Journal of the Royal Society of Western Australia, 94: 407–416, 2011

The Saltwater Crocodile, *Crocodylus porosus* Schneider, 1801, in the Kimberley coastal region

V Semeniuk[1], C Manolis[2], G J W Webb[2,4] & P R Mawson[3]

[1] V & C Semeniuk Research Group
21 Glenmere Rd., Warwick, WA 6024

[2] Wildlife Management International Pty. Limited
PO Box 530, Karama, NT 0812

[3] Department of Environment & Conservation
Locked Bag 104, Bentley D.C., WA 6983

[4] School of Environmental Research,
Charles Darwin University, NT 0909

Manuscript received April 2011; accepted April 2011

Abstract

The Australian Saltwater Crocodile, *Crocodylus porosus*, is an iconic species of the Kimberley region of Western Australia. Biogeographically, it is distributed in the Indo-Pacific region and extends to northern Australia, with Australia representing the southernmost range of the species. In Western Australia *C. porosus* now extends to Exmouth Gulf. In the Kimberley region, *C. porosus* is found in most of the major river systems and coastal waterways, with the largest populations in the rivers draining into Cambridge Gulf, and the Prince Regent and Roe River systems. The Kimberly region presents a number of coastlines to the Saltwater Crocodile. In the Cambridge Gulf and King Sound, there are mangrove-fringed or mangrove inhabited tidal flats and tidal creeks, that pass landwards into savannah flats, providing crocodiles with a landscape and seascape for feeding, basking and nesting. The Kimberley Coast is dominantly rocky coasts, rocky ravines/ embayments, sediment-filled valleys with mangroves and tidal creeks, that generally do not pass into savannah flats, and areas for nesting are limited. Since the 1970s when the species was protected, the depleted *C. porosus* populations have recovered across northern Australia. Monitoring shows large geographical variations in current population abundance between and within rivers of the Northern Territory, Queensland and Western Australia, and modelling shows strong support for linkage to the ratio of total area of favourable wetland vegetation (*Melaleuca*, grass and sedge) to total catchment area, rainfall seasonality, and other climate parameters.

Keywords: Saltwater Crocodile, *Crocodylus porosus*, Kimberley

Introduction

The Australian Saltwater Crocodile or Estuarine Crocodile, *Crocodylus porosus* Schneider, 1801, is the world's largest living reptile and is an iconic species of the Kimberley region of Western Australia. Considerable research has been conducted into the biology and status of *C. porosus* in northern Australia, particularly in the Northern Territory. The species' biology, population dynamics, recovery since protection and management have been the subject of intensive research efforts over the last 35 years (*e.g.* Magnusson 1980a, 1980b; Bayliss & Messel 1990; Messel & Vorlicek 1985, 1986; Webb *et al.* 1983, 1984, 1987b, 2000; Webb & Manolis 1989, 1992; Mawson 2004; Fukuda *et al*. 2007, 2010). As part of the joint Royal Society of Western Australia and Western Australian Marine Science Institute Symposium on Kimberley Marine and Coastal Science, we have endeavoured to provide a summary of the information on the species, outlining its history, palaeontology and phylogenetic relationships, biogeography, biology, habitats, nesting requirements, population dynamics, and some behavioural characteristics, with a literature that the reader can access for further information.

History

The rivers of northern Australia have been well known for the presence of crocodiles since the early days of colonisation and exploration, and as Australia's prominent predator in its northern regions, the Saltwater Crocodile has taken the lives of many unsuspecting people, their pets and livestock (Caldicott *et al.* 2005). In the 1950s and 1960s *C. porosus* was hunted for its skin throughout its distribution, and it is estimated that around 270,000 skins were exported between 1945 and 1972 (Webb *et al*. 1984). The days of unregulated hunting slowly ended as hunters themselves recognised that the resource had been over-exploited, and by the late 1960s there were so few *C. porosus* remaining that hunting was uneconomical. The unsustainable harvesting was formally ended by the Western Australian Government in 1969, followed soon after by the Northern Territory in 1971, and Queensland in 1974. Over the following decade *C. porosus* populations began to recover as a result of legislative protection but also because their habitats across northern Australia were largely intact. At the time of protection, populations comprised mainly juveniles, with few adults. By the late 1970s crocodile sightings became more common, and after several well-publicised crocodile attacks fears that a growing crocodile population would interfere with and inhibit a growing human population led to a more proactive form of crocodile conservation in the Northern Territory (Webb *et al.* 1987a). A major public education program (Butler 1987) and a problem crocodile program were two key elements of a management program designed to enhance public safety. In both the Northern Territory and Western Australia it was recognised that for the public to accept large populations of large Saltwater Crocodiles, they needed to perceive crocodiles as being beneficial to local people. This meant encouraging activities that generated positive linkages with crocodiles, and trying to minimise activities that generated negative linkages. The subsequent management programs have incorporated sustainable use as a means of achieving positive benefits (*e.g.* CALM 2003; DEC 2009; Leach *et al.* 2009), and a problem crocodile program as a means of eliminating negative linkages. To date, the sustainable use of wild *C. porosus* populations has not been adopted in Queensland (Read *et al.* 2004), although some advances are now being made in that direction.

Palaeontology and phylogenetic relationships

The crocodilians appear as a fossil group in the Triassic as part of the archosaurs, the group that includes the dinosaurs (Nash 1975; Buffetaut 1979; Taplin 1984; Bellairs 1987). With the birds, crocodilians are the only surviving archosaurs. The genus *Crocodylus* first appeared in the Palaeocene some 65 million years ago (Archer 1976; Willis & Molnar 1997; Mackness & Sutton 2000). Modern crocodilians, as large amphibious and carnivorous reptiles, and as water's edge predators, have much in common with each other. They inhabit tropical and subtropical lakes, rivers and coasts, lay their eggs in nests constructed on land, and their morphology and physiology have been shaped by similar lifestyles, allowing many generalisations to be made about the group as a whole. Research work on extant forms has emphasised homogeneity within the group rather than the differences (Cohen & Gans 1970; Densmore & Owen 1989; Densmore & White 1991), with the relative homogeneity appearing to be the remnants of a large radiation which peaked in the Mesozoic – their hard parts are very similar to those of fossil forms of the Triassic (Steel 1973, 1989). The three extant lineages (Crocodyloidea, Alligatoroidea and Gavialoidea) were distinct by the Upper Cretaceous. Phylogenetic relationships of crocodyloids suggest the possibility that many or all of the extant crocodylids might be derived relatively recently from marine-adapted ancestors with physiological capabilities similar to *C. porosus* (Taplin *et al*. 1985; Taplin & Grigg 1989; Salisbury & Willis 1996).

In recent years there has been extensive research on the history and systematic relationships of fossil crocodilians discovered in Australia, several from within the range of *C. porosus* and the related Australian Freshwater Crocodile *C. johnstoni* (Willis 1997). The diverse crocodile fauna, which appears to have been dominant for much of the Tertiary, became extinct during the Pliocene in association with the collapse of the Australian megafauna (Willis 1997). *Crocodylus porosus* appears suddenly in the fossil record in early Pliocene deposits at Bluff Downs, Queensland (Archer 1976). Interestingly, *C. johnstoni* appears in the Pleistocene, suggesting that it may have originated from a *C. porosus* ancestor (Willis & Archer 1990).

Distribution

Biogeographically, *C. porosus* is distributed from the east coast of India across to southeast Asia, including Vietnam, Cambodia, Thailand, the Philippines, Malaysia and Indonesia, and through Papua New Guinea and Australia. Australia represents the southernmost extent of the range of the species. In Western Australia *C. porosus* now extends to Exmouth Gulf (Fig. 1), and lone male crocodiles have also been recorded as resident in isolated rivers and tidal creeks in the Pilbara region. Vagrant crocodiles have been recorded in marine habitats as far south as Carnarvon on the mid-west coast.

In the Kimberley region, *C. porosus* is found in most of the major river systems and coastal waterways, including: the Ord, Patrick, Forrest, Durack, King, Pentecost, Prince Regent, Lawley, Mitchell, Hunter, Roe and Glenelg Rivers and Parrys Creek. The largest populations occur in the rivers draining into Cambridge Gulf, and the Prince Regent and Roe River systems of the east and northwest Kimberley region. Much lower densities occur in the rivers draining into King Sound and Stokes Bay in the west Kimberley.

Coastal habitats in the Kimberley region

The Saltwater Crocodile occurs in a range of habitats, including inland freshwater settings such as lakes, swamps, billabongs and river courses, and coastal and marine habitats. The definition of what is a 'crocodile habitat' will depend on whether the crocodile is viewed as permanently occupying a niche as a resident (in which case it is permanent, and may patrol a specific territory, or inhabit a specific tidal creek), or in fact is a temporary resident, or is a vagrant, occupying an environment on a transitory basis.

The Kimberly region presents a number of coastlines to the Saltwater Crocodile (Fig. 1). In the Cambridge Gulf area, there are mangrove-fringed or mangrove inhabited tidal flats and meandering tidal creeks that pass landwards into savannah supratidal flats and savannah floodplains (Fig. 2). This provides crocodiles with a landscape and a seascape where they can feed, bask and nest. The Kimberley Coast (*sensu* Semeniuk 1993) is a ria shore dominantly with rocky coasts, cliffs, bouldery shores, marine-flooded narrow rocky ravines and embayments with sandy beaches and sandy bars at their seaward openings; in the larger river-developed valleys and gulfs, there are sediment-filled valley tracts with mangrove-fringed or mangrove inhabited tidal flats and meandering tidal creeks, but these generally do not pass landwards into savannah supratidal flats and savannah floodplains. Areas for nesting are somewhat limited.

King Sound is similar to Cambridge Gulf in that there are mangrove-fringed or mangrove inhabited tidal flats and meandering tidal creeks but they pass landwards into extensive salt flats and as such do not provide crocodiles with much opportunity to nest. The western

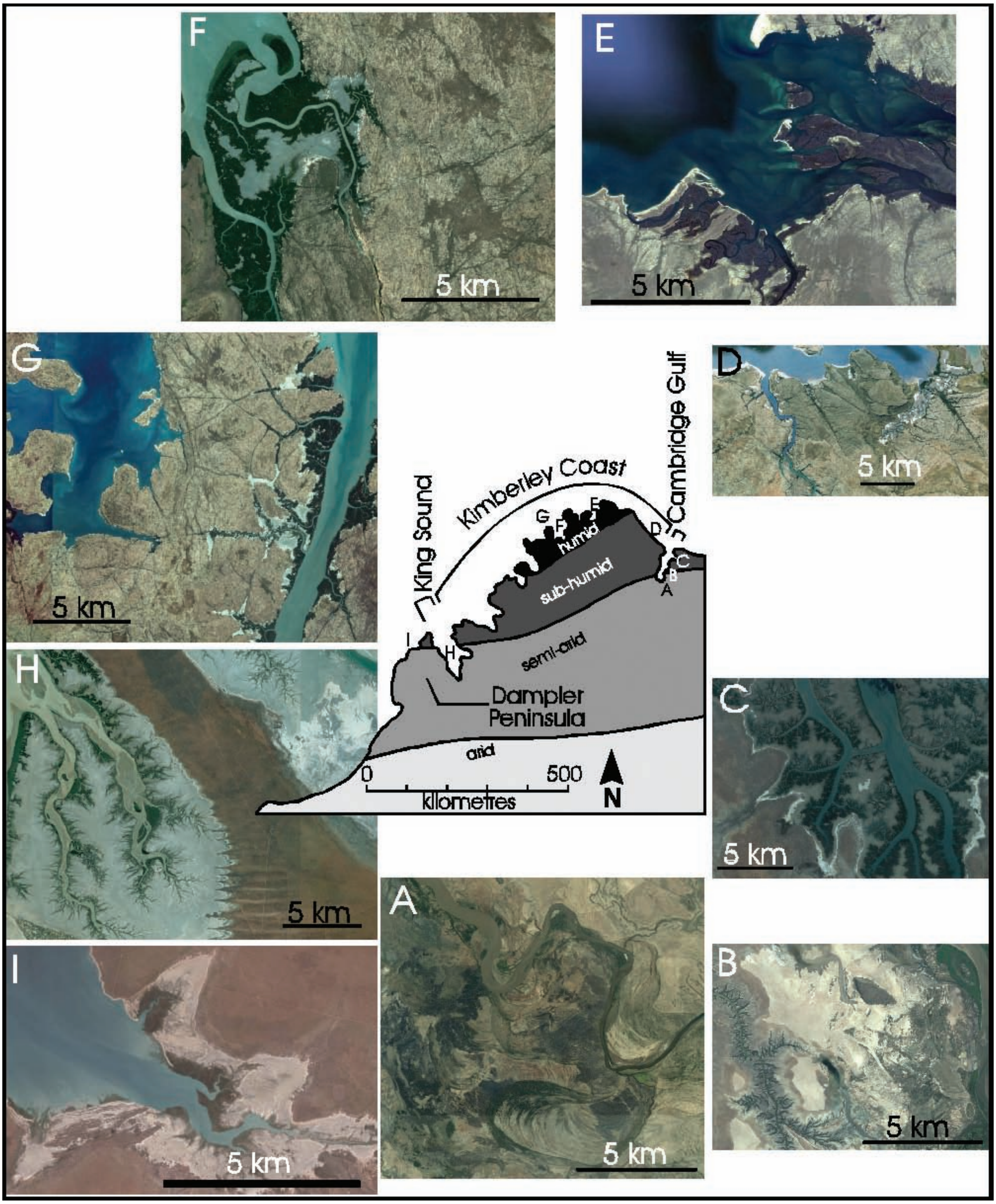

Figure 1. The four coastal types that are habitat to the Saltwater Crocodile, with aerial photographs of the coastal zone typical of each: (1) the Cambridge Gulf area, (2) the Kimberley Coast (*sensu* Semeniuk 1993) with rocky coast, narrow ravines, and deltas, (3) King Sound, and (4) the west coast of Dampier Peninsula. The central map shows the climate setting of the Kimberley region, and the location of aerial photographs: (A) floodplain in southern Cambridge Gulf; (B) mangrove fringed salt flats and tidal creeks of middle Cambridge Gulf; (C) tidal flats, salt flats and tidal creeks more extensively inhabited by mangroves in northern Cambridge Gulf; (D) the dominantly rocky coast and mangrove-filled narrow ravines of the northeastern Kimberley Coast; (E) densely mangrove-inhabited delta of the Drysdale River; (F) densely mangrove-inhabited delta of the Lawley River; (G) rocky shores, narrow mangrove-inhabited ravines west of the Mitchell River, and the narrow (dominantly rocky) gulf of the Mitchell River; (H) mangrove-fringed salt flats and tidal creeks of middle King Sound; and, (I) mangrove-fringed salt flats of the embayment of Beagle Bay.

Figure 2. Images of contrasting habitat; Saltwater Crocodile on a rocky coast at Croc Creek in Yampi Sound opposite Cockatoo Island (photograph courtesy of One Tide Charters, Derby), and on the upper reaches of a floodplain (Ord River) in the Cambridge Gulf area (photograph W.R. Kay).

coast of Dampier Peninsula is comprised of rocky shores and local embayments filled with and with mangrove-fringed or mangrove inhabited tidal flats and meandering tidal creeks; locally the salt flat passes landward into freshwater swamps.

A selection of landscapes and seascapes in the Kimberley region is shown in Figure 2. This shows areas where crocodiles may inhabit and nest, and the areas such as mangrove vegetated tidal flats and tidal creeks, backed by salt flats, where crocodiles may inhabit but with little opportunity for nesting.

Burbidge (1987) also noted that the areas of the Kimberley inhabited by *C. porosus* differ markedly from most of the Northern Territory, describing the Kimberley coastline and hinterland as chiefly composed of steep, rugged, ancient, deeply faulted sandstones with access up many rivers blocked to crocodiles by waterfalls and their associated gorges. There are few areas of floodplain and very few freshwater swamps and hence breeding habitat is relatively scarce.

It would appear, therefore, from the description of coastlines above, that the carrying capacity of the Kimberley river systems and the Kimberley region as a whole is much less than that of the Northern Territory. This notion is supported by an assessment of trade and other statistics from the 1946–74 hunting period (Webb *et al.* 1984).

Biology

Crocodilians are sturdy lizard-shaped reptiles, with a well-armoured head and trunk and with horny skin and scales, reinforced with bony plates. In modern crocodilians, the head is generally flattened and the snout elongated. The skeleton is typical of that of tetrapods in general and of archosaurs in particular, with the skull and pelvis particularly specialised (Romer 1956). The structure of the cervical vertebrae, the osteoderms, and the ribs protect the ventral surface (Steel 1973).

The nasal capsules lie near the tip of the snout, and nostrils which can close in the external nares tend to be raised above the tip of the snout – thus submerged crocodilians are inconspicuous when drifting toward terrestrial prey. During submergence, the palatal flap, a rigid plate of tissue at the rear of the oral cavity, closes the posterior buccal space against the entry of water, and the nostrils can be closed tightly. Skull and jaws are solid and together with the strong peg-like teeth can maintain an effective hold on prey (Iordansky 1973). The vertically undulating jawline coincides with the distribution of the largest teeth, accentuating the pseudo-heterodonty. In the Crocodylidae, upper and lower teeth alternate at occlusion, and the 4th dentary tooth fits into a lateral notch at or near the junction of the pre-maxilla with the maxilla. As a result, the teeth of crocodiles are far more conspicuous than those of alligators when the mouth is closed. Iordansky (1973) and Langstone (1973) provide useful reviews of the structure of both modern and extinct crocodilian skulls.

The skin of crocodiles is covered with keratinised scales, many of which are reinforced with bony plates, or osteoderms (Brazaitis 1987). Saltwater Crocodiles have no osteoderms in the belly scales. All "true" crocodiles, such as *C. porosus*, have Integumentary Sense Organs (ISO) on the scales. The function of ISOs, which are absent in the alligatorids, remains unclear, and it has been suggested that they are osmoreceptors, designed to detect salainity (Jackson *et al.* 1999). The ISOs on the jaws are well vascularised and innervated and considered to be involved in the detection of vibrations in the water – Soares (2002) termed these "Dome Pressure Receptors". Osteoderms are prevalent in the dorsal and nuchal scales, and commonly bear conspicuous ridges. The scales themselves are covered by hard, wear-resistant beta-keratin, and the skin between the scales is covered with less rigid alpha-keratin.

The skin provides a significant barrier to the movement of both water and ions. The Crocodylidae are good ionic and osmotic regulators, and ionic composition is similar between species [see Grigg *et al*. (1986), Taplin (1988) and Mazzotti & Dunson (1989)]. Larger individuals, with a lower surface area/mass ratio, can tolerate exposure to osmotic stress longer than smaller ones. Maintenance of internal homeostasis is frequently managed against a threat of flood or drought in fresh and salt water, respectively. Whereas most crocodilians are found in fresh water, *C. porosus* occurs routinely in hyperosmotic estuarine habitats while many others are exposed at least to brackish environments (Taplin 1988). Hatchlings of *C. porosus* are able to survive and grow without access to fresh water (Grigg *et al*. 1980; Taplin 1984). The presence of functional salt glands on the tongue provides *C. porosus* with an effective means of ridding the body of excess salt without the loss of body water at the same time.

Adult *C. porosus* are large, and the species shows a pronounced sexual dimorphism in terms of size. Males grow larger and often more rapidly than females, reaching an average maximum length of around 5 m (Webb and Manolis 1989) – however, some individual males may reach 6–7 m, and weigh over 1000 kg (Whitaker and Whitaker 2008). Females are much smaller, generally not exceeding 3 m in length. In the wild, males are sexually mature around 3.4 m (16 years) and females at 2.3 m (12 years) (Webb and Manolis 1989). At the same size, males and females cannot be identified on the basis of external characteristics.

Saltwater Crocodiles use behavioural means to regulate body temperature within optimal limits, moving between land and water to heat and/or cool themselves. During the cooler times of the year, basking during the day is prolonged in order to raise body temperature, whereas during the warmer times of the year the hotter parts of the day are spent in the water (see Lang 1987b).

Further description and discussion of crocodile morphology, physiology, natural history, biogeography and phylogeny and general biology may be found in Grigg *et al*. (1980), Taplin (1984, 1988), Wright & Moffat (1985), Webb *et al.* (1987), Mazzotti & Dunson (1989), Cogger (1993, 1996), Grigg and Gans (1993), Cooper-Preston & Jenkins (1993), Molnar (1993), Richardson *et al.* (2002), and Webb and Manolis (1989).

Diet and feeding behaviour

The diet of *C. porosus* varies with the size of individuals. Hatchlings feed mainly on small crabs, prawns and insects (Webb *et al.* 1991; Webb & Manolis 1989). With increasing size, crocodiles feed on a greater variety of larger food items, including fish, crabs, turtles, birds and mammals, with prey such as cattle and horses eaten only by the largest of crocodiles (Taylor 1979).

Saltwater Crocodiles typically employ a “sit and wait” strategy for hunting prey at the water’s edge. The minimum exposure posture allows only the eyes, ears and nostrils to be exposed at the water’s surface, and the body to be hidden underwater. Unsuspecting prey are grabbed quickly, and killed with a single snap of the jaws or by being dragged underwater and drowned. The tail can be used to accelerate the body completely out of the water or to launch a rapid lunge at prey. Small crocodiles will sit at the water’s edge snapping at any movement that occurs near their jaws. Crocodiles may also employ direct hunting methods, such as stalking prey at the water’s edge or in the water, or using the tail to knock prey out of small trees. Large crocodiles will also scavenge carrion, and individuals have been recorded caching dead prey for later retrieval (Doody 2009).

The crocodilian stomach is a simple bag-like structure that allows heavy objects such as stones to be stored (Richardson *et al.* 2002). Stones are likely to assist in breaking down prey (gastroliths), but a hydrostatic function has also been suggested (hydroliths). The stomach is highly acidic (pH 1–2), and even bones are completely digested. Items made of keratin (feathers, hair) or chitin (insect cuticle) are not digested, but mechanically broken down – hairballs are formed in the stomach and later regurgitated. Large crocodiles can go for long periods (up to 12 months) without food.

Nesting

Nesting for Saltwater Crocodiles is a wet season activity, spanning October to April. Females construct a mound of mud and/or vegetation that is typically located close to permanent water (Webb *et al.* 1977). Freshwater swamps and floodplain habitats associated with tidal rivers are the most common nesting habitats (Webb *et al.* 1977; Harvey & Hill 2003). Mangrove swamps are rarely used. The extent and timing of nesting is related to rainfall and water levels in the preceding dry season. Annual nesting effort may vary by more than 50% between years.

Clutch and egg size are largely determined by female size. Mean clutch size is around 50 eggs, with up to 90 eggs having being recorded (see Webb *et al.* 1983). On average, some 75–80% of wild *C. porosus* eggs would not be expected to hatch. Although a mound-nesting strategy is designed to maintain the eggs above the water, flooding is the main cause of embryonic mortality for *C. porosus* (Magnusson 1982; Webb *et al.* 1983). In some cases, overheating caused by the decomposition of certain types of vegetation (*e.g. Phragmites*) used in the construction of the nest may contribute to mortality (Webb and Cooper-Preston 1989). Examination of *C. porosus* nests in the Kimberly area indicated that overheating due to high ambient temperatures was a potential cause of mortality in some areas (G Webb Pty Ltd 1989).

Incubation period is dependent on temperature (*e.g.* 80 days at 32°C, 90 days at 30°C). Like other crocodilians, Saltwater Crocodiles have temperature-dependent sex determination: 100% males are produced at 32°C, 100% females at < 31°C, and 100% females at > 33°C (Webb *et al.* 1987c). When the eggs are ready to hatch the hatchlings make chirping sounds (Britton 2001), and the female helps them by digging them out of the nest, and taking them to the water’s edge in her mouth – she will guard them until they are independent. Extensive studies of nesting, egg characteristics, survivorship, and hatchling dispersal of *C. porosus* has been undertaken by Magnusson (1979a, 1979b, 1979c, 1980a, 1980b, 1982), Webb *et al.* (1983) and Webb & Messel (1978).

Nesting habitat for *C. porosus* is limited in the Kimberley region, and only the Ord, King and Roe River systems support suitable vegetation for significant nesting. A few nests have been recorded in other river systems such as the Drysdale and Prince Regent Rivers and Admiralty Gulf Creek. Saltwater Crocodiles occur in four of the 10 conservation reserves > 2000 ha in area in the Kimberley region that have rivers running through them.

Population dynamics

Mortality rates from egg to maturity are high. Based on available information Webb & Manolis (1993) predicted mean estimates for survival rates for several size classes of wild *C. porosus*: eggs 30% hatch; hatchlings (0–1 year) 12%; 1–2 years 85%; 2–3 years 85%; 3–4 years 85%; and, 4–5 years 85%. Survival rates of older individuals are difficult to estimate, but < 1% of eggs are expected to reach maturity. *Crocodylus porosus* may live for more than 50 years.

As *C. porosus* populations in northern Australia began to recover, it became clear that density-dependent factors were important to the rapid increase in abundance seen in the first few years of protection, and subsequent changes in size structure thereafter. In rivers studied in detail, numbers of small crocodiles over time were negatively correlated with numbers of larger crocodiles. With increasing numbers of large crocodiles, the numbers of small crocodiles decreased, either through exclusion from the river, or through being killed by other crocodiles (Webb & Manolis 1992). Survival rate for hatchlings was unrelated to numbers of larger crocodiles, but was dependent on the number of hatchlings present – the higher the number of hatchlings that were recruited into a river the lower the survival rate to 1-year-of-age This density-dependent survival rate is thought to compensate for the annual egg-harvest in the Northern Territory, which has been sustained, without restocking, for over 25 years.

Behaviour

Like other crocodilians, Saltwater Crocodiles have a rich repertoire of behaviours through which they communicate, including vocal (audible and sub-audible), visual and chemical signals (Lang 1987a). Relative to American Alligators *Alligator mississippiensis*, Saltwater Crocodiles are not as "vocal", although vocalizations are clearly an important means of communication between individuals. For example, hatchlings utilise a high-pitched "bark" in response to danger, to which adults and larger juveniles will respond. Such vocalizations may also serve to maintain hatchlings within a creche in the first few months of life.

Female Saltwater Crocodiles exhibit a high degree of maternal care for their eggs and young. They will aggressively defend their eggs/nests against predators (including humans), assist hatchlings to emerge from the nest, and even carry them to the water.

Relative to other crocodilian species, Saltwater Crocodiles are highly territorial and adults are generally intolerant of conspecifics. Injuries caused by intra-specific fighting are commonplace, particularly in larger individuals (Webb & Messel 1977). Younger subordinate crocodiles may be forced out of areas by larger crocodiles, and forced to seek unoccupied territories elsewhere. This may result in movement out of rivers and subsequent movement around the coast until suitable areas are located. For example, since the late 1970s the Northern Territory's Problem Crocodile Program has captured and removed any crocodiles moving into Darwin Harbour from around the coast (Nichols and Letnic 2008). However, some individuals may move upstream, into freshwater areas typically outside the range of the species, and sometimes into recreational areas used by people – this is a management issue being addressed in the Northern Territory (Letnic and Connors 2006).

In the Ord River the numbers of *C. porosus* in upstream, non-tidal sections of the river have increased significantly in recent years, and some individual *C. porosus* have been recorded from Lake Kununurra and Lake Argyle (DEC, unpublished data). Other movements relate to the reproductive season (*e.g.* females moving to nesting areas, males seeking females; Kay 2004), and satellite telemetry is now revealing as yet "inexplicable" movements by adult *C. porosus* in and out of core areas of activity (WMI, unpublished data).

Saltwater Crocodiles are excellent swimmers, with a relatively higher proportion of their body length represented by the tail, and greatly reduced bony dorsal armour – both characteristics are considered adaptations for swimming long distances. Individual Saltwater Crocodiles are commonly sighted well out to sea, and the record distance is around 2000 km (Manolis 2005). Crocodiles can also travel substantial distances overland (Walsh & Whitehead 1993; Webb and Manolis 1989).

Current management practices, conservation status, and monitoring

The management of crocodiles in northern Australia has been discussed by Webb *et al*. 1987a) in relation to habitat, population dynamics, nesting, harvesting and farming, and in Western Australia by Burbidge (1987) and Mawson (2004). The depleted *C. porosus* populations have recovered strongly across northern Australia in the 40 years since the species was protected (*e.g.* Fukuda *et al*. 2010). The recovery of the *C. porosus* population in the tidal section of the Ord River is shown in Figure 3.

Population monitoring shows large geographical variations in current abundance between and within rivers of the Northern Territory, Queensland and Western Australia. The historical abundance of *C. porosus* also varied between rivers (see Webb *et al.* 1984), and there is no reason to suspect that this will not continue to be the case in the future. The higher abundance of *C. porosus* in the Northern Territory is related to the greater extent of habitat and nesting there.

Broad-scale environmental influences on population abundance have been examined by modelling the species-environment relationships across northern Australia. The models show strong support for the linkage to the ratio of total area of favourable wetland vegetation types (*Melaleuca*, grass and sedge) to total catchment area, a measure of rainfall seasonality, namely the ratio of total precipitation in the coldest quarter to total precipitation in the warmest quarter of a year, and

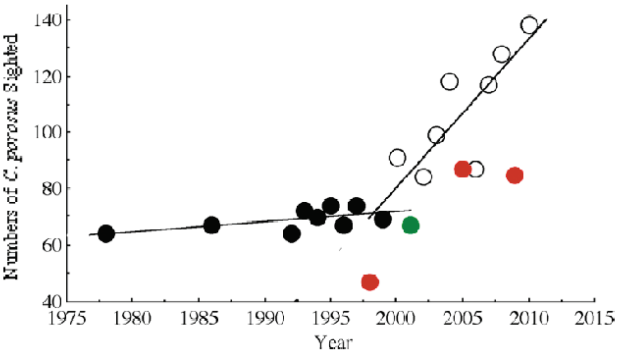

Figure 3. Recovery of the Saltwater Crocodile populations in the tidal Ord River, Western Australia (DEC, unpublished data). Helicopter count index for *C. porosus* in the Ord River monitoring zone, 1978–2010 Line for 1978–1999 indicates the non-significant linear regression (r^2= 0.36, p= 0.09; 1998 excluded due to particularly warm conditions), and the line for 2000–2010 indicates the significant linear regression (r^2= 0.55, p= 0.02; 2001, 2005 and 2009 excluded due to high or low temperatures during surveys).

the mean temperature in the coldest quarter of a year (Fukuda *et al*. 2007). There was not any clear negative association with landscape modification, as indicated by the extent of high-impact land uses or human population density in catchments. Thus geographical variations in crocodile density are mostly due to differences in habitat quality rather than the management regimes adopted in the respective jurisdictions.

In Western Australia, crocodiles usually cannot be commercially harvested in conservation reserves. The conservation estate within the Kimberley region (where most of the crocodiles live) amounts to an area in excess of 2.88 million ha (DEC 2009). Lands supporting other crocodile populations are vested in Crown Reserves and Aboriginal Lands. The proportion of land that actually constitutes riparian habitat suitable for crocodiles is a much smaller subset of these areas. The circumstances whereby crocodiles may be harvested from a conservation reserve includes where such actions are deemed a necessary operation under the *Conservation and Land Management Act 1984* or where an area management plan specifies that the management of overabundant populations was warranted or to protect human life from large crocodiles assessed as posing a direct threat to safety and welfare.

The conservation of crocodiles in Western Australia is potentially threatened by a range of environmental and anthropogenic factors. Many of these, such as drought and flood and disease, are ecosystem and environmental processes that exist in the realm of the larger environment. However, these processes are not considered a long-term threat to the conservation of crocodiles (DEC 2009). Potential anthropogenic threats to the conservation of crocodiles principally arise from the commercial harvest and habitat destruction (through pastoralism, mining and damming of waterways or use of surface water for mining or agriculture purposes). However, in 20 years of commercial harvesting in Western Australia, viable *C. porosus* populations have been maintained across their natural range and, moreover, the distributional range of the species appears to have expanded, with increasing numbers of sub-adult and adult male crocodiles being recorded at Broome, and vagrant animals also being recorded further south along the Pilbara coast, and as far south as Carnarvon (DEC 2009).

However, to ensure that the commercial crocodile harvest in Western Australia remains sustainable and does not jeopardise the viability of crocodile populations across their range, the Department of Environment and Conservation enacts a range of management controls, including regular and ongoing monitoring of crocodile populations, setting commercial harvest quotas at levels considered to be ecologically sustainable for the populations, management of problem crocodiles, providing refuge habitat, and assessing the impacts of commercial crocodile harvest on other species, habitats and ecosystems (DEC 2009).

The conservation status of the commercially harvested crocodiles in Western Australia largely reflects their former abundance and historical utilisation. Commercially harvested crocodiles in Western Australia are currently listed as 'Other Specially Protected Fauna' under the provisions of the *Wildlife Conservation Act*, but are not listed under the Australian Government *Environmental Protection and Biodiversity Conservation Act*. The International Union for the Conservation of Nature's Red List of Threatened Species identifies *C. porosus* as Lower Risk-Least Concern (Jenkins 1987; Webb *et al.* 2010). The Australian population of *C. porosus* is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), thus allowing regulated trade in the species from Australia. At a State level, Western Australia's approved management program (DEC 2009) provides compliance with Australia's obligations to CITES.

Crocodiles and Traditional Owners

Traditional Owners in the Kimberley and northern Australian region have had a long history with the Saltwater Crocodile. The crocodile has figured in their rock art, legends, and stories, and they have hunted them for food. Conversely, the crocodile has preyed on the indigenous people. As such, the crocodile has insinuated itself into Aboriginal culture, and is of particular significance where it is the totem for particular clans (*e.g.* Lanhupuy 1987). In the Northern Territory, landowners benefit economically from Saltwater Crocodiles through the ranching program (Leach *et al.* 2009; Webb *et al.* 1996).

Crocodile attacks in Western Australia and lessons for the future

Records from published newspaper accounts along with government records indicate that since 1947 there have been 11 attacks on humans attributed to *C. porosus* in Western Australia. Of these attacks, three were fatal – one occurred in 1947, and involved a British seaman in Wyndham Harbour, where there was clear evidence that a crocodile had fed on the man, but not conclusive proof that the crocodile had killed him. The other fatal attacks in Western Australia occurred in 1980 (Wyndham) and 1987 (Prince Regent River). Non-fatal attacks have been reported from both riverine and marine habitats (WMI, unpublished data).

With increasing development along the Kimberley and northern Pilbara coastline there is an increased likelihood of adverse interactions between people during works programs or recreational activities. Added to this is the fact that many of the people who will be moving to those areas will be 'crocodile naïve', this indicates that specific public education programs will be necessary to raise worker awareness of the risks of living in areas occupied by crocodiles.

References

Archer M 1976 Bluff Downs local fauna. Memoirs of the Queensland Museum 17: 383–396.

Bayliss P & Messel H 1990 The population dynamics of estuarine crocodiles. An assessment of long-term census data. *In*: Crocodiles. Proceedings 9th Working Meeting IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland. pp 1–44.

Bellairs A (d'A) 1987 The Crocodilia. *In*: G J W Webb, S M Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 5–7.

Brazaitis P 1987 Identification of crocodilian skins and products. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 373–386.

Britton A R C 2001 Review and classification of call types of juvenile crocodilians, and factors affecting distress calls. *In*: G C Grigg, F Seebacher & C E Franklin (eds), Crocodilian Biology and Evolution. Surrey Beatty & Sons, Chipping Norton. pp 364–377.

Buffetaut E 1979 The evolution of the crocodilians. Scientific American 241: 124–132.

Burbidge A A 1987 Crocodile management in Western Australia. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 125–127.

Butler W H 1987 "Living with Crocodiles" in the Nortehrn Territory of Australia. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 229–231.

Caldicott, D G E, Croser D, Manolis C, Webb G & Britton A 2005 Crocodile attack in Australia. An analysis of its incidence, and review of the pathology and management of crocodilian attacks in general. Wilderness and Environmental Medicine 16(3): 143–159.

CALM 2003 Saltwater Crocodile (*Crocodylus porosus*) and Freshwater Crocodile (*Crocodylus johnstoni*) Management Plan for Western Australia 2004–2008. Conservation and Land Management, Perth.

Cohen M M & Gans C 1970 The chromosomes of the Order Crocodilia. Cytogenetics 9: 81–105.

Cogger H 1993 General description and definition of the Order Crocodylia. *In*: C J Glasby, G J Ross & P L Beesley (eds), Fauna of Australia, Vol. 2A, Amphibia and Reptilia. AGPS, Canberra. pp. 235.

Cogger H 1996 Reptiles and Amphibians of Australia. Reed Books, Chatswood.

Cooper-Preston H & Jenkins R W G 1993 Natural history of the Crocodylia. *In*: C J Glasby, G J Ross & P L Beesley (eds), Fauna of Australia, Vol. 2A, Amphibia and Reptilia. AGPS, Canberra. pp. 337–343.

DEC 2009 Management Plan for the Commercial Harvest and Farming of Crocodiles in Western Australia – 1 January 2009–31 December 2013. Department of Environment and Conservation, Como.

Densmore L D & Owen R D 1989 Molecular systematics of the order Crocodilia. American Zoologist 29: 831–841.

Densmore L D & White P S 1991 The systematics and evolution of the Crocodilia as suggested by restriction endonuclease analysis of mitochondrial and nuclear ribosomal DNA. Copeia 1991: 602–615.

Doody J S 2009 Eyes bigger than stomach: prey caching and retrieval in the Saltwater Crocodile, *Crocodylus porosus*. Herpetological Review 40(1): 26–29.

Fukuda Y, Whitehead P & Boggs G 2007 Broad-scale environmental influences on the abundance of Saltwater Crocodiles (*Crocodylus porosus*) in Australia. Wildlife Research 34: 167–176.

Fukuda Y, Webb G, Manolis C, Delaney R, Letnic M, Lindner G & Whitehead P 2011 Recovery of saltwater crocodiles, *Crocodylus porosus*, following the cessation of hunting in tidal rivers of the Northern Territory, Australia. Journal of Wildlife Management (in press).

Grigg G & Gans C 1993 Morphology and physiology of the Crocodylia. *In*: C J Glasby, G J Ross & P L Beesley (eds), Fauna of Australia, Vol. 2A, Amphibia and Reptilia. AGPS, Canberra. pp. 326–336.

Grigg G C, Taplin L E, Harlow P & Wright J 1980 Survival and growth of hatchling *Crocodylus porosus* in salt water without access to fresh drinking water. Oecologia 47: 264–266.

Grigg G C, Taplin L E, Green B & Harlow P 1986 Sodium and water fluxes in free-living *Crocodylus porosus* in marine and brackish conditions. Physiological Zoology 59: 240–253.

G Webb Pty Ltd (1989). Saltwater Crocodile (*Crocodylus porosus*) nesting in the Northeast Kimberley Region of Western Australia (1988/89 season). Unpublished Report to Department of Environment and Conservation, Perth.

Harvey K R & Hill G J E 2003 Mapping the nesting habitats of saltwater crocodiles (*Crocodylus porosus*) in Melacca Swamp and the Adelaide River wetlands, Northern Territory: an approach using remote sensing and GIS. Wildlife Research 30: 365–375.

Iordansky N N 1973 The skull of the Crocodilia. *In*: C Gans & T S Parsons (eds), Biology of the Reptilia. Academic Press, London. pp 201–262.

Jackson K, Butler D G & Youson J H 1999 Morphology and ultrastructure of possible integumentary sense organs in the estuarine crocodile (*Crocodylus porosus*). Journal of Morphology 229(3): 315–324.

Jenkins R W G 1987 The Word Conservation Strategy and CITES; Principles for the management of crocodiles. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 27–31.

Kay W R 2004 Movement and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. Wildlife Research 31: 495–508.

Lang J W 1987a Crocodilian behaviour: implications for management. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 273–294.

Lang J W 1987b Crocodilian thermal selection. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 310–317.

Langstone W 1973 The crocodile skull in historical perspective. *In*: C Gans & T S Parsons (eds), Biology of the Reptilia. Academic Press, London. pp 263–284.

Lanhupuy W 1987 Australian aboriginal attitudes to crocodile management. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 145–147.

Leach G J, Delaney R & Fukuda Y 2009 Management Program for the Saltwater Crocodile in the Northern Territory of Australia, 2009–2014. Northern Territory Department of Natural Resources, Environment, The Arts and Sport, Darwin.

Letnic M & Connors G 2006 Changes in the distribution and abundance of saltwater crocodiles (*Crocodylus porosus*) in the upstream, freshwater reaches of rivers in the Northern Territory, Australia. *Wildlife Research* 33: 529–538.

Mackness B & Sutton R 2000 Possible evidence for intraspecific aggression in a Pliocene crocodile from north Queensland. Alcheringa 24: 55–62.

Magnusson W E 1979a Dispersal of hatchling crocodiles *(Crocodylus porosus)* (Reptilia, Crocodilidae). *Journal of Herpetology* 13: 227–231.

Magnusson W E 1979b Incubation period of *Crocodylus porosus*. Journal of Herpetology 13: 362–363.

Magnusson W E 1979c Maintenance of temperature of crocodile nests (Reptilia, Crocodilidae). Journal of Herpetology 13: 439–443.

Magnusson W E 1980a Habitat required for nesting by *Crocodylus porosus* (Reptilia: Crocodilidae) in northern Australia. Australian Wildlife Research 7: 149–156.

Magnusson W E 1980b Hatching and creche formation by *Crocodylus porosus*. Copeia 1980: 359–362.

Magnusson W E 1982 Mortality of eggs of the crocodile *Crocodylus porosus* in northern Australia. Journal of Herpetology 16: 121–130.

Manolis C 2005 Long-distance movement by a saltwater crocodile. Crocodile Specialist Group Newsletter 24(4): 18.

Mawson P R 2004 Crocodile management in Western Australia.. *In*: Crocodiles. Proceedings 17th Working Meeting IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland. pp 28–37.

Mazzotti F J & Dunson W A 1989 Osmoregulation in crocodilians. American Zoologist 29: 903–920.

Messel H & Vorlicek G C 1985 Population dynamics of *Crocodylus porosus* – a ten year overview. *In*: G Grigg, R Shine & H Ehmann (eds), Biology of Australasian Frogs and Reptiles. Surrey Beatty and Sons, Chipping Norton. pp 71–82.

Messel H & Vorlicek G C 1986 Population dynamics and status of *Crocodylus porosus* in the tidal waterways of northern Australia. Australian Wildlife Research 13: 71–111.

Molnar R 1993 Biogeography and phylogeny of the Crocodylia. *In*: C J Glasby, G J Ross & P L Beesley (eds), Fauna of Australia, Vol. 2A, Amphibia and Reptilia. AGPS, Canberra. pp 344–348.

Nash D S 1975 The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. Annals of the South African Museum 67: 227–329.

Nichols T and Letnic M 2008 Problem crocodiles: reducing the risk of attacks by *Crocodylus porosus* in Darwin Harbour, Northern Territory, Australia. Herpetological Conservation 3: 503–511.

Read M, Wright B & Enoch C 2004 Crocodiles in Queensland – an overview. *In*: Crocodiles. Proceedings 17th Working Meeting IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland. pp 13–27.

Richardson K C, Webb G J W & Manolis S C 2002 Crocodiles: Inside and Out. Surrey Beatty & Sons, Chipping Norton.

Romer A S 1956 Osteology of the Reptiles. Chicago University Press, Chicago.

Salisbury S W & Willis P M A 1996 A new crocodylian from the early Eocene of southeastern Queensland and a preliminary investigation into the phylogenetic relationships of crocodyloids. *Alcheringa* 20: 179–226.

Semeniuk V 1993 The mangrove systems of Western Australia – 1993 Presidential Address. Journal of the Royal Society of Western Australia 76: 99–122.

Soares D 2002 An ancient sensory organ in crocodilians. Nature 417: 241–242.

Steel R 1973 Crocodiles. Christopher Helin, London.

Steel R 1989 Crocodylia. *In*: O Kuhn (ed), Hanbuch der Palaeoherpetologie. Gustav Fisher, Stuttgart.

Taplin L E 1984 Homeostasis of plasma electrolytes, water and sodium pools in the estuarine crocodile, *Crocodylus porosus*, from fresh, saline and hypersaline waters. Oecologia 63: 63–70.

Taplin L E 1988 Osmoregulation in crocodilians. Biological Reviews 63: 333–377.

Taplin L E & Grigg G C 1989 Historical zoogeography of the eusuchian crocodilians. American Zoologist 29: 885–901.

Taplin L E, Grigg G C & Beard L 1985 Salt gland function in freshwater crocodiles: evidence for a marine phase in eusuchian evolution. *In*: G Grigg, R Shine & H Ehmann (eds), Biology of Australasian Frogs and Reptiles. Surrey Beatty & Sons, Chipping Norton. pp 403–410.

Taylor J A 1979 The foods and feeding habits of subadult *Crocodylus porosus* Schneider in northern Australia. Australian Wildlife Research 6: 347–359.

Walsh B & Whitehead P J 1993 Problem crocodiles (*Crocodylus porosus*) at Nhulunbuy, Northern Territory, Australia: an assessment of relocation as a management strategy. Wildlife Research 20: 27–135.

Webb, G J W, Beal A M, Manolis S C & Dempsey K E 1987c The effects of incubation temperature on sex determination and embryonic development rate in *Crocodylus johnstoni* and *C. porosus*. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 507–531.

Webb G J W, Britton A R C, Manolis S C, Ottley B & Stirrat S 2000 The recovery of *Crocodylus porosus* in the Northern Territory of Australia: 1971–1998. *In*: Crocodiles. Proceedings 15th Working Meeting IUCN-SSC Crocodile Specialist Group. IUCN, Gland, Switzerland. pp 196–235.

Webb G J W & Cooper-Preston H 1989 Effects of incubation temperature on crocodilians and the evolution of reptilian oviparity. American Zoologist 29: 953–971.

Webb G J W, Hollis G J & Manolis S C 1991 Feeding, growth and food conversion rates of wild juvenile saltwater crocodiles (*Crocodylus porosus*). Journal of Herpetology 25: 462–473.

Webb G J W & Manolis S C 1989 Crocodiles of Australia. Reed Books, Sydney.

Webb G J W & Manolis S C 1992 Monitoring saltwater crocodiles (*Crocodylus porosus*) in the Northern Territory of Australia. *In*: D R McCullough & R Barrett (eds), Wildlife 2001: Populations. Elsevier Applied Science, London and New York. pp 404–418.

Webb G J W & Manolis S C 1993 Conserving Australia's crocodiles through commercial incentives, *In*: D Lunney & D Ayers (eds), Herpetology in Australia. Surrey Beatty & Sons, Chipping Norton. pp 250–256.

Webb G J W, Manolis S C and Brien M L 2010 Saltwater Crocodile *Crocodylus porosus*. *In*: S C Manolis & Stevenson C (eds), Crocodiles. Status Survey and Conservation Action

Plan. Third Edition. Crocodile Specialist Group, Darwin. Pp 99–113.

Webb G J W & Manolis S C & Whitehead P J 1987a The management of crocodiles in the Northern Territory of Australia. *In*: G J W Webb, S C Manolis & P J Whitehead (eds), Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton. pp 107–124.

Webb G J W, Manolis S C & Whitehead P J (eds) 1987b Wildlife Management: Crocodiles and Alligators. Surrey Beatty & Sons in association with the Conservation Commission of the Northern Territory, Chipping Norton.

Webb, G J W, Manolis S C, Whitehead P J & Letts G A 1984 A proposal for the transfer of the Australian population of *Crocodylus porosus* Schneider (1801), from Appendix I to Appendix II of C.I.T.E.S. Technical Report No. 21. Conservation Commission of the Northern Territory, Darwin.

Webb G J W & Messel H 1977 Abnormalities and injuries in the estuarine crocodile, *Crocodylus porosus*. Australian Wildlife Research 4: 311–319.

Webb G J W & Messel H 1978 Movement and dispersal patterns of *Crocodylus porosus* in Arnhem Land, northern Australia. Australian Wildlife Research 5: 263–283.

Webb G J W, Messel H & Magnusson W E 1977 The nesting biology of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* 1977: 238–249.

Webb G J W, Missi C & Cleary M 1996 Sustainable use of crocodiles by Aboriginal people in the Northern Territory. *In*: M Bomford & J Caughley (eds), Sustainable Use of Wildlife by Aboriginal Peoples and Torres Strait Islanders. Australian Government Publishing Service, Canberra. pp 176–185.

Webb G J W, Sack G C, Buckworth R & Manolis S C 1983 An examination of *C. porosus* nests in two northern Australian freshwater swamps, with analysis of embryo mortality. Australian Wildlife Research 10: 571–605.

Whitaker R & Whitaker N 2008 Who's got the biggest? *Crocodile Specialist Group Newsletter* 27(4): 26–30.

Willis P M A 1997 Review of fossil crocodilians from Australasia. Australian Zoology 30: 287–298.

Willis P M A & Archer M A 1990 A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. Memoirs of the Queensland Museum 28: 159–163.

Willis P M A & Molnar R E 1997 A review of the Plio-Pleistocene crocodilian genus *Palimnarchus*. Proceedings of the Linnean Society of New South Wales 117: 224–242.

Wright D E & Moffat L A 1985 Morphology and ultrastructure of the chin and cloacal glands of juvenile *Crocodylus porosus* (Reptilia, Crocodilia). *In*: G Grigg, R Shine & H Ehmann (eds), Biology of Australasian Frogs and Reptiles. Surrey Beatty & Sons, Chipping Norton. pp 411–422.