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Seasonal Variation in the Macroinvertebrate Fauna of Billabongs along Magela Creek, Northern Territory

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Abstract

The littoral zone of five permanent billabongs along Magela Creek was sampled monthly over 1 year for macroinvertebrates. In three shallow billabongs, greatest numbers of taxa (about 45) and of individuals (about 1000 individuals per minute) were caught in the late wet season and early dry season (April–July); by the end of the dry season (December) these values had decreased to about 18 taxa and about 200 individuals per minute. Fluctuations were not so marked in two deep (or channel) billabongs: rarely were there fewer than 30 taxa and 400 individuals per minute present, and maximal values were similar to those in the shallow billabongs. These changes appeared to be associated with the growth of macrophytes, which occurred during the wet season in all billabongs. There was little variation between billabongs in the mean composition of the fauna.

Introduction

Magela Creek is a seasonally flowing tributary of the East Alligator River in the Northern Territory, about 250 km east of Darwin. Its catchment consists of floodplain, forested lowland and sandstone plateau, and it has a tropical monsoon climate. In this paper, the seasonal variation in the macroinvertebrate fauna of five permanent billabongs located in the lowlands near the Ranger Uranium deposit (Fig. 1) is considered. [Here the term billabong refers to a pool in or nearby the creek bed, although Bayly and Williams (1973) use the term to refer to oxbow lakes.] It is part of a larger study of the biota and water quality of billabongs along this creek (Chaney *et al.* 1979; Walker and Tyler 1979; Hart and McGregor 1980; Bishop *et al.* 1981) designed to provide data on the aquatic communities before mining of uranium starts.

This study consisted of regular systematic collections from a number of sites. No collections of macroinvertebrates have been made in this region before; the nearest previous collections have been taken in north-western Australia in the Kimberleys (Miles and Burbidge 1975; Kabay and Burbidge 1977; Williams 1979). These collections consisted of single samples from a range of localities and did not provide information on seasonal changes in the fauna. It is essential to document such changes in a study such as this so that there is some basis for deciding whether future changes are natural or man-made. The potential impact of uranium mining is through the release of associated heavy metals such as copper and zinc (Davies and Hart 1980).

Study Area

Five billabongs were sampled: Georgetown, Coonjimba, Goanna, Mudginberri, Buffalo; their relation to Magela Creek (12°35′S., 132°52′E.) is shown in Fig. 1. These billabongs always contained water during the study (March 1979–March 1980), but the creek only flowed during the wet season (approximately December–April). The average annual rainfall recorded at Jabiru is 1560 mm (Ranger Uranium Mines, personal communication) with an average annual evaporation of 2400 mm (Walker and Tyler 1979; Williams 1979). The 1978–79 wet season (November–March) delivered 1509 mm of rain and the 1979–80 season (December–April) 1889 mm.

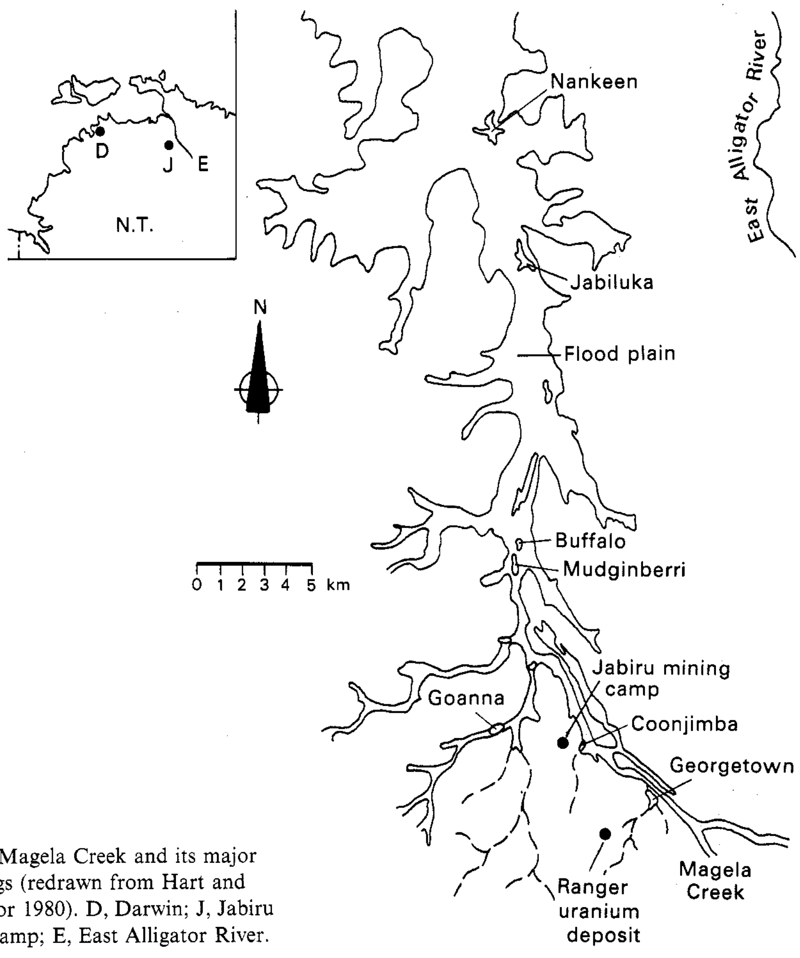

Fig. 1. Magela Creek and its major billabongs (redrawn from Hart and McGregor 1980). D, Darwin; J, Jabiru mining camp; E, East Alligator River.

The two billabongs furthest upstream (Georgetown and Coonjimba) are shallow (2–3 m during the wet season) and are separated from the creek by a levee. These are called backflow billabongs by Hart and McGregor (1980) because water flows in (or back) through a channel in the levee when the creek first flows. The two billabongs furthest downstream (Mudginberri and Buffalo) are on the main channel of the creek, thus having separate inlets and outlets, and are deep (7–10 m during the wet season); these are known as channel billabongs. Goanna is on the main channel of a tributary to Magela Creek, but is shallow (2–3 m during the wet season) and sometimes fills with water from its own catchment and sometimes with water flowing up from the main stream.

The billabongs chosen for sampling are downstream of the uranium deposit and are thus well placed in the event of contamination. Georgetown receives runoff partially from the deposit, and Coonjimba receives runoff from the mining camp of Jabiru and from a retention pond below the dam that will contain tailings from the processed ore. Goanna will receive treated effluent from a permanent town, and Mudginberri and Buffalo receive all flow from the upper catchment of the Magela Creek.

All the billabongs undergo seasonal and diurnal fluctuations in various physical (temperature, depth, turbidity) and chemical (pH, dissolved oxygen, conductivity) variables, which have been documented in detail by Hart and McGregor (1980) and Walker and Tyler (1979). Water depth is greatest in February or March and then falls steadily during the dry season to reach a minimum level in November or December. The temperatures of the surface water vary between a minimum of 22°C in July and a maximum of 38°C in November, with diurnal fluctuations being more marked in the dry season than in the wet season; average surface temperature of the billabongs based on readings taken monthly between 9·00 and 12·00 h is 30°C. Turbidity generally increases throughout the dry season but is reduced during the wet season; the shallow billabongs are invariably more turbid than the channel billabongs. Conductivity increases during the dry season, but generally indicates that the waters are very dilute. The pH mostly varies between 6·0 and 7·0, although somewhat lower values are recorded when the billabongs first fill at the beginning of the wet season. Oxygen levels in the shallows are usually high, and depend to a large extent on ambient temperature and the photosynthesis of phytoplankton and macrophytes.

Bankside vegetation of the shallow billabongs consists of stands of *Melaleuca viridiflora* Gaertn., and the channel billabongs are lined with *Pandanus aquaticus* F. Muell., *Barringtonia acutangula* Gaertn. and several species of *Melaleuca*. During the wet season, considerable growth of macrophytes occurs along the shallow edges of the billabongs. Some of the more common of these plants are *Nymphaea gigantea* Hook, *Nymphoides* spp., *Utricularia* sp., *Najas tenuifolia* R.Br., *Caldesia oligococca* (F. Muell.) Buch., *Aponogeton* sp., *Eleocharis* sp. As water levels in the billabongs fall, the macrophytes die. Mudginberri generally has the least extensive development of these plants because its banks are steep and only at highest water levels are there suitable shallow areas. Buffalo, although also having steep banks, has a permanent stand of *Nymphaea gigantea* around much of its shore.

Methods

Samples of macroinvertebrates were taken monthly for 12 months using a triangular hand net (30 cm wide) with 500-μm mesh. In each billabong, six 10-s sweeps were made in the littoral (< 1 m deep) region. Each sweep vigorously disturbed any macrophytes present as well as the bottom debris which usually consisted of decaying leaves of *Melaleuca* spp., *Pandanus aquaticus* and *Barringtonia acutangula* overlying a mixture of sand and silt. The samples were washed in the laboratory with water to remove the larger debris, before being preserved in 90% ethanol. They were later sorted, identified and counted under a dissecting microscope. When large numbers of a particular taxon were present, usually only 100 individuals were picked. By noting the cumulative number of taxa as each series of six samples was sorted, I found that after four or five samples little increase in number of taxa occurred, indicating that the six 10-s samples provided a reasonably comprehensive collection for each billabong.

The smallest instars of many of the aquatic insects probably passed through the 500-μm mesh of the collecting net. However, this should not seriously alter conclusions about seasonal variations in the abundance of various taxa. The smallest instars would soon reach a catchable size at the fast developmental rates likely to prevail in water at 30°C.

The collections were deposited in the National Museum of Victoria, together with a list detailing the numbers of each taxa caught at each site on each sampling date.

Results

Although the sampling procedure described above enables the catches to be expressed as number of animals per minute (six catches of 10 s), interpretation of this index of density is not always simple: changes in the monthly counts could result not only from changes in total population size, but also from changes in the spread of the population as the extent of the littoral zone varies with fluctuating water level. Therefore, if the highest densities (i.e. counts) occur during the wet season, the total population size is probably also greatest; if they occur when water levels are low, this does not necessarily follow. It should also be realized that the area of the littoral zone on any particular date differs between billabongs, and thus similar densities do not imply similar total populations inhabiting the billabongs.

The mean monthly counts are given in Table 1. For the abundant taxa (mainly Oligochaeta and Chironomidae), of which only 100 individuals were usually picked, these mean values are somewhat underestimated.

Minor Taxa

These include the Porifera, Hydridae, Tricladida, Gordiidae, Oligochaeta, Hirudinea and Hydracarina. Only the Oligochaeta were continually caught throughout the year. They reached their greatest density during the wet season at all sites. The Hydracarina were the next most common group and were present continuously in Goanna, but were only common at the beginning of the wet season in other billabongs. The Tricladida became common in the dry season in the channel billabongs and in the wet season in the others, but were never as abundant as the previous two groups. The remaining taxa occurred sporadically, mainly during the wet season or early dry season, except for the sponge *Pectispongilla botryoides* (Haswell), which was present throughout the year in the channel billabongs, but only during the wet season and early dry season in the others.

Gastropoda

Five species of gastropoda were found, but only *Amerianna* sp. *A* and *Gabbia australis* Tyron were common. These were most abundant in the wet season when they were often found on macrophytes. Presumably those collected at the start of the wet season had survived the dry season by hibernating in the mud, a well-known ability of gastropods (Pennak 1978). *Amerianna* sp. *A* was present in all the billabongs although non-hibernating individuals persisted in some longer into the dry season. *G. australis* was found only in three of the billabongs and reached maximum density in Georgetown and Goanna.

Ferrissia sp. *A* was caught in all billabongs, but generally only during the dry season. This species was invariably attached to fronds of *Pandanus aquaticus* or leaves and could easily have been overlooked in collections. It may well have been present in the wet season but the greater water depth prevented sampling of the debris where it was most likely to occur. *Gyraulus* sp. *A* and *Austropoplea lessoni* (Deshayes) occurred in only two billabongs, mainly during the early dry season.

Crustacea

Ostracoda and Conchostraca (plus Cladocera and Copepoda which were caught but not counted) were present in all the billabongs and generally were most abundant in the early or mid wet season.

The Atyidae and Palaemonidae were also present in all the billabongs. *Caridina* sp. *A* was generally more abundant in the littoral than the two species of *Macrobrachium*, probably because atyids tend to congregate along banks (Williams 1980). In the shallow billabongs, *Caridina* sp. *A* was abundant only in the dry season and it was only at this time that it bred. In the channel billabongs, *Caridina* sp. *A* was common nearly all year and breeding persisted into the wet season when the highest densities were reached.

Macrobrachium sp. *A* was common in all the billabongs, especially during the dry season, but was generally at its highest density in the channel billabongs. *Macrobrachium* sp. *B* was common only in the channel billabongs and rarely occurred in the others. The absence of both species at all sites in January and February is perhaps due to migration downstream as well as migration away from the littoral zone. Ovigerous females were never caught and it is likely that this is because larvae can only develop in saline water. *Macrobrachium* sp. *A* is similar to *M. tolmerum* as described by Riek (1951); Kneipp (1979) has shown that larvae of this species do not survive in fresh water.

One other crustacean occurred occasionally. The crab *Holthusiana transvera* (von Martens) lives in burrows and is only active above the surface during the wet season. It was present commonly along the banks of Goanna.

Ephemeroptera

Seven species occurred, but only *Cloeon fluviatile* Ulmer and *Tasmanocoenis* sp. *A* were found at all sites. In the shallow billabongs, *C. fluviatile* and *Tasmanocoenis* sp. *A* were most abundant in the late wet season and early dry season, but disappeared from the samples towards the end of the dry season. In the channel billabongs, these species showed less seasonal fluctuation in abundance and were present every month, although peak densities usually occurred during the wet season. *Tasmanocoenis* sp. *A* was most common in the channel billabongs and Goanna, but *C. fluviatile* appeared to be equally common in all billabongs. Emergence and reproduction appeared to occur continuously while both species were present.

Tasmanocoenis sp. *B* was only common in Mudginberri where it was caught most of the year but at lower densities than *Tasmanocoenis* sp. *A*. *Thraulus* sp. *A* occurred at a low but almost continuous level in the channel billabongs only. *Atalonella* sp. *A*, *Centroptilum* sp. *A* and *Baetis* sp. *A*, which appeared occasionally in the wet season, were all species found in Magela Creek itself and were undoubtedly washed in to Mudginberri and Buffalo.

Odonata

Nymphs of the two coenagrionid genera *Ischnura* and *Pseudagrion* [each with three species (adults) recorded from Magela Creek by Watson (1980)] were present in all billabongs and reached their highest density in the late wet season and early dry season. The Libellulidae [with 27 species (adults) recorded from Magela Creek] also occurred in all the billabongs. Their nymphs were most abundant in the shallow billabongs during the wet season, but occurred at lesser densities throughout the year in the

Table 1. Mean monthly catches of macroinvertebrates in each billabong
+ Present but not counted; blank space, taxon not present

Macroinvertebrate	Mean monthly catch (No. min^{-1}) George-town	Coon-jimba	Goanna	Mudgin-berri	Buffalo
Porifera					
Pectispongilla botryoides	+	+	+	+	+
Hydridae	1·1	2·6	1·6	0·2	0·8
Tricladida sp. *A*	4·6	2·7	0·2	8·7	13·3
Tricladida sp. *B*	2·3	3·5	0·8	3·0	1·8
Gordiidae	0·4	0·3	0·2	0·3	0·2
Gastropoda					
Amerianna sp. *A*	10·3	21·4	9·5	6·4	11·9
Gabbia australis	17·9		31·0		4·4
Ferrissia sp. *A*	0·1	0·8	1·5	0·7	0·3
Gyraulus sp. *A*			0·3		1·0
Austropeplea lessoni	1·3		0·1		
Oligochaeta	66·7	79·4	60·3	64·6	83·7
Hirudinea					
Richardsonianidae sp. *A*		+	+	+	+
Glossiphoniidae sp. *A*	0·9	4·3	2·6	0·7	
Hydracarina	10·3	40·4	69·3	16·4	7·3
Conchostraca					
Lynceus sp. *A*					0·1
Cyzicus sp. *A*	16·1	33·2	16·9	23·4	10·8
Limnadia sp. *A*	0·1				
Ostracoda	32·5	46·4	42·3	23·5	47·8
Atyidae					
Caridina sp. *A*	14·8	18·8	20·3	23·6	50·1
Palaemonidae					
Macrobrachium sp. *A*	15·3	5·8	3·4	26·8	16·3
Macrobrachium sp. *B*	0·1		0·1	8·3	2·3
Sundatelphusidae					
Holthuisiana transvera			+		
Ephemeroptera (nymphs)					
Cloeon fluviatile	46·5	51·2	50·3	49·5	42·8
Tasmanocoenis sp. *A*	6·6	5·8	36·5	43·1	52·4
Tasmanocoenis sp. *B*	0·2			15·6	1·9
Thraulus sp. *A*				3·7	2·0
Atalonella sp. *A*				0·1	0·3
Centroptilum sp. *A*				0·3	
Baetis sp. *A*				0·5	2·0
Odonata (nymphs)					
Protoneuidae	0·7	0·3	2·9	0·6	0·3
Ischnura spp.	17·0	15·5	13·3	1·3	11·5
Pseudagrion spp.	5·0	1·7	3·3	1·8	4·3
Austrogomphus turneri	0·4	0·3	0·2	1·9	0·3
Antipodogomphus neophytus	0·1			0·1	0·3
Ictinogomphus australis	0·8	0·9	0·5	0·3	0·3
Libellulidae	5·5	6·5	3·3	0·9	4·4
Hemicordulia intermedia	0·3	0·3	0·3	0·2	0·2
Pentathemis membranulata	0·4	0·5	0·2	0·1	0·1
Hemianax papuensis	0·1	0·1		0·3	0·1
Hemiptera					
Agraptocorixa sp. *A*	8·9	14·7	22·3	4·3	10·3
Agraptocorixa sp. *B*	3·3	8·6	20·2	5·3	18·9
Agraptocorixa halei	0·2		1·4	0·4	
Plea brunni	12·1	13·6	12·8	11·5	27·3

Table 1 (*contd*)

Macroinvertebrate	Mean monthly catch (No. min^{-1})				
	George-town	Coon-jimba	Goanna	Mudgin-berri	Buffalo
Ranatra diminuta	1·1	1·0	0·8	0·3	0·2
?Nychia marshalli	4·0	3·2	2·2	10·8	4·6
Enithares sp. *A*	0·1	0·2			0·7
Enithares sp. *B*			0·3		0·9
Enithares sp. *C*		0·1			
Anisops paracrinita	2·3	0·5	1·2	0·2	
Naucoris sp. *A*	1·7		0·3	0·2	0·2
Naucoridae sp. *A*	0·6	1·7	0·2	0·2	0·3
Hydrometra sp. *A*	+	+	+		+
Gerridae	+	+	+	+	+
Veliidae	+	+	+	+	+
Mesovelia sp. *A*	+	+	+	+	+
Neuroptera (larvae)					
Sisyra sp. *A*	0·3	0·2	0·3	0·2	0·6
Diptera (larvae)					
Chironomidae	49·7	66·3	76·6	89·4	93·5
Ceratopogonidae	24·0	26·0	13·7	15·3	14·7
Thaumeleidae	0·1	0·1	0·3	1·0	0·8
Chaoborinae	27·5	5·8	1·0		0·1
Culicinae	1·3	1·9	4·7	1·0	1·4
Tabanidae		0·3		0·2	0·2
Simuliidae					0·2
Lepidoptera (larvae)					
Pyralidae	0·6	3·7	0·8	0·4	4·3
Trichoptera (larvae)					
Tricholeiochiton sp. *A*	1·0	2·3	3·2	1·2	2·0
Hellyethia sp. *A*	2·8	1·4	1·5	3·1	4·9
Orthotrichia sp. *A*	4·3	17·3	27·0	0·8	1·4
Anisocentropus muricatus	0·3	0·1	0·1	14·3	4·8
Ecnomus spp.	5·7	4·2	10·3	3·8	5·8
Oecetis spp.	19·2	6·1	7·0	20·5	6·6
Trianodes sp. *A*	0·9	0·1	0·1	2·9	1·5
Trianodes sp. *B*	0·3	0·1	0·2	3·9	4·8
Triplectides sp. *A*	0·3	0·2	0·1	7·9	5·5
Cheumatopsyche sp. *A*					0·1
Coleoptera					
Dytiscidae larvae	0·2	0·5	1·9	0·2	0·3
Hydroporinae larvae	1·6	1·5	8·7	3·7	1·5
Dytiscidae adults	8·3	13·3	18·7	10·0	6·7
Hydrophilidae larvae	0·2	0·7	0·5	0·8	1·3
Berosus sp. *A* (larvae)	3·6	0·6	1·9	1·3	1·5
Hydrophilidae adults	0·2	1·2	0·9	6·8	5·4
Helodidae sp. *A* (larvae)	0·1				
Haliplus sp. *A* (larvae)	0·2	0·3	0·5	0·1	0·2
Haliplus sp. *A* (adults)	1·1	0·3	0·3	0·4	
Spercheidae adults		0·1			
Ptilodactylidae adults		0·1			
Dineutus sp. *A* (larvae)			0·1		0·4
Dineutus sp. *A* (adults)			+	+	+
Helminthidae sp. *A* (larvae)				0·3	0·1
Helminthidae adults			0·1		
Noteridae larvae					0·1
Hydrochidae adults					0·2

channel billabongs. The Protoneuridae were found in all billabongs, but only for a restricted period at the beginning of the wet season or at the end of the dry season. In Mudginberri they occurred occasionally throughout the year. The Gomphidae *Austrogomphus turneri* Martin, *Antipodogomphus neophytus* Fraser, *Ictinogomphus australis* (Selys); the Corduliidae *Hemicordulia intermedia* Selys, *Pentathemis membranulata* Karsch; and the Aeshnidae *Hemianax papuensis* (Burmeister) occurred sporadically at low densities in all billabongs. Breeding of all species probably occurred mainly during the wet season.

Hemiptera

Twelve species were recorded, but only four commonly. Of the common species, the two unidentified *Agraptocorixa* were found most abundantly during the wet season or early dry season except in Coonjimba and Goanna where greatest densities occurred in the late dry season. The other two species, *Plea brunni* Kirklady and ?*Nychia marshalli* (Scott), were only abundant in the dry season and disappeared during the wet season except in Mudginberri where ?*N. marshalli* reached its highest density in January. *P. brunni* became very abundant towards the end of the dry season in the channel billabongs.

All other species (including *Ranatra diminuta* Montandon) were found at lower densities for restricted periods, again mainly during the dry season. *Anisops paracrinita* Brooks and *Agraptocorixa halei* Hungerford were exceptions, occurring in the early wet season. It is probably as a result of low density that some of these less common species were not recorded in all the billabongs. Of the surface dwelling forms, the Gerridae were found throughout the year, and the Veliidae, *Microvelia* sp. *A* and *Hydrometra* sp. *A* mainly occurred during the dry season.

Neuroptera

The one species, *Sisyra* sp. *A*, feeds exclusively on sponges. It was present in all billabongs but at very low densities. In the shallow billabongs, it only occurred during the wet season when the sponge *P. botryoides* was present. In the channel billabongs, it occurred in both seasons and perhaps was present continuously as was the sponge, but at densities too low to catch.

Diptera

The Chironomidae were continuously present at each site and were usually the most abundant dipteran. They consisted of two subfamilies, the Chironominae and the Tanypodinae, of which the former was usually the commonest except at the end of the dry season when the latter predominated. High densities occurred in all billabongs except at the end of the dry season and the beginning of the wet season, although low densities persisted somewhat longer in Georgetown. Emergence and breeding appeared to occur continuously while large numbers of larvae were present.

The Ceratopogonidae were found in all billabongs and reached their greatest density during the dry season, but tended to disappear in the early wet season. The Chaoborinae were most common in the backflow billabongs where they sometimes reached high densities at the end of the dry season. The other families occurred sporadically at low densities. The Simuliidae were washed into Buffalo once during high flow.

Lepidoptera

A number of species of Pyralidae larvae were caught in small numbers at all sites. The larvae live in cases made of plant material, often of the leaves of the water lily *Nymphaea gigantea*. In Buffalo they were nearly always caught and perhaps were only missing from some samples because they were at densities too low to catch; *N. gigantea* was always present in this billabong. In the other billabongs they appeared to be restricted to the wet season, although Coonjimba was an exception, perhaps because some *N. gigantea* lasted well into the dry season here.

Trichoptera

At least nine taxa were caught in each of the billabongs. In the shallow billabongs, the commonest of these were *Oecetis* spp. (possibly three species), *Orthotricia* sp. *A* and *Ecnomus* spp. (possibly two species). *Oecetis* spp. were continuously present except in Coonjimba where they were not found during the early wet season. The other two species were only present during the late wet season and the first half of the dry season. Maximum densities of all three taxa were reached in the early dry season, although *Oecetis* spp. showed less seasonal variation than the others. Lesser numbers of *Tricholeiochiton* sp. *A* and *Hellyethia* sp. *A* were caught, and only during the late wet and early dry seasons, while the other species occurred only occasionally.

These other species, *Anisocentropus muricatus* (Neboiss), *Triaenodes* spp. *A* and *B* and *Triplectides* sp. *A*, were much better represented in the channel billabongs, probably because more twigs and leaves were available here for cases; maximum density was generally reached in the dry season and the species were present for more of the year. *Tricholeiochiton* sp. *A* and *Hellyethia* sp. *A* were also caught for more of the year in Buffalo, but not in Mudginberri. Densities of *Orthotrichia* sp. *A* and *Ecnomus* spp. were often less than those in the shallow billabongs, but *Ecnomus* spp. were caught continuously in Buffalo and were only absent during the early wet season in Mudginberri. *Oecetis* spp. were continuously present (except once in Buffalo) and were most abundant during the wet season. In Mudginberri they also reached a peak density towards the end of the dry season. *Cheumatopsyche* sp. *A*, a species found occasionally in the creek itself, was washed into Buffalo once during a period of high flow.

Adult Trichoptera were caught throughout the year at a light trap set monthly near Goanna, and adults probably emerged and bred throughout the period when a particular species was present.

Coleoptera

Adult Dytiscidae were the commonest taxon and reached maximum density at the end of the dry season at all sites. Their larvae (including the Hydroporinae) largely occurred during the wet season, although single specimens were found during the dry season in the channel billabongs. A similar pattern was evident for the Hydrophilidae (including *Berosus* sp. *A*) in the channel billabongs. However, in the shallow billabongs, both adults and larvae of this family were mainly caught in the dry season, except *Berosus* sp. *A* which was only recorded in the wet season. The other taxa occurred occasionally except the adult gyrinid *Dineutus* sp. *A* which was often seen at Mudginberri and Buffalo. The larvae of the less common taxa were restricted to the wet season. Thus, except for the Hydrophilidae in the shallow billabongs, breeding of all families appeared to occur during the wet season.

Discussion

Seasonal Variations in the Fauna

The previous account can be summarized by presenting the seasonal variation in the total number of taxa and of individuals in the various billabongs (Fig. 2); this figure includes taxa whose presence only is indicated in Table 1. The total number of individuals is generally underestimated because only 100 specimens of each of the abundant taxa were picked. However, this should not alter the general pattern and will mainly affect only the highest estimates by reducing the extent of their fluctuations.

From Fig. 2 it is clear that in Georgetown, Coonjimba and Goanna the greatest number of taxa and individuals occurred during the late wet season and the early dry season (April–July). Both indices then fell markedly for the rest of the dry season but recovered rapidly in January when water levels in the billabongs rose, despite the diluting effect of the ensuing floods. This dilution was most evident in February and March when water levels were highest. Thus, the period when the maximum number of taxa and greatest abundance of individuals are found starts in the wet season but only

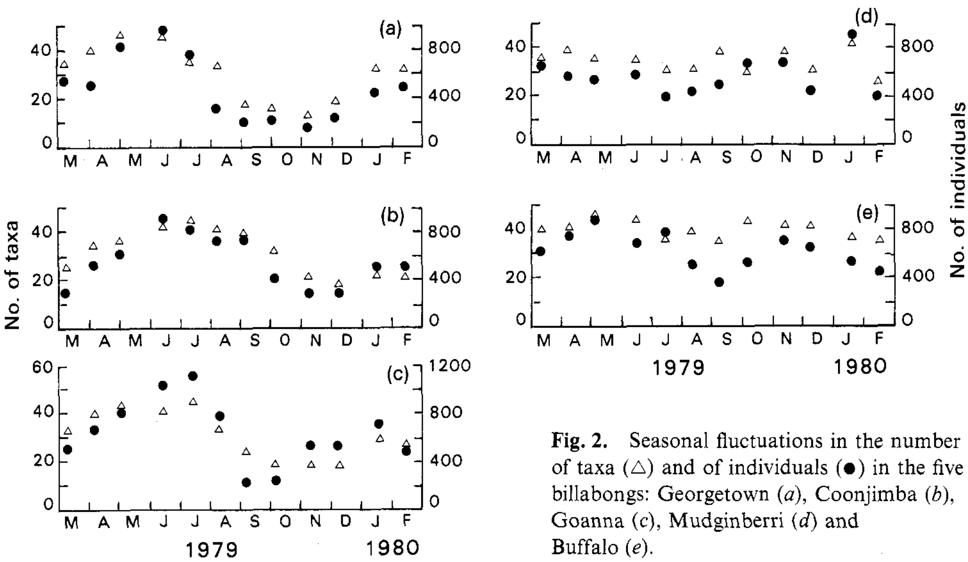

Fig. 2. Seasonal fluctuations in the number of taxa (△) and of individuals (●) in the five billabongs: Georgetown (*a*), Coonjimba (*b*), Goanna (*c*), Mudginberri (*d*) and Buffalo (*e*).

becomes obvious in the early dry season. The numbers of taxa and individuals in the three billabongs were quite similar except that the maxima were reached somewhat later in Coonjimba and Goanna. In Goanna, there was also a rise in the number of individuals, but not taxa, at the end of the dry season due to large catches of Coleoptera and Hydracarina. The similarity of numbers of taxa and of individuals caught at either end of the period of study indicates that sampling was consistent and gives confidence in making these seasonal comparisons.

In the channel billabongs, the seasonal fluctuations in the number of taxa and of individuals (Fig. 2) were not so marked: the number of taxa rarely fell below 30 and the number of individuals varied by a factor of two rather than five as in the shallow billabongs. In Buffalo, the highest numbers of taxa and of individuals also occurred in the early dry season (May), but their subsequent decline only continued until September after which both indices rose near to maximal levels again. During the early wet season, there was another decline in both taxa and numbers, probably because the rising water levels diluted the fauna. More or less the same sequence occurred in Mudginberri, but here both indices fluctuated after August from their lowest to almost their highest levels, reaching their maxima in January.

The probable cause of this seasonal fluctuation in numbers of taxa and of individuals is fluctuation in the amount of macrophytes present. These are best developed during the late wet season and early dry season (April–July) and, by offering the macroinvertebrates food and shelter from predators, promote a large and diverse community. There was no indication of deoxygenation in the shallows of any of the billabongs during the dry season (Walker and Tyler 1979) and it seems unlikely that other chemical factors such as pH or conductivity adversely affected the macroinvertebrate fauna.

In the shallow billabongs, the macrophytes had largely disappeared by August or September (except for a few *Nymphaea gigantea* and *Eleocharis* sp.), after which marked declines in numbers and taxa of macroinvertebrates were evident. Changes in the littoral zone of the channel billabongs were less marked as were fluctuations in the fauna. Macrophytes were only common around Mudginberri during February and March, but *N. gigantea* and others were common throughout the year in Buffalo. In Mudginberri, the absence of macrophytes was perhaps made up for by the complex array of roots of *Pandanus aquaticus* which line the banks, and large quantities of detritus such as leaves and twigs; both of these habitats would offer shelter and food. It is noteworthy that the patterns of feeding by the fishes in the billabongs reflect the patterns of abundance of the macroinvertebrates. Bishop *et al.* (1981) have shown that feeding intensity of the fishes (as indicated by fullness of the guts) is greatest in the late wet season and early dry season.

Organic detritus is probably a major source of food for the macroinvertebrates within the littoral zone; the guts of the Ephemeroptera and Trichoptera were often full of it. The exact nature of this detritus is unknown, but decomposing leaves of *Pandanus aquaticus*, *Barringtonia acutangula* and *Melaleuca* spp. appear to make up much of it. When well-developed zones of macrophytes are present, epiphytic algae on the macrophytes (periphyton) must also be widely eaten. The macrophytes themselves do not seem to be used by the macroinvertebrates except by the Pyralidae larvae for cases.

The fauna that disappear from the samples in the dry season survive by various means. A few, such as the Gastropoda, hibernate in the mud, re-emerging when this is submerged in the next wet season. Others may rely on resistant stages in their life cycle, such as eggs (e.g. the Ephemeroptera, Marchant 1982) or pupae, as many insects do in temperate streams which dry out (Williams and Hynes 1976); or they may persist, but at densities so low they were not recorded. This latter method may also be used by some taxa during the wet season rather than during the dry, e.g. *Caridina* sp. *A*.

It should be recognized that, because of the greater persistence of fauna, the channel billabongs may well act as reservoirs for some species that are actually exterminated in the dry season in the shallow billabongs. Hynes (1975), in a study of the fauna of an intermittent stream in tropical Africa (Ghana), suggested that most recolonization of aquatic insects took place from eggs laid by flying adults rather than through survival of resistant stages. However, as the shallow billabongs in Magela Creek do not dry out completely, resistant stages are not as improbable as in Hynes' stream which became dry and sunbaked.

The rapid resurgence of the fauna at the beginning of the wet season (Fig. 2), which is especially evident in the shallow billabongs, suggests fast growth and reproductive rates for at least some of the fauna. I have shown elsewhere (Marchant 1982) that *C.*

fluviatile and *Tasmanocoenis* sp. *A* have life cycles of about 1 month. Such short cycles probably also prevailed among the other Ephemeroptera and many of the Trichoptera and Diptera. Others such as the Odonata may have spent up to a few months in the non-flying stages. Some of the non-insect groups may have had life cycles of this length; the life cycles of the Gastropoda could have been much longer. Life cycles of one to a few months are similar to those suggested by others who have studied tropical insects in streams. In Uganda, Hynes and Williams (1962) found many insect larvae and nymphs were fully grown 1 month after a stream was denuded with D.D.T. Hynes (1975) concluded from his study of the seasonal changes of the fauna of a stream in Ghana that the average life cycle was 2·5 months.

Faunal Comparisons

Variability in the composition of the fauna of the billabongs can be judged by calculating Czekanowski's coefficient of similarity (Hellawell 1978):

$$C = 2W(A+B)^{-1},$$

where W is the sum of the lesser of the two mean counts (Table 1) for each species common to both billabongs, and A and B are the mean total number of individuals in each billabong. The results (Table 2) indicate that there is little variation in

Table 2. Czekanowski's coefficient of similarity for the various comparisons between billabongs

	Coonjimba	Goanna	Mudginberri	Buffalo
Georgetown	0·76	0·69	0·69	0·68
Coonjimba		0·77	0·67	0·70
Goanna			0·67	0·70
Mudginberri				0·76

composition between billabongs, at the present state of taxonomic discrimination. The shallow billabongs are slightly more similar to each other than to the channel billabongs, which in turn are more similar to each other than to the shallow billabongs, but the differences in the coefficients are not great. This lack of variability is largely due to the fact that differences in the fauna generally occur among taxa that are not very abundant and so do not add much to the estimate of the total number of individuals.

Some sampling of the littoral zones of two billabongs (Jabiluka, Nankeen) on the floodplain and one billabong (Bowerbird) in the upper catchment of Magela Creek, revealed faunas similar to those in the five lowland billabongs. A few collections from comparable habitats in the Kimberleys (Miles and Burbidge 1975; Kabay and Burbidge 1977; Williams 1979) indicate similarities between the regions, at least at the level of genera, but further comparisons of the fauna cannot be made as the taxonomy of many groups is poorly or incompletely known.

Welcomme (1979), in his review of the fisheries ecology of floodplain rivers, comments that information on the benthic macroinvertebrates of slow rivers associated with tropical floodplains is very sparse. The profundal areas of the few rivers that have been sampled are dominated by sparse communities of Oligochaeta and Chironomidae. The same areas in the permanent standing waters of the floodplains are somewhat richer, often containing large biomasses of Mollusca, in addition to the previous two groups. [In the deeper regions of the billabongs in Magela Creek, the mussel *Velesunio angasi* (Sowerby) is common.] The littoral areas of the standing waters are the richest in species: high densities of Ephemeroptera, Trichoptera, Mollusca, Hemiptera and Chironomidae have been reported during the flood season, especially in beds of macrophytes. Thus, the general features of the macroinvertebrate fauna of the Magela billabongs appear similar to the little that is known for the fauna of such habitats from other tropical regions.

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