

## Overview Article

# Biodiversity of the wetlands of the Kakadu Region, northern Australia

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**Abstract.** The biodiversity values of the wetlands in the Kakadu Region of northern Australia have been recognised as being of national and international significance, as demonstrated through their listing by the Ramsar Convention on Wetlands. Analyses of the wetland biodiversity have resulted in the production of species list for many taxa, and some population and community-level analyses of biomass and abundance, and the mapping of habitats at multiple scales. Wetland habitats include inter-tidal mud-flats, mangroves, hyper-saline flats, freshwater flood plains and streams. The tidal influence on the saline wetlands is pronounced, as is the influence of the annual wet-dry cycle of the monsoonal climate on the flood plains and streams. The vegetation is diverse and highly dynamic with rapid turnover of organic material and nutrients. The fauna is abundant with endemism be-

ing high in some habitats. Most fauna analyses have focussed on vertebrates with a large amount of information on waterbirds and fish in particular. However, despite extensive effort over the past two decades much is still unknown about the biota. While the invertebrate fauna in the streams has received some attention, a large taxonomic classification effort is required. The functional inter-relationships between habitats and species have largely not been assessed. Further, the ecology of many species is only cursorily known. At the same time there has been increased attention to pressures on the wetlands, such as weeds and feral animals, water pollution, and the potential impact of climate change and salinisation of freshwater habitats. Importantly, given the social context of the region, increased attention is being directed towards traditional use and management of the wetlands.

**Key words.** Wetlands; wetland fauna; wetland vegetation.

## Introduction

In this paper we summarize data on species numbers and describe the general ecology of major plant and animal

groups in the wetlands within Kakadu National Park and the broader Alligator Rivers Region in northern Australia. The Region is located to the east of the city of Darwin in the Northern Territory of Australia (Fig. 1) and is part of a larger bio-geographical region known loosely as the wet-dry tropics that extends across northern Australia (Finlayson et al., 1997; Finlayson, 2005). Isolated and lowly populated, the wetlands are of immeasurable value for the world's natural and cultural heritage and have at-

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tracted great interest, particularly over the past 20–30 years, for their conservation values (Finlayson and von Oertzen, 1996a). The Alligator Rivers Region comprises the ~20,000 km<sup>2</sup> Kakadu National Park and a further ~8,000 km<sup>2</sup> of land within the western portion of Arnhem Land (a large tract of Aboriginal owned land to the east of Kakadu National Park) that comprises part of the catchment of the East Alligator River. Lowry and Knox (2002, 2006) further extended the areal region to include parts of the adjacent catchments. Given the recognition of the name “Kakadu” and its areal dominance within the Region the general name “Kakadu Region” is adopted here and taken to include the wider region, as done by Finlayson and von Oertzen (1996b) when reporting on the vegetation of the Region.

Wetlands in the Kakadu Region include mangroves, freshwater flood plains, salt flats and small permanent lakes (Finlayson and Woodroffe, 1996). The wetlands of Kakadu National Park have been designated as internationally important under criteria established by the Ramsar Wetlands Convention, due in part, to their importance in a biogeographical context, the outstanding diversity of their plant communities, and their role in conserving the large numbers of waterfowl that congregate on the flood plains during the Dry season (Finlayson et al., 1990; Finlayson and von Oertzen, 1996a). World Heritage listing of Kakadu National Park also refers to the natural heritage value of the tidal flats and flood plains, and the floristic diversity and endemism of the wetland vegetation.

Descriptions of the diversity and ecology of wetland species in the Region reflect large differences in the amount of available information for the taxonomic entities. The information is uneven and incomplete. The descriptive information presented here is followed by an outline of the pressures on the wetlands, as ascertained in recent years using structured and integrated approaches and risk assessment in particular.

### Definition and classification of wetland species

Wetlands in the Kakadu Region comprise a number of hydrological patterns – tidally influenced as well as annually flooded. Whilst the tidal influence extends some 70–90 km along the major rivers, most attention has been directed towards the freshwater flooding of the rivers and adjacent floodplain wetlands. The freshwater wetlands are subject to a reasonably predictable mono-modal flood pulse (Finlayson et al., 1990, 1989; Finlayson and Woodroffe, 1996) that has been related to the rainfall data and the more complex seasonal climatic pattern recognized by the indigenous inhabitants of the Region (Fig. 2; Finlayson, 2005). During the dry months the wetlands may dry completely and can be colonized by terrestrial plant and animal species that may or may not be wetland

specific. As these species are integral parts of the wetlands and may contribute considerably to wetland functions and processes (e.g. energy and nutrient cycles) they are included in this description, although often there is scant information about their biology or ecological role/s.

The concept of a wetland species is based around that used for wetland plants by Finlayson et al. (1989), namely, a plant or animal that is adapted to withstand periods of waterlogging or flooding for a period of time. Under this general definition species found in the seasonally inundated areas (woodlands and grasslands) that fringe the billabongs and flood plains are included along with the wholly aquatic species, as well as species that use the wetland less frequently but are fully dependent on it. This is similar to the approach proposed by Gopal and Junk (2000) who also provided further subdivisions based on the extent of the reliance of the species on the wetland. This more detailed categorization has not been adopted given a lack of information on the taxonomy and ecology of many taxa.

As there is little specific information from the riparian fringes of the streams, except from generic biological surveys, this habitat is not emphasised. The monsoonal forest habitats that fringe or abut the streams and flood plains are not included; Wilson et al. (1996) provide a detailed description of the vegetation of the Region.

### Ecological characterization of the Kakadu Region

#### Landforms

The geological evolution of the Region was summarised by East (1996) who described three major landforms. Lowry and Knox (2002, 2006) provided more detailed mapping of six geomorphic landscape classes across the Region; the distribution of these classes is shown in Figure 3, whilst the area of each is listed in Table 1.

1. *Arnhem Land Plateau* – in the eastern and southern parts of the Region; an average height of 300 m above the adjacent plains; composed predominantly of quartzose sandstone known as the Mamadawerre Formation (previously known as the Kombolgie Formation – Carson et al., 1999); highly dissected with a high proportion of bare rock; bounded in the north and west by a steep escarpment.
2. *Dissected Foothills of Igneous Origin* – a variety of landforms, including rocky hills, boulder-covered strike ridges, stony hillocks and occasional granite pillars; formed through igneous activity and subjected to exposure and/or erosional processes over the last 2.5 billion years.
3. *Mamadawerre (Koolpinyah) Surface* – gently undulating plains and rises of the lowland landscape; composed of sedimentary plains, and found predominantly

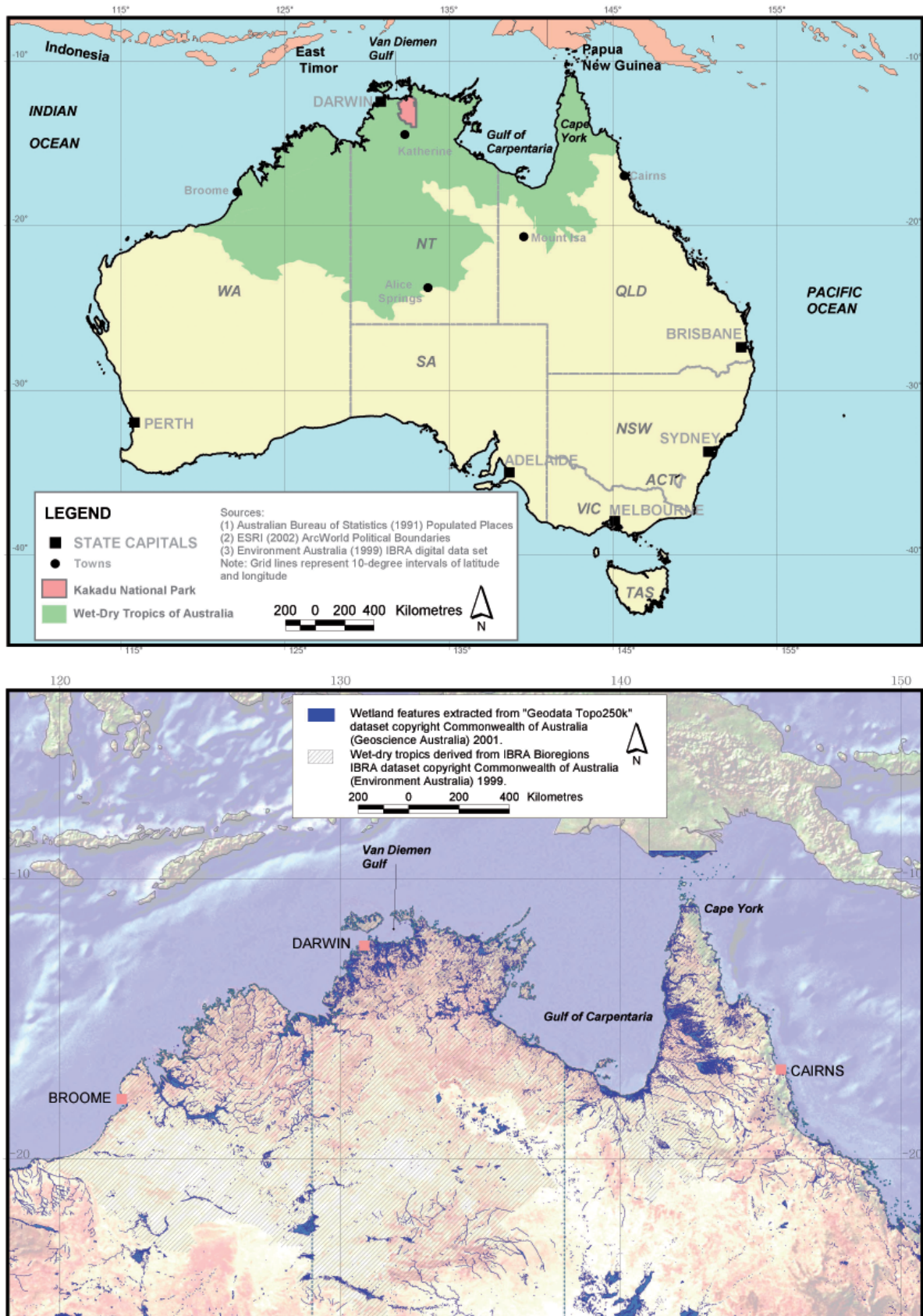
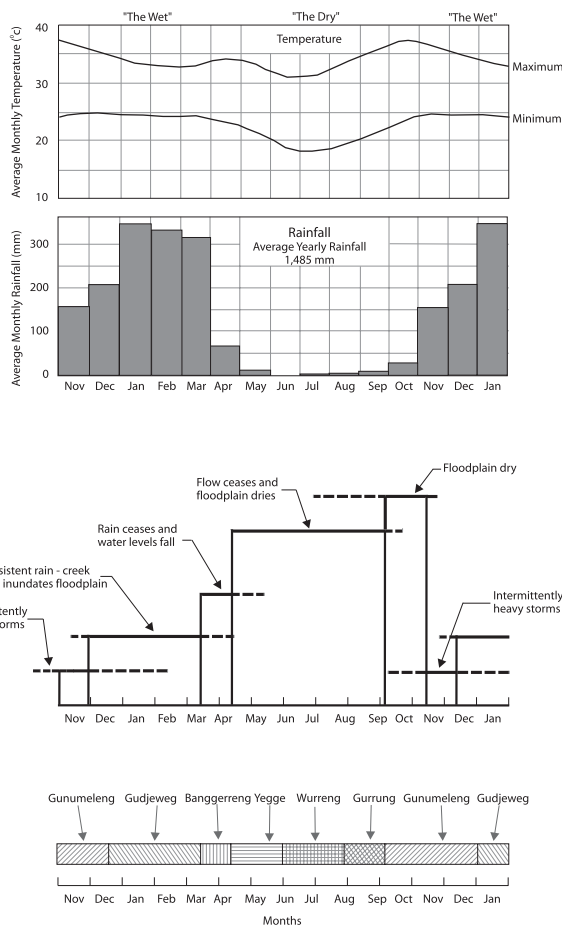


Figure 1. Location of Kakadu National Park and the Alligator Rivers Region in northern Australia’s wet-dry tropics (from Finlayson et al., 1997 and Lowry and Finlayson, 2004).



**Figure 2.** Generalised representation of: a) the climate of the Australian wet-dry tropics; b) hydrological change on the floodplains (variability is represented by dashed lines); and c) an Aboriginal calendar. A 14 month period is used to illustrate the extension of seasons across the calendar year. The hydrological information was adapted from Sanderson et al. (1983) by Finlayson et al. (1990) and the Aboriginal calendar from Ovington (1986) and Morris (1996). The Aboriginal seasons are described in the following manner: *Gunumeleng* pre-monsoon season; *Gudjeweg* monsoon season; *Banggerreng* harvest time; *Yegge* cool weather time; *Wurrung* early dry season; and *Gurrung* hot dry season.

in the south-west of the Kakadu Region; formed by the gradual erosion and retreat of the Arnhem Land plateau exposing the underlying, more resistant substrata and the development of undulating rises and plains.

4. *Deeply Weathered Mamadawerre (Koolpinyah) Surface* – a deeply weathered surface composed of plains, broad valleys, very low-gradient slopes, and isolated hills and ridges of resistant rock; located mainly between the Plateau and the coastal flood plains, although inliers occur in the Plateau.
5. *Alluvial floodplains* – along the middle upper reaches of the major rivers; in the upper reaches of the rivers the floodplains are typically confined within narrow river valleys. The plains have a gentle slope and gradually merge into the coastal flood plains; deposi-

**Table 1.** Geomorphic land classes in the Kakadu Region (from Lowry and Knox, 2002, 2006).

Geomorphic landscape class	Area km <sup>2</sup>
Alluvial floodplains	2960
Arnhem Land plateau and escarpment	9918
Coastal floodplains	3923
Deeply weather, eroded Mamadawerre Surface	13006
Dissected foothills of igneous origin	3435
Mamadawerre Surface – sedimentary plains	7045

**Table 2.** Area (km<sup>2</sup>) of catchments within the Kakadu Region (from Lowry and Knox, 2006).

Catchment	Within the Kakadu Region	Within Kakadu National Park
Mary River	8142	1269
Wildman River	3336	1708
West Alligator River	1444	1444
South Alligator River	11945	10900
East Alligator River	10340	2205
Katherine River*	5168	1601

\* most of Katherine river catchment is outside of the Kakadu Region

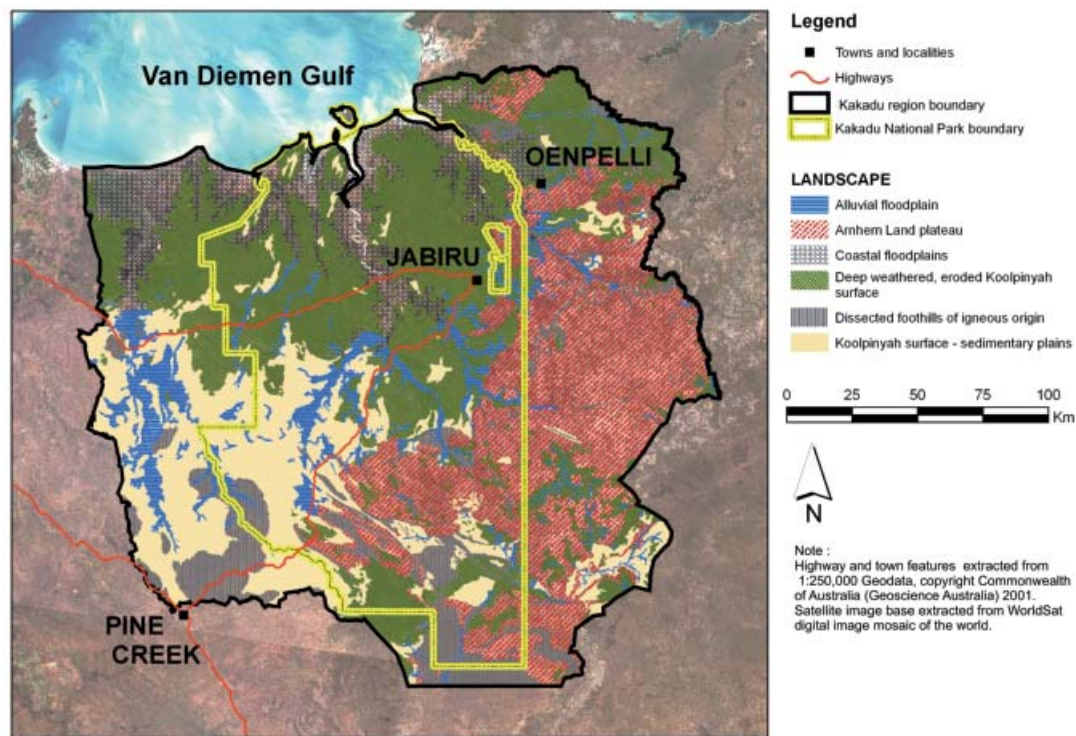
tion of alluvial sediments by the rivers has resulted in the development of flood plains along the rivers.

6. *Coastal floodplains* – bound the coastal margins; poorly drained plains of very low relief; resulted from sea level rise which reached its present level approximately 6000 years ago and drowned the coastal river valleys; infilling of the valleys led to the development of broad coastal flood plains; large meandering rivers form the upper reaches of the coastal flood plain and grade into saline mudflats near the coast.

The Region contains the entire catchments of the Wildman, West Alligator, South Alligator and East Alligator Rivers, as well as part of the Mary and Katherine catchments that are within Kakadu National Park. Lowry and Knox (2002, 2006) also include the adjacent parts of the Katherine and Mary River catchments (Table 2, Fig. 3). More accurate mapping has been prepared recently, confirming that the original map excluded part of the catchment of the East Alligator River and corrected the misconception that Kakadu National Park contained the entire catchment of the South Alligator River (Lowry and Knox, 2006).

### Climate and hydrology

The climate is generally taken to comprise two broad seasons – the Wet season, which commences late in the year (November-December) and lasts for 3–4 months, and the Dry season (Taylor and Tulloch, 1985), as shown



**Figure 3.** Geomorphic land classes in the Kakadu Region (from Lowry and Knox, 2002; 2006).

schematically in Figure 2. The most significant features of the Wet season are thunderstorms, tropical cyclones and rain depressions. As cyclones move inland they form rain depressions and are an important source of rain. Rainfall is also associated with monsoonal troughs, with 2–3 occurring each year, that usually produce widespread cloud and rainfall, regional convection that provides localized showers and easterly disturbances that, in some years, extend the rainy season. The Dry season is characterized by south-east trade winds and very little rain fall.

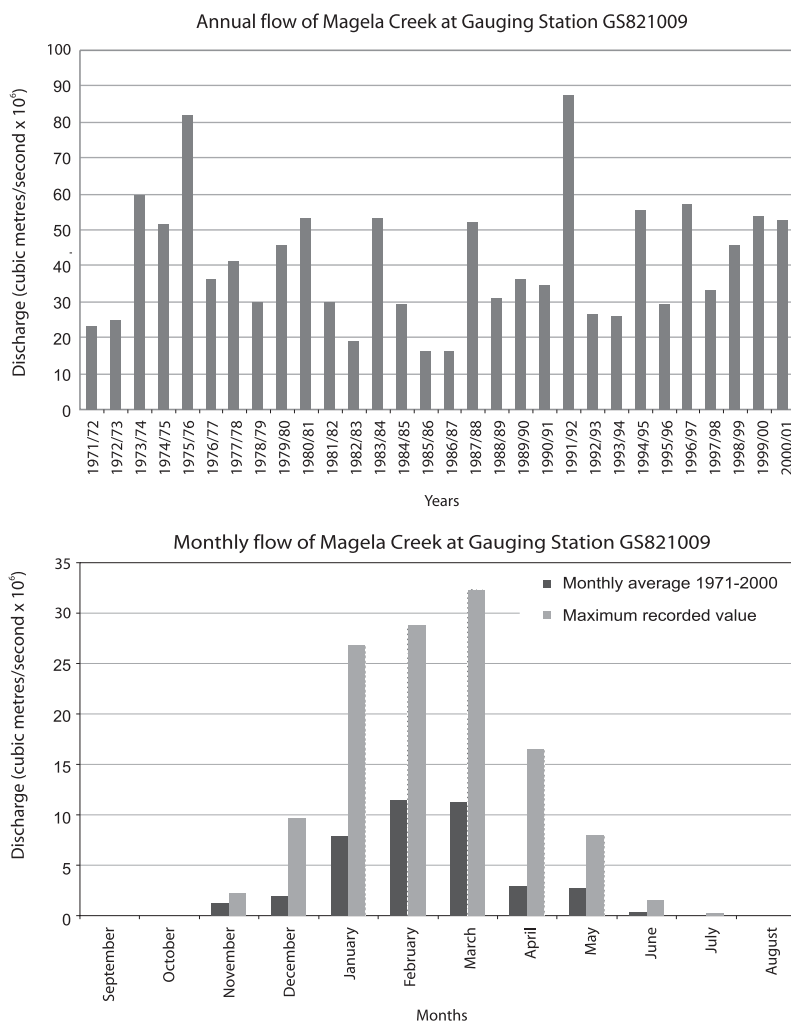
In general, temperatures are warm to hot throughout the year with a mean monthly maxima of 37°C in November and 31.5°C in July. In the Wet season warm temperatures are accompanied by relative humidity of about 80%. Cloud cover is greatest during the Wet season.

Local Aboriginal people have a refined perception of the climate and recognize six seasons based on the relationship between changes in the weather and the availability of food items (Ovington, 1986; Morris, 1996). The calendar they recognize is usually presented in a circular manner, but when presented in a linear manner and compared with the meteorological data the patterns outlined by the Aboriginal calendar are readily identifiable from the meteorological data (Finlayson, 2005; Fig. 2).

Finlayson (2005) also depicted the relationship between the knowledge base developed over millennia by Aboriginal people, the more recently obtained meteoro-

logical data, and a generalized hydrological cycle that was developed separately from field observations at Magela Creek and flood plain in Kakadu National Park (developed by Sanderson et al., 1983, and modified by Finlayson et al., 1990; Fig. 2). At the start of the Wet season intermittent rain storms saturate the soils of the lowland Mamadawerre (Koolpinyah) Surface and as more consistent rain occurs water collects in the creeks and thence in the large tidal rivers. Heavy rainfall over the plateau can send water cascading into the streams on the lowland surface. Once the creeks and rivers are full the freshwater spills across the flood plains and can cover them to a depth of several metres. The base flow in the creeks across the lowlands is less than 5 m<sup>3</sup> s<sup>-1</sup> with peak flows late in the Wet season, reaching and exceeding on occasions, 1000 m<sup>3</sup> s<sup>-1</sup>. The large range in both total annual and mean monthly discharge along the Magela Creek is representative of the water regimes experienced in the lowlands across the Region (Fig. 4); there is little information on the flow patterns in the plateau.

Flooding occurs once the catchment is saturated; heavy falls of rain later in the season generate more wide spread flooding than equivalent rainfall earlier in the season. The water regimes of the creeks and rivers reflect the climatic variability of the region (as shown in Fig. 2). While flow may be maintained in the upper reaches of the watercourses by springs or seeps, freshwater flow in the mid-lower sections of creeks and rivers generally ceases



**Figure 4.** Total annual and mean monthly flow in Magela creek (data from Northern Territory Department of Natural Resources, Environ-

within a few months of the end of the rains. The creeks and flood plains then dry out except for a few permanent swamps and lagoons, known locally as billabongs (Finlayson et al., 1990).

The spring tidal range in van Diemen Gulf is 5–6 m and estuarine water can extend more than 100 km upstream and generally remains within the stream channel (Woodroffe et al., 1989). The groundwater level in the surrounding landscape is recharged by the Wet season rains, but can fall 2–4 m during the Dry season.

**Vegetation/Landcover**

The Region contains in excess of 1800 species of higher plants (macro-algae and vascular plants; Brennan, 1996; Wilson et al., 1996). The floral diversity reflects the range of landscapes and habitats (Hoatson et al., 2000). Many vegetation surveys have been conducted, ranging

from a 1:1,000,000 map compiled as part of a vegetation survey of the Northern Territory to 1:250,000 and 1:100,000 surveys of specific communities. Vegetation in the region can be broadly categorised into 8 broad classes, which reflect the influence of the soils, geology and landform of the area. These include mangrove forests, sedges and herbaceous plants, paperbark forests, grassland and savanna, tall open forest and woodland, monsoon rainforest and woodland, spinifex grassland, and heath shrubland.

Wilson et al. (1996) provide an overview of the vegetation and land cover. Around 55% of the terrestrial vegetation is described as tropical tall grass savanna, composed of eucalypt-dominated open forest and woodland, with a 1–2 m grassy understorey. A further 30% of the Region is covered by heaths, and open woodlands with sparse grass understorey. Closed canopy monsoon rainforests are restricted to lowland springs, rock out-

crops, flood plain and beach levees, and sandstone. Vegetation communities on the freshwater flood plains exhibit marked variations in their composition, due to the extremes of the Wet and Dry seasons (Finlayson et al., 1989, 1990; Finlayson and Woodroffe, 1996; Finlayson, 2005). In the Wet season, flowering plants are profuse and widely distributed across the floodplain with high dry weight production. However, during the Dry season the vegetation is sparse and far less diverse. Mangrove communities are restricted to a narrow coastal strip and to the reaches of the major rivers subject to tidal influence (Finlayson and Woodroffe, 1996).

Fire and invasive plant and animal species have a significant impact on the extent and distribution of plant species and the land cover (Anderson, 1996; Cowie, 1996). Saline intrusion, caused by either climate change, or damage to the natural levees separating freshwater and saline wetland communities, by feral animals (water buffalo) has the potential to cause significant change to the vegetation communities of the floodplains (Bayliss et al., 1997; Eliot et al., 1999). Significant change in the floodplain vegetation has already occurred with the removal of feral buffalo (Skeat et al., 1996).

### Wetland evolution

Stratigraphic studies, particularly those on the wetlands of the South Alligator River have demonstrated that substantial environmental change has occurred over the last 20,000 years, attributed largely to changes in sea-level (see overview in Finlayson and Woodroffe, 1996). About 18,000 years ago, the sea levels across northern Australia were some 150 m lower than today and the coastline was several hundred kilometres north of the present location. The sea has since risen and around 8000 years ago tidal water flooded into the valleys, as illustrated by data from the South Alligator River valley which is now filled to a depth of 14–16 m with fine muds and alluvium.

The stratigraphy of the deltaic-estuarine plain of the South Alligator River, and probably the other river systems in the Region, indicates that the wetlands developed in three major phases: i) transgressive: ii) big swamp; and iii) sinuous/cuspate. Finlayson and Woodroffe (1996) summarised the many studies which generally support the notion of wide-scale change in the vegetation of the plains and rivers. The transgressive phase (8000–6800 years ago) was characterised by marine incursion into the prior valley and terrestrial ecosystems were displaced by mangrove forests as the sea level rose. By 6800 years ago a mangrove forest dominated by Rhizophoraceous species had become established. The onset of the 'big swamp' phase (6800–5300 years ago) followed stabilisation of the sea level around its present level. Mangrove forests established over most of the present-day flood plains for around 6000 years with successional changes

including *Rhizophora* slowly gaining dominance over *Bruguiera/Ceriops* species, a brief period of dominance by *Sonneratia* sp. and subsequent succession from *Sonneratia* through Rhizoporaceous forest to stands of *Avicennia*. The sinuous/cuspate phase began about 5300 years ago and represents a period during which the South Alligator River re-established a distinct channel meandering across the estuarine plains, changing during the last 2500 years from an entirely sinuous form to a predominantly cuspate form in the central part of the tidal section. Associated with the transition from the 'big swamp' to the 'sinuous' phase there was widespread replacement of mangrove species with the grasses and sedges characteristic of the present day freshwater wetlands. The timing of the transition from mangroves to freshwater wetlands probably varied throughout the Region.

### Biodiversity of different plant and animal groups

Wetlands in the Kakadu Region comprise tidally influenced mangroves and salt flats, seasonally inundated flood plains and billabongs, and small permanent lakes (Finlayson et al., 1990). The latter are small and not common. The flood plains (and associated lagoons) cover about 195,000 ha and extend along the major rivers (West Alligator, South Alligator and East Alligator) and creeks (Magela, Nourlangie, Jim Jim and Cooper) throughout the Region. Published studies of the species-level diversity of the wetlands have centred on the flood plain of Magela Creek, a tributary of the East Alligator River.

It is noted that whilst the role of the seasonal wetting and drying has been highlighted the effect of stochastic events on the composition and distribution of species within the wetlands has not been considered in detail - ecological investigations have principally considered species presence and distribution across the wetlands with limited analysis and modelling of ecological interrelationships and processes. While Finlayson (1988) provide an initial summary of the high standing biomass present on the flood plains the inter-relationship between the chemical, physical and biological components of the wetlands are not elaborated, except for pointing out that for some vertebrates much of their food supply comes from the adjacent terrestrial environment.

### Phytoplankton

Taxonomic studies were undertaken mainly in the early 1980s. Thomas (1983) provided a listing of 160 diatom taxa from 32 genera and considered the flora rich and allied to that of south-east Asia with annual changes in water quality and the variable environment contributing to

the diversity. Bedell (2001) confirmed that the distribution and relative abundance of diatom species in artificial and natural wetlands was more strongly related to variations in electrical conductance (EC) and pH than temperature or dissolved oxygen. Out of the 125 species observed, 7 were identified as indicators of pH and/or EC, as shown below:

- acidic conditions: *Aulacoseira granulata*, *Brachysira exilis* var. *lanceolata*, *Brachysira serians* var. *brachysira* (A), and *Navicula radiosa*;
- alkaline conditions: *Achnantheidium minutissimum* and *Nitzschia palea*;
- EC < 100 µS/cm: *Aulacoseira granulata* and *Brachysira serians* var. *brachysira* (A); and
- EC > 100 µS/cm: *Achnantheidium minutissimum*, *Nitzschia gracilis* (A) and *Nitzschia palea*.

A high level of interconnectedness existed between pH, EC, wetland type and species diversity. Artificial sites generally differed from more natural sites with a higher pH and a higher EC than the creek and billabong sites. Species diversity was lower in artificial sites than in natural sites. Further, water quality was a key determinant governing the diatom assemblages present in different wetland types. McBride (1983) also determined that the biomass of diatoms attached to macrophytes was equivalent to about 30 % of the macrophyte biomass of 16,500 t dry weight in the area investigated.

Ling and Tyler (1986) recorded over 530 taxa from groups other than diatoms. The Desmidiaceae (desmids) were particularly rich floristically and, as with the diatoms, were similar to those of south-east Asia. Broady (1984) investigated the widespread desiccated crusts and felts on the floodplain surface during the Dry season and recorded *Microchaete* and *Scytonema* species not previously recorded. Heterogeneous genera, e.g. *Scytonema*, *Calothrix*, *Hapalosiphon* and *Stigonema*, were present and secreted mucilaginous sheaths that combined with the intertwining filaments were assumed to stabilize the soil surface and reduce moisture loss. A characteristic feature of the flood plain during the Dry season is the development of large patches of green and red surface scums comprising phytoflagellates, in particular *Pyramimonas*, *Chlamydomonas*, *Chlorogonium* and *Euglena* species. *Euglena sanguinea* is responsible for the commonly observed red colour, but changes in species composition can cause a change to green.

## Macrophytes

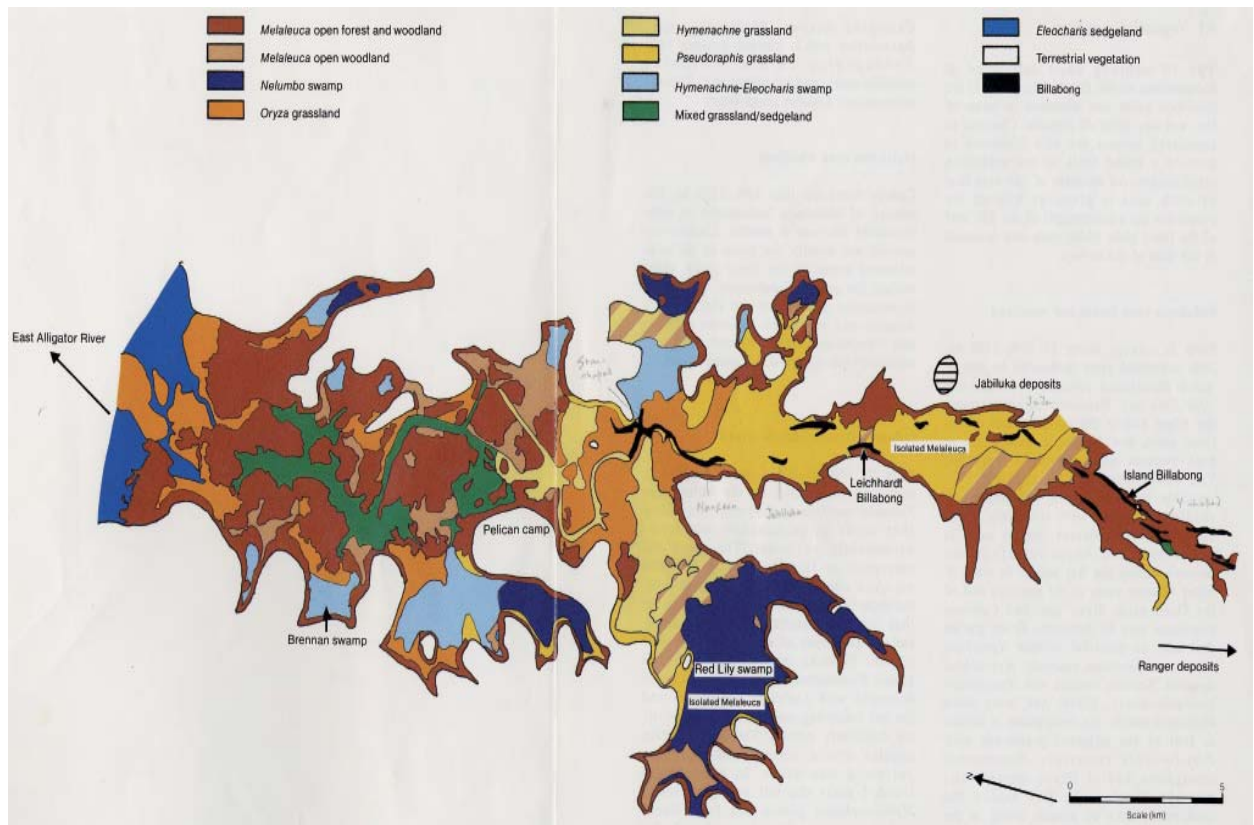
**Distribution.** The summary provided by Finlayson (2005) of the information available on the vegetation of the Magela flood plain has been adapted for use here. A listing of freshwater macrophytes (macro-algae and vascular plants) found in the region was produced by Finlayson et

al. (1989); Finlayson and Woodroffe (1996) provided a list of mangrove species; Brennan (1996) a list of all higher plants; and Cowie et al. (2000a) a flora of the coastal flood plains of the Northern Territory. The following information is taken mainly from Cowie et al. (2000b). The wetland flora consists mostly of widely distributed taxa with only 3 genera, *Hygrochloa*, *Omegeandra* and *Maidenia*, being endemic to Australia. Some 24 % (57 species) of the species that occurred primarily on floodplains were endemic to Australia; 57 % (132 species) were widespread in the Old World; 13 % (30) were pantropical; and 6 % (19 species) restricted to Australia. Of the Australian endemics, only 4 species that were not restricted to the floodplains, *Bambusa arnhemica*, *Hygrochloa aquatica*, *Nymphoides spongiosa* and *Nymphoides subacuta*, were restricted to the Northern Territory. The non-endemic nature of the flora was considered to reflect the many opportunities for exchange of species with other landmasses during recent geological times.

Within the Kakadu Region, Finlayson et al. (1989) built on information provided by other researchers and prepared a generalized vegetation map for the Magela flood plain based on observations from 5–6 years and, in particular, the Wet seasons, when many of the aquatic plants reach their peak biomass and are easier to differentiate and map. The analysis took into account the assertion by Sanderson et al. (1983) that an over-emphasis on detailed and short-term sampling did not account sufficiently for the high natural variability. It is not known how well the description provided for the Magela reflects the situation on other flood plains, especially given changes that have occurred with the removal of feral buffaloes (*Bubalus bubalis*) (Skeat et al., 1996). Ten communities were identified (Fig. 5) and are briefly described below.

- i) Melaleuca open forest and woodland (tree canopy cover of 10-70 %): areas dominated by one or more *Melaleuca* species - *M. viridiflora* and *M. cajaputi* around the edges and at the northern end of the flood plain, and *M. leucadendra* in back-swamps inundated for 6-8 months. The understorey varies.
- ii) Melaleuca open woodland (tree canopy cover < 10 %): *Melaleuca leucadendra* in areas inundated for over 6 months. Understorey species are usually the same as those in adjacent areas of the flood plain.
- iii) Nelumbo-Nymphoides herbland: a mixed community dominated by the water lilies *Nelumbo nucifera* and *Nymphoides indica* that occur in permanently and semi-permanently wet areas.
- iv) Orzya grassland: dominated by *Oryza meridionalis* towards the end of the Wet season. In the Dry season it consists of bare ground and dead *Oryza meridionalis* stems with persistent *Phylla nodiflora* and *Ludwigia adscendens* as xerophytic forms, and *Pseudoraphis spinescens*.





- v) Hymenachne grassland: dominated by *Hymenachne acutigluma* throughout the year.
- vi) Pseudoraphis grassland: dominated by the perennial emergent grass *Pseudoraphis spinescens* which has a turf-like habit during the Dry season and grows up through the water during the Wet season.
- vii) Hymenachne-Eleocharis grass-sedgeland: swampy areas that dry out seasonally and are dominated by *Hymenachne acutigluma* or *Eleocharis* spp., which are slower to establish.
- viii) Mixed grass-sedge-herbland: a variety of species with the dominant species depending on the topographic situation. *Oryza meridionalis* occurs on the drier sites with *Pseudoraphis spinescens* in slightly wetter places, while *Eleocharis* spp. and *Hymenachne acutigluma* occur in the deeper sites. On sites that remain flooded for 10-11 months *Nymphoides indica* and *Nymphaea macrosperma* may be present.
- ix) Eleocharis sedgeland: *Eleocharis* spp. dominate during the Wet season, but are replaced by annual herbs during the Dry season;
- x) Open-water community: permanent billabongs, flow channels, shallow waterholes contain *Nymphaea macrosperma* and *Nymphaea pubescens* and a number of submerged plant species. Floating grass mats comprising *Leersia hexandra*, *Hymen-*

*achne acutigluma* and *Urochloa mutica* along with the herb *Ludwigia adscendens*, occur along the banks of the billabongs.

More recent analyses have shown that these communities still predominate (J. Lowry unpublished information) along with several invasive species, in particular *Salvinia molesta* and *Urochloa mutica*, and the native species *Sesbania sesban* which intermittently dominates some areas of the plain, assumedly in responses to particular flooding and germination conditions that have not been identified.

In addition to the flood plain analyses, Finlayson et al. (1993a) reported a semi-quantitative analysis of vegetation dominance in 5 billabongs from the Magela creek and flood plain – three located on small tributaries and initially filled by water from the main creek rather than from the tributary, and two that represented remnants of deep channels on the flood plain. The three located on the tributaries had a generalised vegetation zonation consisting of:

- i) fringing *Melaleuca* spp. woodland in seasonally inundated areas;
- ii) a mix of grasses and sedges in seasonally inundated areas shaded by woodland;
- iii) a belt of *Eleocharis* sp. in water that is usually <1.5 m deep during the Wet season;

- iv) a small area of open water usually 1.5-2.0 m deep in the Wet season; and
- v) patches of waterlilies and submerged plants along the boundary between the sedges and the open water.

The dominant plant species, based on 'visual biomass' and 'ground cover', are the *Melaleuca* spp. trees and the geophytic, perennial *Eleocharis* spp. sedges. In contrast, the two billabongs located on the flood plain had a generalised vegetation zonation comprising:

- i) fringing *Melaleuca* spp., *Pandanus aquaticus*, and *Barringtonia acutangula* trees along a levee that comprised the western bank;
- ii) a mix of grasses and sedges and a few trees interfacing with the flood plain grass communities along the gently sloping eastern bank;
- iii) a mix of grasses, herbs and sedge overlaying a floating mat of *Salvinia molesta* extending from the banks towards the middle of the billabong; and
- iv) a discontinuous fringe of submerged plants and waterlilies along the edge of the floating mat.

As noted above, in recent decades the floodplain vegetation has undergone considerable change as a consequence of invasion by feral animals, e.g. buffalo and pigs (*Sus scrofa*), as well as weeds, e.g. mimosa (*Mimosa pigra*), salvinia (*Salvinia molesta*) and paragrass (*Urochloa mutica*), changes in fire regimes, and saline intrusion. However, there have been few attempts to predict changes or project future scenarios for vegetation management despite the extent of change and importance of the flood plains.

Finlayson et al. (1989) determined that both the duration and depth of inundation greatly influenced the distribution of plant species, and attempted to explain this through an empirical model of plant succession in wetlands, developed by Van der Valk (1981), to assess changes in vegetation that occur as a result of changes in the annual hydrological pattern (Finlayson, 1990; Finlayson and Woodroffe, 1996). Despite limitations the model provided a framework for predicting changes in vegetation patterns.

*Growth strategies and forms.* Finlayson et al. (1989) assessed the growth forms of the 222 plant species found on the Magela flood plain across four broad habitat categories, seasonally inundated plain, seasonally inundated fringe zone, billabong and permanent swamp. (The taxonomic listing and hence the number of species recorded by Finlayson et al. (1989) have not been updated in accordance with the taxonomy presented in the flora provided more recently by Cowie et al. (2000b). The fringe zone covered the edges of the flood plain and included the *Melaleuca* forests/woodlands, with the seasonally inundated plain habitat covering the remainder of the

**Table 3.** Number of plant species found in four broad habitats areas on the Magela flood plain (from Finlayson et al., 1989).

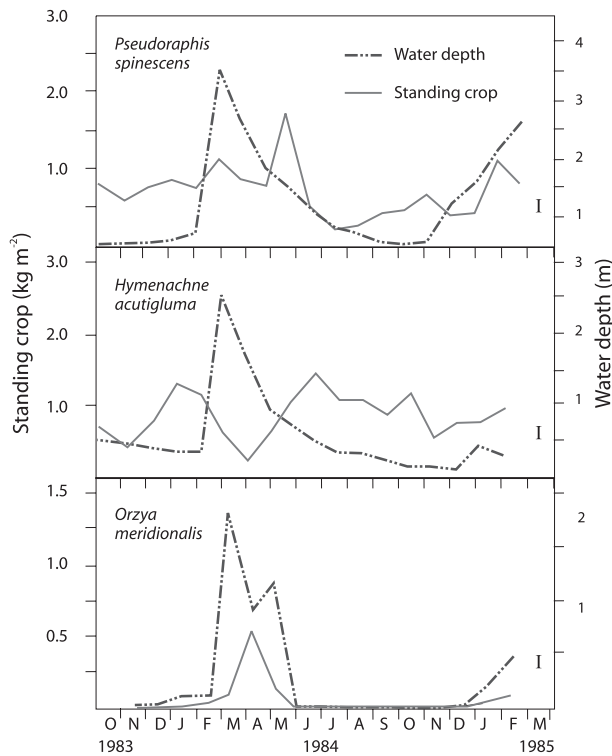
Habitat	Total species	Annuals	Perennials	Geophytic Perennials
Permanent billabongs	46	19	2	6
Seasonally inundated flood plain	94	57	29	8
Fringe zone	158	100	50	8
Permanent swamps	21	5	11	5

flood plain, except for the permanently wet areas. The seasonally inundated plain and the fringe zone contained around 40% and 70% respectively, of the species, compared with 20% in the billabongs and 10% in the permanent swamps (Table 3).

In total there were 139 annual species with 102 terrestrial and 37 aquatic species. Eighty-nine of the terrestrial species occurred in the fringe zone with 27 only on the plain which is seasonally inundated for a longer period than the fringe zone. Finlayson et al. (1989) provide a listing of growth strategy and form for each species. This included 4 growth strategies (annual, perennial, or geophytic perennial) and 2 primary (terrestrial or aquatic) and 7 secondary growth forms (tree, shrub, grass, sedge, vine, palm or herb). Terrestrial annuals represented a diverse group of species with 60 of them classified as herbs, 18 as sedges and 17 as grasses. Twenty-seven of the aquatic annuals are herbs and 6 are shrubs. There were 68 perennial species, 50 in the fringe zone. 34 of the perennials are terrestrial, 26 aquatic, with 8 others difficult to classify. There are 12 terrestrial trees including *Eucalyptus* spp., *Pandanus spiralis*, *Lophostemon lactifluus* and *Syzygium suborbiculare*. The aquatic perennial species are dominated by 12 herbs, including *Hydrilla verticillata*, *Ludwigia adscendens*, *Nelumbo nucifera* and *Nymphoides indica*, and by 5 grasses, including the widespread *Hymenachne acutigluma* and *Pseudoraphis spinescens*. There were 14 geophytic species, the more widespread include the *Nymphaea* and *Eleocharis* species.

Within the broad categorisation of growth strategies and forms there are many morphological and physiological adaptations that enable particular species to occupy various niches within the cycles of dry and wet conditions. Coiwe et al. (2000a) provide an overview of the many specific adaptations that enable plants to survive the variability due to changes in the hydrological cycle.

*Productivity.* The productivity of the floodplain vegetation on the Magela flood plain has been investigated, covering seasonal changes in the dry weight of aquatic grasses and litterfall from *Melaleuca* trees (Finlayson, 1988, 1991; Finlayson et al., 1993b). Changes in the



**Figure 6.** Above-ground dry weight biomass of three aquatic grass species (from Finlayson, 1991). The least significant difference ( $P =$

above-ground biomass (dry weight/unit area) or the widespread aquatic grasses *Pseudoraphis spinescens*, *Hymenachne acutigluma* and *Oryza meridionalis* were determined during 1983–84 (Fig. 6; Finlayson, 1991). The dry above-ground biomass of the grass species was influenced by water depth which in itself is directly related to the rainfall pattern and surface water flow. The annual dry weight production for these species was  $0.51 \text{ kg m}^{-2}$  for *Oryza meridionalis*,  $1.91 \text{ kg m}^{-2}$  for *Pseudoraphis spinescens*, and  $2.09 \text{ kg m}^{-2}$  for *Hymenachne acutigluma*.

Dry weight production of the widespread *Melaleuca* woodlands and forests on the Magela flood plain were estimated through an analysis of litterfall data (Finlayson, 1988; Finlayson et al., 1993b). In an intensively sampled forest the total litterfall was approximately  $0.7 \text{ kg m}^{-2} \text{ y}^{-1}$  compared to  $1.5 \text{ kg m}^{-2} \text{ y}^{-1}$  at a less intensively sampled site (Finlayson, 1988). The value of 0.7 to  $1.5 \text{ kg m}^{-2} \text{ y}^{-1}$  is within the range recorded for other forests at the same latitude (Lonsdale, 1988). The above ground biomass of *Melaleuca* species on the Magela flood plain was also calculated using an algorithm relating diameter at breast height to tree height and fresh weight (Finlayson et al., 1993b). This resulted in a calculated tree weight of  $260 \pm 0.3 \text{ t ha}^{-1}$  based on a tree density of  $294 \text{ trees ha}^{-1}$ ; elsewhere on the floodplain tree densities were much

higher, although an analysis of density across the entire floodplain was not undertaken.

### Aquatic invertebrates

Available taxonomic information, zoogeographical relations and the general ecology of various groups of aquatic invertebrates of the Region were reviewed by Humphrey and Dostine (1994). Summary taxonomic data are presented in Table 4 based on Humphrey and Dostine (1994) with updated information from Corbett (1996) and an unpublished database on voucher specimens (Environmental Research Institute of the Supervising Scientist). This represents approximately 300 micro-invertebrate (Copepoda, Cladocera, Rotifera) and over 600 macro-invertebrate (insects, worms, mites, larger crustacean groups, molluscs and sponges) species from freshwater habitats in the Region, including sandstone plateau streams and springs, upland (but below-escarpment) sections of streams with permanent flow, mid-reaches of streams with seasonal flow, permanent waterbodies on or adjacent to the main stream channels, and seasonally-inundated flood plains near the terminus of major streams.

The composition of the freshwater invertebrate fauna of the Region is both Australian (Williams, 1980) and/or south-east Asian at generic and higher taxonomic levels, depending upon the group. Across all taxonomic groups, more data are required before making accurate comparisons with the invertebrate fauna in other climatic zones, both in Australia and elsewhere (Shiel and Williams, 1990; Humphrey and Dostine, 1994). Nevertheless, mayfly (Ephemeroptera) and caddisfly (Trichoptera) data have been used in comparative global zoogeographical studies (Vinson and Hawkins, 2003), while Cranston (2000) reported high diversity of chironomid flies in both the wet and wet-dry tropics of Australia compared with temperate Australia. Cranston et al. (1997) also observed high chironomid species richness in natural, as well as mining-induced, acidic waters of the Region, contrary to findings in temperate studies. They explained this by the large tropical (Australian and south-east Asian) pool of species tolerant of naturally-occurring acidic waters common to these regions. Despite this, the Australian chironomid fauna is impoverished compared with northern hemispheric faunas (Cranston, 2000).

Kay et al. (1999) remarked upon the similarity of macro-invertebrate families in fresh waters of north-western Australia, compared with elsewhere across northern Australia. Cranston (2000) noted little additional richness and only modest novelty of chironomid species in waters of north-western Australia compared to the Kakadu Region, a pattern that appears to hold generally for most other invertebrate faunal groups (C. Humphrey, unpublished observations). Humphrey (1999) postulated that high seasonality of the extensive lowland aquatic

**Table 4.** Number of families, genera and species of aquatic invertebrates recorded in the Kakadu Region. Numbers in italics are (under)estimates only, while ‘–’ indicates data not available.

Phylum/Class	Order	Families	Genera	Species
Mollusca/Gastropoda	Pulmonata	4	6	7
	Prosobranchiata	2	5 <sup>A</sup>	5
Mollusca/Bivalvia	Unionoida and Veneroida	2	2	2
Arthropoda/Insecta	Diptera	Chironomidae	43	122
		7 (non- Chironomidae)	–	–
	Trichoptera	9	21	105
	Ephemeroptera	3	14	25
	Coleoptera	16	50	100
	Hemiptera	11	–	–
	Odonata	8	54	77
	Lepidoptera	1	–	10
Arthropoda/Crustacea	Isopoda	1	1	20
	Decapoda	5	8	20
	Ostracoda	–	–	6
	Conchostraca	2	–	6
Arthropoda/Crustacea/Copepoda	Calanoida and Cyclopoida	–	7	14
	Cladocera	6	30	48
Arthropoda/Arachnida	Hydracarina	15	29	–
Annelida	Oligochaeta	5	–	–
	Hirudinea	2	–	–
Porifera		–	4	7
Rotifera		–	–	227

A: Includes one exotic species

environments of northern Australia would select animals and plants that were readily dispersed. Moreover, lowland freshwater ecosystems of large parts of northern Australia are relatively young in geological terms – a feature which, together with high seasonality and species vagility, has probably mitigated against endemism at regional and smaller catchment scales (Humphrey, 1999). Some elements of the insect fauna from mainly upland sections of streams, however, may be more restricted in distribution. This includes the mayfly family, the Leptophlebiidae; 7 of the 9 species of Leptophlebiids found in the Kakadu Region appear to be restricted to the Northern Territory (P Suter, unpublished data). Indeed, this insect family contains the only species in the Region (*Tillyardophlebia dostinei*) so far found to be restricted to a single freshwater stream (C. Humphrey unpublished data).

Not only are major invertebrate faunal groups widespread across northern Australia, but at family-level at least, the fauna (including that of the Kakadu Region) has a high year-to-year persistence (constancy) compared with other regions of Australia, a feature that is strongly related to the relatively low degree of inter-annual variability of stream flow (Humphrey et al., 2000).

In contrast to the aquatic insects and the lowland fauna generally of the Region, components of the crustacean groups the Decapoda and Isopoda, occurring in freshwaters of the ancient ‘stone country’ of the eastern part of the Region contain a substantial and significant endemic component. This fauna includes an endemic family of shrimps, the Kakaducarididae, comprising two endemic genera, *Leptopalaemon* and *Kakaducaris* (Bruce, 1993; Bruce and Short, 1993), as well as an endemic genus of phreatoicidean isopod (*Eophreatoicus*), of Gondwanic origin, that has exceptional species-level diversity (G. Wilson personal communication). Most of these macro-crustacean species have very restricted distributions, often limited to single streams, seeps or springs. This diversity and endemism was attributed by Humphrey (1999) to the antiquity and persistence of the plateau/escarpment and associated perennial streams, springs and seeps, and isolating mechanisms including fragmentation of habitat (long-term climate changes, erosion) and the generally poor dispersal characteristics of these crustacean groups.

The invertebrate ecology, including seasonal dynamics, of seasonally-flowing portions of streams near an

**Table 5.** Diversity of freshwater fishes recorded from the Kakadu Region.

Order	Family	Number of genera	Number of species	Marine vagrant (m) or catadromous (c)
Pleurotremata	Carcharhinidae	2	2	m
	Pristidae	1	1	m
Hypotremata	Dasyatidae	1	1	m
Osteoglossiformes	Osteoglossidae	1	1	
Elopiformes	Megalopidae	1	1	c
Anguilliformes	Anguillidae	1	1	c
Clupeiformes	Clupeidae	2	3	m
Siluriformes	Ariidae	1	3	
	Plotosidae	3	5	
Atheriniformes	Atherinidae	1	2	
Synbranchiformes	Synbranchidae	1	1	
Pleuronectiformes	Cynoglossidae	1	1	
	Soleidae	2	2	?
Perciformes	Belontiidae	1	1	
	Melanotaeniidae	1	5	
	Pseudomugilidae	1	2	
	Ambassidae	2	3	
	Centropomidae	1	1	c
	Terapontidae	5	6	
	Apogonidae	1	1	
	Toxotidae	1	2	
	Mugilidae	1	2	c
	Gobiidae	1	3	c
	Eleotrididae	5	8	
	Scatophagidae	2	2	m
	Kurtidae	1	1	
	Gerreidae	1	1	m
<b>Total</b>	<b>27</b>	<b>42</b>	<b>62</b>	

operating uranium mine (Ranger mine) and a uranium ore deposit (Jabiluka) has been investigated for all phases of the hydrological cycle, including recolonisation after early Wet season re-wetting, early-mid Wet season flows, recessional flow period and pool-formation phase. Pattridge et al. (1997) found that upon re-wetting with the first stream flows in Magela Creek, most recolonising taxa were derived from perennial upper reaches through drift, though contributions were also derived from adjacent billabongs and resting stages (especially microcrustaceans) in the sandy substratum. The seasonal dynamics of aquatic invertebrates from permanent waterbodies on or adjacent to the main stream channels have also been studied (Marchant, 1982a, b, c; Outridge, 1988).

Much effort has been directed at the use of aquatic invertebrates for detecting and assessing mining impact (and recovery) in the Region (Humphrey, 1990; Humphrey and Dostine, 1994; Faith et al., 1991, 1995; Smith

and Cranston, 1995; Hardwick et al., 1995; Humphrey et al., 2002). The responses of aquatic invertebrates to a range of natural and human-related disturbances in the Region have also been investigated, including fire regimes, invasive wetland grasses and tourism (Douglas, 1999; Douglas and O'Connor, 1999; M. Stowar unpublished information).

### Fishes

Freshwater fishes are among the most comprehensively studied aquatic organisms in the Region (Taylor, 1964; Midgley, 1973; Pollard, 1974; Bishop et al., 1986, 1990, 2001). The ecology, community structure and biogeographic relationships of the fish fauna are reasonably well known and have been described and reviewed by Bishop and Forbes (1991). Sixty two freshwater fish species have been recorded, represented

by 44 entirely freshwater species, 4 species that reproduce in estuarine or marine waters (catadromous) and 14 marine or estuarine species that commonly enter non-tidal freshwaters (marine vagrants) (Table 5).

All except three Australian freshwater fish (*Neocercatodus forsteri*, *Scleropages leichardti* and *S. jardinii*) are comparatively recent descendents from marine families. When this recent colonisation of freshwater habitats is combined with the small area of freshwater habitats on the Australian continent it is not surprising that the species richness of the continent (302 species) is very low by global standards (Allen et al., 2002). The diversity of freshwater fish is higher in the tropics compared to temperate regions of Australia. Shiel and Williams (1990) suggested that periods of extreme aridity in the southern temperate areas and ease of migration of new species from marine to freshwaters as a result of greater length and low-gradient of tropical rivers were most likely to determine species richness of freshwater fish. However, Bishop and Forbes (1991) and more recently Unmack (2001) have suggested an evolutionary explanation arguing that freshwater fish diversity in Australia is a reflection of the fish diversity in adjacent seas and this is greater in the tropics. The fish diversity in the Kakadu Region is relatively high by comparison to other regions within the continent - this may be related to the rich diversity of marine fish in the Indo-Pacific archipelago.

Catchment size is a major factor determining fish diversity in different drainage systems. Bishop and Forbes (1991) compared the diversity of fish in streams in the Region with a generalised relationship between catchment area and diversity developed for tropical rivers by Welcomme (1979). By separating the drainage basin into sub-catchments they found that streams in the Region had higher diversity than many other streams of similar size elsewhere; however, this seems spurious as it assumes that fish diversity in a sub-catchment is independent of the rest of the catchment. Pusey and Kennard (1996) in comparing the fish diversity of 10 tropical rivers along the far northern east coast of Queensland found that while catchment size is an important factor determining species diversity, differences in fish community structure were related to latitude.

About half the fish species encountered in the Kakadu Region are small to medium in size, being usually less than 30 cm in length. The small-bodied fish fauna of the Region is dominated in overall abundance by centropomids (perchlets), melanotaeniids (rainbow fish) and atherinids (hardyheads); the larger bodied fish fauna is dominated by ariids and plotosids (Fork and Eel tailed Catfish), clupeids (Boney Bream), megalopids (tarpon) and to a lesser extent, terapontids (grunters). Some other larger species include Barramundi (*Lates calcarifer*), Saratoga and three estuarine shark species. Only one shark, the Bull Shark *Carcharinus leucas*, enters non-

tidal waters (H. Larson personal communication). The two other shark species, the Bizant River Shark (*Glyphis* sp. A) and the Northern River Shark (*Glyphis* sp. C) are listed respectively as critically endangered and endangered under IUCN criteria. Their distribution is limited to only a few river systems in northern Australia, although it is acknowledged that further specimens and taxonomic work are required to properly determine the distribution and status of these species (Larson, 2000; Pogonoski et al., 2002).

Longitudinal zonation of fish species is not very pronounced along the major stream channels. Marine vagrants are more likely to be found in freshwater bodies close to the limit of tidal influence. Upstream there is little variation in the species composition until the first dispersal barriers occur near the escarpment of the sandstone plateau. In this lowland zone on most major streams 20 to 30 species are likely to be encountered at a single location. Upstream from dispersal barriers, such as waterfalls and large cascades, species diversity declines greatly and pools on the plateau may contain only one or two species. Most species utilise both riverine and associated lentic wetlands when available. There are 6 species that are restricted to riverine habitats and another 2 that rarely enter lentic wetlands. At least 3 species occur only in small tributaries within the plateau and escarpment zone.

Many of the fish species in the Region are common across northern Australia. Of 114 species known from rivers of the wet-dry tropics of northern Australia 32 occur throughout the entire zone; 11 are restricted to the Arafura bio-region of the Northern Territory; and 3 are endemic to the Region and nearby western Arnhemland, including Mariana's Hardy Head (*Craterocephalus marianae*), the Sharp-nose Grunter (*Syncomistes butleri*) and Midgley's Grunter (*Pingalla midgleyi*). (Recent surveys have extended the known range of the hardyhead and the grunter.) Another 3 species have very disjunct distributions across northern Australia and Papua New Guinea, including the Coal Grunter (*Hephaestus carbo*), Banded Rainbowfish (*Melanotaenia trifasciata*) and Black-striped Rainbowfish (*Melanotaenia nigrans*). The latter reflect an historic freshwater connection between Australia and Papua New Guinea that was severed by sea-level rises within the past 30,000 years.

Upstream escarpment habitats are nutrient poor and are dominated by herbivore/detritivores and omnivores. The Sharp-nose Grunter has specially adapted teeth, jaws and intestines for grazing epiphytes from rocks and logs, whilst the archerfish (*Toxotes chatareus* and *Toxotes lorentzi*) can capture terrestrial prey by emitting a jet of water from the mouth to dislodge the prey from overhanging vegetation (Bishop et al., 2001). A range of trophic categories is represented amongst the fish communities of lowland waterbodies, that are generally nutri-

ent rich. Fish in the Region exhibit a number of breeding strategies, with a high proportion of species exhibiting some form of parental care, including live bearing, buccal incubation and nest guarding (Bishop et al., 2001).

A characteristic feature of the ecology of the fish communities is the movement of fish between habitats with the re-linking of Dry season refuge areas of the escarpment, corridor and floodplain zone once Wet season flows commence (Bishop and Forbes, 1991). Feeding, breeding and recruitment of juveniles mostly occurs during the Wet season months with most species spawning early in the Wet season, taking advantage of the increased area of habitat available to supply resources for growth and reproduction (Bishop et al., 2001). Many species breed in off-river water bodies of lowland streams and in the vast areas of inundated flood plain. In some seasonal tributaries of the larger Alligator Rivers, including Magela and Nourlangie Creeks, there are massive upstream migrations in the late Wet season of mainly small bodied fishes (dominated by ambassids and melanotaeniids) from floodplain nursery areas to Dry season refuges (Humphrey and Dostine, 1994). These spectacular migrations often consist of several hundred thousand fish per hour moving past a single observation point (Bishop et al., 1995).

Large natural fish mortalities, or 'fish kills' are a common occurrence in the Region (Pidgeon, 2001). These are caused by a number of factors with low dissolved oxygen levels the most common cause. Influx of toxic chemicals by natural processes (weakly acidic waters containing toxic levels of aluminium, and leached ichthyocidal compounds such as saponins from trees and shrubs), and disease have also been recorded. Disease rarely results in large-scale mortalities at one time. Most fish kills occur during the early Wet season when the first flows introduce oxygen depleting organic matter from the catchment and concentrated contaminants (described above). Storms and flows can mix anoxic water from the bottom of billabongs and stir up sediment and detritus which can further reduce oxygen levels. Fish kills often result in the deaths of many thousands of fish and usually involve the larger bodied fish such as Barramundi, Fork and Eel-tailed Catfish, Tarpon and Mullet (Bishop, 1980; Bishop et al., 1982; Brown et al., 1981; Noller, 1983; Pidgeon, 2001).

There is no commercial fishery in freshwaters of the Region, but there are important artisanal fisheries by indigenous people and recreational fishery. The latter is largely a sport fishery targeting only one species, the Barramundi. This fishery is highly managed with minimum size limits, small bag limits and seasonal closures that vary with measured fishing pressures. Upland sections of streams in Kakadu are generally off-limits to (non-indigenous) recreational fishing. Otherwise, there is no management for other freshwater species other than not al-

lowing commercial exploitation except for limited catches for the aquarium fish trade.

### Amphibians

Australia's amphibia are represented by five families in the order Anura (the frogs and toads) with four families of native frogs (the Microhylidae, Myobatrachidae (or Leptodactylidae), Hylidae (or Pelodryadidae), and the Ranidae) and the introduced cane or marine toad, *Bufo marinus* from the Bufonidae family (Robert and Watson, 1993). The Kimberley region and the northern part of the Northern Territory which contains the Kakadu Region are considered to be an area of significant amphibian diversity. Despite this general information there are many gaps in the knowledge about the ecology and biology of many frog species of this area, with new species being found as recently as 1997 and 2001 (Northern Territory Frogs Database, 2003).

The first comprehensive study of frogs in the Kakadu Region was undertaken in the Wet seasons of 1978–1979 and 1979–1980 (Tyler et al., 1983). Woinarski and Gambold (1992) undertook a further survey to examine distribution patterns of herpeto-fauna in relation to environmental gradients (substrate, moisture availability, vegetation); frogs were found to be most strongly associated with substrate and moisture availability and occurred in 4 distinct assemblages – a sandstone assemblage, lowland clay-flat assemblage, wet forest assemblage and two species with idiosyncratic ranges (Woinarski and Gambold, 1992). These surveys have recorded 25 frog species from 3 families – the Hylidae with 2 genera and 16 species; the Myobatrachidae with 5 genera and 8 species; and the Microhylidae with 1 genera and 1 species (Table 7). The cane toad is a recent invader (van Dam et al., 2002a).

Most of the frog species display a clear seasonal dichotomy of behaviour, being inactive during the Dry season with at least 9 species aestivating underground (Tyler and Crook, 1987). Some of these species are fossorial (*Cyclorana australis*, *C. longipes*, *Limnodynastes ornatus*), while others (such as *Litoria nasuta*, *L. inermis*, *L. wotjulemensis* and *L. tornieri*) are known to descend down deep cracks in the hardened mud at the edge of billabongs (Tyler and Crook, 1987). In contrast, during the Wet season, frogs are very obvious and abundant (Tyler and Crook, 1987) and are an important food source for a variety of birds, reptiles and fish (Morris, 1996).

The sandstone assemblage of frogs is endemic to northern Australia with species occupying crevices near small perennial streams in the sandstone escarpments and plateaux (Braithwaite et al., 1991; Morris, 1996; Woinarski and Gambold, 1992). These species cope with extreme environmental conditions with the tadpoles tolerating temperatures of around 42 °C, and the adults in the

**Table 6.** Frog species recorded from the Kakadu Region (from Press et al., 1995, taxonomy as per Northern Territory Frogs Database, 2003).

Family	Species	Common name(s)
Myobatrachidae	<i>Crinia bilingual</i>	Bilingual Frog, Ratchet Frog
Hylidae	<i>Cyclorana australis</i>	Burrowing Frog, Giant Frog
Hylidae	<i>Cyclorana longipes</i>	Long-footed Frog
Hylidae	<i>Litoria bicolor</i>	Northern Dwarf Tree Frog
Hylidae	<i>Litoria caerulea</i>	Green Tree Frog
Hylidae	<i>Litoria coplandi</i>	Saxicoline Tree Frog, Copland's Rock Frog
Hylidae	<i>Litoria dahlia</i>	Dahl's Aquatic Frog
Hylidae	<i>Litoria inermis</i>	Peter's Frog
Hylidae	<i>Litoria meiriana</i>	Rockhole Frog
Hylidae	<i>Litoria microbelos</i> (formerly <i>Litoria dorsalis</i> )	Dwarf Rocket Frog, Javelin Frog
Hylidae	<i>Litoria nasuta</i>	Rocket Frog
Hylidae	<i>Litoria pallida</i>	Pale Frog
Hylidae	<i>Litoria personata</i>	Masked Cave Frog, Masked Rock Frog
Hylidae	<i>Litoria rothii</i>	Roth's Tree Frog
Hylidae	<i>Litoria rubella</i>	Desert Tree Frog, Red Tree Frog
Hylidae	<i>Litoria tornieri</i>	Tornier's Frog
Hylidae	<i>Litoria wotjumulensis</i>	Wotjulum Frog
Microhylidae	<i>Austrochaperina aldelphe</i> (formerly <i>Sphenophyrne adelphe</i> )	Northern Territory Frog
Myobatrachidae	<i>Limnodynastes convexiusculus</i>	Marbled Frog
Myobatrachida	<i>Limnodynastes ornatus</i>	Ornate Burrowing Frog
Myobatrachidae	<i>Megistolotis lignarius</i>	Capenter Frog
Myobatrachidae	<i>Notoden melanoscaphus</i>	Northern Spadefoot Toad, Golfball Frog
Myobatrachidae	<i>Uperoleia arenicola</i>	Jabiru Toadlet
Myobatrachidae	<i>Uperoleia inundata</i>	Floodplain Toadlet
Myobatrachidae	<i>Uperoleia lithomoda</i>	Stonemason Toadlet

Dry season with limited surface water, low humidity and high daytime temperatures (Morris, 1996). The sandstone specialist assemblage consists of *Megistolotis lignarius*, *Litoria personata*, *Litoria meiriana* and *Litoria coplandi*. During the Dry season these species seek refuge in sandstone crevices and caves in the escarpment. *M. lignarius* and *L. personata* are endemic to the Kakadu sandstone escarpment.

Two species are found throughout the Region and around Australia, without any strong association to environmental variables. *Litoria caerulea* has a widespread distribution throughout northern Australia and along the east coast (Woinarski and Gambold, 1992). The burrowing frog *Limnodynastes ornatus* also has a widespread distribution throughout Australia, but in the Kakadu Region is most abundant on sandy flats with tall forests (Woinarski and Gambold, 1992). The highest diversity of frogs within the Region occurs on lowland wet clay flats, with open vegetation and extensive tussock grass cover (Woinarski

and Gambold, 1992). Most of these species are burrowing frogs (*Uperoleia* spp., *Limnodynastes convexiusculus* and *Cyclorana australis*). One of the burrowing frog species, *Uperoleia arenicola*, is endemic to the Region. Another group of frogs is most abundant in riparian or monsoon forests, comprising mainly tree frogs (*Litoria* spp., and *Crinia bilingual*) (Woinarski and Gambold, 1992).

### Reptiles

The reptile fauna of the Region is one of the most diverse in Australia, with 127 species recorded (Table 7) and including only one introduced species, the Asian House Gecko (*Hemidactylus frenatus*). The herpeto-fauna comprise 15 families and 62 genera. From a conservation viewpoint, using the IUCN criteria (2000), the Loggerhead Turtle (*Caretta caretta*) is considered endangered whereas there is little concern for the Green Turtle (*Chelonia mydas*); both species of sea turtle have been re-



**Table 7.** Reptile fauna of the Region (from Press et al., 1995).

Order	Suborder	Family	Number of Genera	Number of Species
Crocodylia		Crocodylidae	1	2
Testudines		Carettochelydidae	1	1
		Chelidae	3	5
		Cheloniidae	4	4
Squamata	Sauria	Agamidae	5	9
		Gekkonidae	7	16
		Pygopodidae	3	4
		Scincidae	11	36
		Varanidae	1	11
Squamata	Serpentes	Acrochordidae	1	2
		Boidae	3	6
		Colubridae	8	8
		Elapidae	10	13
		Hydrophiidae	3	3
		Typhlopidae	1	7
<b>Total</b>		<b>15</b>	<b>62</b>	<b>127</b>

ported nesting (Miles, 1998) on an island that is free of most of the mainland egg eaters, such as dingos, feral pigs and humans (Miles, 2000). The Flatback (*Nator depressa*) and Pacific Ridley (*Lepidochelys olivacea*) Turtles have also been recorded nesting (Vanderlely, 1995). The Oenpelli Python (*Morelia oenpelliensis*) is listed as vulnerable.

Eighteen species of large reptiles are listed as using riparian and floodplain habitats of the Magela Creek system within Kakadu (Finlayson et al., 1990) with a further 6 water-dependent species. The latter includes: the Pig-nosed Turtle (*Carettochelys insculpta*); the Mangrove Monitor (*Varanus indicus*), restricted to mangrove communities along the estuaries; the Little File Snake (*Achrochordus granulatus*); and three species of aquatic colubrid snakes (*Cerberus rynchops*, *Fordonia leucobalia* and *Myron richardsonii*), usually found in estuarine and mangrove habitats.

Two species of crocodile have a broad distribution across northern Australia and are plentiful in the region. The Estuarine or Saltwater Crocodile (*Crocodylus porosus*) inhabits coastal rivers extending well inland via major rivers and billabongs on the river floodplains. The Freshwater Crocodile (*Crocodylus johnstoni*) inhabits permanent freshwater rivers, lagoons and billabongs across northern Australia (Cogger, 2000). There are no reliable population estimates for these species in the Region although it is generally considered that they are populous and have recovered from the decimation that occurred as a consequence of hunting activities that were formally stopped in 1971.

Of 11 species of goanna found in the region 5 are found in aquatic or semi-aquatic habitats. In contrast to the Mangrove Monitor, Merten's (*Varanus mertensi*) and Mitchells (*Varanus mitchelli*) Water Monitors are usually associated with freshwater streams and billabongs, obtaining approximately 40% of their food (biomass) from aquatic systems (Shine, 1986a). The sand goannas (*Varanus gouldii* and *Varanus panoptes*) occur over a range of habitats, but frequently use dry flood plains and the edges of watercourses to forage for food. The proportion of prey from aquatic habitats that is eaten by *V. panoptes* is high, up to 30% by weight, but negligible in *V. gouldii* (Shine, 1986a).

Six species of turtle are found in the freshwater reaches of the rivers, creeks and billabongs in the Region. The Pig-nosed Turtle, although common where it occurs in both Australia and Papua New Guinea, has a fairly limited distribution in the Region and, hence, the South Alligator River in Kakadu represents a significant refuge (Press et al., 1995). *Chelodina burrungandjii* and *Elseya latisternum* are found in pools on the sandstone plateau, while *Elseya dentata* inhabits sandy or rocky stretches between the escarpment and floodplains. (Press et al., 1995). The characteristic floodplain turtle is the Northern Long-necked Turtle (*Chelodina rugosa*) which is carnivorous and during the Dry season survives by burying itself in the mud and aestivating.

The Arafura File Snake (*Achrochordus arafurae*) is mainly restricted to the larger billabongs in the Dry season with many more in lower mainstream billabongs than in the upper reaches of creeks (Shine, 1986b). In the Wet

season most are found in shallow, inundated grasslands (Shine, 1986a). They are a popular food item for Aboriginal people in the Region (Shine, 1986b). The Little File Snake inhabits estuarine habitats and feeds on crabs and small fish. Other species of snake that occur on the floodplains include the Water Python (*Liasis fuscus*) and the King Brown Snake (*Pseudechis australis*). The Water Python has been recorded at the extraordinary high density of 714 km<sup>2</sup> on the nearby Adelaide River floodplain (Madsen and Shine, 1996). As water levels drop with the onset of the Dry season a number of species, including the Olive Python (*Liasis olivaceus*) and the Northern Death Adder (*Acanthophis praelongus*) move onto the drying floodplain. The Keelback or Freshwater Snake (*Tropidonophus mairii*) is found in freshwater habitats, whilst several species of colubrid snakes inhabit mangrove areas where they feed on crustaceans and fish. Three species of sea-snakes have been recorded in the estuarine and tidal reaches of the rivers – Hardwick's Sea-snake (*Lapemis hardwickii*), Darwin Sea-snake (*Hydrelaps darwiniensis*) and Stoke's Sea-snake (*Astrotia stokesii*) (Press et al., 1995).

The rate of endemism within the area is high. Sadlier (1990) found 74 reptile species in the Magela Creek region, with 13% appearing to be endemic to the wider sandstone plateau.

### Waterbirds

The coastal floodplains and the alluvial floodplains of the Region are of immense importance for waterbirds (Morton et al., 1991). Of the 20 families of waterbirds accepted under the Ramsar definition and included in the Asia-Pacific Migratory Waterbird Strategy (2001–2005), 16 are found in the Region (Table 8). These families comprise 99 species of waterbirds, of which 52 are shorebirds (or waders) and 32 migratory (Morton et al., 1990; Chatto, 2003).

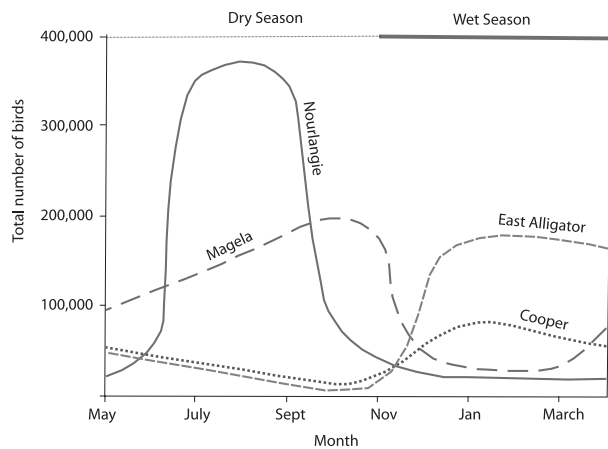
The importance of the Region to waterbirds has been extensively documented over many years. The wetlands support many species of national and international significance, including those protected under the Japan Australian Migratory Bird Agreement (JAMBA) and the China Australia Migratory Bird Agreement (CAMBA). The flood plains in particular provide important refuge areas critical to the conservation of waterbirds throughout northern Australia (Morton et al., 1991). During the Dry season months of August–October the floodplains are used intensively by up to 2 million waterbirds, including large concentrations of geese and ducks (Morton et al., 1991; Bayliss and Yeomans, 1990), such as the Magpie Goose (*Anseranas semipalmata*), the Wandering Whistling Duck (*Dendrocygna arcuata*) and Plumed Whistling Duck (*Dendrocygna eytoni*). The importance of the mosaic of contiguous wetlands across the river

**Table 8.** Waterbirds families listed in the Asia-Pacific Migratory Waterbird Strategy 2001–2005 and found in the Kakadu Region.

Taxonomic Family	Common Name	Number of species
Podicipedidae	Grebes	2
Phalacrocoracidae and Anhingidae	Cormorants and Darter	5
Pelecanidae	Pelicans	1
Ardeidae	Herons, Egrets and Bitterns	12
Ciconiidae	Storks	1
Threskiornithidae	Ibises and Spoonbills	5
Anatidae	Swans, Geese and Ducks	12
Gruidae	Cranes	2
Rallidae	Rails, Gallinules and Coots	7
Jacaniidae	Jacanas	1
Haematopodidae	Oystercatchers	2
Recurvirostridae	Stilts and Avocet	2
Glareolidae	Pratincoles	2
Chradriidae	Plovers	11
Scolopacidae	Sandpipers	22
Laridae	Gulls, Terns and Skimmers	12

systems of Kakadu National Park for waterbirds has been recognised in the listing of the park under the Ramsar Wetlands Convention. The high diversity and abundance of waterbirds species are also a contributing factor to the listing of Kakadu National Park as a World Heritage area.

Within the Kakadu Region numerous roosts of shorebirds, containing 2,000 or more birds, are spread along the coastline with almost 9,000 individuals recorded at Finke Bay in a survey in September 1993 (Chatto, 2003). Ground surveys have also been used with around 12,500 individuals being recorded in late April 1992 and late March 1992, along the coast between the South Alligator River and Minimini Creek. The more numerous species included Whimbrel (*Numenius phaeopus*), Eastern Curlew (*Numenius madagascariensis*), Common Greenshank (*Tringa nebularia*) and Black-tailed Godwit (*Limosa limosa*). The mangroves fringing the river banks provide suitable habitat for nesting colonial waterbirds with large multi-species colonies of Intermediate Egret (*Egretta intermedia*), Cattle Egret (*Ardea ibis*), Great Egret (*Ardea alba*), Little Egret (*Egretta garzetta*), Pied Heron (*Ardea picata*), Little Pied Cormorant (*Phalacrocorax melanoleucos*), Little Black Cormorant (*Phalacrocorax sulcirostris*) and Australian White Ibis (*Threskiornis molucca*) being recorded between 1990 and 1999 (Chatto, 2000). In all 18 species of waterbirds have been recorded in the mangroves and 27 on the inter-tidal flats. Waterbird usage of the flood plains varies seasonally with



**Figure 7.** Seasonal use by waterbirds of four floodplains (Nourlangie, Magela and Cooper Creeks and East Alligator River) in the Kakadu Region, as determined by aerial surveys (from Morton et al., 1984).

some species moving between the floodplains as habitat conditions change in response to rainfall and flooding and become more or less suitable for breeding, roosting and/or feeding (Morton et al., 1984). Waterbird usage of four floodplains in the early 1980s is shown in Figure 7.

The diets of aquatic herbivorous species, such as the Magpie Goose, Wandering Whistling Duck, Plumed Whistling Duck, and the Green Pygmy Goose (*Nettion pulchellus*) are linked to the phenological state of the floodplain plants many which flower and seed towards the end of the Wet season (Morton et al., 1990a, b; Finlayson et al., 1990). As the water recedes during the Dry season, a number of waterfowl species from southern Australia, such as Hardhead (*Aythya australis*), Grey Teal (*Anas gracilis*), Pink-eared Duck (*Malacorhynchus membranaceus*) arrive. The Dry season grasslands host migratory species such as the Little Curlew (*Numenius minutus*) (Garnett and Minton, 1985; Bamford, 1988a, 1990; Morton et al., 1991; Schulz, 1989). The Little Curlew, a species that breeds in Siberia and over-winters in Australia, arrive in the Region in the latter part of September; they build up in numbers until the onset of the Wet season, at which time they move to the sub-coastal floodplains some distance to the east and west of the Region (Bamford, 1990). Morton et al. (1991) estimated approximately 300,000 Little Curlew staging through the Region during October in the early 1980s; Bamford (1990) estimated 50,000 were present in the late dry seasons of 1987–1989. Other migratory shorebirds occurring in large numbers during the migratory periods and using the freshwater wetlands of the Region as well as neighbourhood floodplains include the Sharp-tailed Sandpiper (*Calidris acuminata*) and Marsh Sandpiper (*Tringa stagnatilis*), both species, as with the Little Curlew, being present in numbers that make these wetlands

internationally important (i.e. contain more than the 1% of the population in the East Asian-Australasian Flyway; Chatto, 2003).

Many other bird species that are not regarded as waterbirds, as described above, depend on wetlands in the Region for at least part of their life cycle (Table 9). Whilst the Region is recognised as providing important habitats for these species their ecology and population levels have not on the whole been investigated. The number of wetland-dependent bird species present in the habitat categories used in Table 9 are: coastal habitats 16; mangroves 67; monsoon forests 99; and floodplain and riparian areas 137. The riparian habitats in particular support many wetland-dependent species, such as Kingfishers and the White-breasted Sea-eagle, and small passeriformes, such as Honeyeaters and Flycatchers, with about half of them being endemic to northern Australia (Morton and Brennan, 1991).

### Mammals

Many mammals may be considered wetland-dependent in the sense that they access the water, although very few species spend their entire life cycle in the wetlands. A notable exception is the Dugong (*Sirenia artiodactyla*). A number of mammals are known to make some use of the floodplain environment in the Northern Territory, including 2 species of rodents, 2 species of dasyurids (carnivorous marsupials), 3 macropods, a number of insectivorous bats, 2 species of flying foxes, and the dingo (Cowie et al., 2000a). The Dusky Rat (*Rattus colletti*) seems to be a characteristic species that shelters in cracks in the floodplain soils during the Dry season, feeds on seeds, and stems and corms of sedges and grasses, and reaches high densities (around 150 ha<sup>-1</sup> being recorded on a nearby floodplain; Madsen and Shine, 1996). In the Wet season they move to adjacent higher ground from which it recolonises the floodplain as they dry. The False Water Rat (*Xeromys myoides*) is seemingly not as common as the Dusky Rat and may in fact be vulnerable. The fringing vegetation, in particular the *Melaleuca* trees, provide roosting sites for colonies of flying foxes (*Pteropus scapulatus* and *Pteropus alecto*) and when flowering are a source of nectar which also attracts the Northern Blossom Bat (*Macroglossus minimus*).

Introduced mammals that have invaded or make extensive use of the wetlands include the Asian water buffalo (*Bubalus bubalis*), European domestic pig (*Sus scrofa*), cattle (*Bos taurus*) and horses (*Equus caballus*). All are considered pest species with the water buffalo having overgrazed and degraded the wetlands and except for a small domesticated herd have been removed from the Park (Skeat et al., 1996).

**Table 9.** Other wetland-dependent birds (i.e. those not classed as waterbirds) present in the Kakadu Region.

Family group	Coastal wetland	Mangrove	Moonsoon forest	Floodplain and Riparian areas
Mound-builders		1	1	
Quails				3
Kites-Hawks-Eagles	5	7	10	15
Falcons			1	6
Rails-Crakes-Swamphens-Coots		3	1	5
Bustards				1
Pigeons-Doves		3	6	4
Cockatoos	1	2	4	5
Lorikeets-Parrots		1	3	4
Cuckoos-Koels-Coucals		3	6	8
Owls			3	3
Barn Owls				2
Frogmouth			1	1
Nightjars		1	1	2
Owlet-Nightjars			1	1
Swifts	2	2	2	2
Kingfishers	2	5	5	6
Bee-eaters	1	1	1	1
Rollers	1	1	1	1
Pittas		1	1	
Australian treecreepers				1
Fairy-wrens			1	1
Australian warblers		2	4	4
Honeyeaters-Chats		8	13	15
Robins		2	2	3
Babblers			1	1
Sitellas				1
Whistlers-Shrike-thrushes		5	4	4
Monarchs-Fantails-Drongos and Magpie Larks		9	9	9
Cuckoo-shrikes		4	5	5
Orioles and Figbirds		2	3	3
Woodswallows and Butcherbirds	1	2	3	5
Crows	1	1	1	1
Bowebirds			1	1
Larks				1
Pipits and Wagtails	1			2
Weavers-Waxbills and allies			3	9
Flowerpeckers	1	1	1	1

## Threats

A number of general analyses and reviews over the past few decades have identified the threats and management

issues faced by floodplain wetlands in northern Australia (Storrs and Finlayson, 1997; Finlayson et al., 2005). Many of these affect the Kakadu Region, although the relative importance of each varies across the flood plains.

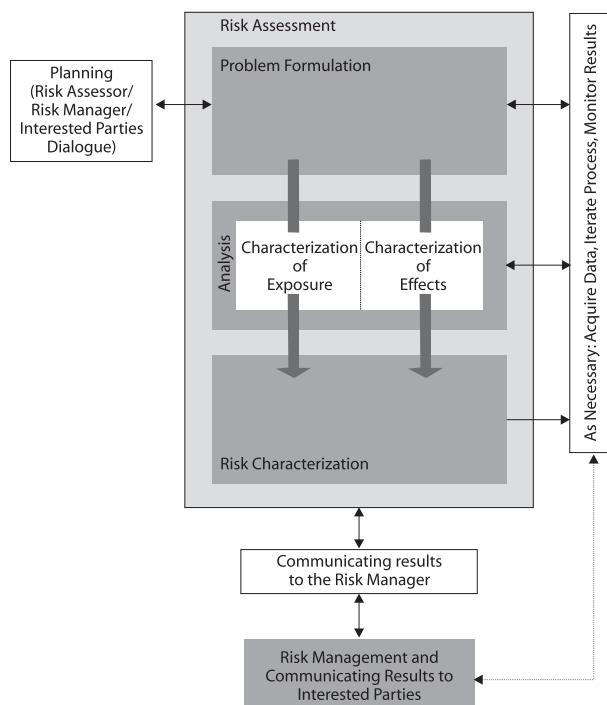
As elsewhere in northern Australia these issues have been assessed in site-based analyses within the Region and some comprehensive databases now exist (e.g. management of specific invasive species – Cook et al., 1996, Rea and Storrs, 1999 - and uranium mining – Humphrey et al., 1999, Gardner et al., 2002). Other issues are being assessed, but not necessarily in a coherent manner (e.g. coastal and climate change – Eliot et al., 1999). The likely impacts of global climate change are perhaps the most insidious and least understood by local managers (Bayliss et al., 1997). It is anticipated that climate change will not only affect the biological, chemical and physical features of wetlands, but will also interact strongly with other existing or emerging pressures on wetlands with synergistic, antagonistic or cumulative effects.

Information on many threats is increasingly being collected through the adoption of structured risk assessment procedures, such as that shown in Figure 8 (Finlayson and van Dam, 2004). For many of the main pest species the extent of their invasion of the wetlands has been assessed to some extent, although often incompletely. In many instances the biology of the species may also be known or is being studied; however, vital information on the ecological changes wrought by these species is often confined to a few isolated studies, if any, and/or anecdotal evidence. Further information is becoming available through risk assessments for *Mimosa pigra* (Walden et al., 2004), cane toads (*Bufo marinus*; van Dam et al., 2002a), the herbicide te-

buthiuron (van Dam et al., 2004), uranium mining (van Dam et al., 2002b) and climate change (Bayliss et al., 1997; Eliot et al., 1999). It is evident that information collation and analysis is not only underway, but is ongoing; the challenge is to translate this information into practical advice for managers and for managers to heed the warnings.

The complexity of managing wetlands within the Kakadu Region is illustrated by two examples raised by Finlayson (2005). The first considers changes in burning patterns on the floodplains. Recent investigations within Kakadu National Park have been trialing the use of fire to establish floodplain vegetation mosaics more suited for access by traditional Aboriginals for hunting and food collection. In this instance access had been restricted by an overabundance of the native grass *Hymenachne acutigluma* that had spread since the removal of buffalo from the plains in the mid-1980s. Thus, we have a scenario where the removal of a feral animal has been accompanied by the expansion of a native plant that restricted Aboriginal access to traditional food resources on the floodplains. Importantly, these investigations are being led by local people with assistance from park managers and researchers (P. Christopherson and P. Bayliss personal communication). The second example covers the complex biotic inter-relationships that occur on the floodplains, such as those between the large populations of magpie geese and the vegetation resources that they require for feeding and nesting. Finlayson (2005) speculated that the number of geese could affect the future extent of at least some of these plant species either through direct consumption or when nesting by damaging the stems with subsequent physiological effects and changes in growth conditions.

On the whole there has been little investigation of the interactions between the ecological components of the floodplain wetlands; some exceptions occur, but such investigations do not seem to be considered *de rigeur* for management planning or indeed for guiding responses to the many threats faced by the wetlands. The recent focus on risk assessments has gone somewhat towards providing information that can be more readily used for management purposes. There is however, an evident gap between collecting information on the biodiversity of the wetlands and providing science-based guidance for management purposes, or for this guidance to be accepted and used. The scenario shown through the assessment of the likely impact of climate change and sea level rise (Bayliss et al., 1997; Eliot et al., 1999) illustrates this disjuncture. Climate change and sea level rise is projected to result in the replacement of many freshwater wetlands with saline wetlands and with consequent displacement or loss of the freshwater species diversity, and to exacerbate the pressure from existing threats and pressures. Yet, management steps have not been agreed, pos-



**Figure 8.** Generalised framework for ecological risk assessment (modified from US EPA, 1998).

sibly due to limited awareness or understanding of the issues, or even resignation that adaptation rather than mitigation is a better response. At the same time full advantage has not been undertaken of monitoring opportunities, in this instance the existence of transects established in the mangroves along the East Alligator River some 20 years ago as well as new technologies using GIS and remotely sensed data, as shown by the mangrove change detection undertaken along the West Alligator River (Lucas et al., 2002). Making better use of such opportunities is a challenge for researchers and managers alike.

## Conclusions

The species diversity of the wetlands of the Kakadu Region is diverse and profuse. Many taxa have been identified and species distributions and seasonal and annual variations investigated. The information base though is incomplete and uneven. Much data have been collected in specific locations with few region-wide investigations and with a few notable exceptions, e.g. Russell Smith et al. (1997), based mainly on surveys undertaken by contemporary scientific means with limited input from the local aboriginal community. The latter is changing and increasingly local people are participating in joint activities or initiating their own analyses in relation to changes due to invasive species and fire management. Obtaining region-wide information is being facilitated through GIS and remote sensing (e.g. Lucas et al., 2002; Lowry and Finlayson, 2004; Lowry and Knox, 2006) although continuing on-ground data collection may be difficult and expensive to achieve, especially given the changing nature of the wetlands within and between years. Further, in recent decades the wetlands have changed in response to deliberate management actions – those addressing invasive species being better known. The outcomes of these management actions have been complex with the removal of large numbers of feral buffalo having been widely supported, but with less understanding of the likely consequences. It may or may not have been possible at the time to project a scenario where the native grass *Hymenachne acutigluma* spread to dominate large parts of the floodplains.

The advent of new technologies provides an opportunity for more effective inventory, assessment and monitoring of the wetland environments; this needs to be explored and suitable investments made. It may also be worthwhile taking a step back and more thoroughly analyzing the information bases available and complementing the mainly qualitative risk assessments with more quantitative and landscape-wide analyses based on statistical probabilities and model scenarios. At the same time if a clear picture of the biodiversity value of the Kakadu

Region is sought it will be necessary to revisit past surveys etc. and ascertain how much has changed – it is not fully known how well the information referred to in this paper reflects the current biodiversity status. It may also be useful to address the priorities for further biodiversity survey – should there be more effort seeking information on endemic or vulnerable species, or are more general surveys required first? Is there sufficient baseline or reference data to assess the effect of existing let alone further invasive species? Does this data correlate with and/or incorporate appropriate local information?

The wetland landscape of the Kakadu Region has received wide recognition and the available data supports this. It is as widely recognized that these wetlands have undergone major change and face major pressures now and in the near-future. Addressing these pressures is possible – the tools are available and more recent management approaches have sought to involve local people and increase transparency in decision making about management actions as well as research priorities. The next steps in ensuring the maintenance of the biodiversity values of the wetlands of the Kakadu Region are complex, especially if they are subject to increasing pressure from both existing and emerging drivers of change. It is further anticipated that more sophisticated ecological understanding of the processes that support the food webs in the wetlands (Douglas et al., 2005) will assist in future management.

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