their functions in the ecosystem and habitats with high diversity. Some invertebrate species have an overall importance for the ecosystem as they have a high productivity, or they threaten the system as neozoans, or they are useful sentinel organisms. This chapter gives an introduction to the key taxa in the Pantanal wetland, its rivers and tributary streams of the Planalto.

15.2 Adaptations of key groups to the floodpulse

In the Pantanal, the floodpulse acts as a landscape filter (sensu Poff 1997) for colonizing invertebrates on different levels. The floodpulse determines (a) the aquatic habitat area in seasonal floodplains, (b) the connectivity between permanent and temporary water bodies, and (c) the habitat resource characteristics including flow conditions, food offer and oxygen concentration (Wantzen et al. 2005). Pantanal invertebrates have highly adapted species traits in order to cope with adverse conditions (Heckman 1998b) and to rapidly profit by changing resources in the pulsing landscape (Wantzen & Junk 2006). Large parts of the Pantanal seasonally dry out, therefore many aquatic species have short life cycles and re-establish quickly after drought, migrate, or they can estivate in muddy sediments. Rising water levels create new habitats and connect formerly disjunct water bodies, making new resources available for aquatic invertebrates – but also for their aquatic vertebrate predators (fish and young caimans). Winged adult insects, especially water bugs (Belostomatidae and Notonectidae) quickly recolonize newly developing water bodies during the freshet (Fig. 15.1).

The **microzoobenthos**, including testaceans, ciliates, rotifers, gastrotrichs, nematodes, and small flatworms, colonizes sediments and aquatic vegetation in permanent and temporary water bodies of the Pantanal (Hardoim & Heckman 1996; Heckman 1998a, b). Due to their ability to disperse in root systems of floating macrophytes and to survive drought in cysts, this group is omnipresent in the Pantanal. The epi- and endobenthic copepod assemblages of the Pantanal appear not to be as diverse and locally restricted as in the Planalto as indicated by studies from the Cerrado near Brasília (Reid 1984, 1997; Reid & Moreno 1990), which have revealed extremely high copepod biodiversity in the small streamside wetlands similar to the tributary streams to the Pantanal. In spite of being little studied, the microbenthos seems to be the key group for the transfer of organic

Fig. 15.1. Survival mechanisms of aquatic invertebrates in the Pantanal.



matter from biofilms to the vertebrates, especially to small floodplain fish species that are specialised in picking microbenthic organisms from plant surfaces. Nearly all small-sized fish, including young stages of large species, are surface-pickers. Large quantities of testacean shells are found in the stomach content of *Moenkhausia dichroura* (F. MACHADO, UFMT, Cuiabá, pers. comm.); however, it is not clear yet if there is a top-down control. HARDOIM & HECKMAN (1996) suggested that limits for the occurrence were set by (a) heat resistance of microzoobenthic species when water bodies are shrinking, (b) drought resistance, i.e. their ability to produce resting cysts for estivation, and (c) by food limitation due to oligotrophic conditions during the high water phase that limit periphytic algal growth.

The longest estivation times have been observed for the **freshwater sponge** *Drulia brownii*, which produce gemmulae that can survive extreme drought for more than a year. The sponges colonize branches of trees in the floodable zone of the riverbanks and margins of capão islands (see chapters 5, 12). where they are exposed to drought for several months (HECKMAN 1998b). There are more sponge species occurring on the rocky outcrops of the large Pantanal rivers, such as *Oncosclera navicella* (CARTER 1881) and *Trochospongilla repens* (HINDE 1888), however, these are less drought resistant as *Drulia brownii* (BOWERBANK 1863) and were not observed above the waterline (EZCURRA DE DRAGO, INALI Argentina, pers. comm.).

Ampullarid snails (Ampullaridae) occurring in the Pantanal, like *Pomacea lineata, P. scalaris*, and *Marisa planogyra,* have special adaptations to survive high temperatures during low water and even drought conditions of several months, including the development of both gills and lungs, a protective operculum, and a very high reproduction rate (KRETZSCHMAR & HECKMAN 1995). When studying ampullarid snail distribution along an inundation gradient at Fazenda Ipiranga near Poconé during the dry season, these authors found high densities of three species, *P. lineata* (20-48 ind.m^{-2})*,* *P. scalaris* (0-180 ind. m^{-2}), and *Marisa planogyra* (32-108 ind.m^{-2}). Egg masses were found throughout the year, however, with a strong bias towards the flooded period, with average (and maximum) clutch sizes of 390 (800), 230 (550) and 70 (270) eggs, respectively, for the three species. The eggs are calcified for protection, however, they do not survive the entire dry period (KRETZSCHMAR & HECKMAN 1995). When the sediments become rewetted at the beginning of the rainy season, many estivating ampullarid snails and trichodactylid crabs return to the sediment surface. Wading birds (e.g. *Aramus guarauna*) and snail kites (*Rostrhamus sociabilis*) then crowd in large flocks and prey upon them in the shallow water.

In spite of their protective shells, the **bivalves** of the Pantanal vary greatly in their resistance to desiccation, even within the same genus. *Anodontites elongatus* (Mycetopodidae) survives complete dryness of the sediments for several weeks while *A. trapesialis* is very vulnerable to drought and dies after one day of exposure (CALLIL 2003). Two survival strategies were observed. In temporary floodplain channels, mussels dig deep hollows into the fine, hard-packed sediments (HECKMAN 1998a), while in floodplain lakes they migrate towards the deepest point in the water body (CALLIL 2003).

Oligochaetes colonize practically all benthic habitats (BRINKHURST & MARCHESE 1991) including other animals like sponges and bryozoans (CORBI et al. 2005). In spite of having a sensitive cutis, they are very well adapted to the wet-and-dry conditions in the Pantanal, as both egg clutches and adults of most species can estivate in drought-resistant cysts. The root systems of floating macrophytes (e.g. *Eichhornia crassipes*) are densely colonized by oligochaetes. Along with the chironomids, this order is one of the best indicator taxa for water quality (see below). The oligochaete faunae of the Pantanal and the Upper Paraná floodplain have many overlapping taxa (EZCURRA DE DRAGO et al. 2004; MARCHESE 1987; MARCHESE et al. 2003; MARCHESE et al. 2005; TAKEDA 1999). Most remarkable is the range of body size in this order, ranging from nearly one meter in the terrestrial giant earthworm *Glossoscolex giganteus,* that produces large earth mounds in the dry-fallen floodplains (ADIS, MPI Plön, pers. comm.) and 2 mm in *Narapa bonettoi*, which colonizes mobile sand dunes in the larger rivers of the Pantanal (TAKEDA et al. 2001; MARCHESE et al. 2005, and see below).

Chironomids are by far the most diverse and abundant aquatic insect group found in benthic assemblages of the Pantanal and its tributaries (ABURAYA & CALLIL 2007; BUTAKKA 1999; BUTAKKA et al., submitted manuscript; HECKMAN 1998b; PAULA 1997; SCHIRMER, unpublished data; SERRANO et al. 1998a; STUR 2000; WANTZEN 1997). They have developed many different survival strategies that enable them to occupy almost all aquatic habitats, such as drought resistance and short life cycles. *Fissimentum* is a genus from the Chironomini tribe which is tolerant to desiccation (CRANSTON & NOLTE 1996). Life cycles of only one week from egg to imago are reported for *Apedilum elachistum* (NOLTE 1995) enabling it to colonize even temporary rock pools (NOLTE et al. 1996). In the Pantanal floodplain, short and partly synchronized life cycles cause that microhabitats that were rich in chironomid larvae one day may be completely devoid of larvae the next day, due to mass emergence (F. SCHIRMER, Stuttgart pers. comm.). Interseasonal variation of larval density is also high. In the Paraguay River, ABURAYA & CALLIL (2007) observed a variation between 180 ind. m^{-2} in May to 840 ind. m^{-2} in August, thus a strong increase from wet to dry season.

Among the **mayfly** species of the Pantanal, *Cloeodes hydation* (Baetidae, Ephemeroptera) is especially adapted to drought. *Cloeodes* larvae that were experimentally dehydrated on petri dishes were able survive up to 9 hours of dryness and could be repeatedly dried up to 5 successive times, moulting within 12 hours after rewetting (NOLTE et al. 1996). These authors calculated a life cycle length of 19 to 25 days. Similarly short cycle lengths were suggested for other stream mayflies in the

Bento Gomes River (Nolte et al. 1997) and in Cerrado streams of the Planalto (Oliveira & Froehlich 1997; Wantzen, unpublished data). Apart from drought, benthic invertebrate assemblages in lakes and connection channels of the Pantanal are subject to periodical alternations between lentic and lotic conditions (Wantzen et al. 2005). When the water and sediment movement increases during the wet season, the larvae of the mayfly *Campsurus notatus* (Polymitarcyidae, Ephemeroptera) perform lateral movements towards the lake margins to avoid the current (Butakka & Wantzen 2002; Takeda & Grzybkowska 1996). The genus *Campsurus* is an important keystone taxon in rivers and lakes of the Pantanal because of its high productivity and because of its function as bioturbator by burrowing tubes in fine **bed** sediments in which they maintain a permanent water flow by gill movements. In Amazonian lakes, life cycle length of three months have been reported for *Campsurus notatus* (Nolte 1987). It prefers sites with low organic matter content in the sediments as shown for Amazonian (Leal & Esteves 1999) and Pantanal lakes (Butakka & Wantzen 2002). Mass emergences of this genus may convey hundreds of kilograms of carbon upriver within few hours in neotropical rivers (Wantzen & Junk 2006).

Some **caddisfly** species of the genera *Neotrichia* and *Oecetis* occur in high densities in the root zone of the floating macrophyte *Eichhornia crassipes.* Gill movements and a small body size (i.e. short respiration tracts) are species traits that enable survival of these larvae under low-oxygen conditions. Marçal & Callil (2008) could identify the oxygen concentration as a control for the occurrence of diverse caddisfly and other benthic species in floodplain lakes of the Paraguay River within the Pantanal National Park. Both mayfly and caddisfly larvae are subject to strong fish predation and are only found in crevices which serve as a refuge. Apart from the root system of macrophytes, caddis fly larvae (mostly hydropsychids of the genus *Leptonema*) are also found in abandoned burrows of *Campsurus* in the clay margins of the larger rivers, or in porous woody debris in the rivers (Marchese et al. 2005).

The Pantanal Region is considered the geodetic centre of South America. This precludes the occurrence of invertebrate species that need to migrate towards marine environments for reproduction. Like in Amazonia (Walker & Ferreira 1985), the decapods occurring in the Pantanal reproduce in fresh water. Two **palaemonid shrimps** are so far known to the Pantanal, the larger *Macrobrachium amazonicum* (Heller 1862) with 50-110 mm body length, and the small (20-37 mm) *Palaemonetes ivonicus* (Holthuis 1950; F. Machado, pers. comm.). Both species are omnivorous and co-occur in shallow areas of standing and flowing water bodies, especially in dense macrophyte beds were they also represent an important food source for larger fish. In the nekton of large lakes such as Chacororé and Sinhá Mariana, small shrimp larvae occur in large quantities during the spawning season of the characids and were caught along with fish larvae (Severi, unpublished data).

In spite of having large numbers of planktonic larval stages (for *Macrobrachium amazonicum*, 10 to 11 plankton-feeding stages are reported for Amazonia (Junk & Robertson 1997), the freshwater shrimps also migrate into the tributary streams of the feeder rivers of the Pantanal. However, their distribution is locally limited by scarcity of calcium and by waterfalls which hamper the colonization of upstream sections of the tributary streams by non-flying aquatic organisms.

Five species of **trichodactylid crabs** were reported from the Pantanal near Poconé (Araújo & Machado, unpublished manuscript). Average clutch sizes were 800 (*Dilocarcinus pagei* Stimpson 1861), 600 (*Silviocarcinus cf. oronensis* Pretzman 1968), and 400 (*Poppiana argentianus* Rathbun 1906) per female. Reproduction of these species and the *Trichodactylus* species, *T. camerani* (Nobili 1869) and *T. parvus* (Moreira 1912), generally takes place at the beginning of the wet season with a peak in October and November. Females carry eggs and juveniles of different developmental stages using the pleopods which form a brood pouch. Juveniles develop directly, without larval stages. In spite of high egg numbers and parental care, low fecundity rates (i.e. number of viable offspring per female and year) of 7.41 for *Dilocarcinus pagei* and 6.65 for *Sylviocarcinus australis* (Magalhaes & Türkay 1996) were reported in the Paraguay River (de Barros Mansur & Hebling 2002). The crabs avoid inadequate environmental conditions by migrating towards deeper water bodies (Fig. 14.1). When the habitats finally dry out completely, the crabs can estivate in deep holes in muddy sediments in monospecific or mixed associations, even along with ampullarid snails (F. Machado, pers. comm.). At river margins, the crabs dig holes of about one meter depth above the waterline. Crabs close them with wet mud, indicating the presence of an active animal. Inactive holes are important habitats for other invertebrates, fish, snakes or kingfishers. The Pantanal crabs are omnivorous and feed i.a. on snails, macrophytes, and fish. Their predators are birds, e.g. *Rostrhamus sociabilis, Busarellus nigricollis, Geranospiza caerulescens, Polyborus plancus*, *Jabiru mycteria,* and crab-eating fox (*Procyon cancrivorous*), caimans, guatí (*Nasua nasua*), *lobinho* (*Cerdocyon thous*), and fish like pacu (*Piaractus mesopotamicus*) and piraputanga (*Brycon microlepis*). They are also much sought after by local fishermen who use them as bait.

15.3 Benthic habitats (choriotopes) and their invertebrate assemblages

Definition of habitats is a difficult task in the quickly changing environment of the Pantanal (Wantzen et al. 2005). The classic definition of Hynes (1970), restricted "benthos" to aquatic bottom sediments, whereas Resh & Rosenberg (1984) extended the term by including the stems of aquatic macrophytes as a substrate. In shallow neotropical floodplains, the transition between these habitats is very smooth and many benthic species of the Pantanal colonize a wide range of habitats. For example, we found ***Campsurus*** spp. (mayflies) in lake sediments, in floodplain channels (Wantzen & Butakka 2002), in the banks of the main channel river sediments (Ezcurra de Drago et al. 2004; Marchese et al. 2005), and in roots of floating macrophyte. Some benthic habitats, however, have clearly defined assemblages.

15.3.1 Rhithral assemblages

There are only few sites where streams directly enter into floodplain habitats, e.g. in the foothills of the sierras that border the Pantanal National Park. Most low-order streams are restricted to the high plains, surrounding the northern part of the wetland. These plains are generally based on arenitic rocks (e.g. the Chapada dos Guimarães), however, parts of the Chapada dos Parecis, of the Serra de Bodoquena and of the hill ranges north of Corumbá have limestone rocks. Sioli's general statement that geochemistry of the catchment has a strong effect on the stream characteristics (Sioli 1968) becomes much evident here as the occurrence of calcium-dependent mollusks and larger crustaceans do not occur at all in calcium-lacking streams.

Rainfall seasonality strongly affects the runoff characteristics of the streams, many of which are intermittent. Connectivity to riparian wetlands is low during the dry season from June to September, however, flow pulses during rainy season increase runoff up to tenfold and allow an exchange of organic matter and biota between stream and riparian wetlands (Junk & Wantzen 2004; Wantzen & Junk 2000).

Cerrado streams from sandstone areas have very low conductivities and calcium is hardly detectable (Heckman 1995; Wantzen 1998b, chapters 6,7). They typically lack mollusks and decapod crustacea, while harpacticoids, some cladocerans and ostracods were the only crustaceans found in these ion-poor streams. Fish are equally rare, thus the trophic structure is ruled by large predatory invertebrates. In streams that had conductivities below 7 $\mu S\ cm^{-1}$, we hardly found more than 2 to 3 species of characid, rivulid, or trichomycterid fish. On the other hand, they harbour a considerable insect fauna (Wantzen & Wagner 2006). Many species have not yet been described, especially chironomids, empidids, and other diptera. The diversity of the orders Ephemeroptera, Plecoptera, Trichoptera (i.e. mayflies, stoneflies, caddis flies) which appears to be lower in Cerrado streams than in temperate zone streams, can be assessed only after thorough revision of the material (e.g. Holzenthal 1995; Froehlich 2002; Dominguez et al. 2006). Benthic sampling, emergence traps and rearing experiments indicate that most of these taxa are polyvoltine (Oliveira & Froehlich 1997; Wantzen 1997; Bispo, Oliveira, Marques & Wantzen, unpublished manuscript).

The trophic guilds (functional feeding groups) of invertebrates in Cerrado streams differ from the distribution of shredders, collectors, grazers and predators reported from the river continuum in temperate zones (Vannote et al. 1980). The density and diversity of shredders is rather low whereas most invertebrates are omnivores or predators (Wantzen 1997; Wantzen & Wagner 2006). Thus, the food webs of these streams depend much less on the direct consumption of leaf litter than e.g. temperate streams. Recent isotope studies in Mata Atlantica streams (Brito et al. 2006) indicate that periphytic and drifting algae are another important food source in tropical streams. Wantzen et al. (2008) suggested that organic matter sources other than leaf litter, e.g. falling terrestrial insects, feces of herbivore insects, flowers, fruits and pollen are important food sources in Cerrado streams, as reflected by the high percentage of predators and scavengers. Odonata (dragonflies) reveal considerable species richness and a high degree of adaptation to special habitats and feeding. In slow-flowing sections, dragonfly larvae are found digging in sand or sand-filled leaf packs (Gomphidae), lurking for prey on vertical woody structures (Aeshnidae), while in fast-flowing sections they hunt on stones (Calopterygidae) and in plants like Podostemaceae (some Libellulidae). Dobsonfly larvae (Corydalidae) are the largest benthic predators in low-conductivity streams of the Cerrado. They are extremely resistant to high current, however, they require high physical and chemical water quality and can therefore be taken as indicator species (Paula 1997; Wantzen 1997). Browsing for prey in stony and woody substrates, they act as ecological engineers by litterally cleaning the intersticial spaces (Wantzen 1997).

Calcarious streams have similar assemblages as the Cerrado streams but they also harbor shrimp and mollusc species such as *Haasica balzani* (see Table 15.1). Due to increased nutrient availability, primary production is generally higher at exposed sites than in the nutrient-poor Cerrado streams, allowing a higher percentage of grazers and a lower abundance of simulids which need bare surfaces for fixation.

Piedmont streams are situated in the transition zone between the Planalto and the Pantanal. Often, cascades limit the upstream migration of fish and decapods. The faunistic overlap of typical wetland species and the fauna of the upstream tributaries causes a high species richness (Wantzen & Junk 2000). Comparing two sets of streams at the same level of taxonomic resolution (family or genus level), a piedmont stream near Caité had almost twice the taxa richness (79 ± 10 taxa) as the Cerrado streams of the Planalto (average of 43 ± 16 taxa), mostly due to higher diversity of caddis flies, mayflies and dragonflies in the piedmont stream (Wantzen 1997). Piedmont streams are permanently well-oxygenated and

Table 15.1 Occurrence of bivalves in the Pantanal due to various authors: 1 = Serrano et al. (1998b), 2 = Heckman (1998a), 3 = Callil(2003), 4 = Oliveira et al. (2006); Marçal & Callil (2008); Callil et al. (2007), 5 = Aguiar (2006), 6 = Colle & Callil (2009)

Taxon	small river	large river	lake	stream	Author
Sphaeriidae					
Pisidium sp1.	x				1,5
Pisidium sp2.	x				5
Pisidium sp3.	x				5
*P. punctiferum (*Guppy,1867),	x				1
P. sterkianum (Pilsbry, 1897*)*	x		x		5,6
Eupera sp.	x				1
E. simoni Jousseaume*,* 1889	x				1
E. tumida (Clessin, 1879*)*;	x				1
Hyriidae					
Castalia ambigua inflata Orbigny,1835	x	x	x		1,2,3,6
Diplodon parallepipedon (Lea, 1834)			x		3
D. guaranianus (Orbigny, 1835)	x				3
Etheriidae					
Batlettia steffanensis (Moricand, 1856) 1*		x			3
Mycetopodidae					
Haasica balzani (Ihering, 1839)		x			3
Bartlettia stefanensis (Moricand, 1856)					
Anodontites trapesialis (Lamarck, 1819)	x	x	x		1,2,3,5,6
A. trigonus (Spix, 1827),	x				1,2,3.6
A. tenebricosus (Lea, 1834)	x				1,5
A. ensiformis (Spix, 1827)		x			3,5
A. crispatus Bruguiere, 1792				x	3
A. elongatus (Swainson, 1823)			x		3,6
A. soleniformes (Orbigny, 1835)		x			1,3,5
Monocondylea parchapii Orbigny*, 1835*	x		x		1,3,5
Fossula fossiculifera (Orbigny, 1835)			x		3
Mycetopoda siliquosa (Spix, 1827)					
M. soleniformes Orbigny, 1835.					
Corbiculidae					
Corbicula largillierti (Philippi, 1844)	x	x			3,5,6
Corbicula fluminea (Müller,1774)		x	6		3
Mytilidae					
Limnoperna fortunei (Dunker, 1857)					4

become important refuges for large invertebrates and fish when the "dequada" phenomenon, i.e. fast decrease of oxygen concentration due to intensive leaching at the beginning of the rainy season (Calheiros & Hamilton 1998), turns the floodplain a hostile environment.

Rhithral parts of rivers such as the Cuiabá River above Nobres are characterized by high water velocities, low water depth, and gravellish and sandy sediments. The clear water and the width of the wide river bed allow an intensive growth of periphytic algae that provide feeding grounds for grazers (e.g. helicopsychid caddis flies and several snail species). Net-spinning caddis flies (mostly hydropsychid *Macronema* and *Smicridea*) cover large areas of the sediments. These sites show a faunistic overlap between tributary and potamal species and high benthic biomasses. Moreover, they harbour rare mollusc species (see Table 15.1) and are important oviposition sites for fish.

15.3.2 Potamal assemblages

The lower sections of the large feeder rivers of the Pantanal like the Paraguay, Cuiabá, São Lourenço, or Itiquira generally characterized by sandy, clayish or rocky substrates which harbour distinct assemblages. In a first study on benthic invertebrate assemblages in 38 sites of the upper section of the Paraguay River, Marchese et al. (2005) identified 69 species and morphospecies, including 22 oligochaetes, 20 chironomids, 6 ephemeropterans, 5 microcrustaceans, 3 nematodes, 2 tubellarians, 2 ceratopogonids, 2 mollusks, 2 hirudineans, and one coleoptera, trichoptera, dragonfly, watermite, and sponge each. In a year-round study on a short stretch of the same river near Cáceres, Aburaya & Callil (2007) found 32 chironomid species, the most abundant taxa being *Polypedilum* (*Asheum*) (45.8%), *Polypedilum* (*Tripodura*) (11.5%), *Polypedilum gr. fallax* (4.22 %), *Labrundinia* sp.1 (11.4%), and *Tanytarsus* (2.68%). Average density of benthic invertebrates varied in the study of Marchese et al. (2005) between 72 and 10,354 ind.m^{-2} in the meandering sector of the river; 3,611 and 49,629 ind.m^{-2} in the straight-transitional sectors. Highest densities were attained in sand-gravel sediments dominated by *Narapa bonettoi*, which occured associated with other oligochaetes such as *Haplotaxis aedeochaeta,* the turbellarian *Myoretronectes paranaensis,* the nematode *Tobrilus*, the copepod *Potamocaris* sp., and chironomids such as *Djalmabatista* sp. and *Lopescladius* sp. A similar assemblage was found in the same type of sediments in the Upper Paraná River by Montanholi-Martins & Takeda (2001) and the Middle and Lower Paraná by Marchese (1984) and Marchese et al. (2002). *Narapa bonettoi* is a typical r- strategist, with asexual and sexual reproduction occurring at the same time (Ezcurra de Drago et al. 2004; Marchese 1994). Its minute body size allows fast (re-) colonisation of mobile sandbeds (Marchese et al. 2002). Habitats with finer sediments were represented mainly by *Parachironomus* sp., *Cryptochironomus* sp., *Nimbocera* sp., *Campsurus* sp., Leptohyphidae, and Hydracarina. Judging from the extremely low biomasses in mobile sandy sediments – individuals are so small that even large numbers of them can hardly be seen in the sample with the bare eye – we suppose that the benthic invertebrate production of these sites does not significantly support the food web. Substantial invertebrate biomasses were found either in clay margins perforated by digging mayflies (*Campsurus* sp.), or in backwaters with accumulations of fine particulate organic matter where large mussels occur, or in snags of large woody debris (Marchese et al. 2005) which represent an important habitat in sand river systems (Benke et al. 1984; Wantzen & Junk 2006).

The limited occurrence of these hot spots of benthic invertebrate biomass (Wantzen & Junk 2006) supports the view that for this type of mostly sand-bedded river, the floodplains are more important to support fish productivity than the proper river channel (Agostinho & Zalewski 1995; Junk et al. 1989). The benthic assemblages of sections of the Paraguay River downriver of the Pantanal have been studied by the AquaRap expedition 1997, which covered the lower section of the Upper Paraguay and upper section of the Lower Paraguay River from the mouth of the Rio Negro in the North (on Brazilian territory) to the mouth of the Rio Aquidauana/Aquidabán (on Paraguayan territory) in the South (Barbosa et al. 2001, Magalhães et al. 2001). A study by Ezcurra de Drago et al. (2004) covers the lowermost section of the river from the Paraguayan/Argentinian border to its confluence with the Paraná river. Sandy river bed sediments provide a monotonous habitat with a similar assemblage dominated by the oligochaete *Narapa bonettoi* along the entire channel of the Paraguay River.

The sediment structure of the upper sections of the feeder rivers of the Pantanal, however, is often gravelly, e.g. in the Cuiabá River near the city of Nobres. These substrates are densely colonized by chironomids and larger invertebrates, e.g. they harbour a large number of bivalves (Table 15.1) and snails (Thiaridae), mayflies (Leptohyphidae, Leptophlebiidae) and caddisflies (Polycentropidae) (Lima 2002). The amount of the input of drifting organisms from these river sections into the sandy channel sections has not been assessed. Using artificial substrates of gravel bags Lima (2002), studied the benthos fauna on a 26-km-long stretch from 10 km above the city of Cuiabá to its downstream perimeter. He found 71 taxa, including 34 families of invertebrates and 47 genera of chironomids which did not show a clear spatial pattern along or across the studied section; however, the total abundance was much higher during the low water period than during the high water.

A recent invader of solid substrates, *Limnoperna fortunei* (see below), might locally increase the in-channel productivity, as shown for the Paraná River (Darrigran & Ezcurra de Drago 2000) and the Paraguay River (Marçal & Callil, 2008; Oliveira et al. 2006).

15.3.3 Benthos of floodplain lakes and channels

The seasonal changes of water depth, flooded area, current velocity, and current direction in lakes and channels of the Pantanal cause strong fluctuations in the populations of benthic invertebrates. These temporal changes interact with spatial heterogeneity in the distribution of the fauna on a large (littoral vs. limnetic sites) and a small (substrate patch) scale (see Wantzen et al. 2005 for a detailed discussion). Moreover, key parameters for the distribution of the benthic invertebrates such as temperature and oxygen covary with the water level fluctuations (Marçal & Callil 2008). Nessimian & Sanseverino (1995) identified water level fluctuations and development of the macrophyte vegetation as the main triggers for chironomid distribution in a Brazilian sand dune lake. Water low level induced changes in chironomid community by substituting grazers such as *Goeldichironomus* sp. and by detritivorous/herbivorous such as *Polypedilum* sp. in several habitats of the Upper Paraná River (Takeda et al. 2004a, 2005).

As an example, we studied the benthic invertebrate fauna, especially chironomids, of the shallow Sinhá Mariana Lake near Barão de Melgaço (Fig. 15.2), at sites which seasonally interchange water with the Cuiabá River (I. Corixo Tarumã), with the nearby Chacororé Lake (II. Corixo do Mato), in the lake centre (III. Limnetic Zone), and in the mouth of a blackwater river (IV. Rio Mutum) during the low and the high water period (Butakka 1999; Wantzen & Butakka 2002). The results of our studies in Pantanal floodplain lakes suggest that water current and connectivity are crucial for the occurrence or lack of adequate food items and substrates for colonization. The seasonal occurrence of the lotic, web-spinning *Rheotanytarsus* at site I and the strong reduction of filter feeders during the wet season can be regarded as indicator for the changes between "limnophase" and "potamophase" of floodplain-lake-systems (sensu Neiff 1990).

Benthic invertebrates, especially chironomid larvae, had generally higher densities at the litoral sites than at the limnetic site (Table 15.2). Most insect taxa and bivalves were restricted to the shallow littoral sites (I, II, IV). Nematoda, oligochaeta and ostracoda were the most abundant taxa at all sites and sampling dates. However, there were strong seasonal differences. Numbers of nematoda, oligochaeta and crustacea (copepods) increased from dry season to wet season whereas chironomids and other insects revealed a complementary pattern. From dry (lentic) to wet (lotic) season, total abundance of invertebrates became reduced in sites I, II, and III (by 60, 30 and 19%, respectively), however, at the inflow site

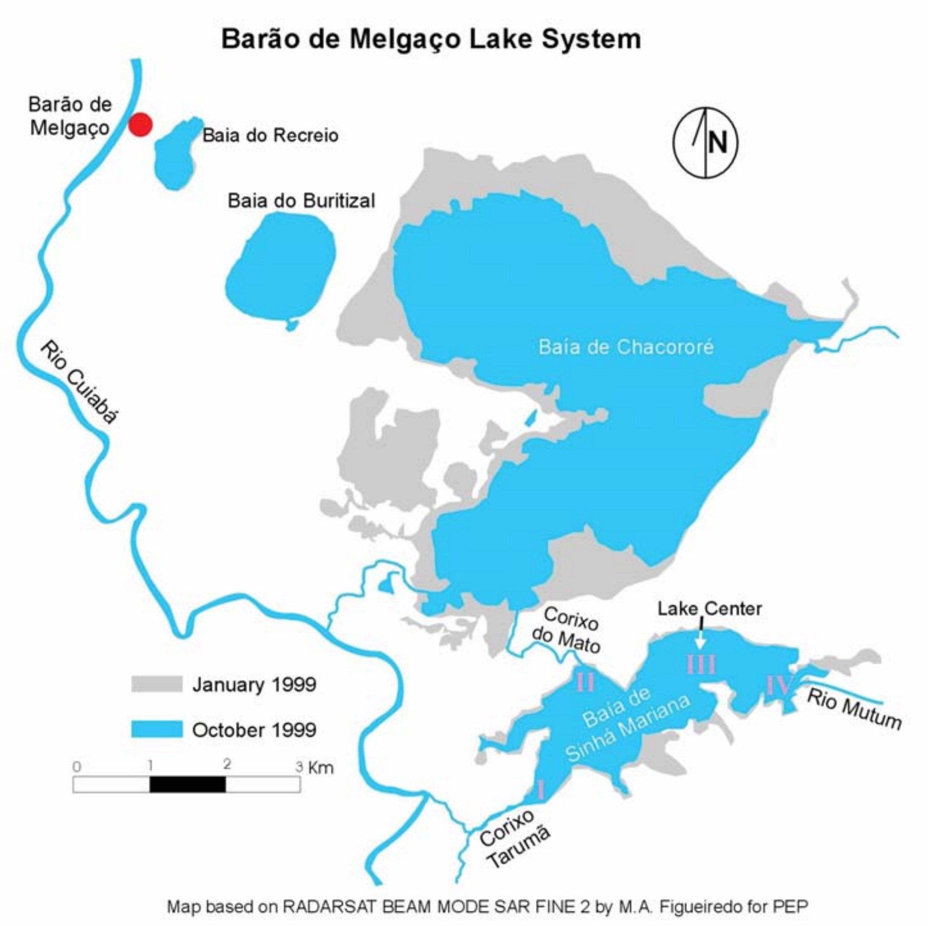


Fig. 15.2 Map showing the sampling sites of BUTTAKA's (1997) study and their possible hydrologic connections to other water bodies.

of the Mutum River (site IV) numbers increased by 134%, indicating a large input of drifting invertebrates from the river.

In the Sinhá Mariana lake, 28 morphospecies of chironomids have been identified so far (BUTAKKA 1999). The littoral stations were characterized by filter feeders (*Caladomyia*), gatherer-collectors (*Polypedilum*, *Aedokritus, Fissimentum*), and predators (*Cryptochironomus* and *Ablabesmyia* (*Karelia*). Some taxa occurred only during the low water period, including collectors like *Zavrelliela* and predators like *Larsia*. Others occurred only during the high water period, such as gatherer-collectors (*Chironomus gr. salinarius*, *Beardius*, *Chironomus gr. decorus*), filterer-collectors (*Rheotany-*

Table 15.2 Densities of taxonomic groups in the Sinhá Mariana Lake during the dry and wet season 1998/1999 (average values from 3 parallel samples per month, 3 months per season, ± standard deviation, from BUTAKKA 1999).

site/season	**unit**	**I-Dry**	**I-Wet**	**II-Dry**	**II-Wet**	**III-Dry**	**III-Wet**	**IV-Dry**	**IV-Wet**
variable									
Chironomidae	ind/m^2	4698 ±3941	924 ±954	2416 ±1592	303 ±286	685 ±1127	44 ±21	2484 ±1771	408 ±861
other insects	ind/m^2	5994 ±5645	1147 ±519	173 ±181	31 ±60	54 ±59	36 ±23	264 ±133	155 ±146
Nematoda	ind/m^2	5643 ±3918	1549 ± 904	6664 ±4470	2377 ±3310	2455 ±2647	1417 ±521	8309 ±6661	14667 ±5651
Crustacea	ind/m^2	745 ±627	885 ±819	1518 ±2295	1604 ±1627	3120 ±4018	1100 ± 889	7180 ± 4466	24872 ±19163
Oligochaeta	ind/m^2	3341 ±3599	3605 ±2608	2694 ±2173	4922 ±4858	404 ±174	2858 ±1294	2946 ±2304	12827 ±9743
Mollusca		10 ±16	85 ±137	2 ±7	59 ±67	-	-	5 ±10	70 ±102
other invert.	ind/m^2	277 ±317	111 ±108	41 ± 89	199 ±285	18 ±25	10 ±12	215 ±124	599 ±989
Total	ind/m^2	20711 ±12126	8309 ±4104	13512 ±9887	9498 ±9495	6739 ±5464	5467 ±2475	21407 ±8276	53600 ±28565
Taxa number (Chironomidae)	n	3.55 ±1.66	4.22 ±1.39	4.77 ±0.83	2.11 ±0.92	1.66 ±1.32	0.88 ±0.33	3.77 ±1.71	3.33 ±1.65
Diversity (Chironomidae)	H’	0.49 ±0.16	0.52 ±0.05	0.45 ±0.11	0.41 ±0.14	0.48 ±0.03	-	0.48 ±0.09	0.75 ±0.08

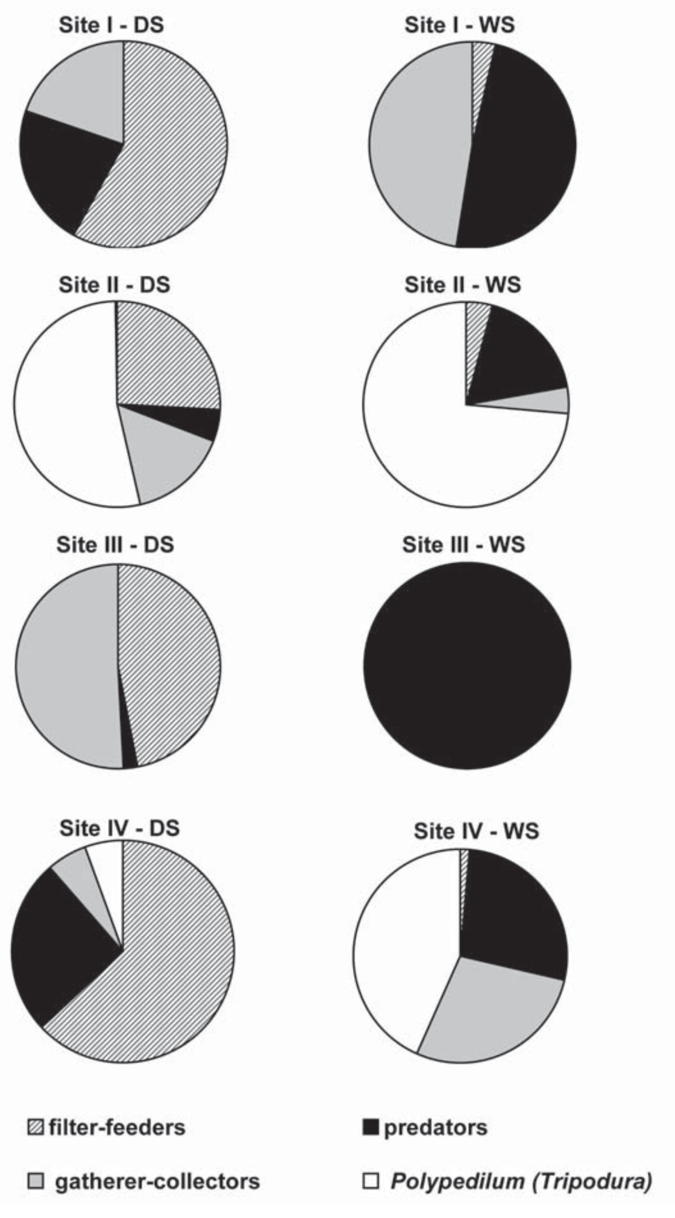


Fig. 15.3 Relative abundance of chironomids of functional feeding groups in the Sinhá Mariana lake, Brazil. The genus *Polypedilum* (Tripodura) belongs to both feeding groups, shredders and gatherer-collectors. Note that an increase in relative abundance can coincide with a decrease in total abundance of a certain group. Sites are described in the text. DS = dry season (low water period), WS = wet season (high water period).

tarsus), and one predator (*Tanypus punctipennis,* BUTAKKA et al., unpublished). Only one scraper (*Phaenopsectra* sp.) was found occasionally.

The proportions of the functional feeding groups of chironomids varied greatly between seasons (Fig. 15.3). **Filter feeders** (mainly *Caladomyia* in the littoral sites and *Tanytarsus* at the limnetic site) became reduced from the dry/lentic to the wet/lotic season. At the lake centre (site III) only few predatory chironomids (*Coelotanypus*) were found. Similarly, the genus *Polypedilum* (*Tripodura*) which has variable feeding behaviour as shredder and gatherer-collector, increased its relative density but decreased in total abundance during the wet season. Chironomid genera studied by HENRIQUES-OLIVEIRA et al. (2003) in streams also showed a change in their feeding habits, having more generalists and opportunistic feeding on what was available.

Other insect taxa included mayflies, predatory chaoborid and ceratopogonid midges, herbivorous elminthid beetles, very few predatory hemipterans and dragonflies, and hydropsychid caddisflies (only at site I). The burrowing mayfly genus *Campsurus* was present throughout the sampling period, with highest larval densities of 3,866 ind.m^{-2} at site I during decreasing water levels, indicating that these larvae profit by the suspended food sources from the floodplain areas. Mussels (*Castalia inflata*) occurred only in the littoral sites, maintaining a high biomass of filterers during the wet season (WANTZEN & BUTAKKA 2002).

MARCHESE et al. (2005) found similar density values for benthic invertebrates of the sediments in floodplain lakes (682-5,962 ind.m^{-2}) and floodplain channels (1,704-2,208 ind.m^{-2}) of the Upper Paraguay River. The Shannon-Wiener diversity index ranged from 0.75 at river sites to 2.08 in lake sites. Sites with silt-clay sediments and relatively low organic matter content were characterized by *Paranadrilus descolei, Aulodrilus pigueti*, and *Campsurus* sp., while floodplain lakes with high organic matter content showed a dominance of *Paranadrilus descolei, Tubifex tubifex, Aulodrilus pigueti, Pristina osborni*, and *Fissimentum* sp. (Table 15.2). Similar oligochaete species were found in river and floodplain habitats of the Negro River in the south-eastern part of the Pantanal (TAKEDA et al. 2000). Oligochaetes also show seasonal variation in the density due to the floodpulse. MENEGAZZO (2006) could show for the Santa Rosa Lake, that during falling water levels (June-October 2004) biodiversity of oligochaetes decreased (from 12 to 7 taxa), while the density significantly increased (from 1,441 to 2,097 ind. m^{-2}). The naidids *Pristina osborni* and *P. americana* accounted for most of this variation.

A comparison of the invertebrate fauna between the root systems and the "true" benthic habitats of floodplain lakes shows that the latter generally have lower densities, biomass, and diversity than the macrophytes (BUTAKKA & MIYAZAKI 1998). The benthic assemblages of the root systems of *Eichornia crassipes* in fifteen lakes in the Pantanal National Park (confluence of Cuiabá and Paraguay

Table 15.3 Occurrence of aquatic oligochaete in bank and channel habitats of the Upper Paraguay River and in its floodplain habitats. Abundance classes: 1 = <100 ind. m^{-2}; 2 = 101-1,000 ind. m^{-2}; 3 = 1,001-10,000 ind. m^{-2}. Data from MARCHESE et al. (2005) for the Pantanal and from TAKEDA et al. (2000) for the Rio Negro (11 sampling sites including river and floodplain habitats).

Oligochaete species	Bank	Channel	Floodplain	Rio Negro
Narapa bonettoi	3	3	1	3
Bothrioneurum americanum	1	1	1	1
Limnodrilus udekemianus	1			
cf. Rhyacodrilus sp.	1	1		
Tubifex tubifex	1	1	1	
Paranadrilus descolei	1	1	2	1
Aulodrilus pigueti	1	1	2	1
Aulodrilus adetus				1
Dero hymanae	1		1	
Dero cf. Gravelyi	1	1	2	
Dero pectinata	1	1	1	1
Dero righii	1	1	1	1
Dero nivea			1	
Dero borellii				1
Dero vagus				1
Dero digitata				1
Dero furcatus				1
Dero multibranchiata				1
Pristina osborni	1	1	1	1
Pristina americana	1	1	1	1 – 2
Pristina aequiseta				1
Pristina macrochaeta				1
Pristina proboscidea				1
Pristina synclites				1
Stylaria sp.				1
Nais shubarti	1		1	
Nais elinguis			1	
Nais variabilis				1
Stephensoniana trivandrana	1	1	2	1
Slavina evelinae			1	1
Trieminentia corderoi	1			
Haplotaxis aedeochaeta	1	1		
Brinkhurstia americana	1	1	1	1
Bratislavia unidentata				1
Pristinella longidentata				1
Opistocysta serrata				1
Enchytraeidae	1			1

River) were analyzed in several studies. Marçal & Callil (2008) identified 14 taxa of trichoptera, the densities of which varied between 357 and 4,448 ind.m^{-2}. The most common taxa were *Oecetis* sp., *Polycentropus* sp., and *Macronema* sp. Coleoptera were represented by 29 genera of 19 families, the most common being Noteridae (75%), Dytiscidae (10%), and Hydrophilidae (7%), while the families Apionidae, Scarabaeidae, Byphyllidae, Coccinilidae, and Liminichidae together contributed only 0.5% of the individuals (Sorubim 2007). The density of mollusks varied between 1,648 and 38,480 ind. m^{-2}, mostly represented by the families Hydrobiidae (55%), Sphaeridae (25%), while *L. fortunei* represented 12%, Planorbidae 6%, and Ancylidae 2% (Silva 2007).

Information on standing crop of zoobenthos in the Pantanal is very scattered. In a first survey on benthos and sediment characteristics for 12 stations in a pond, some lakes and the rivers Taquari, Miranda and Paraguay, Fukuhara & Mitamura (1985) report average values of formol-fixed benthic invertebrates larger than 130 µm of 401 mg wet weight.m^{-2} (range: 2–2,804 mg wet weight.m^{-2}). Presence of large and heavy mayfly and gomphid dragonfly larvae strongly influenced the results. Zoobenthos biomass in both lakes of the Paraguay River was low (163–295 mg wet weight m^{-2}), although the organic matter content was high (ignition loss 6.9–8.1%, carbon content: 1.03–2.28%). Even though no precise mass data are available yet, our studies have shown that the density and biomass of benthic invertebrates in river-floodplain lakes depends very much on the connectivity between river and lake.

Lakes with depositional character tend to have very low invertebrate biomasses due to the high oxygen consumption of the accumulated organic matter. The dense black layers of undecomposed *Eichhornia* fibres on the bottom of shallow lakes were hardly colonized at all by macrozoobenthos probably due to temporary lack of oxygen. Studies in Amazonia revealed that oxygen depletion and development of H_2S in deeply flooded floodplain lakes strongly reduced planktonic and benthic invertebrates (see discussion in: Junk & Robertson 1997). The situation in the Pantanal seems to be opposed: Here, disconnected water bodies during the dry season have low oxygen concentrations (see Nogueira et al. 2002) while flooding triggers connectivity and supply of oxygenated water. Those lakes that have a strong connectivity (i.e. permanent throughflow in secondary channels) have relatively low detrital biomass available and medium benthic biomass. Highest biomass values were found in lakes that have a temporary connection to the river so that fresh detritus becomes delivered regularly however old, recalcitrant and highly oxygen-demanding detritus become washed out of the system during flood events (Marchese et al. 2005). Burrowing activity of invertebrates and loricariid fish provide sponge-like habitat structures in clayish riverbanks and driftwood jams that are hot spots for both benthic invertebrate abundance and biomass

(Wantzen & Junk 2006). Gatherer and filter feeders, including mayflies and caddisflies (Polymitarcyidae and Hydropsychidae), chironomids, and – more recently – the invasive mussel *Limnoperna fortunei*, settle on these surfaces, where they can exploit the large amounts of suspended organic particles. A longitudinal profile of the benthos of the Paraguay River in 2000 and 2001 (Ezcurra de Drago et al. 2004; Marchese et al. 2005) revealed that in the upper section, driftwood logs were densely colonized by benthic invertebrates while in the lower section, the wooden surfaces were literally cleaned by *sábalo* fish (*Prochilodus* sp.). It is not yet clear if this effect was caused by a different fish community in both sections or by the fact that in the lower section, which was infested by *L. fortunei* earlier, and the fish already learned to use this species as a food item (Montalto et al. 1999) and changed their foraging behaviour (see next section).

15.4 Native and invasive bivalves in the Pantanal

Mussels are important players in the trophic structure of freshwater ecosystems as they can remove a considerable amount of particulate organic matter and algae from rivers and lakes (Descy et al. 2003) and transfer it into biomass which is often the highest of all taxa in benthic assemblages. In spite of good historical records (Ihering 1915; Pilsbry 1933), bivalves have re-gained interest only recently along with their dramatic worldwide decline (Lyons et al. 2007). In the Pantanal, a large number of bivalves occurs, however, their diversity, ecology, and taxonomy are only poorly known. Early expedition data from Pilsbry (1933) and Ihering (1915) on the Paraguay report *Anodontites exoticus* (Lamarck 1819), *A. mortonianus* (Lea 1834), and *Diplodon* (*Ciclomya*) *paranensis* (Lea 1834). Recently, the list is increasing as a result of more intensive studies (Table 15.1).

Current studies on bivalve ecology in the Pantanal deal with ecophysiology, reproductive cycles and with anatomical features which support taxonomic and bioindicator assays (Callil & Junk 2001). In a recent study (Callil 2003), it was shown that *Anodontites trapesialis* and *A. elongatus*, two common Mycetopodidae species, show very different reactions to a variable degree of connectivity of the floodplain lakes and the river mainstem. In the Poço Lake, which is permanently connected to the Cuiabá River, shells of *Anodontites trapesialis* presented only one third of the weight of shells from the isolated Conchas Lake. However, the average fresh weight, i.e. body mass plus shell mass, was not significantly different between both sites, indicating a higher biomass production in the connected lake which regularly receives freshwater inputs by the Cuiabá River. The co-occurring species, *Anodontites elongatus*, did not show these effects. Bivalves living in temporarily oxygen-free environments have to cope with the accumulation of acidic substances from the anaerobic respiration (e.g. succinate) in the extrapallial fluid which reduce the deposition of calcium in the shell or even dissolve it (Wilbur & Saleuddin 1983). The shell weight differences between populations can be attributed to this mechanism and the variable environmental conditions (Callil 2003). Callil & Mansur (2005) assume that the energetic investment in either shell weight or body mass is an adaptive variable of the survival strategy of mussels which can become optimized for the current oxygenation situation.

Globalization favours the spread of exotic species, especially mussels (Karatayev et al. 2007). Currently, several exotic mussel species are invading the Pantanal (Callil et al. 2007). They may cause changes and damages to the ecosystem, e.g. by outcompeting the large native bivalve species. Recent and future research will evidence if these species are able to establish on the long run. First records of the Asian freshwater clams *Corbicula fluminea* and *C. largillierti* (Corbiculidae) in the Pantanal in 1996 reported densities of 192 ind. m^{-2} (Callil & Mansur 2002) which were relatively low compared to 5,191 ind.m^{-2} at Lagoa Mirim (Mansur et al. 1988), 4,173 ind.m^{-2} at Rio Caí (Mansur et al. 1994) in southern Brazil, 2,495 ind.m^{-2} in Argentina (Darrigran, unpublished), and 9,257 ind.m^{-2} for North America (Isom 2007). This fact may be related either to the recent colonisation by this genus or to the high water temperatures during the low water period which often exceed the upper lethal limit for this species which is close to 36 °C (McMahon & Williams 1986). At high temperatures, *Corbicula fluminea* reduces its feeding rate (Viergutz et al. 2007). At present**,** the species *C. largillierti* has colonized the Cuiabá river and many of its tributaries (Callil, unpublished data). *Corbicula fluminea* is known as an invader of sandy and gravelly sediments also for European rivers and lakes (Rajagopal et al. 2000, Werner et al. 2007). It can feed both by filtering and pedal-feeding, *i.e.* using cilia on the food to collect subsurface organic matter and may have an impact on the carbon budget of small streams by burial or removal of particulate organic matter (Hakenkamp 1999). In Brazilian territory, this species has been documented firstly in the Paraná River floodplain (see review in Takeda et al. 2004b). Since the 1990s, there has been an accentuated decrease in the density of native species. In the Pantanal, we could not state any nuisance effect by this species yet.

On the contrary to the previous species, the golden mussel *Limnoperna fortunei*, a mytilid from Asian fresh and brackish waters, has a strong impact on the biota. This species is migrating rapidly upstream the Paraná River from the Río de la Plata (Callil et al. 2007; Oliveira et al. 2006; Takeda et al. 2004b). Due to transport of the planktonic larvae in ballast water of ships, the invasion carried on very quickly (Darrigran & Ezcurra de Drago 2000) upstream of the Río de la Plata system. In 2000, we could neither detect larvae nor attached mussels in the section 200 km below the city of Cáceres (Marchese et al. 2005), however, they had already arrived at the rocky outcrops in the Pantanal National Park 400 km downriver by that time. Today (2007), the species has colonized the whole Pantanal (Callil et al. 2007). Attached with byssus threads, it can colonize and completely cover all kinds of solid substrates, including living native mussels which become outcompeted by the exotic species (Darrigran 2002). Along with large woody debris, mussel shells (including those of living mussels) represent the only hard substrates in wide areas of the Pantanal. The Upper Paraguay River, for example, has a sand-clayish sediment which is interrupted by rocky outcrops on average every 40 km (Ponce 1995; Wantzen et al. 2003). Therefore, *L. fortunei* settles in large quantities to the shells of native mussels and eventually starves them by covering the filtering openings (Callil et al. 2007; Oliveira et al. 2006). Due to a short tolerance to desiccation (a drought period longer than 12 days is generally lethal), natural floodpulsing seems to be the best natural control for the spread of the species (Ezcurra de Drago et al. 2004). Current studies have confirmed that even today (2007) the upper section of the Paraguay River (between Taiamã and Cáceres) has not been colonized by stable populations (as indicated by the lack of larvae and post-larvae) in spite the fact that individual adults were regularly observed near ships (where they occur in ballast and bilge water, Callil et al., unpublished data).

Other effects of mass development of the golden mussel were an increase in density and diversity of invertebrates other than mollusks (Darrigran 1998) and an enlargement of the food spectra of various fish, e.g. Potamotrygonidae, Anostomidae, Doradidae, Pimelodidae, and Loricariidae in which it makes up to 90% of the stomach content (Montalto et al. 1999). We assume that the limited desiccation tolerance and the adaptation of the diverse fish to the new food item will reduce the general impact of this species; however, the large native mussel species of the Pantanal are severely threatened. A control of bilge water of ships should become mandatory to reduce the spread of the species.

15.5 Benthic invertebrates as bioindicators in the Pantanal

Benthic invertebrates are commonly used as sentinels for environmental changes in aquatic ecosystems. In the past, bioindicator systems developed in temperate zones were often directly applied in the tropics without considering the regional differences of both impact type and indicator group. For most aquatic insects, for example, indicator values are available only for northern-temperate congeners of South-American species and conclusions drawn with these data for biomonitoring in the tropics may be misleading (Pérez 1999). Empirical and experimental studies are needed to improve this situation.

The water bodies of the Pantanal are threatened by a series of impacts, including physical pollution (Wantzen 2006), toxic pollution (Laabs et al. 2002), and organic pollution. Various studies have focused on developing indicator systems for these impacts.

15.5.1 Indicator systems for physical pollution

Physical water pollution has been neglected for a long time as an important element of water quality assessment (Waters 1995). Erosion in the catchment of the tributaries to the Pantanal puts a serious threat on the aquatic and riparian biota due to scouring and covering food sources and habitats, increasing turbidity of the water and interacting with suspended organic particles (Hamilton et al. 1998; Wantzen 1997, 1998b, 2006). During a three-year study near the city of Jaciara, ten streams with variable degrees of siltation were studied using newly developed artificial substrates in order to standardize colonization conditions for benthic invertebrates. Colonization densities of the artificial substrates (Wantzen & Pinto-Silva 2006) were significantly lower comparing high impact sites and low impact sites during the same time, or comparing times of high sediment input and low input at the same site. Filter-feeders (e.g. Trichoptera) and visually foraging predators (e.g. Odonata excluding Gomphidae) were especially reduced by siltation (Wantzen 1997). Erosion gullies act as point sources for sediment input into streams which have detrimental effects on all benthic invertebrate taxa and algae (Wantzen 1998b).

Impact effects increase during rain events which mobilize additional amounts of sediments (Fig. 15.4). As riparian structures including vegetation also become impacted by siltation, those species that depend on both aquatic and riparian habitats such as dragonflies or caddis flies become affected during different life stages. Therefore, joint analysis of instream metrices and habitat structure indicators is strongly recommended (Wantzen 1998a; Wantzen et al. 2006).

15.5.2 Indicator systems for toxic pollution

Mercury spills are considered an environmental impacts in the district of Poconé as a side effect of gold mining in the northern border of the Pantanal (Hylander et al. 1994, (see chapter 25). Aquatic molluscs are considered good indicators of heavy metals (Callil & Junk 2001). They occur in larger quantities in wetlands form Mato Grosso and are important food items for top predators like fish, aquatic birds and caimans, which accumulate mercury by the uptake

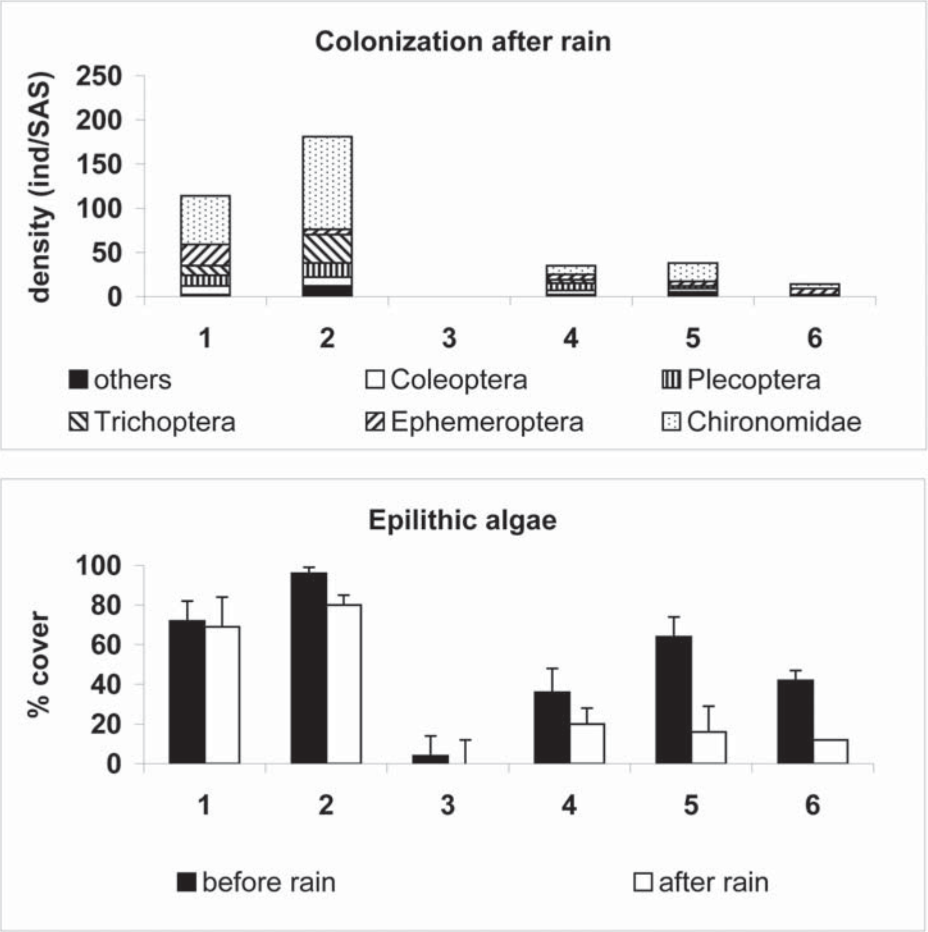


Fig. 15.4 Average density data from the most common taxa (a, b) of benthic and (c) of epilithic algae before and after a rain event at the Tenente Amaral Stream, Mato Grosso. Data from Wantzen (1998b).

of contaminated snails. Almost 2 tons of mercury are estimated to lie in the deposits of the gold mines (Tümpling Jr et al. 1995) of the area which provokes concern about their mobilisation and uptake into the foods webs. When determining the total mercury concentration in *Pomacea scalaris*, *P. lineata*, and *Marisa planogyra,* maximum values of 1.99 ± 0.39 μg Hg.g^{-1} were found in *P. scalaris* at sites with direct or indirect influence of the gold mines near the Bento Gomes River (Callil & Junk 2001). High values of 1.12 ± 0.05 μg Hg.g^{-1} were found for the same species in lake areas which act as a sink for fine particles

(Nogueira et al. 1997). Gastropods turned out to be especially suited for active and passive biomonitoring as they showed representative accumulation rates of mercury, are commonly found in the field, and are easy to rear for laboratory experiments.

Apart from mercury, toxic pollutants in the Pantanal region include pesticides from the large agricultural areas in the catchments, industrial waste, and leachates from garbage dumps. In a study on pesticides along the Rio São Lourenço catchment, Laabs et al. (2002) found measurable concentrations of 29 substances, mostly endosulfan compounds, in rain water, surface water, and sediments. They identified rain water as an important vector from the Planalto to the Pantanal and calculated a maximum input of 2,800 kg for the whole wetland in 3.5 months. The effects of all these toxic pesticides on the biota of the Pantanal have not been studied yet, and the large piles of garbage in the outskirts of cities, which become burnt several times a year and which do not have drainage systems for their leachates, cause additional concern about future groundwater pollution.

15.5.3 Indicator systems for organic pollution

In spite of increasing effort by public organs, organic pollution is still a severe problem in urban zones of the entire Paraguay River Basin. Only a small percentage of urban waste water receives adequate treatment (see chapter 30). Additionally, acideous or toxic effluents from industries impede autopurification mechanisms in streams and rivers. Most urban streams turn into cloaca few meters below their sources and do not improve water quality until flowing into the main river. Bathing on the beaches downriver the city of Cuiabá becomes regularly forbidden during the low water season due to hygienic risk (excessive numbers of fecal coliforms). In the outskirts of the cities, human settlements in the riparian zones increase both organic pollution and erosion/siltation. Most rural agglomerations industries, and even some slaughter houses which produce large quantities of oxygen-demanding substances lack waste water treatment. Most domestic waste water percolates from drainage pits into the soils, however, there are few published studies on its effects on groundwater quality and human health (Heckman et al. 1997).

The effects of organic pollution on benthic invertebrates have been studied by (Paula 1997) in the Coxipó River near Cuiabá and by Lima (2002) in the Cuiabá River. The Coxipó River flows from the Chapada dos Guimarães high plain where it forms a large cascade through the Cuiabá Plain and discharges into the Cuiabá River. Using the artificial substrates developed by our group (Wantzen 1997; Wantzen & Pinto-Silva 2006), Paula's study shows the effects of increasing organic pollution at 5 stations along the run length of 70 km. Different metrices, including diversity of all taxa, diversity of families, diversity of insects, density of oligochaeta, and evenness of all taxa, yielded similar results. 178 invertebrate taxa were identified without separating chironomid species. Stoneflies and dobsonflies were limited to the uppermost site which was the least polluted, had highest oxygen and lowest temperature values, while leeches only occurred in the most polluted sites. Most taxa did not occur sufficiently often in the samples to attribute them to a potential indicator value. Relative density data of chironomids, oligochaetes and other invertebrates pooled for "dry season" (May to September) and "rainy season" (October to April) show a very clear pattern of reduction of chironomids and "other" species and an increase of oligochaetes along with the increasingly polluted river (Fig. 15.5).

Oligochaetes and chironomids also dominated the benthos fauna in the Cuiabá River (LIMA 2002), where effects of the pollution inputs of the city of Cuiabá did not cause accumulative trends in the faunal assemblages along the 26-km-long stretch. Instead, species richness, equitability, and Shannon-Wiener diversity had the lowest values at individual, highly polluted sites in the centre of the city, while they were equally high above and below it. Apparently, the benthic invertebrate communities in the studied stretch are adapted to the organic pollution even in the section above the City of Cuiabá (there are other pollutants such as the cities of Rosario Este, Acurizal, and Guia above Cuiabá), so that the pollution from Cuiabá only had a limited effect.

Seasonal variation of the benthic densities was higher than local variation, and it covaried with discharge in LIMA's study (2002). The discharge of the Cuiabá River became reduced from 1999 to 2000 due to low rainfall and the closing of the Manso Dam. The average of the rainy seasons' discharge was reduced from 684 to 352 $m^3 s^{-1}$, and in the dry season from 110 to 95 $m^3 s^{-1}$. The total abundance of benthic invertebrates in 2000 was increased during the rainy season but reduced during the dry season compared with 1999 (LIMA 2002). Apparently, the short-lived aquatic invertebrates were able to quickly use the extraordinarily low wet season discharge like a dry season situation.

We conclude from these two studies that the Coxipó River has already reached the limits of self-purification and that the Cuiabá River is still within its limits. Considering taxonomical difficulties for identification, metrices such as family diversity, chironomid density, oligochaete density, and the presence/absence of hirudineans appear to be the economically most feasible methods for large-scale rapid appraisals and for long term monitoring programs. However, changes in discharge and sediment composition must be included in environmental impact analysis of organic pollution.

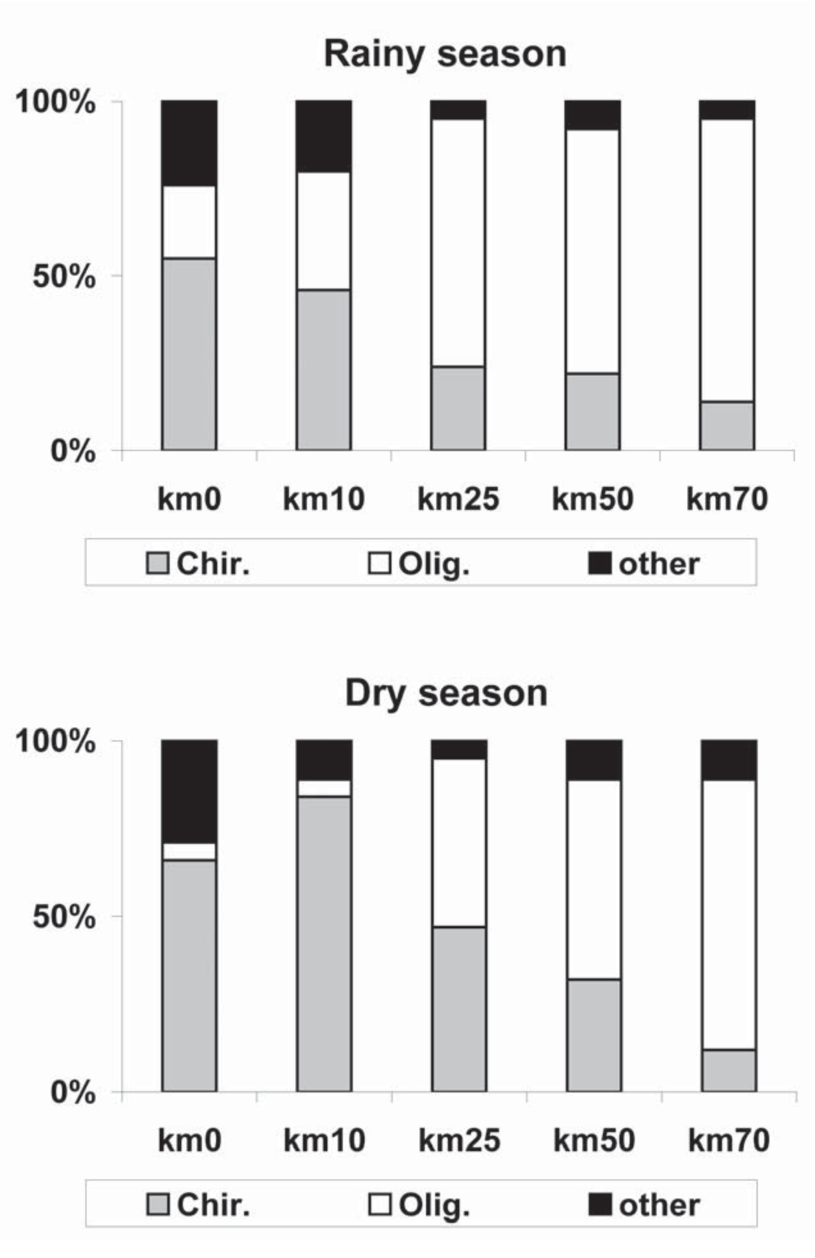


Fig. 15.5 Relative density data of chironomids, oligochaetes and other invertebrates pooled for "dry season" (May to September 1995) and "rainy season" (October 1995 to April 1996) of 5 stations along the Coxipó River near Cuiabá City following a gradient of increasing pollution and decreasing sediment diversity. Data from Paula (1997).

15.6 Discussion and conclusions

Generally, short life cycles and a wide array of different species traits enable benthic invertebrates to cope with the fast changing hydrological conditions of the Pantanal and its tributaries. Preliminary results show that propagule-banks in dried sediments vary considerably. Both very low amounts (Wantzen, unpublished) and very high amounts (Callil, unpublished) of permanent eggs and other viable propagules were found in the Pantanal. In other large seasonal wetlands with long periods of complete dryness this mechanism is known to be very important, e.g. in Australia (Finlayson 1995). Invertebrates with longer life spans and special habitat requirements, such as bivalves and dobsonflies, are most sensitive to environmental changes while short-lived r-strategists quickly recolonize new habitats by "island-hopping" (Junk et al. 2006, Fig. 15.1).

The knowledge of the benthic invertebrate faunas of different regions of the Pantanal is yet incongruent and the taxonomic status of many taxa is uncertain. Most studies work with morphotaxa. We could identify some habitat-specific faunal assemblages which support the view that the species inventory of the Pantanal is not unique but rather typical of other large South American wetlands. There is a large faunistical overlap between some habitats because many organisms are tolerant to a broad variation in ecological conditions. Many species change between "true benthic" and "epiphytic" habitats according to flow conditions, water level, and oxygen concentrations.

Littoral zones and connection channels of the floodplain habitats exert important ecological functions as biological filters and sites of benthic production. The type of connectivity between lake, river and channels (corixos) strongly influences physical setting, functional feeding groups, and taxonomic composition of benthic invertebrate communities. Sites that are connected to nutrient-rich rivers or lakes (that provide large amounts of phytoplankton and suspended organic matter) are characterized by filter feeders, while those sites connected to nutrient-poor and/or humic rivers are dominated by gatherer-collectors. Marginal and channel habitats provided significantly higher diversity and density values than the lake centre. This makes these sites important fish feeding grounds especially during the dry season when surrounding floodplain areas dry out. Recent developments in waterway planning threaten these important habitats in various ways. Channel work and large vessel traffic on the so-far not accepted waterway on the Paraguay River has lead to siltation of connection channels and disruption of the connectivity of various lakes (Wantzen et al. 1997). Recent construction of a dam in the Manso River, a main tributary of the Cuiabá River, has led to dramatic decrease of the water level in the river and its adjacent lakes (e.g. the Chacororé Lake). The maintenance of the natural hydrological dynamics should be considered as a major goal in landscape planning in the Pantanal (see chapter 30). "Hot spots" for benthic biodiversity and production (Wantzen & Junk 2006) should deserve special attention in conservation and management planning.

Acknowledgements

We thank Ines Ezcurra de Drago and Mercedes Marchese for valuable comments on the manuscript. The studies were financially supported by several cooperation programs, including the tropical ecology support program (TÖB-GTZ), the SHIFT-Pantanal (BMBF/CNPq), Biodiversity of the Upper and Lower Paraguay (DLR/CNPq and DAAD/FONCYT).

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