POPULATION ECOLOGY OF *CROCODYLUS POROSUS* (SCHNEIDER 1801) IN THE KIMBERLEY REGION OF WESTERN AUSTRALIA

A thesis submitted for the degree of Doctor of Philosophy at the University of Queensland in May 2004

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STATEMENT OF ORIGINALITY

I declare that this thesis is my original work, except where duly acknowledged, and has not been submitted, in whole or in part, for any other degree or diploma at any other university.

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May 2004

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LIST OF PUBLICATIONS AND PRESENTATIONS

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Kay W. R., Fitzsimmons N. N., Buchan J. C. and Grigg G. C. Evidence for site fidelity and a recent genetic bottleneck in *Crocodylus porosus* populations from the Kimberley region in Western Australia. *Conservation Genetics.* (under revision).

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Additional publications

The following publications are relevant to the thesis but do not form part of it:

Moravec F., Kay W. R. and Hobbs R. P. (2004). *Micropleura australiensis* n. sp. (Nematoda: Micropleuridae) from the body cavity of *Crocodylus johnsoni* in Western Australia. *Journal of Parasitology* **90**, 322-326.

Kamata, R., Kay W. R., Shibata Y., Edmonds J. S. and Morita M. (2002). DDT metabolite and toxaphene residues in wildlife (fish and crocodiles) following high applications to an isolated farming area in tropical NW Australia: possible endocrine disrupting effects (ABSTRACT).' *Fifth International Symposium on Environmental Endocrine Disrupters*. International Conference Centre: Hiroshima, Japan, 26-28 November 2002.

FitzSimmons, N. N., Buchan, J. C., Read, M. A., Miller, J. D., Kay, W. R, Moritz, C., Limpus, C. J., Blair, D. and Grigg, G. C. (2004). Population genetics of Australia's crocodiles: a comparison between *Crocodylus johnstoni* and *C. porosus* (ABSTRACT). p. 65. *In*: Crocodiles. Proceedings of the 17th Working Meeting of the Crocodile Specialist Group, IUCN – The World Conservation Union, Gland, Switzerland and Cambridge, UK.

Shibata Y., *et al.* Persistent organochlorine compounds in Ord River crocodiles. (in preparation).

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Kay, W. R. (2001). 'Population ecology of estuarine crocodiles (*Crocodylus porosus*) in the Kimberley region of Western Australia.' *Guest speaker* at SEEKS monthly meeting. Kimberley Development Commission: Kununurra, 18 April 2001.

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ABSTRACT

Crocodylus porosus is the most widely distributed crocodilian species and suffered widespread population decline during the 20th century, principally due to commercial hunting for their hides, but also from habitat destruction and persecution. An estimated 270,000 to 330,000 animals were killed in Australia before the species was protected in the early 1970s. Populations of *C. porosus* in Western Australia are poorly studied and the number of animals taken during the hunting era is unknown. However, by 1970, hunting was no longer considered to be commercially viable. Over the last two decades, adding commercial value to crocodiles through sustainable use has been an integral part of the management strategy throughout Australia. Despite this, demographic parameters remain unquantified for most life-history stages. This study attempts to provide quantified demographic information for some populations of *C. porosus* in Western Australia.

Patterns of movement are a fundamental component to the dynamics of animal populations. VHF radio tags were attached to 16 estuarine crocodiles, which were tracked between October 2001 and May 2003. Male (n = 12) and female (n = 4) crocodiles exhibited distinctly different patterns of movement. Females occupied a small core linear range (1.3 ± 0.9 km) on the main river channel during the dry season and moved distances of up to 62 km to nesting habitat during the wet season, returning to the same core area the following dry season. Males moved considerable distances along the Ord River throughout the year. The largest range recorded was 87 km for a 2.5 m juvenile male, which had not stabilized. However, male ranges did not appear to be related to body size, with the largest two ranges recorded for the smallest (2.5 m) and largest (4.3 m) males tagged. Rates of male movement did not differ significantly between three size classes of males but there were significant seasonal differences, with the highest mean rates of movement occurring during the summer wet season (4.0 ± 5.4 km/d). The highest rate of sustained movement was 9.8 km/d for a

translocated 2.6 m juvenile male, which travelled 118 km in 12 days to return to the area of its capture. Neither males nor females showed exclusive habitat preferences for any of four broad riverine habitats identified on the Ord River. Males had substantial range overlaps with no obvious spatial partitioning, suggesting territoriality is not an important behavioural characteristic of free-ranging male crocodiles along the Ord River.

Rates of migration were also examined indirectly using genetic data, which integrates patterns of movement at the population level over many generations. One hundred and twenty three tissue samples were collected from three river systems between April 2001 and September 2002. Levels of genetic diversity and structure were quantified at nine microsatellite loci. Genetic data indicated that *C. porosus* shows strong site fidelity. However, indirect estimates of migration from fixation indices suggest gene flow is sufficient to maintain genetic diversity and population substructure but not so low as to cause inbreeding. Genetic diversity was similar in all three populations examined with allelic richness ranging from 4.6 to 5.0 alleles per locus and mean observed heterozygosity ranging from 0.63 to 0.74. Inbreeding coefficients indicated there was only moderate differentiation among the populations (F_{ST} = 0.08, R_{ST} = 0.06) but differences in allele frequencies were highly significant. Assignment tests designated 80% of individuals to their population of origin and identified only five individuals (4%) as first generation migrants. Populations that experience a severe and rapid reduction in size, such as occurred with *C. porosus* following the Second World War, are susceptible to losing a significant component of their genetic variation. There was compelling evidence for a recent genetic bottleneck in the three populations sampled.

Survivorship in *C. porosus* in unknown for most life-history stages so a mark-recapture study was implemented to investigate the dynamics of the *C. porosus* population in the King River. A total of 162 animals were marked between June 2001 and July 2002 of which 75 marked animals were recaptured on 123 occasions. The size of the hatchling

population (age < 1 year old) was estimated to be 91 ± 2 (SE) in 2001, which was effectively an estimate of successful recruitment for the King River during that year. The size of the non-hatchling population (age > 1 year old) was estimated to be 69 ± 13 but the precision of the estimate was low and should be treated cautiously. Survival of the 2001 cohort of hatchlings was high (> 95%) between June and December and did not vary between the sexes. Hatchlings grew rapidly from June 2001 to July 2002, doubling in length and showing a ten-fold increase in body mass. There were no significant differences in growth rates between females and males during the first 18 months of life. Crocodiles showed a significant behavioural response to capture, with capture probabilities decreasing over time for two groups classified by age. Furthermore, differences in capture probabilities between age groups were significant on all occasions. This has important implications for monitoring crocodile populations, particularly if sightability is influenced by human disturbance.

This study has provided some insights into important ecological processes operating within Western Australian populations of *C. porosus*, but the number of populations examined and period of study were small for such a long-lived animal. More work is needed to determine whether the patterns that have emerged are typical throughout the species' range and longer term studies will be required to quantify vital statistics for most life stages.

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A: the number of alleles per locus.

AIC: Akaike's information criterion (Akaike 1973).

AMAE: animal movement analyst extension (see Hooge 2002).

BM: body mass.

CALM: Department of Conservation and Land Management, Western Australia.

CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora.

CJS: Cormack-Jolly-Seber method for analysis of mark-recapture data (Cormack 1964; Jolly 1965; Seber 1965).

CV: coefficient of variation.

DNA: deoxyribonucleic acid.

ESRI: Environmental Systems Research Institute, Redlands, California.

GIS: geographic information system.

GPS: global positioning system.

H_E: expected heterozygosity - the heterozygosity expected for a random mating population with the given allele frequencies according to the Hardy-Weinberg equilibrium (Frankham *et al.* 2002).

H_O: observed heterozygosity - the actual level of heterozygosity measured in a population (Frankham *et al.* 2002).

IAM: infinite alleles model of mutation (Kimura and Crow 1964).

IUCN: The World Conservation Union (formerly the International Union for Conservation of Nature).

K-wires: Kirschner wires.

LOA: longevity of attachment in days.

LRT: likelihood ratio test.

MCP: minimum convex polygon.

MLE: maximum likelihood estimate.

MSLR: mid-stream linear range in kilometres.

MTBS: macro-tidal brackish-saline reach.

mtDNA: mitochondrial DNA.

MTF: macro-tidal freshwater reach.

NA: not applicable.

N_e: effective population size.

N_m: number of migrants per generation.

NT: Northern Territory.

NTF: non-tidal freshwater reach.

OTC: oxytetracycline hydrochloride.

PCR: polymerase chain reaction.

PIT: passive integrated transponder.

PWCNT: Parks and Wildlife Commission of the Northern Territory.

RCA: river channel area in hectares.

ROM: rate of movement in kilometres per day.

$\bar{r}$: observed rate of increase (see McCallum 2000).

R_s: allelic richness corrected for unequal sample sizes using the rarefaction method of El Mousadik and Petit (1996).

SD: standard deviation.

SE: standard error.

SEEKS: Save Endangered East Kimberley Species, Kununurra, Western Australia.

SMM: stepwise mutation model (Kimura and Ohta 1978).

TF: tidal freshwater reach.

TL: total length.

TPM: two-phase model of mutation (Di Rienzo *et al.* 1994).

VHF: very high frequency.

WA: Western Australia

WMI: Wildlife Management International Pty Ltd, Sanderson, Northern Territory.

1. INTRODUCTION AND GENERAL METHODS

1.1 Historical perspectives and regional focus

There has been a strong regional focus to field research on estuarine crocodiles (*Crocodylus porosus*) in Australia. Most studies have been undertaken in the Northern Territory, which is a reflection of both the legacy of Sydney University's Crocodile Research Programme (e.g. see Messel 1977; Grigg 1982) and the efforts of the Conservation Commission of the Northern Territory to address specific management issues and to support the establishment of an industry based on the sustainable use of the species (e.g. see Webb *et al.* 1987; Webb and Manolis 1993). Despite this large research effort, information is lacking on key demographic parameters that are fundamental to investigating the population dynamics of the species. Additionally, there may be considerable geographic variation in these parameters, as is the case for the smaller endemic freshwater species, *Crocodylus johnstoni*, (see Tucker 1997a) but is unknown as yet for its larger relative.

1.1.1 *Western Australia*

In contrast to the substantial scientific information available for the Northern Territory populations, very little is known about the biology of *C. porosus* in the Kimberley region of Western Australia. Wild stocks of *C. porosus* were rapidly depleted in all of northern Australia between 1945 and 1970 due to unregulated hunting for their hides. An estimated 270,000 to 330,000 animals were killed during this period, most from the Northern Territory (Webb *et al.* 1984a). The number of animals taken in Western Australia is unknown but, by 1970, only one commercial hunter was still working in the Kimberley region and the species was considered to be on the verge of extinction (Bustard 1970). The state government acted quickly in response to the recommendations of Bustard (1970) and in 1970 Western Australia became the first state in Australia to protect *C. porosus*. However, subsequent information on the Kimberley population is limited to abundance and distribution data collected by Messel and Burbidge during the 1970s and 1980s (Messel *et al.* 1977; Burbidge and Messel 1979; Messel *et al.* 1987) and more recent survey work commissioned by the Department of Conservation and Land Management (CALM) (e.g. WMI 2003).

The population recovered strongly in the Northern Territory following protection (PWCNT 2000) but the situation for Western Australia is less clear. Surveys by Messel *et al.* (1987) suggest a similar pattern of recovery to the Northern Territory between 1975 and 1986 (Fig. 1.1). Notably, numbers increased in some systems but declined in others. More recent surveys in Cambridge Gulf indicated stable or declining trends between 1986 and 2000 with recent fluctuations (WMI 2003). The total non-hatchling *C. porosus* population in the Kimberley was estimated to be about 2,000 in 1978 and 2,500 in 1986 (Messel *et al.* 1987). Assuming that the observed rate of increase ($\bar{r}$: see McCallum 2000) in the Kimberley population was similar to that in the Northern Territory ($\bar{r} = 6.5\%$: Webb and Manolis 1993), the total Kimberley population in 2000 (30 years after protection) would be about 6,200 to 8,400. This is probably a very generous estimate. The habitat of *C. porosus* in the Kimberley is markedly different from much of the Northern Territory (Burbidge 1987). The Kimberley is largely composed of ancient, deeply-faulted sandstone escarpments and plateaus with access up many rivers blocked to crocodiles by waterfalls and their associated gorges (Burbidge 1987). There are limited floodplains and associated freshwater swamp complexes, therefore breeding habitat is considered scarce (Burbidge 1987). Paucity of breeding habitat is corroborated by nest surveys which have found very low densities of nest over much of the Kimberley (G. Webb Pty Ltd 1989). Consequently, the carrying capacity of the Kimberley river systems and the Kimberley as a whole is considered to be much less than that of the Northern Territory (Burbidge 1987). A more plausible estimate for the size of the Kimberley

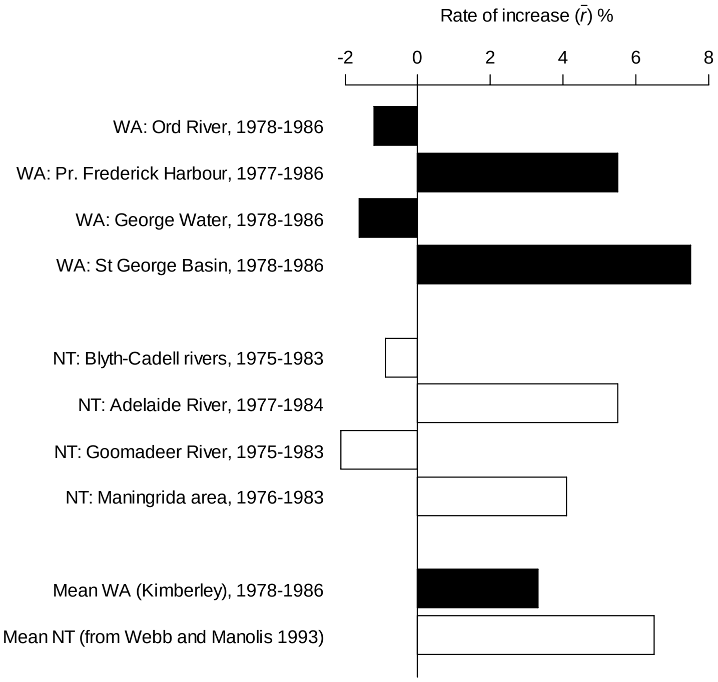


Fig. 1.1. Observed rates of increase ($\bar{r}$) in selected *Crocodylus porosus* populations between 1975 and 1986. Data are from Messel *et al.* (1987) except the mean estimate for the Northern Territory, which comes from Webb and Manolis (1993).

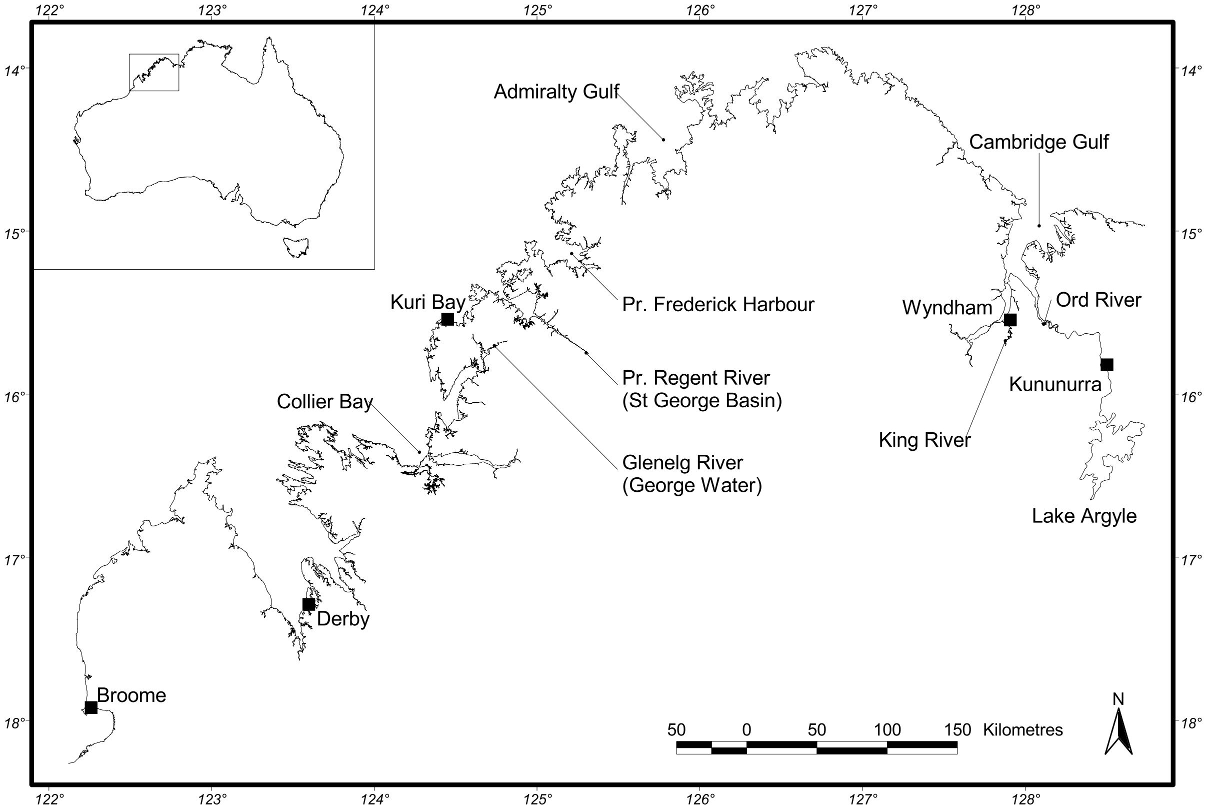


Fig. 1.2. The Kimberley region in Western Australia.

population in the year 2000 would probably be 4,000 to 4,200 based on the mean $\bar{r}$ (3.3%) calculated from data in Messel *et al.* (1987).

1.2 Crocodile movements

Patterns of animal movement must be known in order to understand basic population processes and may themselves be important demographic parameters (Hutton 1989; McCallum 2000). Dispersal is seldom measured in population studies and, in most cases, it is assumed that there is zero net migration (Krebs 1985). This assumption is highly questionable because dispersal is an essential part of the life cycle for most organisms. It helps to prevent inbreeding by facilitating gene flow between local populations, sets limits on geographic distributions and affects community composition (Krebs 1985). Some populations sustain net emigration and export individuals while others are maintained only by net immigration (Pulliam 1996). Thus dispersal may be a critical parameter in population changes.

Despite the potential importance of movement, home range behaviour and dispersal to crocodilian life histories, these factors have received careful examination only in *Alligator mississippiensis* (Hutton 1989). The data for other species of crocodilian are either non-existent or very limited in scope. Most studies indicate that crocodiles move around little for most life-history stages (e.g. Joanen and McNease 1970; Webb *et al.* 1983a; Hutton 1989; Muñoz and Thorbjarnarson 2000). However, there a numerous reports of *C. porosus* undertaking large-scale ocean voyages over hundreds of kilometres (e.g. Allen 1974; Bustard and Choudhury 1980) and they have been shown to have osmoregulatory plasticity over a broad range of salinities (Taplin 1988). Tucker *et al.* (1997) found that pubescent male *C. johnstoni* were essentially nomadic and had much larger home ranges than other stages. This suggests that sex-biased dispersal may be an important characteristic of the reproductive biology of crocodilians (Tucker *et al.* 1998).

1.2.1 *Homing*

Homing behaviour is a phenomenon that has been reported for a number of crocodilian species (e.g. Chabreck 1965; Gorzula 1978; Webb *et al.* 1983b; Rodda 1984a), mostly in juveniles, but data for *C. porosus* are equivocal. Walsh (1993) found that < 50% of problem crocodiles that were translocated from Nhulunbuy in the Northern Territory returned to the original site of capture. The probability of recapture could not be related to distance and direction of release, nor size and sex of the released animal. The frequency of capture for individual crocodiles was also unrelated to these variables. The time between consecutive recaptures of the same crocodile was highly variable ranging from 10 days to > 3.7 years (mean = 289 ± 317 days, $n = 56$). The highest ratio of coastal return distance to time elapsed between captures was 3.9 km/d (mean = 0.2 km/d). The comparatively slow rate of return to the original site of capture would seem to suggest that the instinct to home is not strong for such a large and mobile animal that has the capability to move long distances (see Allen 1974; Bustard and Choudhury 1980). An alternative hypothesis to explain the homing instinct is that dominant animals with established territories displace the translocated animals, which eventually return to the original site of capture (see Messel and Vorlicek 1986). However, Walsh (1993) found that only 7% of recaptured animals had injuries that could be attributed to other crocodiles, which would suggest that territorial aggression was not a significant factor influencing homing. This assumes that non-recaptured crocodiles were not killed by conspecifics and that trap shyness was not a significant factor. The mechanism may be density-dependent and become more significant as crocodile populations recover from exploitation.

1.2.2 *Radio-telemetry*

All information on movements of *C. porosus* have so far been inferred from mark-recapture studies (e.g. Webb and Messel 1978b; Walsh and Whitehead 1993). Radio-telemetry has been used successfully to track a number of crocodilian species (e.g. Joanen and McNease 1970; Rodda 1984b; Magnusson and Lima 1991; Hocutt *et al.* 1992; Muñoz and Thorbjarnarson 2000) but, surprisingly, there are no published radio-tracking studies for either species of crocodilian found in Australia. Early attempts to radio-track *C. porosus* were unsuccessful, perhaps due to the limitations of prototype equipment or attachment difficulties (see Webb and Messel 1978b; Yerbury 1980). Signal attenuation in brackish or salty water may also have been a contributing factor (Kenward 2001). While recapture studies have provided baseline information on the movements of *C. porosus*, telemetry is more suitable for clarifying theories about patterns of movement and advancing our understanding of dynamic activity budgets and seasonal patterns of habitat use by different life-history stages (Tucker *et al.* 1997)

1.3 Population genetics

Maintenance of genetic diversity should be a major objective for the conservation and management of species because genetic diversity represents evolutionary potential (Frankham *et al.* 2002). The World Conservation Union recognizes the need to conserve diversity at three levels: genetic diversity, species diversity and ecosystem diversity (Frankham 1995a). Large populations show greater adaptive evolutionary capabilities than small or fragmented populations because selection is less effective at removing deleterious alleles in small populations, which are also more likely to become fixed (Frankham *et al.* 2002). Consequently, the evolutionary potential of species with a small population size is compromised because they have less initial genetic diversity, and lose genetic diversity at a greater rate in each generation, than species with a large population size (Frankham *et al.* 2002). It is the effective size of a population (N_e), as opposed to census size, that determines the loss of genetic diversity and extent of inbreeding (Frankham *et al.* 2002).

1.3.1 *Choice of markers*

There has been rapid progress in the development and use of molecular markers over the last decade (Davies *et al.* 1999) with concomitant progress in the development of statistical tools for analysing molecular data (Luikart and England 1999). Consequently, there are a number of innovative molecular techniques available for studying not only phylogenetics but also wide-ranging questions in population ecology (Frankham 1995a; Neigel 1996; Luikart and England 1999).

Traditionally, mitochondrial DNA (mtDNA) has been the most commonly used genetic marker in population studies (Davies *et al.* 1999). This is because mutation rates vary in different regions of the mtDNA genome and areas can be selected to have high enough variation to distinguish divergence, but not so high as to create background noise (FitzSimmons *et al.* 2001). However, mtDNA is maternally inherited in vertebrates and therefore only provides information on female lineages within populations (FitzSimmons *et al.* 2001). Furthermore, the reduction in diversity associated with population bottlenecks is exacerbated for mitochondrial genes because they have only a quarter of the effective population size (N_e) of nuclear genes (Davies *et al.* 1999). Studies of allozymes in *A. mississippiensis* (Adams *et al.* 1980) and *Crocodylus niloticus* (Lawson *et al.* 1989) have revealed low levels of variation indicating that this approach may be of limited value in other crocodilian species as well (Glenn *et al.* 1998). Fortunately, markers are now available that assay nuclear DNA directly, such as microsatellites, introns, randomly amplified polymorphic DNA (RAPDs) and restriction fragment length polymorphisms (RFLPs) (Davies *et al.* 1999). These markers still reveal high levels of diversity when mtDNA and allozymes are relatively impoverished (Davies *et al.* 1999).

Microsatellite markers have been used in studies of *A. mississippiensis* (e.g. Glenn *et al.* 1998; Davis *et al.* 2000; Davis *et al.* 2001; Davis *et al.* 2002) and have been recently developed for a number of other crocodilian species including *C. porosus* and *C. johnstoni* (FitzSimmons *et al.* 2001). They are rapidly becoming the genetic markers of choice for addressing questions concerning genetic diversity and relatedness in wild and captive populations because they are highly polymorphic and amenable to automated analysis (Glenn *et al.* 1998).

1.3.2 *Assignment tests*

Microsatellite variation contains far more information about population history than is currently being used in most studies (Luikart and England 1999). One of the more exciting developments in recent years has been assignment tests, which are based on multilocus genetic data and use both individual genotypes and population level allele frequencies (Davies *et al.* 1999). They enable an individual to be assigned to a population of origin (Luikart and England 1999) and have their conceptual origins in forensic applications where, for example, the objective is to determine whether an animal trophy originates from a protected population rather than the legal source its owner may claim (Waser and Strobeck 1998). The trophy is genotyped at multiple loci and the expected frequency of the genotype in each putative source population is calculated. The genotype is then assigned to the population where its expected frequency is highest *i.e.* where it has the greatest probability of occurrence (Waser and Strobeck 1998).

One of the most promising applications of assignment tests is estimating dispersal rates (N_{m}) among wild populations directly via the identification of immigrant individuals (Luikart and England 1999). The direct estimate can then be compared with indirect methods such as estimating N_{m} from F_{ST} using the same genetic data (Luikart and England 1999). Moreover, Bayesian assignment tests have been shown to have sufficient power to identify not only immigrant individuals but their F_1 offspring as well. Additional approaches are being developed to detect sex-biased dispersal by comparing the distribution of relatedness among males and females within a population (Favre *et al.* 1997). This is of particular interest in crocodilian biology since sex-biased dispersal has been described for *A. mississippiensis* (Davis *et al.* 2000) and *C. johnstoni* (Tucker *et al.* 1998). The population genetic structure should reflect a pattern of male-mediated gene flow if there is significant male-biased dispersal (Davis *et al.* 2000).

1.3.3 *Bottlenecks*

When a population experiences a severe and rapid reduction in size, such as occurred with *C. porosus* in northern Australia prior to 1970, it is susceptible to losing a significant component of its genetic variation. This is known as a population bottleneck and has important implications for conservation and management of species. Identifying recently bottlenecked populations is important because bottlenecks can increase rates of inbreeding, loss of genetic variation and fixation of deleterious alleles, thereby reducing adaptive and evolutionary potential, which increases the risk of extinction (see Cornuet and Luikart 1996; Frankham and Ralls 1998; Luikart *et al.* 1998a; Luikart and Cornuet 1998; Saccheri *et al.* 1998; Frankham *et al.* 1999; Garza and Williamson 2001).

Micro- and minisatellite loci are probably the best markers currently available for detecting recent bottlenecks because of their generally high level of variability (Cornuet and Luikart 1996). Cornuet and Luikart (1996) developed two tests that use micro- and mini-satellites for detecting recent bottlenecks. When a population experiences a rapid reduction of its effective size, it generally develops a heterozygosity excess at selectively neutral loci (Cornuet and Luikart 1996). The tests compare the difference between the observed heterozygosity (H_O) and the heterozygosity expected (H_E) from the observed number of alleles. Populations exhibiting a significant heterozygosity excess are considered to have experienced a recent genetic bottleneck (Cornuet and Luikart 1996).

Only recent population declines are detectable because the heterozygosity excess only persists for a finite number of generations (~0.25 to 2.5 × $2N_e$; where N_e = the effective population size) before a new equilibrium is established. However, these tests can help identify which populations have suffered a severe reduction of N_e along with a reduction of census size, and therefore identify populations (or sub-populations) at high risk of extinction due to genetic factors in addition to risks due to demographic factors (Cornuet and Luikart 1996). The *M*-ratio test of Garza and Williamson (2001) is also relevant and tests for a loss of intermediate allelic states due to recent bottlenecks.

1.4 Demography

Crocodiles are *K*-selected organisms whose life history strategies are characterized by slow development, long life, and delayed and repeated reproduction where the risk of reproductive failure is minimized through repeated breeding rather than by maximizing reproductive output. Consequently, crocodiles have limited capacity to compensate for unregulated long-term harvests (Tucker 1995). Vital statistics (survivorship, fecundity, growth rates and age structure) must be quantified for the sound management of commercially exploited species (McCallum 2000). Harvesting practices that derive stock from the wild function as demographic sinks through the emigration of eggs, juveniles or adults from wild source populations (Tucker 1995). Unless demographic parameters are known, the cumulative impacts of harvesting will be difficult to predict.

Despite having been commercially exploited in Australia for nearly two decades, demographic parameters for *C. porosus* remain unquantified. Survivorship is unknown for most life history stages other than eggs (e.g. Webb *et al.* 1977; Magnusson 1982; Webb *et al.* 1983c). Mortality of hatchling crocodiles is generally reported as high during the first year of life but, where the method of estimation has been stated, it has failed to account for the probability of recapture.

1.5 Detailed aims and thesis structure

The specific aims of this study were:

- to document patterns of movement for *C. porosus* in selected rivers of the Kimberley region, Western Australia, using direct (radio-tracking) and indirect (genetic) methods.
- to test for evidence of recent bottlenecks in *C. porosus* populations in the Kimberley region as a result of past widespread hunting, and for evidence of consequent deleterious changes in genetic structure, using microsatellite markers.
- to examine past and present sizes of *C. porosus* populations in the Kimberley region, using genetic and mark-recapture methods.
- to quantify survival and growth rates for *C. porosus* in the King River using mark-recapture methods. However, given that the species has a generation time of between 12 and 15 years, survivorship could only be investigated for a cohort of hatchling crocodiles within the time frame of this project.

Following the revised University of Queensland guidelines for preparation of PhD theses (UQ Graduate School 2004), this thesis is written as a series of stand-alone papers for the main data chapters (Chapters 2 to 5) with a general introduction to the topics (Chapter 1) and a synopsis of the main findings at the end of the thesis (Chapter 6). This format inevitably dictates a certain amount of repetition, particularly when introducing topics and reviewing the results.

1.6 Study area

1.6.1 *Physical environment*

The Kimberley region in Western Australia encompasses an area of > 300,000 km^2 and has in excess of 10,000 km of coastline between Broome and the Northern Territory border (Fig. 1.2). The area contains 35 major river catchments (> 1000 km^2) and 13 minor catchments (< 1000 km^2). Fringing mangrove communities occur on tidal mud in the more sheltered bays and inlets of the coast. Mangrove species richness reaches a maximum for Western Australia in Cambridge Gulf (Fig. 1.3), with 15 species documented, which may occur in pure stands or form mixed associations (Thom *et al.* 1975; Beard 1990). The region has semi-diurnal tides with spring tidal amplitudes of up to eight metres in Cambridge Gulf and about 12 metres in Collier Bay. The riparian vegetation of freshwater reaches is dominated by *Eucalyptus camaldulensis*, *Melaleuca leucadendra* and *Pandanus aquaticus* (Beard 1990). The region is sparsely populated with most of its *ca* 34,000 residents living in the towns of Broome, Derby or Kununurra.

1.6.2 *Bioclimate*

The bioclimate is classified as Dry Hot Tropical and characterized by summer rainfall with a long dry season. More than 80% of rain falls between December and March and precipitation is insufficient to sustain plant growth for eight months of the year (Beard 1990). Rain results from monsoonal southward movements of moist tropical air and is normally received from tropical depressions and thunderstorms but infrequent tropical cyclones can bring widespread and extremely heavy rains (Gentilli 1972). The seasonal alternation of flood and drought is a highly predictable and dominant feature of the climate (McDonald and McAlpine 1991). The climate favours grassland vegetation so most of the region is covered by tropical savannas, which are utilized primarily for grazing cattle (Beard 1990) but there are 12,000 ha of irrigated farmland surrounding Kununurra. Mean daily maximum temperatures at Wyndham range from 31°C in June/July to 40°C in November with > 45 days per annum exceeding 40°C. Minima range from 17°C in June/July to 27°C in November. Mean relative humidity ranges from 32% in July to 68% in February and mean annual rainfall is about 700 mm at Wyndham and 1300 mm at Kuri Bay (Bureau of Meteorology 1996). Fires are a

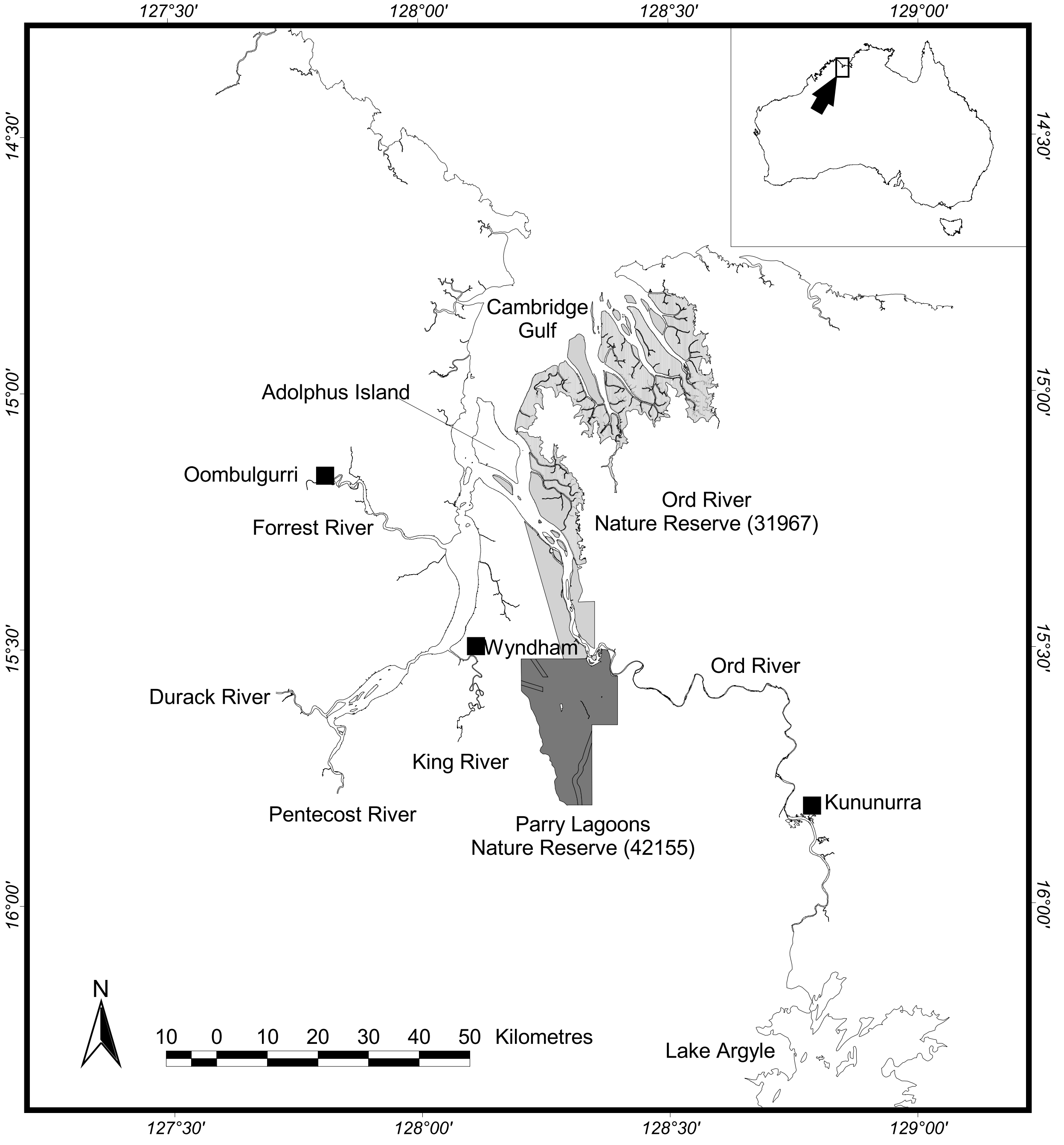


Fig. 1.3. The Cambridge Gulf region in Western Australia.

ubiquitous feature of the northern Australian savannas during the dry season (Haynes 1991) with as much as 50% to 70% of some regions burning every year (Dyer *et al.* 2001).

1.6.3 *Ord River*

The Ord River (Fig. 1.3) is one of the major rivers in Western Australia and has a catchment area of 50,000 km^2. The largest recorded instantaneous flow on the Ord River was approximately 30,800 cumecs in February 1956 (Ruprecht and Rodgers 1999). Since then, the construction of two dams to service an irrigation scheme has reduced the average annual river flow at the mouth from about 4,500 GL to 3,200 GL (Ruprecht and Rodgers 1999). Overflow and discharge from the dams has transformed the flow regime from seasonal to perennial and there has been a substantial reduction in the magnitude of floods. The suppression of large flood events has resulted in appreciable siltation within the lower Ord estuary where the cross-sectional area of the river has decreased by about 50% over the last 30 years (Wolanski *et al.* 2001) and there have been considerable changes to riparian vegetation in the freshwater reaches (Start and Handasyde 2002).

Most of the lower Ord estuary is gazetted as nature reserve (Fig. 1.3), but small areas in the east are within Carlton Hill pastoral lease or are Unallocated Crown Land. It is listed as a Wetland of International Importance under the Ramsar Convention because of its significance as waterbird and crocodile habitat and the extent, structural complexity and diversity of mangroves in the area. It is also listed as a wetland of national importance (Larmour *et al.* 2001). The Ord River Nature Reserve was declared primarily to protect *C. porosus* after the recommendations of Bustard (1970), who felt the area was ideal for a crocodile reserve because it contained excellent habitat and still held a number of crocodiles, which could repopulate the area if rigidly protected (Burbidge *et al.* 1991).

1.7 Legislative framework

C. porosus is declared as specially protected fauna under the Western Australian Wildlife Conservation Act 1950 and is also protected under the federal Environment Protection and Biodiversity Conservation Act 1999. It is not listed on the 1996 IUCN Red List and is classified as Lower Risk, Least Concern because numbers total in the tens of thousands and the population is considered secure in Australia and Papua New Guinea, despite being seriously depleted throughout most of its range (Ross 1998). Principal threats include illegal hunting and habitat destruction (Ross 1998). Australia is a signatory to CITES and *C. porosus* is listed under Appendix II for Australia, Papua New Guinea and Indonesia (with special conditions), and Appendix I for all other countries (Ross 1998). Appendix II enables regulated international commercial trade provided that trade will not be detrimental to the survival of the species in the wild. Species listed under Appendix II are not necessarily threatened with extinction but may become so unless trade is closely controlled (<www.cites.org>). Species listed under Appendix I are considered to be threatened with extinction and CITES generally prohibits commercial international trade in specimens of these species.

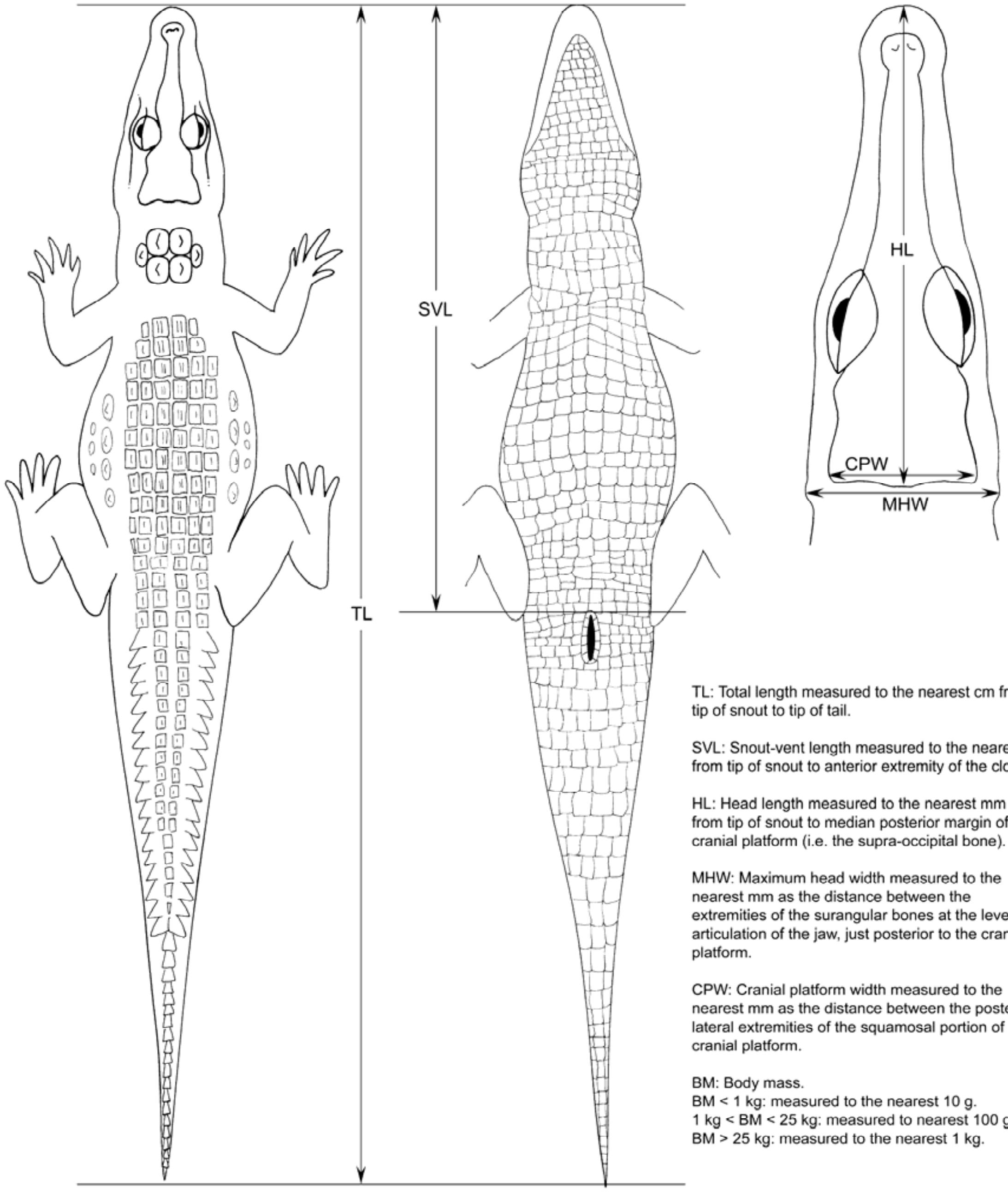
1.8 General field methods

1.8.1 *Crocodile capture*

Crocodiles were caught under permits SF003288 and SF003616 issued by the Department of Conservation and Land Management (CALM). All procedures were approved by the CALM Animal Ethics Committee (approval number: CAEC/15/2000) and the University of Queensland Animal Experimentation Ethics Committee (approval number: ZOO/ENT/350/00/CLM/PHD). Animals were mostly caught at night from a small (4.5 m) boat using a variety of size-dependent techniques that included hand-catching small crocodiles (< 1.2 m total length [TL]) and noosing animals between 1.2 and 2.2 m TL. Crocodiles > 2.2 m TL were caught using either the harpooning technique described by Webb and Messel (1977) or with baited cage traps (Walsh 1987). Once restrained, animals were sexed by visually inspecting the genitalia (Webb *et al.* 1984b) and a subset of morphometric measurements described by Webb and Messel (1978a) taken (Fig. 1.4). Crocodiles were mostly processed onboard the boat but larger animals were sometimes towed to the bank and processed on land. Animals were released as near as possible to the site of capture.

1.8.2 *Marking crocodiles*

Crocodiles were uniquely marked by clipping the caudal verticils with a scalpel or sharp knife using the numbering system detailed in Fig. 1.5, which is similar to that used by the Queensland Parks and Wildlife Service (see QDEH 1995). Portions of skin tissue were kept and preserved in 95% denatured ethanol for later genetic analysis. In addition, passive integrated transponders (PIT tags: 2.12 × 11.5 mm) were subcutaneously implanted in all animals > 60 cm TL, along the dorsal mid-line between the posterior margin of the cranial platform and the nuchal scales (Fig. 1.5).



TL: Total length measured to the nearest cm from tip of snout to tip of tail.

SVL: Snout-vent length measured to the nearest cm from tip of snout to anterior extremity of the cloaca.

HL: Head length measured to the nearest mm from tip of snout to median posterior margin of the cranial platform (i.e. the supra-occipital bone).

MHW: Maximum head width measured to the nearest mm as the distance between the extremities of the surangular bones at the level of articulation of the jaw, just posterior to the cranial platform.

CPW: Cranial platform width measured to the nearest mm as the distance between the posterior lateral extremities of the squamosal portion of the cranial platform.

BM: Body mass.
BM < 1 kg: measured to the nearest 10 g.
1 kg < BM < 25 kg: measured to nearest 100 g.
BM > 25 kg: measured to the nearest 1 kg.

Fig. 1.4. Morphometric measurements taken during the study.

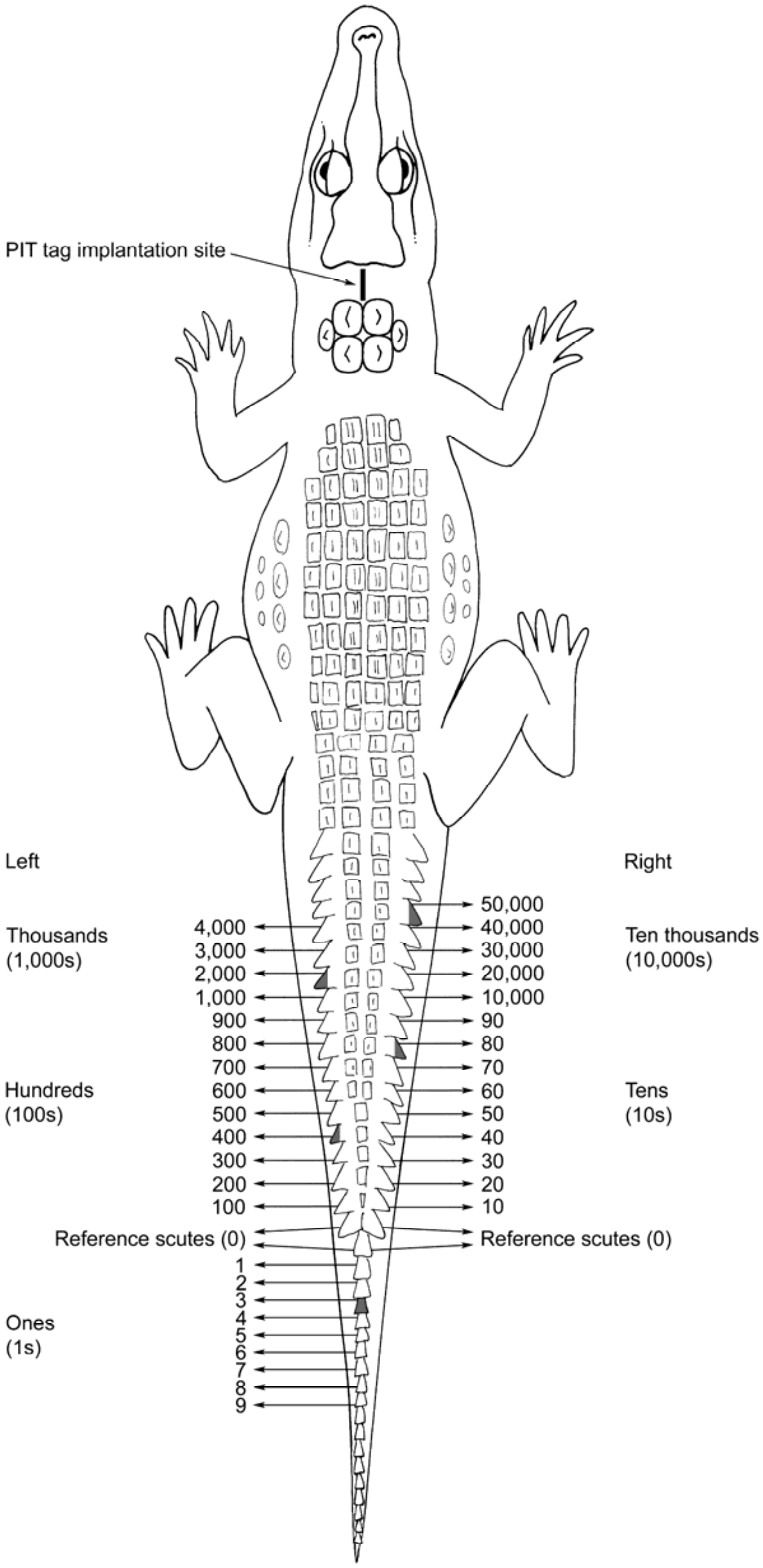


Fig. 1.5. Scute numbering system used for uniquely marking individual crocodiles. For example, if the greyed scutes above were clipped, it would identify the animal as number 52,483. Reference scutes, where the double caudal verticils converged with the single caudal verticils, were never marked because they served as a point of reference. Additionally, PIT tags were subcutaneously implanted in all animals > 60 cm total length, along the dorsal mid-line between the posterior edge of the cranial platform and the nuchal scutes.

2. A NEW METHOD FOR ATTACHING TAGS

Despite the potential importance of movement patterns to crocodilian life histories; movement, home range behaviour and dispersal have received careful examination only in *Alligator mississippiensis* (Hutton 1989). Data for other species of crocodilian are deficient and stem mostly from mark-recapture studies, which have provided baseline information on many species (e.g. Gorzula 1978; Webb and Messel 1978b; Walsh and Whitehead 1993; Tucker *et al.* 1997). However, telemetry is more suitable for clarifying theories about patterns of movement and advancing our understanding of dynamic activity budgets and seasonal patterns of habitat use by different life-history stages (Tucker *et al.* 1997).

Radio-telemetry has been successfully used to track *A. mississippiensis* (e.g. Joanen and McNease 1970, 1972; McNease and Joanen 1974; Goodwin and Marion 1979; Rootes and Chabreck 1993), *Crocodylus acutus* (Rodda 1984b), *Crocodylus niloticus* (Hutton 1989; Hocutt *et al.* 1992), *Crocodylus intermedius* (Muñoz and Thorbjarnarson 2000), *Paleosuchus trigonatus* (Magnusson and Lima 1991) and *Melanosuchus niger* (Martin and da Silva 1998). Attachment configurations for radio tags have included neck collars (e.g. Joanen and McNease 1970), tethering (Rodda 1984a,b; Martin and da Silva 1998; Muñoz and Thorbjarnarson 2000), ingestion (Magnusson and Lima 1991) and surgical implantation (Magnusson and Lima 1991; Hocutt *et al.* 1992). The most successful methods in terms of longevity have been neck collars (Taylor 1984) and surgical implantation (Hocutt *et al.* 1992), which have enabled animals to be radio located for periods in excess of 3 and 2 years, respectively. This paper describes a new method used for attaching VHF radio tags to *Crocodylus porosus* that could easily be modified to attach other electronic devices such as satellite tags, GPS data loggers or time-depth recorders.

Captured crocodiles were physically restrained during the attachment procedure by binding the front and rear legs alongside the body with nylon webbing, and tying the animal to an aluminium ladder padded with burlap sacks. Subject animals were blindfolded with eye pads and electrical tape to reduce visual stimulation. Once restrained, the animals rarely struggled during the procedure unless provoked by loud human voices or the sound of an approaching boat. Anaesthesia was not used, partly because of difficulty finding an appropriate treatment regimen that effectively and reliably sedated the animals for the intended procedure, but more importantly because of the lengthy recovery periods involved (see Loveridge and Blake 1987; Bennett 1996). Priority was given to returning the animals to the water as quickly as possible at the end of the procedure. The procedure was performed near the site of capture either onboard a small (4.5 m) boat or on the riverbank. Animals were released as close as possible to the site of capture.

Tags were attached to the enlarged nuchal scales on the dorsal surface of the neck because the pronounced keel of these scales was conducive to the use of bone pins (Fig. 2.1). The tags fit between the central nuchal scales of large animals (> 3.5 m) and sat above these scales on smaller individuals. One animal had a large gash on its throat and a necrotic wound festering beneath the nuchal scales. Therefore, the tag was attached to the dorsal scales midway between the front legs.

An aluminium angle bracket was pop-riveted to the tag (Fig. 2.1A), which was then placed over the central nuchal scales to assess the fit (Fig. 2.1C). Depending on the size of the nuchal scales, the bracket could be trimmed with tin snips as required to minimize the height of the tag above the dorsal surface. The ventral surface of the tag and the bracket were sanded with emery paper to roughen the surface to aid bonding with the glue. The tag was then sprayed with 70% ethanol and allowed to dry.

Two brands of equally satisfactory glue were used: Loctite Fixmaster Underwater Repair Epoxy (<http://www.loctite.com>) or Selleys Knead It Aqua (<http://www.selleys.com.au>). Both are hand-kneadable, fast-setting, co-extruded epoxy

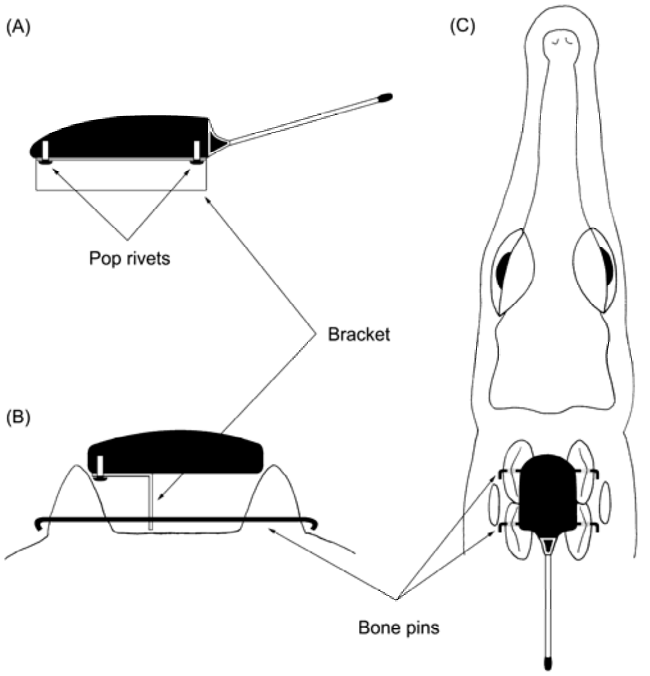


Fig. 2.1. Placement and orientation of the radio tag, bracket and bone pins on the nuchal scales. The attachment was further augmented with glue, which bonded sufficiently well to the tag and bone pins that the bracket is now considered redundant.

Fig. 2.2. Male 184 basking on the banks of the Ord River, 28 May 2002 (36 days after capture).

repair systems that come in roll form, with the hardener encapsulated in the resin. They harden 5 to 10 minutes after mixing to a white solid material and cure fully within an hour. Both will adhere to damp or wet surfaces and cure underwater. The glues are slightly exothermic while curing but were tested on human skin and temperatures generated were mild.

The nuchal scales were scrubbed clean with a disposable chlorhexidine scrub, rinsed with river water and dried with a clean cloth. The area was sprayed with 70% ethanol, which was allowed to evaporate. A lump of glue was placed on the ventral surface of the tag, which was then placed between the central nuchal scales. The tag and glue were moulded to remove any air pockets and minimize the tag's profile above the dorsal surface while leaving the outside lateral edges of the central nuchal scales exposed to enable the placement of bone pins (Fig. 2.1B).

The bone pins used were 31 cm, 1.6 mm diameter, stainless steel Kirschner wires (K-wires), which were cut in half and secured directly into the chuck of a cordless drill. They were then sprayed with 70% ethanol for sterilization. Two pins were used, one through the anterior central nuchal scales and a second through the posterior central nuchal scales (Fig. 2.1C). The K-wires had a trocar spike at each end, which enabled them to drill directly through the osteoderms and bracket without pre-drilling any holes, but the process was fairly slow. Care was required to ensure the orientation of the bone pins was horizontal and that they penetrated only the raised keel of the scales and the bracket (Fig. 2.1B). Once the bone pins protruded through the osteoderms they were bent with pliers, to stop them from pulling through, and trimmed with wire cutters (Fig. 2.1B,C). The area was sprayed again with 70% ethanol, which was allowed to evaporate. Additional glue was then placed around the tag and moulded to provide smooth contouring, and totally encase and seal the central nuchal scales, bone pins and the lower half of the tag (Fig. 2.2).

Table 2.1. Longevity of attachment (LOA) achieved for 16 animals tagged during the study.

Crocodile	Sex	Total length (m)	Body mass (kg)	Date attached (dd/mm/yy)	Bracket (Y/N)	LOA at last fix (days)	Comments
146	M	2.65	59	15/10/2001	Y	15	Tag detached escaping trap
147	M	2.09	26	22/10/2001	Y	241 +	
350	M	2.13	32	23/10/2001	Y	277 +	
164	F	2.72	76	25/10/2001	Y	412 +	
183	F	3.08	103	11/04/2002	Y	281-384	Tag detached in snag
184	M	3.25	91	22/04/2002	Y	377 +	
186	M	3.27	141	24/04/2002	Y	375 +	
188	M	3.53	151	07/05/2002	Y	361 +	
189	F	2.72	82	07/05/2002	Y	360 +	
190	M	2.63	62	09/05/2002	Y	49-67	Tag detached in snag
185	F	2.74	76	24/04/2002	N	370	Tag removed 29/04/2003
191	M	4.34	337	12/05/2002	N	287 +	
192	M	3.12	111	16/05/2002	N	352 +	
193	M	3.17	116	21/05/2002	N	348 +	
194	M	3.07	103	25/05/2002	N	132-195	Tag detached in snag
195	M	2.53	62	26/05/2002	N	341 +	

+ Tag still attached and operational at last fix

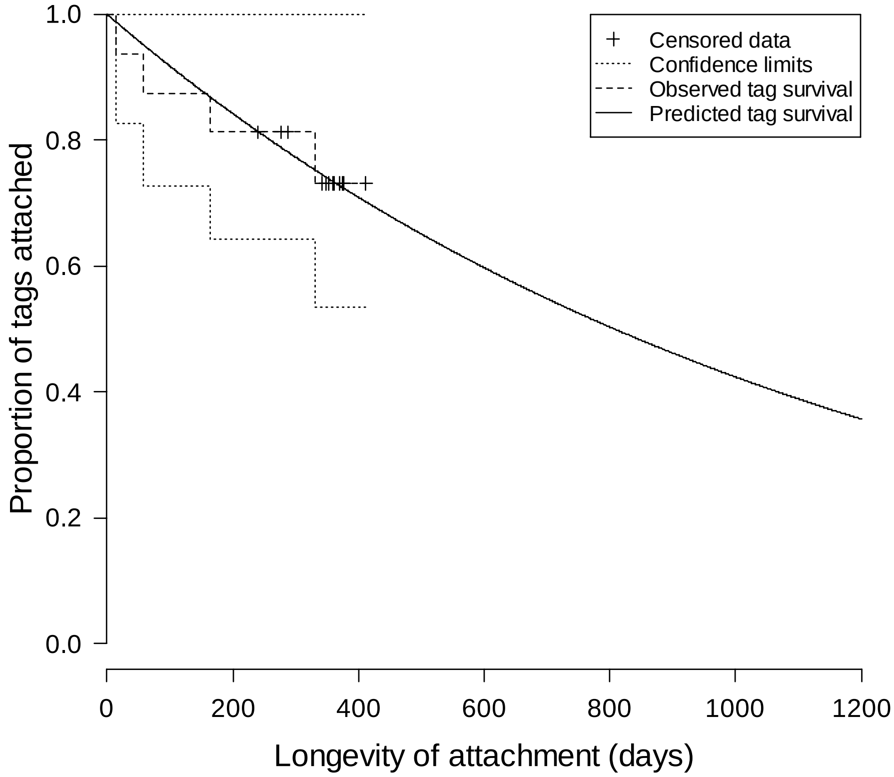


Fig. 2.3. Exponential survival function fitted to longevity of attachment data. The dashed line is the observed tag attachment time with each step down representing a detachment event. The crosses represent censored data, that is, individuals where the tag was still attached and operational at the final observation. The solid line is the tag attachment time predicted by fitting an exponential function to the observed data.

Ten tags were attached using brackets but, because it was thought that the glue bonded sufficiently well to the tag alone, no bracket was used for 6 other attachments (Table 2.1). The length of time a tag stayed attached to a crocodile was similar, irrespective of whether a bracket was used (15 to > 412 days) or not (132 to > 370 days), and I now consider the bracket to be superfluous. Elimination of the bracket not only reduced the materials required but also the time taken to attach a tag. Time taken to attach a tag ranged from 60 minutes (bracket and inexperience) to about 30 minutes (no bracket and experience).

Tag attachment without a bracket was a much simpler procedure. The nuchal area was prepared as before. Holes for the bone pins were pre-drilled through the keel of the nuchal scales with a sterilized drill bit, which was much faster than trying to drill holes using the trocar spike at the end of the K-wires. Also, aligning the bone pins was much easier. After the bone pins were placed through the scales, they were bent and trimmed as before, and the area was then sterilized with 70% ethanol. Once the ethanol evaporated, the glue and tag were placed over the central nuchal scales and moulded into place so that the glue enclosed and sealed the bone pins and scales, and held the tag in place.

Every effort was made to use as sterile a procedure as possible, given the limitations of working under field conditions. Because bone pins were used, a single phrophylactic dose of a broad-spectrum antibiotic, oxytetracycline hydrochloride (OTC), was administered by intramuscular injection as a precaution prior to commencement of the attachment procedure. Dose rates were calculated by allometrically scaling the therapeutic dose recommended by the manufacturer for placental mammals, to that for a generic reptile, using the methods described by Pokras *et al.* (1992) or Sedgwick and Borkowski (1996). OTC has the added advantage of being a suitable biomarker (see Coles *et al.* 2001). It is worth noting that crocodiles, in common with other reptiles and non-mammalian vertebrates, have a renal portal system.

Therefore, it is prudent to inject any medications, especially nephrotoxic drugs, into the anterior half of the animal to avoid the renal portal system (Jenkins 1996).

Tags weighed 140 g but, when combined with glue, pins and bracket, the mass of the assembly increased to about 500 g. In general, tags should weigh < 3-5% of body mass to avoid adverse effects (Kenward 2001). Therefore, using this method with current tag specifications, animals would need to be > 17 kg or about 1.8 m total length. The greatest confirmed longevity of attachment (LOA) achieved during the study was > 412 days and most tags remained attached for > 340 days (Table 2.1). The study ended in May 2003, however, aerial crocodile surveys flown in July 2003 sighted three tagged animals, confirming one tag had remained attached for > 637 days and two others for > 420 days. Four tags (25%) are known to have detached during the study: three detached naturally in submerged snags and one when an animal escaped from a cage trap (Table 2.1). Dislodgement of a tag is most likely during a flight response when an animal is startled, especially when it is among thick or fallen vegetation, whether submerged or on the bank.

A simple mean LOA would not provide a meaningful estimate of expected attachment time because most tags were still attached and operational at the end of the study (= censored data, see McCallum 2000; Crawley 2002). Therefore, survival analysis on LOA was performed to estimate the mean time to failure using the survival package within R software (ver. 1.6.2, R Development Core Team 2004). No evidence was found that the risk of detachment increased with attachment time (Weibull distribution, scale = 1.33, $P = 0.5$ for H_0 scale = 1). Therefore, it was assumed that the risk of detachment was constant throughout life, and an exponential survival function was fitted to the data using parametric regression (McCallum 2000; Crawley 2002). The mean time to failure was estimated to be 1164 days. The precision of the estimate was low, having a 95% CI of between 437 and 3103 days, because most of the data were censored with few failures occurring during the study period (Fig. 2.3).

Crocodile 185 was re-captured after 370 days and the tag removed to evaluate possible deleterious effects of the attachment procedure. The skin appeared healthy with only a slight loss of pigmentation (see Kirshner 1985) and there was no infection or necrosis visible in the underlying tissue. Skull dimensions, total length and body mass had all increased suggesting the attachment had not adversely affected growth or body condition. Furthermore, all females tagged during the study moved to nesting habitat during the wet season and one was detected near a recently constructed nest. Therefore, attachment of the tags did not appear to have interfered with courtship, mating or nesting behaviour. On the basis of this evidence, I consider the technique to be relatively benign.

In summary, this technique provides a reliable medium to long-term method for attaching small electronic devices to crocodilians. It has some advantages over other successful methods of tag attachment. First, it does not constrict an animal's neck as would a collar and it is not as invasive as surgical implantation. Also, signal propagation is better than with an implanted tag, which improves detectability. Examination of underlying tissue on one animal 370 days after attachment suggests that the method is relatively benign. There are a number of ways the technique could be refined. Ideally, the tag should have as low a profile as possible above the dorsal surface of the animal. In hindsight, it would have been preferable to design a narrower tag that would fit between the central nuchal scales on a greater size range of animals to reduce the overall profile of the tag assembly above the dorsal surface. However, there is a compromise in that the tag itself would have a higher profile. Additionally, the flexible whip antenna could be orientated vertically without greatly increasing the risk of detachment, which may improve signal propagation and reception (see Kenward 2001). The use of alternative materials may also be advantageous. For example, bone pins made from titanium or Delrin plastic (<http://plastics.dupont.com>) are probably more inert than stainless steel. It would be well worth testing the use of a less dense, flexible polyurethane glue such as Sikaflex-291 (<http://www.sika-industry.com>), which would reduce the overall weight of the tag assembly. However, curing times for this product are lengthy and would need to be accelerated to be of practical use in the field.

3. RADIO-TRACKING MOVEMENTS

3.1 Introduction

Crocodylus porosus is the most widely distributed crocodilian species, occurring throughout southeast Asia and ranging from northern Australia to southern India and Palau (Ross 1998). It is regarded as the crocodilian that most readily takes to the sea because it is extremely euryhaline and can maintain homeoosmotic conditions over a broad range of salinities (0 to 60 ‰, see Taplin 1988; Taplin and Grigg 1989). There are numerous reports of individuals undertaking ocean voyages over hundreds of kilometres (e.g. see Bustard and Choudhury 1980) and Allen (1974) reports an account of a 3.8 m male that arrived at the eastern Caroline Islands, > 1300 km by sea from the nearest known population. While this species is obviously capable of very large-scale movements, these are likely to be atypical. Most studies indicate that crocodilians move around little for most life-history stages (Webb and Messel 1978b; Magnusson 1979; Webb *et al.* 1983a; Taylor 1984; Hutton 1989; Rootes and Chabreck 1993; Tucker *et al.* 1997; Muñoz and Thorbjarnarson 2000). However, Tucker (1997) found that pubescent male *Crocodylus johnstoni* were essentially nomadic and had much larger home ranges than other life stages.

Patterns of animal movement must be known in order to understand basic population processes and may themselves be important demographic parameters (Hutton 1989). Movement, home range behaviour and dispersal have received careful examination only in *Alligator mississippiensis* despite their potential importance to crocodilian life histories (Hutton 1989). Radio-telemetry has been used successfully to track *A. mississippiensis* (Joanen and McNease 1970, 1972; McNease and Joanen 1974; Goodwin and Marion 1979; Rodda 1984a; Taylor 1984; Rootes and Chabreck 1993), *Crocodylus acutus* (Rodda 1984b), *Crocodylus niloticus* (Hutton 1989; Hocutt *et al.* 1992), *Crocodylus intermedius* (Muñoz and

Thorbjarnarson 2000), *Paleosuchus trigonatus* (Magnusson and Lima 1991) and *Melanosuchus niger* (Martin and da Silva 1998).

Surprisingly, there are no published radio-tracking studies for either species of crocodilian found in Australia. All data on movements of *C. porosus* have been determined by mark-recapture studies (e.g. Webb and Messel 1978b; Messel and Vorlicek 1987; Walsh and Whitehead 1993). Early attempts to radio-track *C. porosus* were unsuccessful, perhaps due to the limitations of prototype equipment or attachment difficulties (see Webb and Messel 1978b; Yerbury 1980). Signal attenuation in brackish or salty water may also have been a contributing factor (Kenward 2001). Webb and Messel (1978b) discussed radio-tracking *C. porosus* and described the movements of five animals with attached transmitters, except it appears much of the information presented on their movements was derived from re-sightings and it is unclear how often animals were radio-located. While recapture studies have provided baseline information on the movements of *C. porosus*, telemetry is more suitable for clarifying theories about patterns of movement and advancing our understanding of dynamic activity budgets and seasonal patterns of habitat use by different life-history stages (Tucker *et al.* 1997). This is the first study reporting the movements of *C. porosus* using telemetry data.

3.2 Methods

3.2.1 *Tracking methods*

Crocodiles were caught using either the harpooning technique described by Webb and Messel (1977) or with baited cage traps (see Walsh 1987). VHF radio tags (150 MHz) manufactured by Sirtrack Ltd (<http://sirtrack.landcareresearch.co.nz>) were attached to the nuchal scales of 16 animals using the techniques described in Chapter 2. Initially, tags were attached to three crocodiles caught on the King River and one to a problem animal caught at Wyndham Port (Fig. 1.3) in a pilot study that commenced in October 2001. The remaining 12 tags were attached to animals caught on the Ord River during April and May of 2002. Eleven of the 12 Ord River crocodiles were caught within a 7 km reach of river and all were caught within a 13 km reach. By the end of the study, the Ord River animals had dispersed over a 108 km section of river. Most tracking was undertaken on the Ord River because large sections contain fresh water due to perennial discharge from Lake Argyle which made locating tags on submerged animals more likely (see Kenward 2001).

Animals were tracked manually, mainly from a boat and occasionally from a variety of aircraft, using a point sampling approach (Kenward 2001). Only one location per tracking day was recorded for each crocodile. When tracking from a boat, signals were initially detected using a scanning receiver (Telonics TR2) connected to an omni-directional antenna. Under optimal conditions, such as with a crocodile basking on the bank and an unobstructed line of sight, signals were discernible from 2 to 3 km. Mostly, however, signals were detected from 0.2 to 0.5 km, particularly when animals were submerged. Signals were perceptible at depths of 4 to 5 m in fresh water. Once detected, a portable three-element Yagi antenna was used to pinpoint the location of a crocodile. Animals were routinely located to within a few metres, especially in fresh water, and their position was recorded to the nearest second of latitude and longitude (40 m) with a GPS receiver (Lowrance GlobalMap 100). Tracking in brackish or saline water was much more difficult because signals were lost as soon as animals submerged. Crocodiles could still be located to within 50 m depending on behaviour but some animals no doubt evaded detection.

Not surprisingly, animals that had been trapped were more tolerant of being approached by a boat than those that were harpooned. Crocodiles responded to an approaching boat by submerging and utilizing prevailing currents to move to deeper water away from the vessel. While all animals showed avoidance behaviour as they were being approached, I doubt it had a major influence on long-term patterns of movement. Boats are common along the Ord River and most animals are accustomed to seeing them, as well as being approached by curious fishermen and tourists. Furthermore, all tagged females inhabited a small section of river for many months, despite being tracked regularly. Three of the females were harpooned in the same section of river they occupied during the dry season.

Aerial tracking was occasionally used to find missing animals and during the wet season when access to the river became difficult. Under optimal conditions, signals were detectable over a distance of approximately 10 km at an altitude of 750 m. Judging by signal behaviour, crocodiles reacted to aircraft flying at altitudes below 750 to 900 m by submerging. Altitude was not a critical factor over fresh water but became an important consideration when tracking over brackish to saline water. Locations were recorded with a GPS receiver. The accuracy of aerial fixes depended on the type of aircraft, its speed and altitude. Signal propagation is greatest immediately overhead when tags are submerged (Kenward 2001). Helicopters enabled the most accurate fixes because they could hover over a location at low altitude to pinpoint the strongest signal. They also had the added advantage of being able to land nearby so that tracking could be undertaken on foot if necessary. The accuracy of locations obtained from fixed-wing aircraft was variable and ranged from 40 m, based on known locations, to about 400 m. Obvious errors, such as terrestrial fixes, were identified and corrected using geographic information system (GIS) software by recalculating the position at the shortest straight-line distance to the river.

Ord River crocodiles were tracked during the day for logistical reasons. A routine tracking run involved searching a 60 to 70 km reach of river (120 to 140 km round trip). Crocodiles were tracked for 5 to 15 d/mo between April and September. Thereafter, they were tracked for approximately 2 to 6 days every 2 months from October 2002 until the study ended in May 2003. King River animals were mostly tracked at night on an irregular basis. Crocodiles are probably more active at night, so diurnal tracking would bias estimates of short-term daily movements. However, diurnal tracking was considered sufficient for estimates of space use and home range over the longer term. Patterns of movement were consistent between Ord and King River crocodiles, although sample sizes were small.

Time tabling was a minor issue while tracking on the Ord River. There were a limited number of locations from which the boat could be launched and the linear habitat meant that some animals were often encountered at similar locations at similar times on consecutive days. From April to October 2002, the boat was launched at a location that enabled an upstream and a downstream tracking run which could be varied between morning and afternoon to reduce this effect though the choice was sometimes made with respect to tidal movements on any particular day. The locations recorded were sometimes varied between forward and return runs as well, however, the logistics of manually tracking in this region imposed a significant constraint on sampling strategy.

3.2.2 ***Analysis of home range***

The vast majority of telemetry studies of animal movements have been of mammals and birds (Millspaugh and Marzluff 2001). Consequently, much of the literature describes the analysis and interpretation of data from species whose movements are largely unrestricted in two-dimensional space. One of the simplest ways to measure movements and home ranges of animals that are geographically restricted to a drainage channel is to measure linear river distances. This approach has been used to quantify home ranges for Australian freshwater crocodiles (Tucker *et al.* 1997) and river otters (Melquist and Hornocker 1983). Linear home ranges have also been used to describe the movements of rats in farmland (Hardy and Taylor 1980). Kenward's (2001) definition of home range as an area traversed repeatedly by an animal is particularly apt for a river-dwelling animal like a crocodile, because, given any two points along the river, the path the animal traversed to travel between them is known at the broad scale.

Tucker *et al.* (1997) regarded conventional calculations of home-range size that required *x*-*y* coordinates as inapplicable for linear habitat like a river. However, a straight line can be described by an infinite number of *x*-*y* coordinates since both are continuous variables. More importantly, the range and variance of the coordinates is determined by the length, orientation and shape of the line. Provided the locations obtained from the movements of an animal are representative of the shape of the river section over which it traverses, any of the conventional algorithms could be used to calculate a home range that is then corrected by subtracting encroaching terrestrial habitat. This approach is relatively straight forward with the use of GIS software. Advantages of using one of the conventional methods include a standardized approach for greater comparability between studies and relatively objective criteria for identifying ‘normal’ movements and activity centres (see Kernohan *et al.* 2001).

If locations are not representative of river shape, which will be a consequence of sampling intensity/interval, many of the conventional methods result in a disjointed utilization distribution. Disjointed utilization distributions are not uncommon when using methods like the 95% home range of a fixed kernel estimator, which is one of the shortcomings of this method (Powell 2000). The problem becomes untenable in linear habitat like a river because the interpretation of a disjointed 100% utilization distribution is that the probability of finding an animal in a section of river that it used to travel between two areas is zero, which is biologically dubious.

Unfortunately, none of the conventional methods could be used in this study because sampling intensity was insufficient for locations to be representative of the shape of the river section a crocodile inhabited. Consequently, two measures of home range were used: mid-stream linear range (MSLR) and river channel area (RCA). MSLR was the mid-stream linear distance in kilometres between the most upstream and downstream locations for a particular crocodile and RCA was the river area in hectares encompassing the MSLR, which was effectively a minimum convex polygon (MCP) approach within the river channel. Many of the conventional methods used for home-range analysis assume independence between successive locations. Home-range size will tend to be underestimated when data are serially correlated (Swihart and Slade 1985) but minimum area techniques are not affected in this way (Harris *et al.* 1990). Therefore, all locations collected for each animal were used to calculate MSLRs in this study. Many authors now consider that strict adherence to the time to independence concept in movement studies is ill advised (Otis and White 1999; Kenward 2001; Kernohan *et al.* 2001).

Spatial analyses were performed using ArcView GIS software (ver. 3.3, ESRI: Redlands, California) in conjunction with the animal movement analyst extension (AMAE ver. 2.0, Hooge and Eichenlaub 2001) and 1:50,000 scale geo-referenced topographic data as base layers. Area-observation curves were plotted to determine whether an animal’s home range had stabilized for the number of locations collected, using the MCP sample size bootstrap function of AMAE (see Hooge 2002). This function bootstraps an MCP home range for a user specified number of iterations and observation interval. Obviously an MCP home range is only an index of the true home range for a crocodile inhabiting linear habitat like a river.

It was not possible to objectively identify centres of activity using conventional methods such as the 50% utilization distribution of a fixed kernel estimator. This was because serially correlated data would have resulted in the erroneous identification of activity centres, as animals were often detected close to their previous location on consecutive days. Therefore, activity centres are reported for individual animals, where considered appropriate, based on knowledge of movements from tracking experience and visual inspection of data using GIS.

3.2.3 *Habitat selection*

Four broad habitat types were recognized based on water chemistry and knowledge of the river: 1. Macro-tidal brackish-saline (MTBS) reaches; 2. Macro-tidal freshwater (MTF) reaches; 3. Tidal freshwater (TF) reaches and Non-tidal freshwater (NTF) reaches. Tracking data were insufficient to make quantitative assessments of habitat selection (see Alldredge and Ratti 1986; White and Garrott 1990; Samuel and Fuller 1996) so qualitative assessments of habitat preference were made for individual animals, based on the frequency of occurrence in a particular habitat and knowledge of movements. Furthermore, while boundaries of the habitat types were relatively static during the dry season, they became dynamic during the wet season as a result of floods so interpretations should be treated cautiously. For example, the salinity at Adolphus Island (Fig. 1.3) ranges from 24 ‰ on neap tides to 30 ‰ on spring tides during the dry season yet can be a low as 5 ‰ during the wet season (D. Palmer, Water and Rivers Commission, Kununurra, personal communication).

3.2.4 *Analysis of movements*

Crocodile movements showed distinct sexual differences, so movements of males and females were analysed separately. Female movements were analysed with simple descriptive statistics and GIS. Analyses of male movements used data from Ord River males only but interesting records are presented for males 146 and 350. No data are presented for King River male 147 due to the small number of locations recorded.

3.2.5 *Rates of male movement*

Rate of movement (ROM) was calculated as the ratio of distance travelled in kilometres to the time interval in days between successive locations. Histograms were constructed to investigate the frequency distribution of ROM. Due to the shape of the distribution, Kruskal-Wallis tests were used to determine whether ROM varied between male size classes, season or tidal phase. Three size classes were used: males between 50 and 100 kg (n = 3); males between 100 and 140 kg (n = 3); and males > 140 kg (n = 3). Categorical variables used for season were: wet (December to March), post wet (April/May), dry (June to August), and late dry (September to November); and, for tidal phase: neap first quarter; neap last quarter; spring full moon and spring new moon. Only rates of movement where the time interval between successive locations was < 8 days were used in analyses. Analyses of ROM were performed using R software (ver. 1.6.2, R Development Core Team 2004).

3.2.6 *Interactions between males*

Static interaction between Ord River males was measured using a simple percentage MSLR overlap. This measure of space sharing was calculated as:

$$HR_{1,2} = \frac{A_{1,2}}{A_1} \quad \text{and} \quad HR_{2,1} = \frac{A_{1,2}}{A_2}$$

where $HR_{1,2}$ is the proportion of animal 1's home range overlapped by animal 2's home range, $HR_{2,1}$ is the proportion of animal 2's home range overlapped by animal 1's home range, and $A_{1,2}$ is the area of overlap among HR_1 and HR_2 (Kernohan *et al.* 2001).

3.2.7 *Directionality of male movements*

Chi-square tests were used to evaluate whether the cumulative distance travelled up- or downstream by Ord River male crocodiles was biased in either direction. Tests were performed using R.

3.3 Results

Area-observation curves suggest female dry season core areas (see Section 3.3.1 below) approach an asymptote between 30 and 40 locations (e.g. Fig. 3.1A), whereas male home ranges probably asymptote between 40 and 50 locations (Fig. 3.1C). Estimates of the size of female core areas (Table 3.1) are considered reliable but home ranges appear to have stabilized for males 184, 188 and 193 only (e.g. Fig. 3.1C), with MSLRs for other males likely to be underestimates (e.g. Fig. 3.1B).

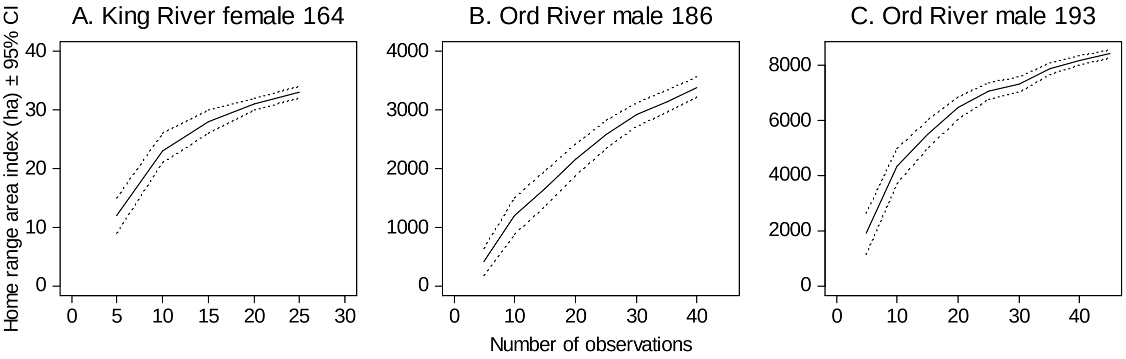


Fig. 3.1. Area-observation curves for three crocodiles radio-tracked between October 2001 and May 2003. The home range area index is a minimum convex polygon area bootstrapped for 500 iterations at intervals of five observations. All observations were used for males but only dry season core area observations were used for females. The axes are not to uniform scale.

3.3.1 *Female movements*

All females occupied different core area habitats, however they showed consistent patterns of movement: all inhabited a small core area on the main river channel during the dry season and moved to areas of suitable nesting habitat at the beginning of the wet season, where they remained until the following dry season (Fig. 3.2, Table 3.1). Dry season core areas ranged from 0.3 to 2.5 km mid-stream linear distance (mean ± SD: 1.3 ± 0.9 km) and encompassed an RCA of 5 to 20 ha (15 ± 7 ha). Females occasionally made excursions away from their core areas during the dry season and the maximum excursion distance detected was 15 km. Mean rates of female movements were generally low (< 1 km/d) because they occupied small core areas during the dry season. The maximum rate of movement detected was a 10.1 km/d upriver movement by female 189 when she was returning to her core area after a downriver excursion. Females moved 15 to 62 km from their dry season core areas to nesting habitat during the wet season (Fig. 3.2, Table 3.1). Two of the four females returned to the same dry season core area following the wet season. Female 183’s tag detached at her wet season habitat and female 189 was not known to have returned to her previous core area when the study ended in early May 2003.

All females tagged during this study were quite large (Table 3.1) and thought to be reproductively mature. Female 164 had a swollen abdomen when she was caught in October 2001 and was thought to be gravid although palpation of the abdomen was inconclusive. She was not detected moving from her dry season core area from December 2001 to March 2002 (n = 6) and either nested nearby or did not nest that season, possibly due to the stress of capture in late October (see Seymour *et al.* 1987; Elsey *et al.* 1991; Rooney and Guillette 2000; Jessop *et al.* 2003). She was detected 15 km upriver from her dry season core area in December 2002, where most nesting activity is reported for the King River. Female 189 was tracked to a recently constructed nest in December 2002 and all females moved to what were presumably nesting habitats during the 2002/2003 wet season. Females were exclusively tracked from the air during the wet season and all but 189 were detected near or under canopy, which made it difficult to confirm the presence or absence of a nest.

Following the wet season, both female 164 and 185 returned to the same core area they occupied the previous dry season. In April 2003, female 189 was still on the floodplain of the lower Ord on the opposite bank to the one on which she had constructed a nest in December 2002. Inspection of the nest mound in April 2003 failed to detect any egg-shell residue and she may have abandoned the site due to below average rainfall during the previous the wet season. By May 2003, she had moved back to the main channel of the Ord River and may have returned to the core area she inhabited the previous dry season. Unfortunately no funds were left to continue the tracking study.

Female 183 moved between the main Ord channel and a small backwater during the 2002 dry season. Signals were reliably detected in the main channel yet disappeared when approaching 183 in the backwater. The backwater was tidally influenced although the water

Table 3.1. Summary statistics for four mature *Crocodylus porosus* females radio-tracked between October 2001 and May 2003.

Crocodile		164	183	185	189	Mean ± SD
Date captured (dd/mm/yyyy)		25/10/2001	11/04/2002	24/04/2002	07/05/2002	
Total length (m)		2.72	3.08	2.74	2.72	
Body mass (kg)		76	103	76	82	
Study interval (d)		412	384	370	360	
Total number of locations (*n*)		30	37	44	41	
Max. rate of movement detected[a] (km/d)		-1.1	-2.4	<1	10.1	
Dry season core area	MSLD[b] (km)	1.5	2.5	1.0	0.3	1.3 ± 0.9
	Area (ha)	17	20	17	5	15 ± 7
Number of core area locations (n_c)		27	32	41	33	
Core area habitat[c]		MTBS	TF	NTF	MTF	
Max. excursion distance detected[a] (km)		7	4	0	-15	
Wet season movement[a] (MSLD[b] km)		15	±21	-62	-15	28 ± 22.7

[a] Negative values indicate downstream movement while positive values indicate upstream movement.

[b] MSLD = mid-stream linear distance.

[c] MTBS = macro-tidal brackish-saline reach; TF = tidal freshwater reach; NTF = non-tidal freshwater reach; and MTF = macro-tidal freshwater reach.

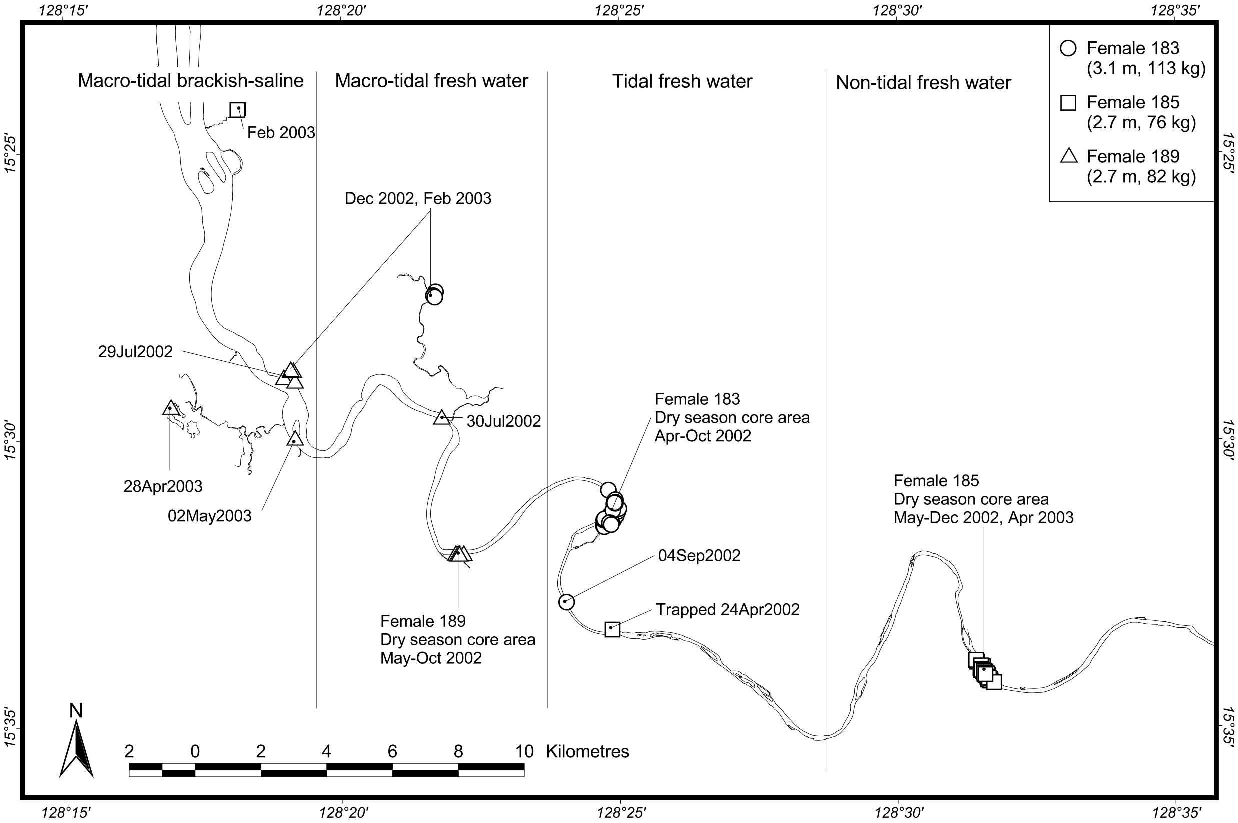


Fig. 3.2. Movements of three mature female *Crocodylus porosus* within the Ord River system between April 2002 and May 2003.

was fresh. Maximum depth ranged from about 2 to 3.5 m depending on tide and the signal should have been detectable. One possible explanation was that she was using an underwater den for refuge, which formed a physical barrier to the tag's signal. Between October and December 2002, female 183 moved 21 km from her dry season core area up a tributary to a non-tidal pool that was possibly spring-fed and where crocodile nests had been seen previously by a local pilot. Her tag was recovered in April 2003 and had detached between October 2002 and April 2003. Signals had been detected from the air in December 2002 and February 2003. Preliminary inspection of the tag indicated damage consistent with a bullet hole. Subsequent examination in Perth by a forensic chemist concluded that the damage and hole dimensions were consistent with calibres commonly used in the region, indicating that female 183 had probably been shot.

3.3.2 *Male movements*

Patterns of male movement were substantially different to those of females (Table 3.2). Males traversed large sections of river and had MSLRs of between 11 and 87 km. The size of the MSLR or RCA appeared to be unrelated to body size with the smallest male tagged (195) having the largest MSLR (87 km), which had not stabilized by the end of the study. The second largest MSLR was 67 km for the largest male tagged (191), which had not stabilized either. MSLRs ranged from 33 to 44 km for the three animals with stabilized estimates (Table 3.2). It was unclear whether river area was important for crocodiles and the large RCAs observed for males 191, 192 and 194 may reflect a habitat preference for the lower Ord estuary where the river channel was broad.

Most males did not show site fidelity to particular sections of river, based on tracking experience and GIS analysis, nor were there any exclusive habitat preferences. The MSLR of

Table 3.2. Summary statistics for nine *Crocodylus porosus* males radio-tracked between April 2002 and May 2003.

Crocodile		195[a]	190[a]	184	194[a]	192[a]	193	186[a]	188	191[a]
Date captured (dd/mm/yyyy)		26/05/2002	09/05/2002	22/04/2002	25/05/2002	16/05/2002	21/05/2002	24/04/2002	07/05/2002	12/05/2002
Total length (m)		2.53	2.63	3.25	3.07	3.12	3.17	3.27	3.53	4.34
Body mass (kg)		62	62	91	103	111	116	141	151	337[b]
Study interval (d)		341	67	377	195	352	348	375	361	287
Total number of locations (*n*)		34	19	44	18	22	45	43	38	26
Mid-stream linear range (km)		87	11	36	62	51	44	29	33	67
River channel area range (ha)		1734	127	985	6427	4160	626	416	658	4988
Mean (± SD) rate of movement (km/d)		0.7 ± 0.6	0.6 ± 1.0	2.1 ± 2.2	1.2 ± 1.6	1.8 ± 1.4	1.3 ± 2.6	1.2 ± 1.6	2.0 ± 4.0	3.3 ± 6.5
Max. rate of movement detected[c] (km/d)		-2.1	3.6	-9.5	4.6	-4.5	-13.1	5.4	19.4	-23.3
Cumulative distance travelled (km)		215	19	207	158	131	138	136	193	190
Centres of activity[d]	*n*	0	0	0	0	0	0	1	1	1
	% locations	NA	NA	NA	NA	NA	NA	84	68	62
	MSLD[e] (km)	NA	NA	NA	NA	NA	NA	4.6	2.6	2.4
	Habitat type	NA	NA	NA	NA	NA	NA	TF	MTBS	TF
Habitats utilized[f]		1,2,3,4	3	1,2,3	1,2,3	1,2,3	2,3,4	3,4	1,2,3	1,2,3,4
Habitat preference[f]		NTF	NA	NA	MTBS	MTBS	NA	TF	MTBS	MTBS

[a] Home ranges for these individuals are likely to be underestimates (see Fig. 2).

[b] Body mass was estimated from skull dimensions and total length using equations from Webb and Messel (1978a).

[c] Negative values indicate downstream movement while positive values indicate upstream movement.

[d] NA = not applicable

[e] MSLD = mid-stream linear distance.

[f] 1 = macro-tidal brackish-saline reach (MTBS); 2 = macro-tidal freshwater reach (MTF); 3 = tidal freshwater reach (TF); and 4 = non-tidal freshwater reach (NTF).

most males encompassed three or four different habitats (Table 3.2). However, the three largest males had centres of activity that comprised 4% to 16% of their MSLR. They moved away from and returned to these centres throughout the year. The largest male (191) may have had multiple centres of activity as he was thought to have spent much of the dry season in 2002 on the lower reaches of the Ord River well outside the routine tracking section. Therefore, his habitat preference was thought to be MTBS despite the recorded centre of activity being in a TF reach (Table 3.2). There did not appear to be strong seasonal patterns of movement for most males, however the four largest animals tended to make more excursions to the upriver sections of their MSLR during the late dry and wet seasons.

Rates of male movement appeared to be bi-modally distributed (Fig. 3.3). This was consistent with observations while tracking. Most males tended to occupy a small section of river for a period of days or weeks where the ROM was low. They then moved to another section of river, often with a high ROM, where they spent variable periods of time. There were no significant differences in ROM between three size classes of males ($H = 0.71$, $P > 0.70$) or between different tidal phases ($H = 0.88$, $P > 0.83$) but there were significant differences between seasons ($H = 13.10$, $P < 0.005$). Mean (± SD) rates of movement were highest during the summer wet season (4.0 ± 5.4 km/d), followed by late dry (1.6 ± 2.3 km/d), dry (1.3 ± 3.3 km/d) and post wet (1.1 ± 1.4 km/d) seasons. However, males were still quite mobile during the dry season and the highest rate of movement detected was a 28 km downriver movement in 1.2 days by male 191 during neap tides at the end of July 2002 (Table 3.2). Conversely, the second highest rate of movement detected was a 19 km upriver movement in one day by male 188 during spring tides in December 2002. The highest rates of movement detected were for the two largest males (Table 3.2), despite there being no significant differences in ROM for different male size classes.

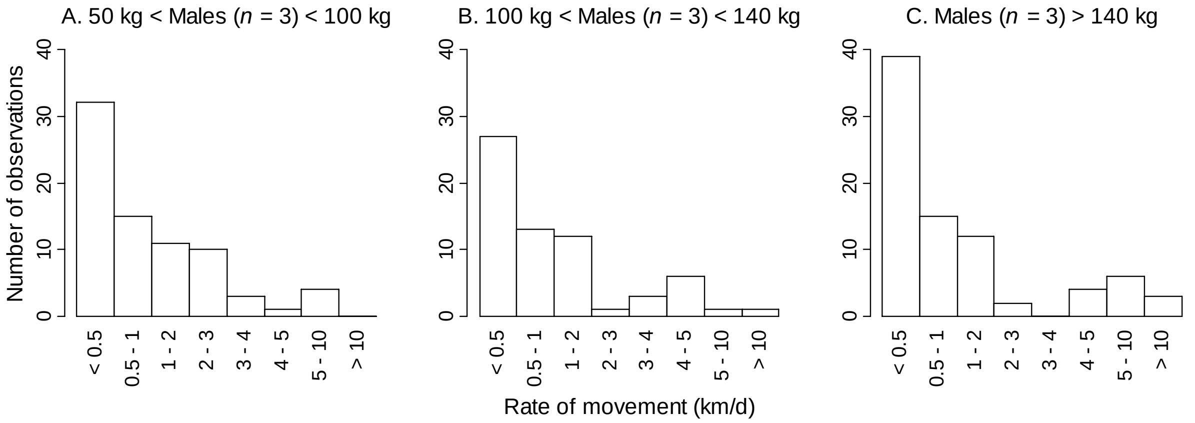


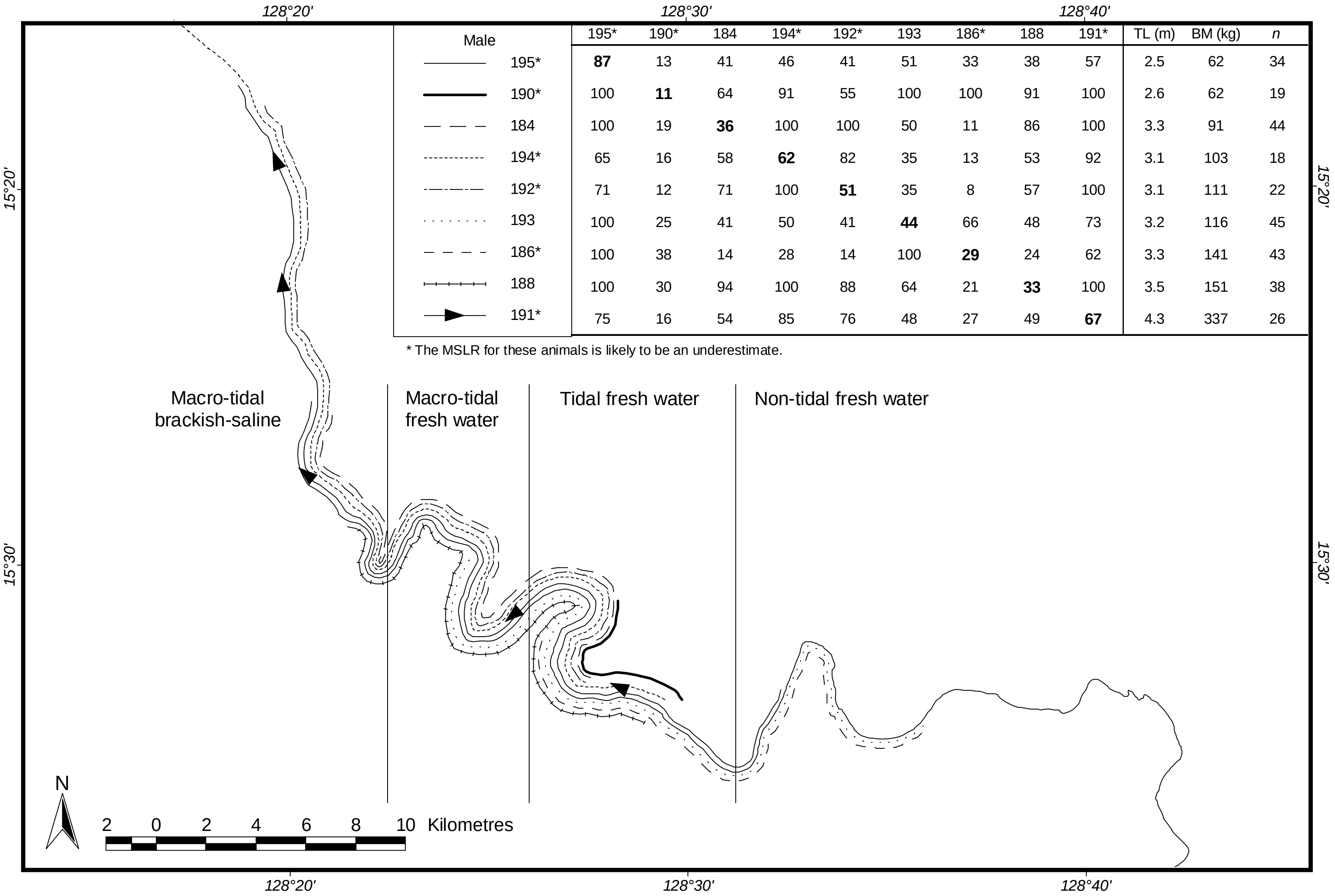
Fig. 3.3. Frequency histograms of rates of movement (km/d) for three size classes of Ord River male *Crocodylus porosus*.

3.3.3 *Interactions between males*

There was substantial overlap of MSLRs for most Ord River males with no obvious exclusion or spatial partitioning evident (Fig. 3.4).

3.3.4 *Directionality of male movements*

Males moved both up- and downstream within any given period and throughout the year. Only male 195 showed significant directional movement ($X^2 = 6.97$, $P < 0.01$) during the study. He reached Skull Rock at the end of July 2003 and was tracked over the next 10 weeks moving between Skull Rock and Tarrara Bar (Fig. 3.5). Tarrara Bar appeared to act as a natural physical barrier to further upstream movement. The lower section of Tarrara Bar had a small gorge where the water was much deeper and slower flowing than in the adjacent upstream section. Male 195 was often detected at the upstream limit of the gorge in an eddy near a small sandbank that was used for basking. However, 195 negotiated this section of river between late February and early May 2003, most likely when river levels were elevated during the wet season, and was detected 12 km further upstream in May 2003 (Fig. 3.5).



Male		195*	190*	184	194*	192*	193	186*	188	191*	TL (m)	BM (kg)	*n*
———	195*	**87**	13	41	46	41	51	33	38	57	2.5	62	34
━━━	190*	100	**11**	64	91	55	100	100	91	100	2.6	62	19
— — —	184	100	19	**36**	100	100	50	11	86	100	3.3	91	44
-----------	194*	65	16	58	**62**	82	35	13	53	92	3.1	103	18
-·—·—·—	192*	71	12	71	100	**51**	35	8	57	100	3.1	111	22
········	193	100	25	41	50	41	**44**	66	48	73	3.2	116	45
— — — —	186*	100	38	14	28	14	100	**29**	24	62	3.3	141	43
┼┼┼┼┼┼	188	100	30	94	100	88	64	21	**33**	100	3.5	151	38
—►—	191*	75	16	54	85	76	48	27	49	**67**	4.3	337	26

* The MSLR for these animals is likely to be an underestimate.

Fig. 3.4. Mid-stream linear ranges (MSLR) of, and static interactions between, nine Ord River male *Crocodylus porosus*. Bold diagonal values in the table are the MSLR for each male in kilometres. The other values are the percentage of MSLR overlap between males.

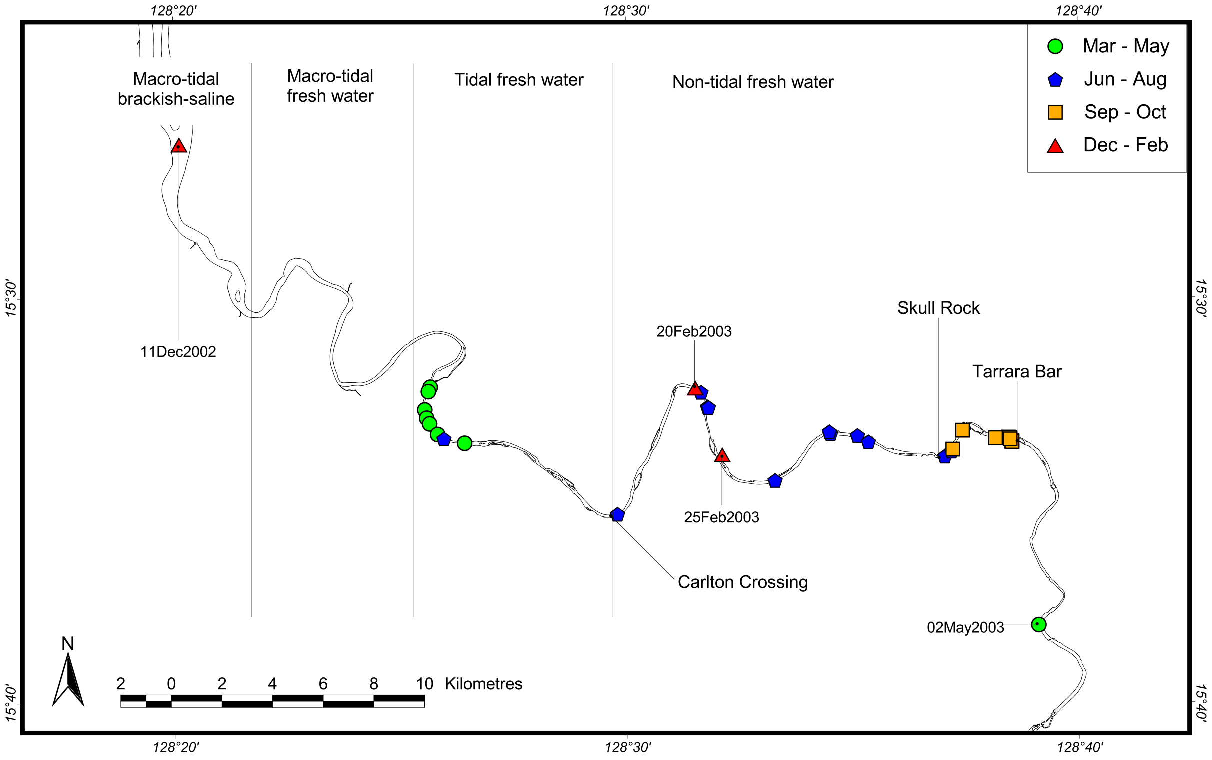


Fig. 3.5. Movements of Ord River male 195 (2.5 m, 62 kg) between May 2002 and May 2003. There was significant directional movement upstream ($P < 0.01$) but both up- and downstream movements occurred within any given period.

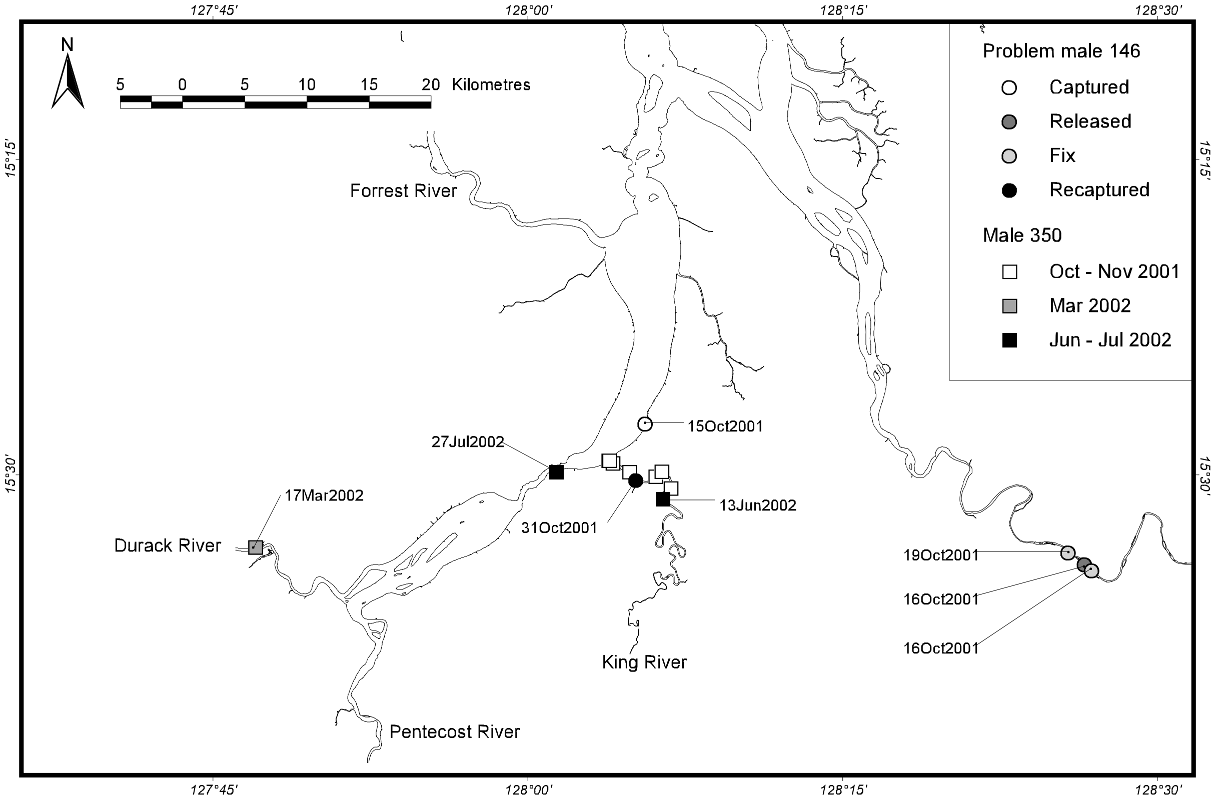


Fig. 3.6. Movements of immature *Crocodylus porosus* males 350 (2.1 m, 32 kg) and 146 (2.6 m, 59 kg). Male 146 was a problem male that was translocated from Wyndham port to the Ord River.

Movement upstream through the TF and NTF reaches required animals to traverse numerous sand, gravel or rock bars with sections of shallow, fast-flowing water, especially upstream from Carlton Crossing (see Fig. 3.5) where tidal movements no longer provide any assistance. Four of the nine Ord River males were detected upstream from Carlton Crossing at some point during the study including two of the three largest males.

3.3.5 *Males 146 and 350*

Male 146 was a 2.6 m problem male that was translocated from Wyndham Port to the Ord River (Fig. 3.6). He showed the highest rate of sustained movement detected during the study by travelling 118 km in 12 days at an average rate of 9.8 km/d to return to the area of capture. This is likely to be a conservative estimate because it assumes he entered a trap set on the King River immediately on return, having overshot the original site of capture.

Male 350 was the only crocodile detected moving to another river system during the study (Fig. 3.6). He was caught and tagged in the King River in October 2001. From October to December 2001, he spent most of his time near the mouth of the King River and was not detected in the river in January or February 2002. In March 2002 he was detected in the Durack River, approximately 44 km from the mouth of the King River. He returned to the King River in June 2002 and was detected in Cambridge Gulf in July 2002, 14 km from his previous location.

3.4 Discussion

3.4.1 *Inter-species comparisons*

Data on home ranges and movements of crocodilians are scarce for all species other than *A. mississippiensis,* providing limited opportunities for making comparisons within and among species. Furthermore, all movement studies of *A. mississippiensis* and *C. niloticus* have occurred in lacustrine systems whereas the present study investigated movements of *C. porosus* in riverine environments. Nevertheless, comparisons across habitats are informative for examining broad differences between species. Home ranges and rates of movement found for *C. porosus* in this study are generally greater than those reported for other species of crocodilian but, even so, are thought to be conservative. The highest ROM detected was 23.3 km/d for the largest male (4.3 m) tagged and a translocated juvenile male (2.6 m) travelled 118 km in 12 days. In comparison, the highest ROM reported for *A. mississippiensis* and *C. niloticus* was 8.5 km/d (Joanen and McNease 1972) and 2.9 km overnight (Hocutt *et al.* 1992) respectively, both by large (> 3 m) males. However, Bustard and Singh (1983) have reported adult gharials travelling distances of 12 km in two hours.

Male and female *C. porosus* showed distinctly different patterns of movement as do male and female *A. mississippiensis* and *C. niloticus*. Male *C. porosus* had linear ranges of between 33 (smallest stabilized estimate) and 87 (largest estimate, unstabilized) km (RCA: 626-4988 ha). However, MSLRs had stabilized for only three of nine males, with stabilized estimates ranging from 33 to 44 km. Mean rates of movement for male *C. porosus* ranged from 0.6 to 3.3 km/d but ROM appeared to be bi-modally distributed and maximum rates were much higher. There were significant differences in rates of male movement between seasons with the highest mean rates occurring during the summer wet season.

Stabilized MSLRs for *C. porosus* males are comparable with linear ranges reported for gharials, which ranged from 23 to 44 km (Bustard and Singh 1983). Australian freshwater crocodiles have much smaller linear ranges. Tucker (1997) found that pubescent male *C. johnstoni* were probably nomadic and had linear ranges of about 30 km yet all other life stages had small (< 2 km) linear ranges. Male alligator home ranges vary from 183 to 5083 ha (Joanen and McNease 1972; Goodwin and Marion 1979), which are comparable with RCAs found in this study for male *C. porosus*. The mean daily movement reported for male alligators by Joanen and McNease (1972) was 0.7 km/d, which is also comparable with the smaller *C. porosus* males. Mature male *C. niloticus* had distinct home ranges, the largest of which was 80 ha (Hutton 1989), which was considerably smaller than those found for *C. porosus*. *C. niloticus* also showed seasonal patterns of activity and were more active during the warmer months (Hutton 1989; Hocutt *et al.* 1992).

Female *C. porosus* occupied small core areas during the dry season (1.3 ± 0.9 km, 15 ± 7 ha) where mean daily movements were generally < 1 km/d. However, movements of 10.1 km/d were detected during excursions. Females travelled distances of up to 62 km to nesting habitat during the wet season. Female *A. mississippiensis* also show distinct seasonal patterns of movement. A number of authors have reported female activity being greatest during the spring breeding season (Joanen and McNease 1970; Goodwin and Marion 1979; Rootes and Chabreck 1993) although Taylor (1984) found females were most active during summer. Mean home ranges for mature female alligators range from 8 (Joanen and McNease 1970) to 56 ha (Taylor 1984) and are quite variable (1 to 256 ha) between individuals (Taylor 1984). They are generally larger than the dry season core areas of female *C. porosus* found in this study but daily movements reported for female alligators are very low. Most studies report movements of < 0.06 km/d for mature female alligators (Taylor 1984; Rootes and Chabreck 1993). The maximum daily movement reported was 0.46 km/d by Joanen and McNease (1970). In contrast, female *C. porosus* tracked during this study were usually quite mobile within their core areas and movements of up to 10.1 km/d were detected. Hutton (1989) found that mature female *C. niloticus* had home ranges of about 15 ha, which are comparable to the dry season core areas found for female *C. porosus* in this study. However, *C. niloticus* females maintained their home ranges near prime nest sites, whereas *C. porosus* females moved considerable distances to nesting habitat during the wet season.

3.4.2 *Male movements, territoriality and mating systems*

Ord River males were very mobile and showed no consistent pattern of movement. There were no obvious patterns of seasonal site selection although the four largest males tended to make more excursions to the upriver sections of their MSLRs during the late dry and wet seasons. ROM increased during the late dry season and was greatest during the wet season. However, the highest ROM detected was 23.3 km/d downriver during the dry season. Crocodiles are probably more active at night but Ord River males were quite mobile during the day. They were often observed utilizing prevailing currents to move with minimal effort, especially making upriver movements on flooding tides. Despite this observation, no significant differences in ROM were found between different tidal phases. However, more intensive investigation would be desirable to analyse whether there was differential use of tidal cycles.

Of all crocodilian species, *C. porosus* is thought to be the least tolerant of conspecifics (Lang 1987). Data showed no convincing evidence of exclusive territories held by Ord River males. MSLRs overlapped substantially and there was no obvious exclusion or spatial partitioning of home ranges (Fig. 3.4). The three largest males had centres of activity but made numerous excursions away from these areas throughout the year both up- and downriver. Their MSLRs included the activity centres of the other largest males except for male 186, whose MSLR did not include male 188’s activity centre. Nevertheless, males 186 and 188 had > 20% overlap of MSLRs. Many other large untagged males were often seen in the routine search area and had obviously overlapping MSLRs with the tagged males without any indication of tagged males being displaced or receiving injuries. It also seems unlikely that a large male could successfully exclude all other males from MSLRs that mostly exceed 30 km.

Bi-modality of male movements may indicate dynamic interactions (see Kernohan *et al.* 2001) between males, where a male spends time in a particular section of river until provoked into moving by another male, but it is also difficult to reconcile male territoriality with patterns of female movement. *C. porosus* are thought to have a polygynous mating system where dominant males mate with multiple females (Lang 1987). However, multiple paternity has been demonstrated in *A. mississippiensis* (Davis *et al.* 2001) and, more recently, genetic studies have found evidence of multiple paternity in captive *C. porosus* (Jamerlan 2003). Ord River females in this study occupied small sections of river from May to October, which included part of the courtship and mating season. A 2.7 m female dissected on 18/9/2002 had abundant mature follicles and oviducal eggs (plasma estradiol = 683 pmol/L; testosterone = 0.7 nmol/L). A 3.4 m male dissected on 9/9/2002 had enlarged testes and appeared to be in full spermatogenesis (plasma testosterone = 17 nmol/L) (see Lance 1987, 1989; Kofron 1990; Coutinho *et al.* 2000; Guillette and Milnes 2000). Females were detected making excursions during the dry season, though these were uncommon. While it remains possible that females move in search of males during the mating season, it seems more likely that males move in search of females occupying dry-season core areas. Mean male ROM increased during the late dry season and reached a maximum during the wet season. Additionally, the four largest males tended to make more excursions to the upriver sections of their MSLRs during the late dry and wet seasons. These patterns of movement were consistent with males actively seeking females during the breeding season. High mobility would be advantageous for males, enabling them to search for females occupying small core areas and would also facilitate multiple paternity in wild populations. This would make defending territories from rival males unnecessary. Size-based dominance hierarchies were clearly evident while observing interactions among Ord River crocodiles. Therefore, aggressive interactions among crocodiles are probably more likely to occur between evenly matched individuals.

3.4.3 *Site fidelity*

Most crocodiles remained within the river in which they were caught and only one animal showed any significant directional movement during the study. Furthermore male 350, which was the only animal detected moving to another river system, returned to the King River. These patterns of movement suggest at least some site fidelity, which is corroborated by genetic data. There are highly significant differences in allele frequencies between the King and Ord River populations and > 74% of individuals were designated to their source population using assignment tests (Chapter 4). Three Ord River males (191, 192 and 194) were thought to have spent much of the dry season in 2002 in the lower Ord estuary outside the routine search area. It is possible they moved into Cambridge Gulf and beyond. However, they were all detected further upriver during the late dry and wet seasons. Male 350 had been scute-marked previously but, unfortunately, no records were available to confirm his previous capture history and point of origin. It was assumed he was an escapee from the crocodile farm in Wyndham.

3.4.4 *Translocation and homing*

The tendency for translocated animals to home has been reported for a number of crocodilian species including *C. porosus* (e.g. Gorzula 1978; Webb and Messel 1978b; Webb *et al.* 1983b; Rodda 1984a). Translocated male 146 travelled 118 km in 12 days (9.8 km/d) to return to the area of capture. He was blindfolded and chemically sedated at the site of capture and was still quite heavily sedated when released. He was quite likely disorientated after release but took only a few days to recover and returned rapidly to the area of capture. This would seem to have required good navigational ability as the return path was by no means obvious (see Murphy 1981; Rodda 1985; Phillips 1996).

However, Walsh and Whitehead (1993) found that < 50% of problem crocodiles translocated from Nhulunbuy in the Northern Territory returned to the original site of capture. It is unknown whether the remainder were translocated successfully and/or killed by conspecifics and/or returned but were trap shy. Only 4 of 23 recaptured individuals had injuries attributable to other crocodiles and some were recaptured up to eight times. The probability of recapture could not be related to distance and direction of release, nor size and sex of the released animal. Frequency of recapture of individual crocodiles was also unrelated to these variables. The time between consecutive recaptures of the same crocodile was highly variable, ranging from 10 days to > 3.7 years (Walsh and Whitehead 1993). The highest ROM detected between recaptures was 3.9 km/d (Walsh and Whitehead 1993), which was quite low when compared with rates of movement detected in this study. Furthermore, release distances ranged only from 17 to 282 km by coast, which are quite small given the capacity of the species for large-scale ocean voyages (see Allen 1971; Bustard and Choudhury 1980). Homing may well be density-dependent for translocated problem animals but the data are equivocal (see Walsh and Whitehead 1993). Reciprocal translocations of electronically tagged animals of similar size and sex over different spatial scales would clarify the effectiveness of translocation as a possible solution to problem animals (Tucker *et al.* 1997).

3.4.5 *Conclusions*

Estuarine crocodiles are large, mobile and long-lived animals that interact with their environment over large spatial and temporal scales. This study has provided an insight into their movements, though the sample size and period of study were small. Data are needed from more animals of both sexes, over a more complete size range, in different geographic regions and habitat types and over a longer time frame to establish whether the patterns that have emerged are typical. It has become increasingly apparent from a number of simulation studies that large sample sizes are required to define the home range of an individual animal reliably, and that large numbers of animals from a particular class must be studied in order to make inferences about movements at the population level (see White and Garrott 1990; Garton *et al.* 2001; Kernohan *et al.* 2001). Automated telemetry systems using satellite tracking technology would be the most efficient and cost-effective approach for collecting the large amount of data required for analysing the movements of *C. porosus* in any future studies, especially in remote areas, and would be less likely to influence animal behaviour than manual tracking techniques.

4. POPULATION GENETICS

4.1 Introduction

Conservation biology is a broad and dynamic field, with a new emphasis on genetic variation in both natural and managed populations (Neigel 1996). Furthermore, the World Conservation Union recognizes the need to conserve diversity at three levels: genetic diversity, species diversity and ecosystem diversity (Frankham 1995a). Genetic techniques can be applied to conservation in many different ways. Most importantly, genetic markers are able to quantify current levels and distributions of genetic variation, which is an important determinant of population viability and evolutionary potential (Neigel 1996). They may also be used to resolve taxonomic uncertainties, define effective conservation units, provide non-destructive means to genotype endangered species, monitor inbreeding and loss of genetic variation in captive, small or fragmented populations, determine paternity and detect illegal hunting (Frankham 1995a). Moreover, genetic markers can be used indirectly to measure processes such as migration, which may be important for ecological as well as genetic reasons (Neigel 1996; Luikart and England 1999). Additionally, genetic markers can be used to identify population bottlenecks (Cornuet and Luikart 1996; Luikart *et al.* 1998a; Luikart and Cornuet 1998; Garza and Williamson 2001), which have significant implications for conservation and management of species. Identifying recently bottlenecked populations is important because bottlenecks can increase rates of inbreeding, loss of genetic variation and fixation of deleterious alleles, which reduces adaptive and evolutionary potential and increases the risk of extinction (see Cornuet and Luikart 1996; Frankham and Ralls 1998; Luikart *et al.* 1998a; Luikart and Cornuet 1998; Saccheri *et al.* 1998; Frankham *et al.* 1999; Garza and Williamson 2001).

There has been rapid progress in the development and use of molecular markers over the last decade and a number of genetic markers are now available that assay nuclear DNA directly (Davies *et al.* 1999). Microsatellite markers have become the preferred marker in many studies because they reveal high levels of genetic diversity when other markers such as allozymes are relatively impoverished (Bruford *et al.* 1996; Davies *et al.* 1999; Luikart and England 1999). For example, studies of allozymes in *Alligator mississippiensis* revealed low levels of genetic diversity (Gartside *et al.* 1977; Adams *et al.* 1980) whereas microsatellites found heterozygosities 20 times higher than values obtained using isozymes (Glenn *et al.* 1998).

Crocodylus porosus is the most widely distributed crocodilian species and suffered widespread population decline during the 20th century, principally due to commercial hunting for their hides but also from habitat destruction and persecution (Ross 1998). An estimated 270,000 to 330,000 *C. porosus* were killed in Australia alone between 1945 and 1972 (Webb *et al.* 1984a). The Western Australian population is poorly studied and historical information on the size of the population and number of animals killed during the hunting era is scarce. However by 1970, when the species was protected, hunting was no longer considered commercially viable (Bustard 1970; Burbidge 1987). A reduction of this magnitude in such a short period of time could cause a genetic bottleneck and make a population susceptible to losing a significant component of its genetic diversity. The purpose of this study was to quantify levels of genetic variation in *C. porosus* populations from three river systems in the Kimberley region of Western Australia and test for evidence of recent population bottlenecks. Some management implications of the findings are discussed.

4.2 Methods

4.2.1 *Genetic sampling*

One hundred and twenty three skin samples were collected from three river systems (Glenelg River: $n = 33$; King River: $n = 50$; and Ord River: $n = 40$) between April 2001 and September 2002 (Fig. 1.2). The mouths of the King and Ord rivers are separated by only 38 km (Fig. 1.3) whereas the Glenelg River is separated from the Ord River by > 4500 km of coastline (Fig. 1.2). The shortest marine route between the Glenelg and Ord rivers is about 690 km. Crocodiles were caught using a variety of size-dependent techniques (see Webb and Messel 1977; Walsh 1987), measured, sexed by visual inspection of the genitalia (Webb *et al.* 1984b), scute clipped to uniquely identify individual animals (see Chabreck 1963) and released. Skin samples were kept and preserved in 95% denatured ethanol. Skin tissue was digested with proteinase-K in a lysis buffer and nuclear DNA isolated using a salt extraction protocol (Miller *et al.* 1988).

DNA markers developed by FitzSimmons *et al.* (2001) were amplified using polymerase chain reaction (PCR) at nine microsatellite loci (Cj16, Cj18, Cj101, Cj104, Cj119, Cj127, Cj131, Cp10 and CUD68). PCR products from the King and Ord rivers were measured with an ABI 373 sequencer and alleles scored using Genotyper software. Samples from the Glenelg River were analysed with a Corbett Research Gel-Scan 2000 using polyacrylamide gel electrophoresis and alleles scored against known size standards with One-Dscan software. Fourteen samples from the King and Ord rivers (16%) were re-analysed using the Gel-Scan 2000 to ensure consistency of results. There were no discrepancies for the re-analysed samples at five loci, a consistent one base pair difference at one locus and a consistent two base pair difference at the remaining loci. Consequently, values for allele sizes from the Glenelg samples were adjusted where necessary to ensure comparability among samples.

4.2.2 *Population structure and differentiation*

Allele frequencies within populations were tested for conformity with Hardy-Weinberg expectations with an unbiased estimate of Fisher's exact probability for the null hypothesis using the Markov chain method described by Guo and Thompson (1992). Linkage disequilibrium between pairs of loci was tested using a similar approach (see Rousset 2001). For each locus, differences in allele frequencies among populations, including pairwise comparisons between populations, were assessed with an unbiased estimate of Fisher's exact probability for the null hypothesis that the allelic distribution was identical across populations, using the Markov chain method described by Raymond and Rousset (1995a). These tests were performed with GENEPOP software (version 3.4, Raymond and Rousset 1995b).

Genetic diversity was assessed by comparing the number of alleles (A), allelic richness (R_S), observed heterozygosity (H_O) and expected heterozygosity (H_E) among populations. A, H_O and H_E were calculated with GENEPOP (Raymond and Rousset 1995b). Because the observed number of alleles (A) is strongly dependent on samples size, R_S was calculated using rarefaction methods described by El Mousadik and Petit (1996) with FSTAT software (version 2.9.3, Goudet 1995). R_s is independent of sample size, which enables unbiased comparisons of allelic richness among populations with unequal sample sizes. The significance of differences in A, R_S, H_O, and H_E among populations were evaluated with a Kruskal-Wallis test using R software (version 1.6.2, R Development Core Team 2004).

The process of mutation underlying microsatellite evolution is complex and must be considered in developing appropriate statistics that accurately reflect genetic structuring in populations (Balloux and Lugon-Moulin 2002). At two extremes are the Infinite Alleles Model (IAM: Kimura and Crow 1964) and the Stepwise Mutation Model (SMM: Kimura and Ohta 1978), neither of which perfectly describe mutation processes at microsatellite loci

(Jarne and Lagoda 1996; Balloux and Lugon-Moulin 2002). This led to the development of the two-phase mutation model (TPM) by Di Rienzo *et al.* (1994), which assumes most mutational changes result from the addition or deletion of one repeat unit, but that mutations of larger magnitude also occur. Therefore, both traditional estimators of population subdivision: Wright's (1951; 1965) F-statistics (IAM), and microsatellite-specific estimators, Slatkin's (1995) R-statistics (SMM), are reported here (see Balloux and Lugon-Moulin 2002). Both parameters were calculated using a weighted analysis of variance approach. F_{ST} and F_{IS} were estimated with θ and f respectively (Weir and Cockerham 1984), and calculated using FSTAT (Goudet 1995). R_{ST} was estimated with ρ and calculated using R_{ST} CALC software (version 2.2, Goodman 1997). Permutation tests were used to evaluate the significance of the estimates and calculate their 95% confidence intervals. The TPM was considered when testing for population bottlenecks (see Section 4.2.5 below). Alpha levels were adjusted with a Bonferroni correction in all analyses when performing multiple comparisons (Sokal and Rohlf 1995).

4.2.3 *Assignment tests*

Assignment tests were used to calculate the probability of an individual belonging to its source population on the basis of its multilocus genotype. Individuals were assigned to populations using the Bayesian likelihood assignment criterion of Rannala and Mountain (1997) and the resampling algorithm of Paetkau *et al.* (2004) with 1000 simulations and an alpha threshold of 0.01. Where the probability of an individual belonging to any of the populations sampled was < 0.01, the individual was classified as unassigned. First generation migrants were identified using a similar approach. L_h (where L_h is the likelihood of drawing that individual's genotype from the population in which it was sampled, given the observed set of allele frequencies) was used as the test statistic because some source populations were clearly missing from the reference population (Paetkau *et al.* 2004). Assignment tests were performed using GENECLASS2 software (Piry *et al.* 2004).

4.2.4 *Gene flow*

Two indirect measures of gene flow between populations were calculated from pairwise estimates of F_{ST} and R_{ST} assuming a d-island model at equilibrium (Slatkin 1995). The number of migrants per generation (N_m) was calculated as:

$$M_R = \frac{1}{4}\left(\frac{1}{R_{ST}} - 1\right)$$

where M is the estimate of N_m and the subscript R indicates that the estimate was based on R_{ST} (Slatkin 1995). A corresponding estimate of N_m was calculated from F_{ST} as:

$$M_F = \frac{1}{4}\left(\frac{1}{F_{ST}} - 1\right)$$

Because F_{ST} was estimated with θ (Weir and Cockerham 1984) and R_{ST} with ρ (Goodman 1997), sampling considerations are already incorporated in the estimators so that the expression $(d_s - 1)/d_s$ discussed by Slatkin (1995), where d_s is the number of populations used to calculate the estimator, is obsolete for the calculation of N_m.

4.2.5 *Population bottlenecks*

Three methods were employed to test for evidence of a recent bottleneck within Kimberley populations of *C. porosus*. First, a Wilcoxon's signed rank test was applied to test for an excess of heterozygous loci under three different models of mutation assuming that populations were in mutation-drift equilibrium (Cornuet and Luikart 1996; Piry *et al.* 1999). Second, the M-ratio test of Garza and Williamson (2001) was used to test whether the average percentage of intermediate allelic states that are occupied within a locus fell below a critical level. Third, a qualitative graphical method was utilized to determine whether there was a mode-shift distortion in allele frequencies using methods described by Luikart *et al.* (1998a). The Wilcoxon and mode-shift tests were performed with BOTTLENECK software (version 1.2.02, Piry *et al.* 1999) and the *M*-ratio test with software available from: <http://www.pfeg.noaa.gov/tib/staff/carlos_garza/carlossoftware.html>.

4.2.6 *Population size*

Three methods were used to estimate effective population size (N_e) indirectly from genetic data. N_e is defined as the size of an ideal population that experiences genetic change at the same rate as the population under consideration (Waples 1991). In an ideal population, mating is random, sex ratios are equal and the variation in family size has a Poisson distribution where mean = variance = 2. First, N_e was estimated as:

$$\hat{N}_e \approx \frac{H_E}{4\mu(1-H_E)}$$

where H_E is the expected heterozygosity and μ is the rate of mutation (Kimura and Crow 1964). Estimates were calculated for mutation rates ranging from 10^{-3} to 10^{-4} (see Weber and Wong 1993; Di Rienzo *et al.* 1994; Jarne and Lagoda 1996). This method represents the long-term effective size for the Kimberley population as a whole, rather than sub-populations (Waples 1991). Second, the linkage disequilibrium method of Hill (1981) was used to estimate the current N_e for each river sampled. Third, current N_e was estimated from cohorts of hatchling crocodiles in the Glenelg and King rivers using the heterozygote-excess method of Pudovkin *et al.* (1996). Samples were insufficient to use this method to estimate N_e for the Ord River. Estimates of N_e from the linkage disequilibrium and heterozygote-excess methods were calculated with NeESTIMATOR software (version 1.2, Peel *et al.* 2004).

Indirect (genetic) estimates of population size were then compared with direct methods for the King River, which included spotlight surveys and mark-recapture data. Animals were classified into two age groups for each estimate: animals < 1 year old (hatchlings) and animals > 1 year old (non-hatchlings). Standard spotlight surveys (see Messel *et al.* 1981; Bayliss 1987) were conducted on 5/06/2001, 15/06/2001 (WMI 2001) and 26/07/2001. The mean number of animals sighted in each age group was calculated from the three surveys. Mark-recapture data were collected between June and December 2001. Recruitment occurs during the wet season (December to March) and migration was likely to be negligible within the sampling period based on genetic and radio-tracking (Chapter 3) data. Therefore, population estimates from mark-recapture data were calculated from closed population models (see Chapter 5) using Program MARK (version 3.2, White and Burnham 1999). Data were unavailable to use direct methods to estimate population sizes for the Glenelg and Ord rivers.

4.3 Results

4.3.1 *Genetic diversity and structure in Kimberley populations*

Allele frequencies for all loci conformed with Hardy-Weinberg expectations within populations and there was no significant linkage disequilibrium between any pairs of loci. A total of 53 alleles were identified of which 16 (30%) were rare (frequency < 0.05) (Table 4.1). The proportion of rare alleles within each population was 22%, 27% and 24% for the Glenelg, King and Ord rivers, respectively. Eight private alleles were found of which five occurred in the Glenelg River (12% of Glenelg River alleles), two in the Ord River (4%) and one in the King River (2%). Significant differences in allele frequencies among all populations were found for eight of nine loci analysed (Table 4.1). Furthermore, significant differences in allele frequencies were found in most pairwise comparisons of populations for the same eight loci (Table 4.1).

Genetic variation was similar in the three populations examined (Table 4.2). The number of alleles per locus ranged from 4.6 in the Glenelg River to 5.1 in the Ord River.

There were no significant differences in A, R_S, H_O and H_E among populations (Table 4.2). H_O ranged from 0.30 to 0.88, with overall values of 0.61 to 0.74 across populations. Overall F_{IS} was -0.023 (Table 4.3) and there was no indication of inbreeding in any of the populations. F_{IS} values for the Glenelg and Ord Rivers were mostly less than zero and, while values were higher in the King River, no values were significant (Table 4.2).

Overall F_{ST} and R_{ST} values were similar (0.08 and 0.06, respectively) and indicate moderate genetic differentiation (*sensu stricto* Wright 1978) among Kimberley populations of *C. porosus* (Table 4.3). This level of subdivision was consistent across pairwise comparisons of populations for both parameters, as were inferred patterns of gene flow (Table 4.4). Estimates of migration ranged from 2.0 to 4.8 migrants per generation with highest rates occurring between the Ord and King rivers (4.8 and 4.3 for F_{ST} and R_{ST}, respectively). Assuming a generation time of 15 years (see Webb *et al.* 1987), estimated rates of migration would equate to about one animal every three years between the Ord and King rivers to one animal every five to seven years between the Glenelg and the Ord/King rivers (Table 4.4).

4.3.2 *Assignment of individuals*

Ninety-nine individuals (80%) were assigned to their source population (Table 4.5). One individual, Glenelg River female 250 (total length [TL] = 110 cm), was unlikely to belong to any of the reference populations sampled and was also identified as a first generation migrant ($P \leq 0.01$). Four more individuals were identified as first generation migrants: King River male 58 ($P \leq 0.01$, TL = 93 cm); King River male 123 ($P \leq 0.01$, TL = 135 cm); Ord River female 128 ($P \leq 0.01$, TL = 178 cm); and Ord River female 160 ($P \leq 0.01$, TL = 101 cm). From the three reference populations sampled, the most likely population of origin was the Ord River for King River male 123; the Glenelg River for Ord River female 128; and the King River for Ord River female 160. King River male 58 was unlikely to have originated from any of the reference populations sampled based on P-values.

Table 4.1. Allele frequencies at nine microsatellite loci for three Western Australian populations of *Crocodylus porosus*. Allele designation is the molecular size in base pairs.

Locus	Allele	Glenelg River ($n = 33$)	King River ($n = 50$)	Ord River ($n = 40$)
Cj16 *	156	0	0.040	0.013
Glenelg & King *ns*	158	0.485	0.290	0.613
Glenelg & Ord *ns*	162	0	0.010	0.013
King & Ord *	164	0.318	0.460	0.275
	168	0.182	0.190	0.075
	183	0	0.010	0.013
	190	0.015	0	0
Cj18 ***	186	0.045	0.230	0.075
Glenelg & King ***	208	0.091	0.300	0.050
Glenelg & Ord ***	210	0.197	0	0
King & Ord ***	214	0.167	0.350	0.400
	218	0.500	0.120	0.475
Cj101 ***	351	0.250	0.030	0.050
Glenelg & King ***	357	0	0.040	0.013
Glenelg & Ord ***	363	0.188	0.010	0.013
King & Ord *	365	0.047	0.020	0.075
	367	0.234	0.790	0.538
	369	0.219	0.060	0.250
	373	0.062	0.050	0.062
Cj104 **	207	0	0.190	0.225
Glenelg & King **	209	0.379	0.220	0.325
Glenelg & Ord **	211	0.621	0.590	0.450
King & Ord *ns*				
Cj119 **	178	0.500	0.580	0.637
Glenelg & King ***	180	0.182	0.180	0.175
Glenelg & Ord *ns*	187	0.045	0.210	0.038
King & Ord *	189	0.273	0.030	0.150
Cj127 ***	355	0.424	0.260	0.150
Glenelg & King **	357	0.061	0.070	0.100
Glenelg & Ord ***	365	0	0.080	0.250
King & Ord *	369	0.303	0.400	0.200
	371	0	0	0.013
	373	0.045	0.160	0.237
	375	0.045	0.010	0
	389	0.121	0	0.025
	398	0	0.020	0.025
Cj131 *ns*	232	0.045	0	0
Glenelg & King *ns*	234	0.061	0.010	0.038
Glenelg & Ord *ns*	238	0.106	0.160	0.287
King & Ord *ns*	242	0.303	0.190	0.175
	244	0.273	0.370	0.287
	246	0.212	0.270	0.200
	248	0	0	0.013
Cp10 ***	196	0.333	0.080	0.075
Glenelg & King **	198	0.197	0.290	0.087
Glenelg & Ord ***	202	0.273	0.520	0.625
King & Ord *ns*	204	0.197	0.110	0.213
CUD68 ***	120	0	0.010	0
Glenelg & King ***	121	0.030	0	0
Glenelg & Ord ***	136	0	0.130	0.062
King & Ord *ns*	138	0	0.360	0.387
	142	0.576	0.060	0.112
	144	0.379	0.440	0.438
	146	0.015	0	0

* $P \leq 0.001$; ** $P \leq 0.0001$; *** $P \leq 0.00001$; *ns* = not significant

For individual loci over all populations: $\alpha = 0.05/(9 \text{ loci}) = 0.0056$

For pairwise comparisons of populations per locus: $\alpha = 0.05/(9 \text{ loci} \times 3 \text{ pairwise comparisons}) = 0.0018$

Table 4.2. Nuclear genetic variation and inbreeding coefficients for three Western Australian *Crocodylus porosus* populations by locus and river system.

	Glenelg River (n = 33)					King River (n = 50)					Ord River (n = 40)				
Locus	A	R_S (n = 32)	H_O	H_E	F_{IS}	A	R_S (n = 32)	H_O	H_E	F_{IS}	A	R_S (n = 32)	H_O	H_E	F_{IS}
Cj16	4	3.97	0.64	0.64	0.006	6	5.27	0.66	0.67	0.020	6	5.40	0.40	0.55	0.275
Cj18	5	5.00	0.79	0.68	-0.156	4	4.00	0.76	0.73	-0.045	4	4.00	0.65	0.61	-0.060
Cj101	6	6.00	0.88	0.81	-0.087	7	6.45	0.30	0.37	0.192	7	6.60	0.80	0.64	-0.246
Cj104	2	2.00	0.58	0.48	-0.209	3	3.00	0.52	0.57	0.094	3	3.00	0.73	0.65	-0.118
Cj119	6	6.00	0.70	0.65	-0.073	7	6.51	0.60	0.59	-0.013	8	7.72	0.55	0.55	-0.008
Cj127	6	6.00	0.76	0.72	-0.058	5	4.64	0.70	0.74	0.058	6	5.79	0.83	0.82	-0.009
Cj131	4	4.00	0.85	0.78	-0.084	4	4.00	0.72	0.74	0.022	4	4.00	0.70	0.77	0.095
Cp10	4	4.00	0.88	0.75	-0.178	4	3.96	0.62	0.63	0.021	4	3.99	0.60	0.56	-0.076
CUD68	4	3.97	0.61	0.53	-0.142	5	4.64	0.58	0.66	0.126	4	4.00	0.75	0.65	-0.156
Mean	4.6	4.55	0.74	0.67		5.0	4.72	0.61	0.63		5.1	4.95	0.67	0.64	
All loci					-0.105					0.044					-0.035

A = number of alleles (*ns*); R_S = allelic richness (*ns*); H_O = observed heterozygosity (*ns*) and H_E = expected heterozygosity (*ns*).
ns = no significant difference among populations.

Table 4.3. Inbreeding coefficients across three *Crocodylus porosus* populations for nine microsatellite loci. Values in parentheses are the 95% confidence interval of the estimate.

Locus	F_{IS}	F_{ST}	R_{ST}
Cj16	0.089	0.055	0.044
Cj18	-0.079	0.125	0.177
Cj101	-0.072	0.154	0.108
Cj104	-0.052	0.036	0.055
Cj119	-0.029	0.036	0.015
Cj127	0.005	0.058	-0.005
Cj131	0.017	0.011	0.024
Cp10	-0.069	0.080	0.104
CUD68	-0.030	0.154	0.043
All loci	-0.023	0.080* (0.048 – 0.114)	0.063** (0.049 – 0.102)

* $P < 0.001$
** $P < 0.0001$

Table 4.4. Pairwise comparison matrix of multilocus F_{ST}/N_m (below the diagonal) and R_{ST}/N_m (above the diagonal) values among three *Crocodylus porosus* populations in Western Australia, where N_m is an indirect estimate of the number of migrants per generation. Values in parentheses are the 95% confidence interval of the estimate.

	Glenelg River ($n = 33$)	King River ($n = 50$)	Ord River ($n = 40$)
Glenelg River	—	0.066** (0.044 – 0.113) 3.5 (2.0 – 5.4)	0.073** (0.050 – 0.122) 3.2 (1.8 – 4.7)
King River	0.110* (0.050 – 0.174) 2.0 (1.2 – 4.8)	—	0.055** (0.032 – 0.109) 4.3 (2.0 – 7.5)
Ord River	0.084* (0.043 – 0.131) 2.7 (1.7 – 5.6)	0.050* (0.023 – 0.081) 4.8 (2.8 – 10.6)	—

* $P < 0.001$
** $P < 0.0001$

Table 4.5. Number of individuals assigned to their population of origin based on the likelihood of multilocus genotypes.

Source population	Assigned population				Proportion
	Glenelg River (*n*)	King River (*n*)	Ord River (*n*)	Unassigned (*n*)	correctly assign. (%)
Glenelg River (*n* = 33)	32	0	0	1	97
King River (*n* = 50)	2.5	36	11.5	0	72
Ord River (*n* = 40)	3	6	31	0	80
Overall					80

4.3.3 *Evidence for bottlenecks*

Results of Wilcoxon tests for recent population bottlenecks varied with the model of mutation (Table 4.6). The Glenelg River showed a significant heterozygosity excess at most loci for all three models of mutation. The Ord River showed a significant heterozygosity excess under the IAM but results for other models of mutation were not significant. The King River showed a heterozygosity excess at the majority of loci but the results of Wilcoxon tests were insignificant (Table 4.6). Mean values of M were significantly less than critical values indicating a loss of intermediate alleles and a recent bottleneck in all populations examined. However, mode-shift tests did not show a distortion in allele frequency distributions for any of the populations tested.

4.3.4 *Effective population size* (N_e)

Under the assumptions of the IAM (Kimura and Crow 1964), estimates of the long-term N_e for the Kimberley *C. porosus* population range from about 500 to 5,000 animals (Table 4.7). Estimates based on the linkage disequilibrium method of Hill (1981) suggest the current N_e ranges from about 27 in the Glenelg River to about 78 in the King River. The heterozygosity-excess method of Pudovkin *et al.* (1996) estimates the current N_e is about four in the Glenelg River and about 13 in the King River (Table 4.7). The N_e/N_c ratio based on the method of Pudovkin *et al.* (1996) and mark-recapture estimates for the King River is ~ 0.19 for the non-hatchling population and ~ 0.08 for the entire population, where N_c is the census population size (see Frankham 1995b). The sex ratio in all populations was heavily skewed (Table 4.7).

Table 4.6. Results of tests for a recent bottleneck in three *Crocodylus porosus* populations from Western Australia using data from nine microsatellite loci.

Test	Mutation model [a]	Parameters [b]	Glenelg River ($n = 33$)	King River ($n = 50$)	Ord River ($n = 40$)
Wilcoxon	IAM		9:0 ($P < 0.001$) [c]	8:1 ($P < 0.065$)	7:2 ($P < 0.005$)
	TPM	$\sigma^2 = 12$; $p = 0.95$	7:2 ($P < 0.007$)	6:3 ($P < 0.249$)	5:4 ($P < 0.411$)
	SMM	$p = 1.0$	7:2 ($P < 0.019$)	5:4 ($P < 0.411$)	5:4 ($P < 0.545$)
M-ratio	TPM	$p = 0.90$; $\Delta_g = 3.5$; $\mu = 5 \times 10^{-4}$	$\bar{M} = 0.543$	$\bar{M} = 0.570$	$\bar{M} = 0.625$
		$N_e = 50$	$M_c = 0.839$ ($P = 0$) [d]	$M_c = 0.841$ ($P = 0$)	$M_c = 0.841$ ($P = 0$)
		$N_e = 250$	$M_c = 0.802$ ($P = 0$)	$M_c = 0.802$ ($P = 0$)	$M_c = 0.802$ ($P = 0$)
		$N_e = 500$	$M_c = 0.773$ ($P = 0$)	$M_c = 0.773$ ($P = 0$)	$M_c = 0.775$ ($P < 0.001$)
		$N_e = 1000$	$M_c = 0.733$ ($P = 0$)	$M_c = 0.742$ ($P < 0.001$)	$M_c = 0.742$ ($P < 0.001$)
Mode-shift	Not applicable		No	No	No

[a] IAM = Infinite alleles model; TPM = Two-phase model; SMM = Stepwise mutation model.

[b] σ^2 = variance; p = proportion of one-step mutations; Δ_g = the average size of non one-step mutations; μ = mutation rate (/locus/generation); and N_e = effective population size prior to the bottleneck occurring.

[c] The ratio is the number of loci with a heterozygosity excess ($H_E > H_{eq}$) to the number of loci with a heterozygosity deficit ($H_E < H_{eq}$).

[d] M_c = the critical value of M, where 95% of equilibrium values of $M > M_c$.

Table 4.7. Comparisons of population estimates using a variety of census techniques. Genetic estimates are based on nine microsatellite loci. Values in parentheses are the 95% confidence interval unless otherwise specified.

Population estimate	Method	Parameters	Glenelg River	King River	Ord River
Genetic	$\hat{N}_{\mathrm{e}}$ [a]	$\mu = 10^{-3} – 10^{-4}$	508 – 5,076	426 – 4,257	444 – 4,444
	$N_{\mathrm{e}}(D)$ [b]		27 (20 – 40; $n = 33$)	78 (50 – 151; $n = 50$)	40 (29 – 59; $n = 40$)
	$N_{\mathrm{e}}(H_{\mathrm{x}})$ [c]		4 ($\infty – \infty$; $n = 10$)	13 ($\infty – \infty$; $n = 18$)	NA
Surveys 2001 ($n = 3$)	Spotlight	< 1 year old	NA	67 ± 13 (SD)	NA
		> 1 year old	NA	65 ± 17 (SD)	NA
Total animals caught in 2001	Capture data	< 1 year old	10 (2002)	89 (+ 5 in 2002)	5 (2001/2)
		> 1 year old	23 (2002)	50 (+ 18 in 2002)	59 (2001/2)
Mark-recapture 2001	Program MARK [d]	< 1 year old	NA	91 (89 – 94)	NA
		> 1 year old	NA	69 (50 – 95)	NA
Sex Ratio (Females per male)	Capture data	< 1 year old	0.43 ($n = 10$)	0.49 ($n = 94$)	1.50 ($n = 5$)
		> 1 year old	1.09 ($n = 23$)	0.33 ($n = 68$)	0.55 ($n = 59$)

[a] This method provides an estimate of the long-term effective population size of the Kimberley population and is not an estimate of N_{e} for individual sub-populations (Waples 1991). H_{E} for pooled sub-populations is 0.68 suggesting the long-term N_{e} for the Kimberley ranges from 542 to 5,420.

[b] This method estimates the effective population size using the linkage disequilibrium method of Hill (1981).

[c] This method estimates the effective population size using the heterozygote-excess method of Pudovkin *et al*. (1996). Infinity values indicate the signal is obscured by sampling error, which is associated with small samples of loci or individuals (Luikart and Cornuet 1999).

[d] See Chapter 5.

4.4 Discussion

4.4.1 *Population structure and gene flow*

Oceans generally lack obvious barriers to migration and dispersal despite the potential influence of currents, sea floor topography and other geographical features (Waples 1998). Therefore, the habitat of *C. porosus* could be considered as continuous via coastal and marine environments. Moreover, *C. porosus* is regarded as the crocodilian that most readily takes to the sea because it is extremely euryhaline, even when recently hatched, and can maintain homeoosmotic conditions over a broad range of salinities (0 to 60‰) due to the presence of lingual salt glands (Taplin and Grigg 1981) and a skin of low permeability that provides insulation from osmotic gradients in the surrounding environment (Taplin 1988; Taplin and Grigg 1989). There are numerous reports of individuals undertaking ocean voyages over hundreds of kilometres (e.g. Allen 1974; Bustard and Choudhury 1980).

Population differentiation is dependent on levels of gene flow and should therefore be related to the dispersal abilities of species. In a meta-analysis involving 333 species across 20 animal groups, Bohonak (1999) found a strong negative correlation between F_{ST} and dispersal ability as expected. *C. porosus* appears to be one of the more mobile species of crocodilian (Chapter 3) so low levels of differentiation are predicted. However, panmixia is rare in natural populations (Hartl and Clark 1997) and moderate genetic differentiation (*sensu stricto* Wright 1978) was found among *C. porosus* populations in this study ($F_{ST} = 0.08$, $R_{ST} = 0.06$).

While population differentiation was considered to be only moderate, differences in allele frequencies among populations were highly significant (Table 4.1). Furthermore, assignment tests designated > 80% of individuals to their population of origin. Only 5 of 123 individuals were identified as probable first generation migrants. Given the potential vagility of *C. porosus* and the limited geographic barriers to dispersal posed by the marine and coastal environments, the significance of differences in allele frequencies among populations found here would suggest at least some site fidelity, or most migrants do not contribute substantially to gene flow. This is corroborated by the results of assignment tests and also supported by radio-tracking data that found most animals stayed within the river system in which they were tagged (Chapter 3), at least in the short term.

Many marine species exploit opportunities for dispersal in the marine environment with extended pelagic larval stages and/or substantial migratory capabilities as adults (Waples 1998). About 60% of species of marine fishes reviewed by Ward *et al.* (1994) had an $F_{ST} < 0.03$ indicating low levels of population differentiation and high levels of gene flow (see Waples 1998). F_{ST} values for *C. porosus* in this study are higher than those of most marine fishes but much lower than average values reported for other species of reptile ($\bar{F}_{ST} \approx 0.26$) and also mammals ($\bar{F}_{ST} \approx 0.24$) (Ward *et al.* 1992). Interestingly, they are similar to average values reported for birds ($\bar{F}_{ST} \approx 0.05$) (Evans 1987), which are also a group with potentially high vagility. F_{ST} values for *C. porosus* are similar to those reported by Dever *et al.* (2002) for *C. moreletii*. However, studies of *A. mississippiensis* at similar geographic scales found much greater differentiation among populations than exists between *C. porosus* populations in the east and west Kimberley. F_{ST} values between alligator populations in the eastern and western parts of their range were 0.13 to 0.30 (Davis *et al.* 2002), indicating greater gene flow occurs between *C. porosus* populations.

F_{ST}- and R_{ST}-based estimates of migration suggest similar patterns of gene flow among Kimberley populations. Higher rates of migration occurred between the two closest rivers with a slight isolation by distance (Wright 1943, 1946) effect between the east and west Kimberley populations (Table 4.4). However, the magnitude of the effect was not concordant with the orders of magnitude difference in geographic scale. Isolation by distance has been reported for *A. mississippiensis* (Davis *et al.* 2002; Ryberg *et al.* 2002) and *C. moreletii*

(Dever *et al.* 2002). F_{ST}-estimates showed slightly better agreement with geographic scale than R_{ST}-estimates but the difference was minor. In a simulation study, Gaggioti *et al.* (1999) found that F_{ST}-based estimates of N_m were always better than R_{ST}-based estimates when sample sizes are moderate or small (≤ 10) and the number of loci scored is low (< 20). Also, the performance of F_{ST}-based estimates is thought to improve as N_m becomes large because mutation plays a lesser role in creating local differentiation than genetic drift (Slatkin 1995). Assignment tests corroborate patterns of gene flow inferred from indirect estimates as more individuals were mis-assigned between the Ord and King rivers, indicating greater migration than occurs with the Glenelg River (Table 4.5).

One of the major effects of migration on the genetic structure of populations is to reduce divergence that may otherwise occur as a result of genetic drift or natural selection (Neigel 1996). Gene flow also reduces inbreeding and may allow the spread of favourable adaptations among populations (Neigel 1996). Between one and ten migrants per generation is considered desirable to minimize the loss of polymorphism and heterozygosity within subpopulations while allowing for divergence in allele frequencies among subpopulations (Mills and Allendorf 1996).

Indirect estimates of gene flow for *C. porosus* are within this range but should be treated cautiously. In a study of population structure in Australian barramundi, Keenan (1994) concluded dimensionality was fundamentally important in the development of population structure and recommended application of the one-dimensional stepping-stone model in studies of populations distributed within river systems. Application of the island model, which effectively is a two-dimensional stepping stone model, is likely to underestimate rates of migration by up to two orders of magnitude (Keenan 1994). Whitlock and McCauley (1999) also criticised the estimation of N_m using Wright's (1931) formula because real populations were very likely to violate the assumptions of the underlying mathematical model and concluded estimates were likely to be correct only within a few orders of magnitude. Furthermore, genetic estimates of migration are measures of gene flow, where migrants have successfully reproduced in a new location (Neigel 1996), so actual rates of migration are likely to be higher (Whitlock and McCauley 1999). Even so, assignment tests, which assess dispersal more so than gene flow, identified $< 5\%$ of individuals as being probable first generation migrants.

Genetic methods for estimating migration generally do not specify directionality (Neigel 1996) but assignment tests have the potential to identify populations as sources or sinks (see Pulliam 1996; Waser and Strobeck 1998; Luikart and England 1999). Using a Bayesian likelihood method and where $H \approx 0.6$, a 100% correct assignment rate can be achieved by scoring about 10 microsatellite loci on 30 to 50 individuals from each of ten reference populations when F_{ST} is near 0.1 (Cornuet *et al.* 1999). From limited data here, migration between the Ord and King rivers appears to be bi-directional (Table 4.5) and dispersal does not appear to be sex-biased. Moreover, dispersal appears to occur across a broad range of size classes when considered in combination with other data on movements (e.g. see Allen 1974; Bustard and Choudhury 1980; Walsh and Whitehead 1993). However, data were insufficient to draw firm conclusions given the comparatively low rates of inferred migration and inadequate replication among different size and sex classes within sub-populations.

4.4.2 *Genetic diversity*

Genetic diversity was similar across all three rivers studied, with no significant differences in allelic richness or observed heterozygosity among Kimberley populations (Table 4.2). The number of alleles per locus was similar to that found for *Crocodylus moreletii* (Dever *et al.* 2002) but heterozygosity was > 30% higher for *C. porosus*. However, Dever *et al.* (2002) studied population subdivision in *C. moreletii* at a much smaller spatial scale. Observed heterozygosities in *C. porosus* were similar to those found in *A. mississippiensis* studied over large geographic scales (Davis *et al.* 2000; Davis *et al.* 2002; Ryberg *et al.* 2002) but the number of alleles per locus was 33% to 69% greater in *A. mississippiensis*, although estimates were not corrected for unequal sample sizes. The comparatively low allelic richness in combination with high heterozygosities may be the result of a recent bottleneck in Kimberley populations of *C. porosus* (see Section 4.4.3 below, and Cornuet and Luikart 1996).

4.4.3 *Population bottlenecks*

When inferring population processes from genetic data, it should be kept in mind that it is difficult to discriminate between current and historical processes and most species in need of conservation have undergone dramatic changes in population size, structure and connectivity in the recent past (Moritz 1995). There is compelling evidence to suggest that all populations sampled have suffered from a recent bottleneck, which has caused a loss of alleles (Table 4.6). Any population where $M < 0.68$ can be considered as having gone through a recent reduction in size when seven or more loci are used and there is confidence in the assumed model of mutation (Garza and Williamson 2001). Furthermore, significant heterozygosity excess (see Cornuet and Luikart 1996) was present in the Glenelg River for all three mutation models tested. Results for the other river systems varied with the model of mutation.

Strictly speaking, heterozygosity excess has been demonstrated only for loci evolving under the IAM and may not be observed where a locus evolves under a strict one-step, stepwise mutation process (Cornuet and Luikart 1996; Piry *et al.* 1999). The Ord River had a significant heterozygosity excess under the IAM and it would be prudent to conclude from this test also that the population has suffered from a recent bottleneck (see Cornuet and Luikart 1996). There is some evidence for excess heterozygosity in the King River but the test results were not significant. Both the *M*-ratio and heterozygosity excess tests rely on the differential rate of post-reduction decline in the number of alleles and heterozygosity. The major difference is that the *M*-ratio method measures and compares these two indices directly and then compares the results with a test that is mutation model-dependent, whereas the method of Cornuet and Luikart (1996) relates the same two indices with a mutation model-dependent estimation (Garza and Williamson 2001).

Allele frequencies did not show a mode-shift distortion in any of the populations examined (Table 4.6). The test has a power of 0.78 to detect a mode-shifted distribution after a bottleneck of < 20 breeding individuals but will not detect a mode-shift about 22% of the time when eight to ten polymorphic microsatellite loci are screened (Luikart *et al.* 1998a). Furthermore, it may take five to ten generations for a mode-shift distortion to occur after a bottleneck of 20 breeders (Luikart *et al.* 1998a). The most recent and widespread population decline of *C. porosus* ended 30 years ago when the species was protected (Webb *et al.* 1984a). This amounts to less than three generations, which may not be long enough for a mode-shift distortion to manifest. It is also possible that the relatively high rates of migration, estimated from fixation indices, may have mitigated some of the genetic consequences of a bottleneck (Luikart *et al.* 1998a). In contrast, however, it is also possible that high rates of migration may lead to a false bottleneck signature (Pope *et al.* 2000). More sensitive tests are available than the ones applied here but they require historical data because they test for temporal changes in allele frequencies and for the loss of alleles (Luikart *et al.* 1998b; Luikart *et al.* 1999; Spencer *et al.* 2000).

There is likely to have been a loss of genetic diversity from the Kimberley population of *C. porosus* due to post-1945 population decline. Given that bottlenecks can seriously compromise adaptive and evolutionary potential, further investigation would be valuable. First, to quantify allelic richness and heterozygosities in museum specimens collected prior to

1945 (if sufficient material is available), which would confirm whether there have been historical changes; and second, to monitor changes in genetic diversity in forthcoming generations, which will also determine whether a mode-shift distortion occurs.

4.4.4 *Management implications*

While the *C. porosus* population in the Kimberley appears to be recovering (Messel *et al.* 1987), annual surveys conducted in Cambridge Gulf since 1989 indicate there has been an increasing trend only since 1999/2000 (WMI 2003). The increase in the King River is probably due to a reduction in harvesting between 2000 and 2002 (WMI 2003). The King River is the only system surveyed annually by boat and spotlight (see Messel *et al.* 1981; Bayliss 1987), whereas the remainder of the Gulf has been surveyed from the air by helicopter. The value of aerial surveys has been questioned by Stirrat *et al.* (2001) because they are thought to have insufficient power to detect significant population changes within management time frames.

Genetic data suggest the long-term N_e in the Kimberley region was probably quite large (Table 4.7). Indeed, large effective population sizes are required to maintain high levels of heterozygosity (Keenan 1994). The accuracy of the estimate using the method of Kimura and Crow (1964) is only as precise as the estimated mutation rate (Waples 1991) but indicates the Kimberley had an N_e ranging from about 500 to 5,000 animals historically. This translates into a census population size ranging from 2,700 to 27,000 non-hatchlings based on N_e/N_c ratios calculated from King River data. However, the N_c for the Kimberley could have been in excess of 50,000 using either the N_e/N_c ratio calculated for the entire King River population or an average N_e/N_c ratio of 0.1 calculated across a broad range of taxa (see Frankham 1995b). This method is more sensitive when estimating large population sizes than small, whereas the reverse is true for the other methods used (Waples 1991).

Estimates of N_e using the linkage disequilibrium of Hill (1981) are reasonably high, particularly for the King River where the N_e is greater than the census size for non-hatchlings, and may be influenced by historical population sizes given that there have been fewer than three generations since protection. However, N_e estimated from cohorts of hatchling crocodiles using the heterozygosity excess method (Pudovkin *et al.* 1996) indicate the current N_e of the breeding population in the Glenelg and King rivers is low (Table 4.7). In fact, it is substantially lower than N_e estimated from linkage disequilibrium and may be indicative of an N_e that continues to decline due to small population sizes. Data for estimating N_e from linkage disequilibrium comprised 33 to 50 samples per population analysed at nine microsatellite loci so the estimate should be reasonably robust (but see Waples 1991; Bartley *et al.* 1992; Schwartz *et al.* 1998). However, sample sizes for estimating N_e using the heterozygosity-excess method were probably insufficient to provide a reliable estimate (Luikart and Cornuet 1999) and may have been confounded by a recent genetic bottleneck (Cornuet and Luikart 1996). Regardless, sex ratios in all populations sampled are heavily skewed, especially in the King River (Table 4.7). While skewed sex ratios are not uncommon in crocodilian populations (Thorbjarnarson 1997; Lance *et al.* 2000), they further reduce N_e (Frankham 1995b).

There is some anecdotal evidence to support the hypothesis that the size of the Kimberley population historically was larger than previously thought. Bustard (1970) reported > 3000 animals were shot between 1963 and 1965 in the Admiralty Gulf region alone, and four hunters shot 582 animals in Collier Bay in four months in 1961 (Fig. 1.2). Furthermore, an experienced shooter from the Northern Territory, who had hunted the Mary River which was renowned for its high density of crocodiles, described the west Kimberley in the early 1960s as “a croc shooter’s paradise” and the “last untouched place for shooting” where “you could get as many as you wanted in a night” (T. Baldwin, personal communication). In one five-month trip in 1961, T. Baldwin collected about 600 skins between Derby and the Prince Regent River (Fig. 1.2). In contrast, the total non-hatchling *C. porosus* population in the Kimberley was estimated to be about 2,500 in 1986 (Messel *et al.* 1987), 16 years but only one generation following protection.

It has been suggested that the Kimberley is poor habitat for *C. porosus* due to the geomorphology of its rivers and, consequently, its carrying capacity much less than that of the Northern Territory (Burbidge 1987). However, genetic data suggest the long-term N_e of the Kimberley was probably quite large and there is some anecdotal evidence to support this. The region is sparsely populated and mostly undeveloped so it is unlikely food resources or habitat degradation are factors limiting the size or recovery of the Kimberley population. Like all ectotherms, *C. porosus* has a low energy demand and does not require large quantities of food (see Pough 1980). The observed rate of increase ($\bar{r}$) for the Northern Territory population was estimated to be 6.5% by Webb and Manolis (1993), which amounts to a population that doubles about every 11 years. Of the Kimberley systems that were monitored by Messel *et al.* (1987), a comparable rate of increase was evident in the Prince Regent and Roe Rivers (Fig. 1.2) but not throughout the Kimberley as a whole. It seems most likely that paucity of nesting habitat is a significant factor limiting recovery of *C. porosus* populations in the Kimberley. What is clear is that there has been a significant reduction in the size of the Kimberley population and a probable loss of genetic diversity.

The significant genetic structure among Kimberley populations and results of assignment tests suggest *C. porosus* has a tendency for site fidelity to natal rivers. Similar results from other *C. porosus* populations in Australia (N. FitzSimmons, unpublished data) suggest that Northern Territory populations are not contributing substantially to recovery of the Kimberley population. It would be prudent to manage the Western Australian population of *C. porosus* conservatively until a sustained and long-term recovery has been demonstrated, and priority should be given to identifying and protecting areas of significant nesting habitat.

Finally, the definition of conservation units within species is fundamental to prioritize and conduct management (Moritz 1995). While there has been considerable effort expended on monitoring wildlife populations, all too often little consideration has been given to defining the appropriate geographic scale (Moritz 1994a). Moritz (1994b) defined Management Units (MUs) as populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles. He suggested MUs could be treated as synonymous with the term "stock" used in fisheries biology, and should be used primarily for short-term management issues. Data suggest *C. porosus* has fidelity to individual river systems. Therefore, it is recommended that MUs in the Kimberley be demarcated at the level of river catchment boundaries. Samples were collected from only three river systems and more rivers need to be sampled to determine whether the patterns that have emerged are typical throughout the Kimberley. However, given the results of assignment tests and the significance of differences in allele frequencies between the Ord and King rivers, where the river mouths are separated by only 38 km, delineation of MUs at the catchment boundary level would seem appropriate. This provides a clear and simple definition for managers to identify the appropriate geographic scale for managing *C. porosus* populations in the Kimberley region.

5. SURVIVAL AND GROWTH OF HATCHLINGS

5.1 Introduction

Crocodylus porosus is the most widely distributed crocodilian species and suffered widespread population decline during the 20th century, principally as a result of commercial hunting for their hides but also from habitat destruction and persecution (Ross 1998). An estimated 270,000 to 330,000 animals were killed in Australia before the species was protected in the early 1970s (Webb *et al.* 1984a). The population recovered strongly in the Northern Territory following protection and adding value to the resource through sustainable use became an integral part of the management strategy throughout Australia (Webb and Manolis 1993). Data on the Western Australian population are limited and suggest the population has increased in some systems but has decreased in others (Messel *et al.* 1987; WMI 2003).

Monitoring populations plays a critical role in animal ecology and wildlife conservation (Gibbs 2000). Quantifying changes in abundance is the key to understanding temporal dynamics in animal populations, assessing the effectiveness of management strategies for harvested or endangered species, documenting compliance with regulatory requirements and detecting incipient changes (Gibbs 2000). Crocodiles are *K*-selected organisms whose life-history strategies are characterized by slow development, long life, and delayed and repeated reproduction where the risk of reproductive failure is minimized through repeated breeding rather than by maximizing reproductive output (Tucker 1995). Consequently, crocodiles have limited capacity to compensate for unregulated long-term harvests (Tucker 1995). Vital statistics (survivorship, fecundity, growth rates and age structure) must be quantified for the sound management of commercially exploited species, otherwise the cumulative impacts of harvesting will be difficult to predict.

Despite *C. porosus* having been exploited commercially in Australia for nearly two decades, demographic parameters for the species remain unquantified. Survivorship is unknown for most life history stages other than eggs (e.g. Webb *et al.* 1977; Magnusson 1982; Webb *et al.* 1983c). Mortality of hatchling crocodiles is generally reported as high during the first year of life but, where the method of estimation has been stated, it has failed to account for the probability of recapture. This study quantifies survival and growth for a cohort of hatchling crocodiles in the King River and discusses some of the implications of behavioural responses to capture for monitoring crocodile populations.

5.2 Methods

5.2.1 *Mark-recapture study*

A mark-recapture study of the *C. porosus* population in the King River (Fig. 1.3) was initiated in 2001 and ended in 2002. The study was originally planned as a robust design experiment (Pollock 1982) with three primary sampling periods (June/July 2001, October/November 2001 and June/July 2002) and six secondary sampling periods of four catch nights each (3 x 6 x 4 = 72 total catch nights). Unfortunately, recapture probabilities during 2002 were confounded by the removal of an unknown number of animals to stock the local crocodile farm, so 2002 data were omitted from mark-recapture analyses. However, morphometric data collected in 2002 were used to examine growth rates. Because capture probabilities were generally low, secondary sampling periods were pooled into six periods of eight catch nights each for analysis of the 2001 data.

Crocodiles were caught at night from a small (4.5 m) boat using a variety of size-dependent techniques that included hand-catching small animals (< 1.2 m), noosing animals between 1.2 and 2.2 m and harpooning animals > 2.2 m (see Webb and Messel 1977; Walsh 1987). Cage traps were trialled during October/November 2001 with limited success. Spring tidal amplitudes of up to 8 m made the placement of traps on banks inefficient along large sections of river and the use of floating traps difficult, due to tidal flows. Animals were caught along a 42 km reach of river that has been surveyed by spotlight annually since 1989 (e.g. WMI 2003). Captured crocodiles were marked by clipping tail scutes (see Chabreck 1963) using a numbering system that enabled individuals to be uniquely identified (Fig. 1.5). Furthermore, passive integrated transponders (PIT tags) were implanted subcutaneously in animals > 60 cm total length along the dorsal mid-line, between the posterior edge of the cranial platform and the nuchal scales. Animals were sexed by visual inspection of the genitalia (Webb *et al.* 1984b) and measured using a subset of morphometric measurements described by Webb and Messel (1978a), before being released near the site of capture.

It was obvious during fieldwork that capture probabilities decreased with increasing size of crocodile and that recapture probabilities decreased over time (see also Webb and Messel 1979). Therefore, data were stratified into two groups for analysis: age < 1 year old (hereafter referred to as hatchlings) and age > 1 year old (hereafter referred to as non-hatchlings). Further stratification of age/size classes would have been desirable to examine hypotheses concerning survival and capture probabilities but data were insufficient, which is often the case when stratifying data in mark-recapture studies (Otis *et al.* 1978). Mark-recapture data were analysed with Program MARK (version 3.2, White and Burnham 1999). Model naming conventions follow those advocated in Lebreton *et al.* (1992) for Cormack-Jolly-Seber (CJS: Cormack 1964; Jolly 1965; Seber 1965) open population models and Otis *et al.* (1978) for closed population models (see footnotes in Tables 5.1 and 5.2 for a description of model names).

5.2.2 *Analysis of survival (ϕ) and model selection strategy*

Data were sufficient to analyse survival for the 2001 cohort of hatchling crocodiles only. The data were stratified by sex to examine differences in survival between the two groups and secondary sampling occasion four was omitted from the analysis because capture effort targeted larger animals during this time period. Initially, a group of candidate models were chosen based on *a priori* knowledge of biological characteristics of the information (Anderson and Burnham 1999a). A general model (CJS time-dependent survival and capture probabilities with a group effect by sex: $\phi_{sex*t}\, p_{sex*t}$) was selected and tested for goodness-of-fit with the data using the parametric bootstrap procedure in MARK with 1000 simulations (Cooch and White 2002). This procedure also enables the overdispersion parameter ($\hat{c}$) to be estimated for inflating variances and quasi-likelihood model selection (White *et al.* 2001). Finally, a good approximating model for inference was chosen based on the principle of parsimony (see Stanley and Burnham 1998; Anderson and Burnham 1999b). Models were selected using Akaike's information criterion (AIC: Akaike 1973), which is an estimate of relative Kullback-Leibler distance (Kullback and Leibler 1951) among models, but likelihood ratio tests (LRTs) were also used to compare nested models. However, information criteria have been found to outperform model selection based on LRTs for both open (Burnham *et al.* 1995) and closed (Stanley and Burnham 1998) mark-recapture models. In practice, AIC_c (Hurvich and Tsai 1989) or $QAIC_c$ were used to compensate for small sample sizes and overdispersion in the data (Anderson *et al.* 1994).

5.2.3 *Population estimate*

Closed population models described by Otis *et al.* (1978) were used to estimate the size of the King River population in 2001. The finite-mixture models of Pledger (2000) enable maximum likelihood estimates (see below) of model parameters for all closed population models described by Otis *et al.* (1978). Model M_0 served as a basic model against which more complex candidate models were compared. Models of increasing complexity (*i.e.* increasing parameterization) were abandoned once data were no longer sufficient for complete parameter estimation. LRTs were utilized to examine hypotheses about capture probabilities for nested models. Demographic closure was not an unreasonable assumption for the 2001 data because recruitment occurs during the wet season (December to March) and migration was likely to be minimal based on radio-tracking experience (Chapter 3) and genetic data (Chapter 4). Also, survival is assumed to be constant for population estimates using closed models but, provided mortality affects marked and unmarked individuals uniformly, the population estimate produced is valid for the beginning of the study in June 2001 (Otis *et al.* 1978; White *et al.* 1982).

5.2.4 *Parameter estimation*

MARK estimates model parameters using maximum likelihood theory (Anderson and Burnham 1999a). Furthermore, demographic parameters and population estimates were calculated using AIC-weighted, model-averaging procedures in MARK to compensate for uncertainty in model selection (Buckland *et al.* 1997; Stanley and Burnham 1998).

5.2.5 *Hatchling growth rates*

Growth rates for the 2001 cohort of hatchling crocodiles were examined using five growth indices calculated from morphometric data collected during the mark-recapture study. The five indices used were: mm total length (TL) per day; grams body mass (BM) per day; grams per mm TL per day; TL increment factor (TL*x*); and, BM increment factor (BM*x*). The latter two indices were calculated as:

$$\mathrm{TL}x = \frac{\mathrm{TL}_{i+1}}{\mathrm{TL}_i} \times \frac{(y \times 365\ \text{days per annum})}{(t_{i+1} - t_i)} \quad \text{and} \quad \mathrm{BM}x = \frac{\mathrm{BM}_{i+1}}{\mathrm{BM}_i} \times \frac{(y \times 365\ \text{days per annum})}{(t_{i+1} - t_i)},$$

where $(t_{i+1} - t_i)$ is the time interval in days between captures, $y = 1$ for annual growth, and $y = 0.5$ for seasonal growth. These two indices are proportional increases in total length and body mass scaled for annual (12 months) and seasonal (6 months) growth, and for variable time intervals between captures. Differences in growth rates between female and male crocodiles were tested with a Wilcoxon two-sample test because the error distribution for each growth index was non-normal (Sokal and Rohlf 1995) using R (version 1.9.0, R Development Core Team 2004).

5.3 Results

A total of 139 individual animals (89 hatchlings and 50 non-hatchlings) were caught and marked in 2001 and an additional 23 individuals (5 hatchlings and 18 non-hatchlings) were caught and marked in 2002. During 2001, 63 marked individuals were recaptured on 100 occasions. The most parsimonious model to estimate population size from the data was model M_{t+age} based on AIC_c values (Table 5.1). The selection of this model was corroborated by LRTs that indicated more complex models fitted the data significantly better ($P < 0.001$) than simpler nested models. Model M_{t+age} indicated there was temporal variation in capture probabilities with an additive main effect from age group. Furthermore, LRTs suggested capture probabilities differed significantly over time (M_0 vs M_t: $X^2 = 74$, $df = 5$, $P < 0.001$) and between age groups over time (M_t vs M_{t+age}: $X^2 = 34$, $df = 3$, $P < 0.001$). The data suggest a considerable behavioural response to capture (Fig. 5.1). Data were insufficient to estimate all parameters for model M_{tb} (Otis *et al.* 1978) with an age group effect, or to assess individual capture heterogeneity for even the simplest finite-mixture model (e.g. model M_h, see Pledger 2000).

5.3.1 *Survival (ϕ)*

The deviance of the general CJS model ($\phi_{sex*t}\, p_{sex*t}$) did not differ significantly from expectation under the null hypothesis ($P > 0.26$) suggesting the model adequately fitted the data and there was no major violation of model assumptions (Cooch and White 2002). $\hat{c}$ was

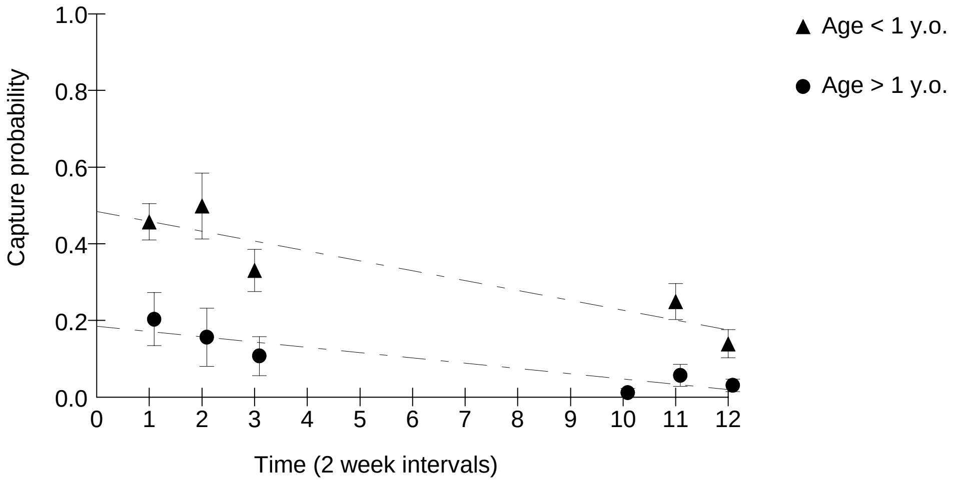


Fig. 5.1. Capture probabilities (± SE) for two groups of *Crocodylus porosus* caught in the King River during 2001. Data from the fourth sampling occasion are omitted for the young group because capture effort was targeting larger animals during this time period. Trend lines are linear relationships fitted by the graphics package in Program MARK.

Table 5.1. Ranking of candidate closed population models and parameter estimates from *Crocodylus porosus* mark-recapture data collected from the King River in 2001. The most parsimonious model has the lowest AIC_c score.

Model[a]	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	Parameters[b]	Deviance
M_{t+age}	-102.60	0.00	0.81	1.00	10	94.32
M_{t*age}	-99.55	3.05	0.18	0.22	14	89.13
M_t	-94.84	7.76	0.02	0.02	10	102.08
M_{tb}	-74.36	28.24	0.00	0.00	7	128.69
M_{b*age}	-61.73	40.87	0.00	0.00	6	143.35
M_{0*age}	-40.47	62.13	0.00	0.00	4	168.67
M_b	-32.11	70.50	0.00	0.00	3	179.05
M_0	-10.76	91.84	0.00	0.00	2	202.41

Parameter[c]	Age group	
	Hatchlings (age < 1)	Non-hatchlings (age > 1)
p (probability of initial capture at t_1)	0.45 ± 0.047 (0.37 – 0.55)	0.20 ± 0.069 (0.10 – 0.37)
c_2 (probability of recapture at t_2)	0.50 ± 0.086 (0.34 – 0.66)	0.16 ± 0.076 (0.06 – 0.36)
c_3 (probability of recapture at t_3)	0.33 ± 0.055 (0.23 – 0.45)	0.11 ± 0.051 (0.04 – 0.25)
c_4 (probability of recapture at t_4)[d]	0.03 ± 0.019 (0.01 – 0.10)	0.01 ± 0.011 (0.001 – 0.08)
c_5 (probability of recapture at t_5)	0.24 ± 0.047 (0.17 – 0.35)	0.06 ± 0.029 (0.02 – 0.15)
c_6 (probability of recapture at t_6)	0.14 ± 0.037 (0.08 – 0.23)	0.03 ± 0.016 (0.01 – 0.08)
N (population estimate for June 2001)	91 ± 1.9 (89 – 94)	69 ± 13.4 (50 – 95)

[a] Model naming conventions follow those of Otis *et al.* (1978): M_0 indicates no variation in capture probabilites; M_b indicates a behavioural response to capture; M_t indicates temporal variation in capture probabilities; **age* indicates an age group effect with interaction; and, +*age* is an additive main effect for age group.

[b] The number of parameters that were estimable from the data, which is not necessarily the total number of parameters specified for the full model.

[c] The AIC-weighted, model-averaged estimate for each parameter ± SE. Values in parentheses are the 95% CI.

[d] Catch effort was targeting large animals during this period.

estimated to be 1.12 by dividing the observed deviance for the general model with the mean deviance from the bootstrap simulations (White *et al.* 2001). The most parsimonious model for estimating survival was model $\phi\, p_{linear}$ based on QAIC$_c$ values (Table 5.2). This was a constrained model (see Cooch and White 2002) in which recapture was constrained as a linear trend with time. The model suggested hatchling survival did not vary between the sexes and was constant throughout the study period but that crocodiles showed a linear behavioural response to capture (see Fig. 5.1). LRTs support this result, indicating survival did not vary between the sexes ($\phi\, p_t$ vs $\phi_{sex}\, p_t$: $X^2 = 0.29$, $df = 2$, $P = 0.59$), over time ($\phi\, p_t$ vs $\phi_t\, p_t$: $X^2 = 0.29$, $df = 2$, $P = 0.87$), or between the sexes over time ($\phi_{sex+t}\, p_t$ vs $\phi_{sex*t}\, p_t$: $X^2 = 1.89$, $df = 5$, $P = 0.86$). There was no evidence to suggest recapture probabilities of hatchling crocodiles differed between the sexes ($\phi\, p_t$ vs $\phi\, p_{sex+t}$: $X^2 = 1.03$, $df = 1$, $P = 0.31$).

5.3.2 *Growth rates*

Growth rates for hatchling crocodiles were quite variable among individuals (Fig. 5.2) and no significant differences between the sexes were evident in any of the growth indices for either dry season (June to November 2001) or annual (June 2001 to July 2002) growth ($P >> 0.05$, Table 5.3). Hatchlings grew allometrically, with TL doubling from June 2001 to July 2002 and BM increasing ten-fold. Proportional increases in size slowed for TL after the dry season (and the first year of life) but continued to increase for BM. Most growth indices except TLx appeared to increase over the wet season, especially BM, but data were insufficient to test seasonal differences rigorously given the variation among individuals and small sample sizes.

Table 5.2. Ranking of candidate open population models for estimating survival of *Crocodylus porosus* hatchlings caught in the King River in 2001. The most parsimonious model has the lowest QAIC$_c$ score.

Model[a]	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight	Model likelihood	Parameters[b]	QDeviance
$\phi\, p_{linear}$	268.78	0.00	0.56	1.00	2	43.96
$\phi_{sex+t}\, p_{linear}$	270.12	1.34	0.29	0.51	4	41.09
$\phi_{sex+t}\, p_t$	273.47	4.69	0.05	0.10	6	40.12
$\phi\, p_t$	274.21	5.43	0.04	0.07	5	43.03
$\phi\, p_{sex+t}$	275.36	6.58	0.02	0.04	6	42.01
$\phi_{sex+t}\, p_{sex+t}$	275.66	6.88	0.02	0.03	7	40.09
$\phi_{sex}\, p_t$	276.10	7.32	0.01	0.03	6	42.75
$\phi_t\, p_t$	278.31	9.53	0.00	0.01	7	42.75
$\phi_{sex*t}\, p_t$	282.98	14.20	0.00	0.00	11	38.23
$\phi_{sex*t}\, p_{sex*t}$	288.66	19.88	0.00	0.00	14	36.65

Parameter[c]	Sex	
	Male	Female
ϕ_1 (apparent survival from t_1-t_2)	99.9 ± 0.22 % (99.5 – 100)	99.9 ± 0.14 % (99.7 – 100)
ϕ_2 (apparent survival from t_2-t_3)	99.9 ± 0.22 % (99.9 – 100)	99.9 ± 0.13 % (99.7 – 100)
ϕ_3 (apparent survival from t_3-t_5)[d]	99.8 ± 0.93 % (98.0 – 100)	99.9 ± 0.43 % (99.0 – 100)
ϕ (hatchling survival: June-December 2001)[e]	98.1%	99.9%

[a] Model naming conventions follow those of Lebreton *et al.* (1992): ϕ = apparent survival; p = recapture probability; t = time dependence; *sex* = sex dependence; *sex*t* indicates an interaction between sex and time; *sex+t* indicates an additive main effects model for sex and time; and, *linear* means the recapture probability was constrained as a linear covariate.

[b] The number of parameters that were estimable from the data, which is not necessarily the total number of parameters specified for the full model.

[c] The AIC-weighted, model-averaged estimate for survival ± SE. Values in parentheses are the 95% CI.

[d] Catch effort was targeting large animals during t_4, so t_4 data were omitted from the analysis.

[e] Hatchling survival from June to December 2001 was estimated as: $\hat{\phi}_{dry} = \prod_{i=1}^{3} \phi_i^{t_i}$.

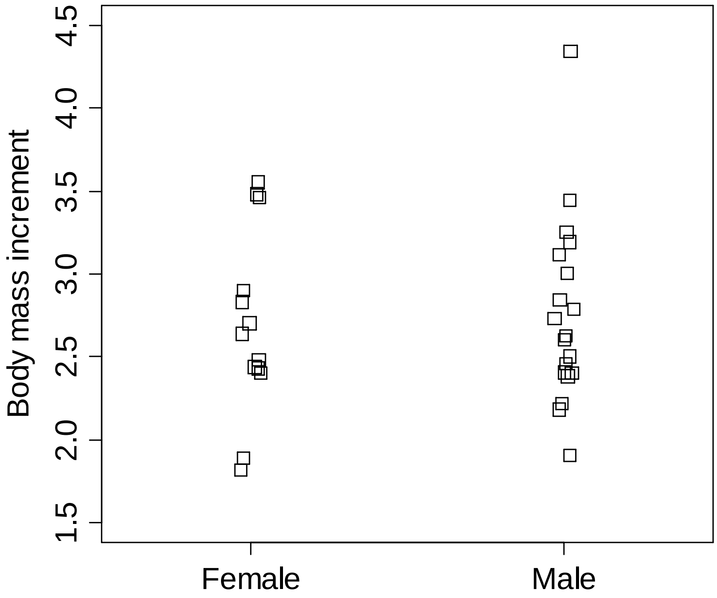


Fig. 5.2. Increments in body mass for King River hatchling *Crocodylus porosus* during the dry season in 2001.

Table 5.3. Growth rates for the 2001 cohort of hatchling *Crocodylus porosus* in the King River, Western Australia.

Season	Growth index [a]	Mean growth rate (± SD)		
		Female	Male	Combined (F+M)
June - Nov. 2001 [b]	TL: mm/d	0.84 ± 0.17 (*n* = 13)	0.84 ± 0.16 (*n* = 19)	0.84 ± 0.16 (*n* = 32)
(Dry 2001)	TL increment factor	1.59 ± 0.16 (*n* = 13)	1.56 ± 0.21 (*n* = 19)	1.57 ± 0.19 (*n* = 32)
Δt = 153 ± 16 days [c]	BM: g/d	1.53 ± 0.45 (*n* = 13)	1.48 ± 0.45 (*n* = 19)	1.50 ± 0.45 (*n* = 32)
	BM increment factor	2.69 ± 0.56 (*n* = 13)	2.76 ± 0.56 (*n* = 19)	2.73 ± 0.55 (*n* = 32)
	g/mm TL/d × 10^2	1.23 ± 0.24 (*n* = 13)	1.16 ± 0.33 (*n* = 19)	1.19 ± 0.29 (*n* = 32)
Dec. 2001 - July 2002	TL: mm/d	1.34 ± 0.20 (*n* = 2)	1.18 ± 0.09 (*n* = 2)	1.26 ± 0.16 (*n* = 4)
(Wet + early dry 2002)	TL increment factor	1.33 ± 0.05 (*n* = 2)	1.31 ± 0.01 (*n* = 2)	1.32 ± 0.03 (*n* = 4)
Δt = 202 ± 7 days	BM: g/d	6.21 ± 2.40 (*n* = 2)	4.10 ± 0.38 (*n* = 2)	5.16 ± 1.86 (*n* = 4)
	BM increment factor	3.36 ± 0.27 (*n* = 2)	3.24 ± 0.05 (*n* = 2)	3.30 ± 0.18 (*n* = 4)
	g/mm TL/d × 10^2	2.27 ± 0.65 (*n* = 2)	1.73 ± 0.36 (*n* = 2)	2.00 ± 0.53 (*n* = 4)
June 2001 - July 2002 [b]	TL: mm/d	1.08 ± 0.16 (*n* = 4)	1.17 ± 0.17 (*n* = 5)	1.13 ± 0.16 (*n* = 9)
(Annual)	TL increment factor	2.03 ± 0.17 (*n* = 4)	2.13 ± 0.30 (*n* = 5)	2.09 ± 0.24 (*n* = 9)
Δt = 357 ± 12 days	BM: g/d	3.30 ± 1.50 (*n* = 4)	3.44 ± 0.76 (*n* = 5)	3.38 ± 1.07 (*n* = 9)
	BM increment factor	8.88 ± 1.89 (*n* = 4)	10.58 ± 4.59 (*n* = 5)	9.83 ± 3.56 (*n* = 9)
	g/mm TL/d × 10^2	0.85 ± 0.33 (*n* = 4)	0.82 ± 0.16 (*n* = 5)	0.83 ± 0.23 (*n* = 9)

[a] TL = total length in mm; BM = body mass in grams; d = day.

[b] There were no significant differences between female and male growth rates for any growth index during the dry season in 2001 nor for annual growth (Wilcoxon two-sample test, $P >> 0.05$).

[c] Δt is the mean interval between recaptures in days ± SD.

5.4 Discussion

5.4.1 *Size of the King River population*

The population estimate for the 2001 cohort of hatchling crocodiles is considered to be robust because capture probabilities were generally adequate for parameter estimation (> 0.2) and the coefficient of variation (CV) < 10% (see White *et al.* 1982). However, the estimate of the size of the non-hatchling population needs to be treated cautiously because recapture probabilities were low (<< 0.2) and the CV high. Both age classes showed a significant behavioural response to capture, with capture probabilities decreasing over time. Moreover, capture probabilities were significantly lower for larger animals on most occasions. These results indicate a need to review the sampling strategy in future mark-recapture studies to increase capture probabilities, especially for larger animals. However, there are limited practical modifications that could be easily adopted. Techniques that minimize capture stress should be utilized at all times. Greater use of traps for larger animals in preference to harpooning is recommended but managing traps in macro-tidal regions is challenging. Immediate processing (e.g. marking, measuring, etc.) and release of all animals is probably preferable to bulk processing and time-delayed release in terms of minimizing stress and subsequent wariness.

5.4.2 *Survival of hatchlings*

Survival of the 2001 cohort in the King River was high (> 95%) from June to December, though may have been lower from January to June. However, environmental conditions from January to April are more favourable for ectotherms because temperatures are higher and there is also a greater abundance of food during the wet season (Webb 1991). Neonatal crocodiles also show higher rates of growth when hatching occurs early in the wet season (Magnusson and Taylor 1981). Furthermore, Webb *et al.* (1977) considered survival to be high during the first three months post-hatching once juveniles had moved from nest sites to the main river channel.

5.4.3 *Sex ratios*

Crocodiles do not have sex chromosomes and sex is determined by nest temperatures during incubation (Lang and Andrews 1994). This may lead to skewed sex ratios, which are often observed in crocodilian populations (e.g. see Thorbjarnarson 1997). The sex ratio in the King River was heavily skewed: 66% of hatchlings and 76% of non-hatchlings were males. For the 2001 cohort of hatchlings, this was probably due to skewed sex ratios at birth since neither recapture probabilities nor survival appeared to differ between the sexes.

5.4.4 *Growth of hatchlings*

There are limited published data on growth rates for wild *C. porosus*. Most are from animals < 120 cm TL and many based on small (or unreported) sample sizes with short intervals between measurements. There are only odd growth records for larger individuals (> 1.5 m TL). Most data come from the Liverpool-Tomkinson Rivers in the Northern Territory (Webb *et al.* 1977; Webb *et al.* 1978; Grigg *et al.* 1980; Magnusson and Taylor 1981) but there are also data from the Klias River in Malaysia (Sah and Stuebing 1996). King River growth rates are comparable with, and mostly higher than, other reported rates, especially for increments in body mass. A common feature of growth data for juvenile *C. porosus* is the variability among individuals (Fig. 5.2, see also Webb *et al.* 1978; Grigg *et al.* 1980).

Webb *et al.* (1978) fitted a linear model to growth data that suggested males grew faster than females, growth rates decrease as size increases and rates were higher during the wet season. While it would seem intuitive that males grow faster than females given the sexual dimorphism of the species, sexual differences in growth rates were not evident in this study during the first year of life, and probably the first 18 months, assuming animals hatched in January. The data do suggest that proportional increments in TL slow over the first 18 months but proportional increments in BM increase. Growth rates over the wet season appear to be much higher than the dry season but the sample size was small. Survival of hatchling crocodiles in the King River was high during 2001 and growth rates comparable with or higher than reported for other regions, suggesting recruitment into the system should be good in the absence of harvesting. However, monitoring indicates that recruitment was poor from 1989 to 2000 (WMI 2003).

5.4.5 *Monitoring populations*

Considerable effort and resources are spent on monitoring populations and it is generally assumed that systematic surveys in different years will detect the same proportion of the population each year and that changes in numbers will reflect changes in population size (Gibbs 2000). It is encouraging that the number of animals sighted during the spotlight survey for annual monitoring in the King River in 2001 (81 hatchlings and 68 non-hatchlings: WMI 2003) was so close to mark-recapture estimates (91 ± 1.9 hatchlings and 69 ± 13.4 non-hatchlings). However, assumptions of systematic surveys are often violated (Gibbs 2000) and the power to detect significant population trends is reduced when variability is high.

Bayliss *et al.* (1986) cautioned that, although spotlight surveys can provide precise indices of abundance, they are inherently inaccurate because of visibility biases. This may be an overly-pessimistic assessment, especially if rigorous standardization is applied, but the behavioural responses to capture found in this study have important implications for monitoring crocodile populations because they suggest disturbance may add an additional source of bias to sightability. For example, the number of animals counted during three spotlight surveys conducted on the King River in June and July of 2001 (W. R. Kay unpublished data and WMI 2003) showed a decreasing trend. Both hatchling and non-hatchling numbers decreased by about 25% over the three surveys. These were not controlled experiments and a number of factors, including different observers and environmental conditions, may have affected the number of animals sighted. However, hatchling mortality was unlikely to have been a factor based on survival estimates for the 2001 cohort. Furthermore, the number of non-hatchlings sighted in the 2002 survey (see WMI 2003) increased by 69%, mostly due to animals < 3 years old (~ 120 cm TL), but this was not attributable to recruitment over the previous wet season (see Fig. 6.2 and WMI 2003) and was unlikely attributable to substantial immigration (Chapters 3 and 4). Therefore, behavioural responses can likely be decomposed into severity of disturbance and time since disturbance ceased. Unless disturbance is uniform, proportionality constants (correction factors) used to convert indices to population estimates may have regional or local specificity and vary over time. Moreover, the correction factors quantified by Bayliss *et al.* (1986) were calibrated against a Petersen estimate of population size, which assumes equal capture probabilities over time for all animals. Therefore, their population estimate and corresponding correction factors are likely to be biased upwards and hence overestimate population size from adjusted spotlight indices.

5.4.6 *Historical implications of behavioural responses*

Behavioural responses to disturbance have interesting historical connotations. Webb *et al.* (1984a) estimated the size of the *C. porosus* population in the NT to be about 40,000 in 1984. Monitoring suggests the population increased at 5% to 8% per annum during the 1980s but had slowed by the early 1990s (Webb *et al.* 1984a; PWCNT 2000). Assuming the rate of increase was constant through time, back calculation suggests the NT population in 1971, when the species was first protected, would have been 14,000 to 21,000 non-hatchlings. At the cessation of hunting in Australia in the early 1970s, *C. porosus* was considered to be rare where it had once been common (Webb *et al.* 1984a) and there were genuine concerns for its long-term survival (Bustard 1970). A behavioural response to hunting, characterized by increased wariness that declined with time since protection, would imply the actual rate of recovery had been slower and/or the initial population size higher than previously thought. This is not to say there was not a substantial reduction in the size of the *C. porosus* population throughout Australia following the Second World War. Only that behavioural responses to hunting are likely to have influenced results of, and conclusions drawn from monitoring programs to a certain extent, especially immediately following protection of the species. While the significance of this example may be problematic for monitoring crocodile populations, it may also offer some cause for optimism for the recovery of crocodilian species in regions where they are still threatened by hunting and persecution, provided habitats remain intact.

6. SYNOPSIS

6.1 Overview of main findings

This study has provided some insights into important ecological processes relevant not only to the Kimberley population of *Crocodylus porosus*, but also to the species as a whole. A new method was developed for attaching electronic devices to crocodilians, which achieved good medium to long-term attachment times and did not appear to have detrimental effects on tagged animals (Chapter 2). It enabled the first study of *C. porosus* movements using radio-telemetry (Chapter 3). The results showed that male and female crocodiles, in Cambridge Gulf at least, have distinctly different patterns of movement. Females occupied small sections of river during the dry season, where mean daily movements were generally < 1.0 km/d, but moved distances of up to 62 km to nesting habitat during the wet season (Table 3.1). Also, females appear to return to the same dry season core areas following the wet season. Neither females nor males showed exclusive habitat preferences for any of the four broad categories of river habitat along the Ord River that were distinguished on the basis of tidal amplitude and salinity. Males moved considerable distances along the Ord River throughout the year and movements appeared to be bi-modally distributed (Fig. 3.3).

C. porosus appears to be one of the more mobile species of crocodilian. It has highly efficient osmoregulatory mechanisms for surviving in marine environments (Taplin and Grigg 1989) but large-scale ocean voyages (e.g. see Allen 1974; Bustard and Choudhury 1980), while being an important component of dispersal and gene flow, are likely to be atypical. Only one animal showed significant directional movement (Fig. 3.5) and most stayed within the river in which they were tagged. Three males spent much of their time outside the routine search area and may have moved into Cambridge Gulf and beyond, but none were detected doing so. Aerial searches undertaken specifically to locate them found them all in the lower reaches of the Ord River. Only one animal was detected moving to another river system but returned to the river where he was tagged (Fig. 3.6).

Sub-adult males are quite mobile and may be nomadic like pubescent male *Crocodylus johnstoni* (Tucker *et al.* 1997) but, unlike *C. johnstoni*, large male *C. porosus* are also very mobile. Linear ranges had stabilized for only three of nine males during the study period, which ranged from 33 to 44 km (Table 3.2). Home ranges did not, however, appear to be related to body size, with the largest range (87 km) recorded for the smallest tagged male, and this had still not stabilized by the end of the study. The largest tagged male (4.3 m) had the second largest linear range (67 km), which had not stabilized either. The highest rate of movement detected was 23 km/d for the largest male.

Intra-specific aggression is an often-reported feature of a number of crocodilian species, especially *C. porosus* (Lang 1987). However, mid-stream linear ranges of male crocodiles in this study overlapped substantially (Fig. 3.4) and there was no evidence for spatial partitioning, suggesting that territoriality is not an important behavioural characteristic of free-ranging male crocodiles. It is also difficult to see how a male crocodile could actively exclude all other males from linear ranges that mostly exceed 30 km of river. Bi-modality of male movements may indicate dynamic interactions (see Kernohan *et al.* 2001) between males, where a male spends time in a certain section of river until provoked into moving to another section by a larger male. However, it is difficult to reconcile territoriality with patterns of female movement. Mobility may be an advantage for males, enabling them to search actively for females occupying small core areas during the breeding season. This would make defending territories from rival males unnecessary. Aggressive interactions between males may result from chance encounters between evenly matched individuals as they move in search of females. This is in contrast to the traditional view about male-male agression in *C. porosus*, and ideas about defence of territory.

One animal was translocated during this study and travelled 118 km in 12 days to return to the area of its capture (Fig. 3.6). This suggests a strong instinct to home. Homing has been reported for a number of crocodilians, mostly in juveniles (e.g. Gorzula 1978; Webb and Messel 1978b; Webb *et al.* 1983b; Rodda 1984a). However, Walsh and Whitehead (1993) found that fewer than 50% of 'problem' crocodiles translocated from Nhulunbuy in the Northern Territory returned to the original site of capture (see Section 1.2.1 for more details). It is unknown whether the remainder were translocated successfully and/or killed by conspecifics and/or returned but were trap shy and not recorded again. Homing may well be density-dependent for translocated problem animals but the data are equivocal (see Walsh and Whitehead 1993). Reciprocal translocations of electronically tagged animals from similar size and sex classes over different spatial scales would clarify the effectiveness of translocation as a possible solution to problem animals (Tucker *et al.* 1997).

Radio-tracking data has provided some insights into patterns of movement for this large, mobile and long-lived species, but the sample size and period of study were small. Data are needed from more animals of both sexes, over a more complete size range, in different geographic regions and habitat types and over a longer time frame to establish whether the patterns that have emerged are typical. Such a study would be very expensive and would have to be undertaken over quite a long period of time. It has become increasingly apparent from a number of simulation studies that large sample sizes are required to define the home range of an individual animal reliably, and that large numbers of animals from a particular class must be studied in order to make inferences about movements at the population level (see White and Garrott 1990; Garton *et al.* 2001; Kernohan *et al.* 2001). Automated telemetry systems using satellite tracking technology and/or archival and downloadable GPS systems would be the most efficient and cost-effective approach for collecting the large volume of data required for analysing the movements of *C. porosus* in any future studies, especially in remote areas.

Furthermore, remote data collection would be less likely to influence animal behaviour than manual tracking techniques.

Indirect estimates of migration from genetic data (Chapter 4) corroborate results of the radio-tracking study, suggesting *C. porosus* shows strong fidelity to well-defined areas despite being highly mobile within them. Furthermore, assignment tests correctly designated 80% of individuals to their population of origin on the basis of multilocus genotypes (Table 4.5). While there was only moderate differentiation (*sensu stricto* Wright 1978) among the Kimberley populations examined ($F_{\mathrm{ST}} = 0.08$, $R_{\mathrm{ST}} = 0.06$), differences in allele frequencies were highly significant (Table 4.1). Indirect estimates of rates of migration are within the range considered sufficient to maintain genetic diversity while allowing for divergence in allele frequencies among sub-populations (Mills and Allendorf 1996).

Genetic diversity was similar in all three Kimberley populations examined, with allelic richness ranging from 4.6 to 5.0 alleles per locus (Table 4.2). However, the number of alleles per locus was 25% to 41% lower than found in *Alligator mississippiensis* (Davis *et al.* 2000; Davis *et al.* 2002; Ryberg *et al.* 2002) and there is compelling evidence for a recent bottleneck in all Kimberley populations sampled (Table 4.6), most likely caused by widespread hunting following the Second World War. Bottlenecks can seriously compromise adaptive and evolutionary potential, therefore, further investigation would be valuable. Firstly, to quantify allelic richness and heterozygosities in museum specimens collected prior to 1945, if sufficient material is available. This would confirm whether there have been historical changes. Secondly, monitoring changes in allelic richness in forthcoming generations will determine whether the consequences of a bottleneck continue to reduce genetic diversity.

Survivorship in *C. porosus* in unknown for most life-history stages so a mark-recapture study was implemented in the King River to examine the dynamics of its *C. porosus* population (Chapter 5). Crocodiles showed a significant behavioural response to capture (Fig.

5.1), which has important implications for monitoring crocodile populations (Section 5.4.5). Survival of hatchlings has been reported as low during the first year of life (e.g. Webb and Manolis 1993) but survival for the 2001 cohort of hatchlings in the King River was high (> 95%) between June and December (Table 5.2). Growth rates for King River hatchlings were comparable with, and mostly higher than, other reported rates of growth (e.g. see Webb *et al.* 1978; Grigg *et al.* 1980; Magnusson and Taylor 1981; Sah and Stuebing 1996). Hatchlings doubled in length and showed a ten-fold increase in body mass between June 2001 and July 2002 (Table 5.3) but rates of growth were highly variable among individuals (Fig. 5.2). There were no significant differences in rates of growth or survival between female and male hatchlings. Demographic parameters for *C. porosus* remain unknown for most life-history stages and are unlikely to be quantified in short-term studies of long-lived species. Skeletochronology in osteoderms is a promising technique for ageing crocodilians but will require material from animals of known age for validation (Tucker 1997b).

6.2 Historical perspective for Western Australia

Genetic data integrate population processes over many generations and provided some information on the historical size of the Kimberley population prior to widespread hunting. The long-term effective size (N_e) of the *C. porosus* population in the Kimberley was probably much larger than previously thought (Table 4.7). The accuracy of the estimate is only as precise as the estimated mutation rate (Waples 1991) but indicates the Kimberley may have had a long-term census size in excess of 50,000 (but see Section 4.4.4).

There is some anecdotal evidence to support this hypothesis. Bustard (1970) reported more than 3,000 animals were shot between 1963 and 1965 in the Admiralty Gulf region alone, and four hunters having shot 582 animals in Collier Bay in four months in 1961 (see Fig. 1.2). Furthermore, an experienced shooter from the Northern Territory who had hunted the Mary River, which was renowned for its high density of crocodiles, described the west

Kimberley in the early 1960s as “a croc shooter’s paradise” and the “last untouched place for shooting” where “you could get as many as you wanted in a night” (T. Baldwin, personal communication). In one five-month trip in 1961, T. Baldwin collected about 600 skins between Derby and the Prince Regent River (Fig. 1.2). In contrast, the total non-hatchling population of *C. porosus* in the Kimberley was estimated to be about 2,500 in 1986 (Messel *et al.* 1987), 16 years but only one generation following protection.

An advertisement that appeared in the Sunday Times in Perth on 4 November 1962, suggested some hunters were earning £8,000 to £9,000 per season (Fig. 6.1). Under the terms of the membership agreement with the International Monetary Fund, the Australian Government set the par value of the Australian pound at 1.99062 grams of fine gold from September 1949 until the introduction of decimal currency in 1966 (<www.abs.gov.au>). Therefore, the advertised earnings were the equivalent of about 15.9 to 17.9 kg of fine gold per season. The current value of gold is around 540 Australian dollars per ounce, so hunters were possibly earning from $300,000 to $340,000 dollars per season in today’s money. The accuracy of the advertisement is unknown and the conversion is sensitive to the volatility of global markets, but it does suggest there may have been considerable financial incentives to shoot crocodiles. The five-month trip undertaken by T. Baldwin in 1961 enabled him to purchase Annaburroo Station in the Northern Territory for £5,000 in 1962 (Baldwin and Baldwin 2000). However, a long-term resident of Wyndham found fishing more lucrative than shooting crocodiles but said he “could have made wages” as a full-time shooter (J. Weir, personal communication). Nevertheless, J. Weir said he shot about 1,000 crocodiles in the Cambridge Gulf systems over a long period and thought there were probably more crocodiles in the Kimberley than the Northern Territory by the 1950s because numbers had been depleted in the Northern Territory by this time.

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Fig. 6.1. The Sunday Times, Perth, 4th November 1962.

6.3 Implications of the results for conservation and management

The Kimberley is considered to be poor habitat for *C. porosus* due to the geomorphology of its rivers and, consequently, its carrying capacity much less than that of the Northern Territory (Burbidge 1987). However, genetic data suggest the long-term N_e of the Kimberley was probably quite large and there is some anecdotal evidence to support this. The region is sparsely populated by humans and mostly undeveloped, so it is unlikely that food resources or habitat degradation are factors limiting the size or recovery of the Kimberley crocodile population. Like all ectotherms, *C. porosus* have a low energy demand and do not require large quantities of food (see Pough 1980). The observed rate of increase ($\bar{r}$) during recovery of the Northern Territory population has been estimated at 5% to 8% (Webb and Manolis 1993; PWCNT 2000).

Of the Kimberley systems that were surveyed by Messel *et al.* (1987), high rates of increase were evident in the Prince Regent and Roe Rivers (Fig. 1.2) but not throughout the region as a whole (Fig. 1.1). It seems most likely that paucity of nesting habitat is a significant factor limiting recovery of *C. porosus* populations in some areas of the Kimberley. In a programme to ensure the continued viability of *C. porosus* populations in this region, priority should be given to identifying and protecting significant nesting habitat. There have been only limited surveys for nests in the Kimberley, and these found very low nest densities (G. Webb Pty Ltd 1989). However, remote sensing and GIS would enable more strategic searches for potential nesting areas (Harvey and Hill 2003).

The significant genetic structure found among Kimberley populations and results of assignment tests, as well as radio-tracking data, suggest *C. porosus* have a tendency for site fidelity to natal rivers (Chapters 3 and 4). Similar results from other *C. porosus* populations in northern Australia (N. FitzSimmons, unpublished data) suggest that Northern Territory populations are not contributing substantially to the recovery of the Kimberley population.

Therefore management units (*sensu* Moritz 1994b) should be demarcated at the level of river catchment boundary. Samples were collected from only three river systems and more rivers need to be sampled to determine whether the patterns that have emerged are typical throughout the Kimberley. However, given the results of assignment tests and the significance of differences in allele frequencies between the Ord and King Rivers, where the river mouths are separated by only 38 km, delineation of management units at the catchment boundary level would seem appropriate. This provides a clear and simple definition for managers to identify the appropriate geographic scale for managing stocks of *C. porosus* in the Kimberley region.

It is clear is that there was a significant reduction in the size of the Kimberley population of *C. porosus* following World War II, which probably resulted in a reduction in genetic diversity. Data from cohorts of hatchlings suggest the N_e in the King and Glenelg Rivers is low based on the method of Pudovkin *et al.* (1996), although sample sizes were small. The size of the Glenelg River population decreased between 1978 and 1986 (Fig. 1.1) and when the system was visited in 2002, to collect tissue samples, *C. porosus* densities appeared to be only low to moderate. Data suggest there has been a bottleneck in all three Kimberley populations examined, especially the Glenelg River (Table 4.6). Furthermore, sex ratios in all populations sampled are heavily skewed, especially in the King River (Table 4.7), which reduces N_e (Frankham 1995b).

The number of animals sighted during spotlight surveys in the Ord River was lower in 1986 than in 1978 (Messel *et al.* 1987). More recent aerial surveys showed a stable trend between 1986 and 1998 (WMI 2003), during which time significant numbers of animals were being removed from Cambridge Gulf as breeding stock for farms (CALM 1999). However, there has been an increasing trend since 1999 (Fig. 6.2). The Ord River Nature Reserve was declared primarily to protect significant habitat for *C. porosus* after the recommendations of

Bustard (1970). The lower Ord estuary is listed both as a Wetland of International Importance under the Ramsar Convention and also as a Wetland of National Importance (Larmour *et al.* 2001). During the study, hundreds of cattle were observed grazing along the banks of the Ord River throughout the year in both Parry Lagoons and Ord River Nature Reserves (Fig. 1.3), in areas known to be utilized by *C. porosus* for nesting. This situation has occurred for many years and needs to be addressed. Furthermore, there are high levels of pesticide contamination in Ord River crocodiles (Y. Shibata, unpublished data), which is known to cause significant reproductive and physiological impairment in crocodilians (Guillette *et al.* 1996; Guillette *et al.* 1999; Guillette and Milnes 2000; Pickford *et al.* 2000; Gunderson *et al.* 2001; Lind *et al.* 2004).

Survival of hatchling crocodiles in the King River was high during 2001 (Table 5.2) and growth rates comparable with or higher than reported for other regions (Section 5.4.4) suggesting recruitment into the system should be good in the absence of harvesting. However, hatchlings are vulnerable to over-harvesting because they are readily approachable at night by boat and spotlight (Webb and Messel 1979). Monitoring indicates that recruitment in the King River was poor from 1986 to 1999 (WMI 2003). The spike in the number of animals sighted during surveys between 2000 and 2002 is probably due to the cessation of egg and hatchling harvests during this period. The increase appears almost entirely attributable to young animals (Fig. 6.2). These data suggest harvesting in the King River has limited recruitment for almost a generation. Further, a total of 266 crocodiles were removed from Cambridge Gulf between 1983 and 1997 (Fig. 6.2) as breeding stock for crocodile farms (CALM 1999). This represents more than 10% of the estimated total Kimberley population in 1986 (Messel *et al.* 1987). In comparison, in the Northern Territory, where the *C. porosus* population is known to total in the tens of thousands, only 67 crocodiles have been removed from the wild to stock farms with breeding animals over the last two decades (PWCNT 2000). Most of the commercial

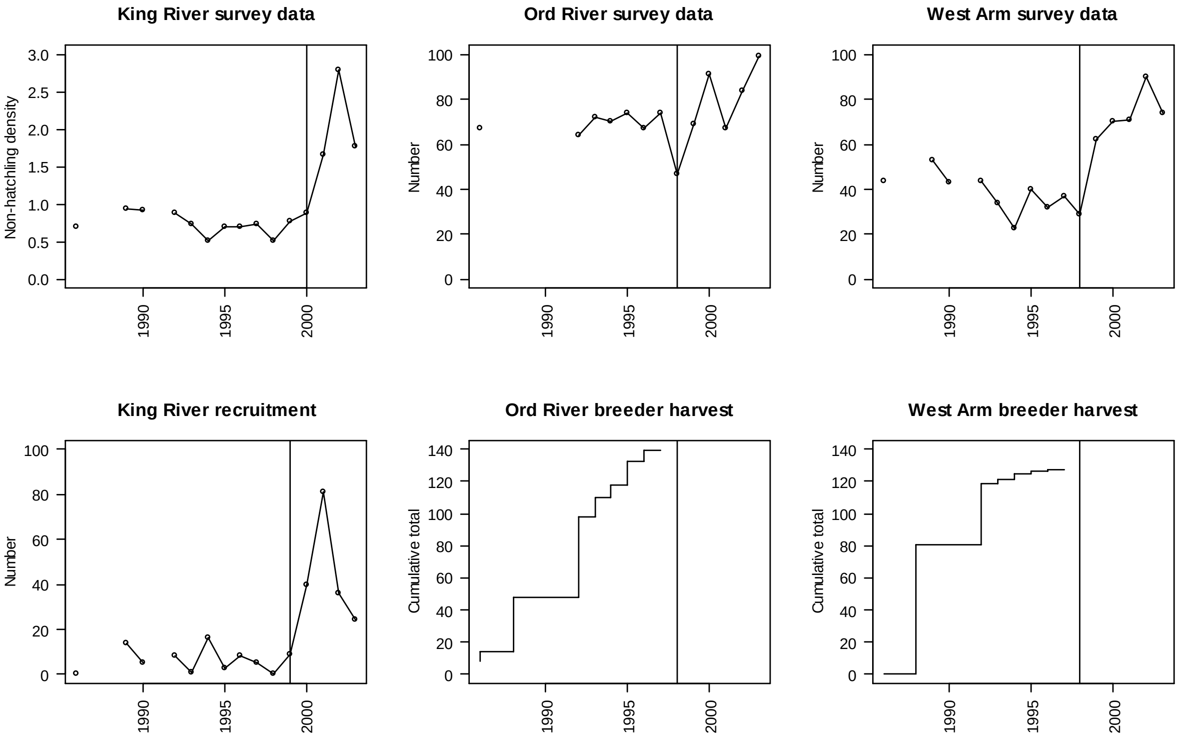

Fig. 6.2. Summary of survey and harvesting data for the Cambridge Gulf region between 1986 and 2003. Data are from WMI (2003) and CALM (1999).

harvest in the Northern Territory has been of eggs, with only minimal collection of hatchlings (PWCNT 2000).

The reproductive strategy of crocodilians is characterized by slow development, long life, and delayed and repeated reproduction where the risk of reproductive failure is minimized through repeated breeding rather than by maximizing reproductive output (Tucker 1995). Consequently, crocodiles have limited capacity to compensate for unregulated long-term harvests (Tucker 1995). Demographic parameters for *C. porosus* remain unquantified for most life-history stages but accurate estimates of key parameters are not necessarily prerequisites for successful management if populations are in secure habitats and subject to light harvest only (Tucker 1995). Conservative harvest quotas, well below predictions of maximum sustainable yield, incorporate buffers to insure against uncertainty when the dynamics of the population is poorly understood (Tucker 1995). This may sound reasonable to a wildlife manager in charge of setting harvest quotas but is probably unappealling to a commercial harvester who is expected to limit current takes to increase future yields (Tucker 1995). Because natural mortality of eggs is high (Webb *et al.* 1977; Magnusson 1982; Webb *et al.* 1983c), selective harvests of eggs are likely to have minimal impact on wild stocks. Furthermore, if an environmental variable, such as rainfall, can be identified as a reliable predictor of nest success, collecting eggs would offer a very conservative approach to harvesting wild stocks of *C. porosus*. Egg quotas could be set high when egg mortality is expected to be high (e.g. high and low rainfall years) and low when recruitment is expected to be good (e.g. medium rainfall years). This strategy is likely to have local or regional specificity.

While the *C. porosus* population in the Kimberley appears to be recovering (Messel *et al.* 1987), annual surveys conducted in Cambridge Gulf since 1989 indicate there has been an increasing trend only since 2000 (WMI 2003). The increase in the King River is probably due to a reduction in harvesting between 2000 and 2002 (WMI 2003). The King River is the only system surveyed annually by boat and spotlight (see Messel *et al.* 1981; Bayliss 1987), whereas the remainder of the Gulf has been surveyed from the air by helicopter. The value of aerial surveys has been questioned by Stirrat *et al.* (2001) because they are thought to have insufficient power to detect significant population changes within management time frames. It would be prudent to manage the Western Australian population of *C. porosus* conservatively until a sustained and long-term recovery has been demonstrated, and priority should be given to identifying and protecting areas of significant nesting habitat.

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Such is Life

Rail caution

A quote from the marketing manager of FreightLink (the mob running the Alice Springs to Darwin railway) Wayne Webster: "When I first got involved with railways I was told there was one rule - don't carry anything that walks or talks." However the company intends to carry cattle and the Ghan will carry passengers once a week in both directions.

Dob 'em in

Hey, what's happening Kununurra, Halls Creek and Wyndham? We didn't have one single Such is Life last week. Dob in your mates. Call us up. Buttonhole us in a pub or anywhere. Make an anonymous phone call. Drop in a funny photo. Anything with a funny or weird story will do. This is your column as well as ours.

Darwin lockout

A well-travelled businessman (once the cream of Ord Valley farmers) got caught out in Darwin recently. The shuttle bus to the airport turned up 10 minutes early, so he grabbed a couple of bags and ran down to meet it. When he attempted to return to his room for other minor articles (such as his wallet, tickets, credit cards and cash) the self-locking door had closed. Reception wasn't yet open. Luckily the taxi driver managed to contact security to let him back into the hotel. We are happy to report he made it to Kununurra in time for the Mockauction.

Foot finding crocs

We reported on the shooting of crocodiles to check DDT levels on October 3. What we didn't know was that recovering the carcases for disposal would be such an onerous task. One local spotted the 'crocodile man' up to his armpits in muddy water feeling with his toes for a large dead croc and hoping he didn't encounter a live one.

Sign of the times

Here at the Kimberley Echo we don't need signs to tell us where to go; there always seems to be someone only too happy to tell us where to go. However, we wonder how many of our tourists are quick enough to take in all the ramifications of this sign at the roundabout. Don't worry, if you miss what's on the front of the sign, you can always look in your rear vision mirror (while you're going into the roundabout) and see a shorter version on the back.

The Kimberley Echo, Kununurra, 24th October 2002.