ECOLOGY OF *Crocodylus porosus* IN NORTHERN AUSTRALIA

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Much of the information which follows was obtained during the 15 year study of *Crocodylus porosus* in northern Australia, by various researchers of the University of Sydney Crocodile Research Group.

C. porosus ranges from Sri Lanka and the west coast of India through south-east Asia, across to the Philippines and down through the islands to New Guinea and northern Australia (Fig. 1). The species is regarded (generally) as that crocodilian which most readily takes to the sea (Ditmars 1910, Smith 1931, Loveridge 1945, Wermuth 1964, Neill 1971, Guggisberg 1972, Brazaitis 1973) and its wide distribution is attributed to an ability to make long sea journeys (Wermuth 1953, Neill 1971, Brazaitis 1973, Webb and Messel 1978). Its reputation for sea travel is based on sightings at sea (Hornaday 1926) and on the appearance of individuals well away from known populations (Neill 1971). A 3.8 m male *C. porosus* was found at Ponape, Eastern Caroline Islands, some 1,360 km from the nearest population (Allen 1974), while a 3.2 m male with a telemetry transmitter travelled 130 km, of which 80 km was along the sea coast (Webb and Messel 1978).

The species reaches the southernmost limit of its range in Australia (Fig. 1). Here it is restricted to the coastal regions of the far north in Western Australia, Northern Territory and Queensland (Cogger 1975). It occurs primarily in rivers as far upstream as tidal influence extends, but is found also in swamps (fresh and salt), billabongs, lakes and non-tidal rivers up to 150 km or more, inland (Messel, pers. obs.). *Crocodylus johnstoni*, Australia's only endemic species of crocodile, overlaps the range of *C. porosus* in fresh water and also can be found in the saltwater sections if the density of *C. porosus* is low (Messel et al. 1978-1986, 1:459).

The two species can be easily distinguished; the snout of *C. johnstoni* is narrow in comparison to that of *C. porosus*.

The habitat in Australia for *C. porosus* is generally much drier and more inhospitable than in wetter areas of Asia like Papua New Guinea, Malaysia and Burma. Swamp as habitat is much less significant than it is in Papua New Guinea for example.

HABITAT

Messel et al. (1978-1986) give detailed descriptions of rivers surveyed from the Kimberley region in Western Australia to Cape York Peninsula in Queensland. Taylor (1979) presents a useful

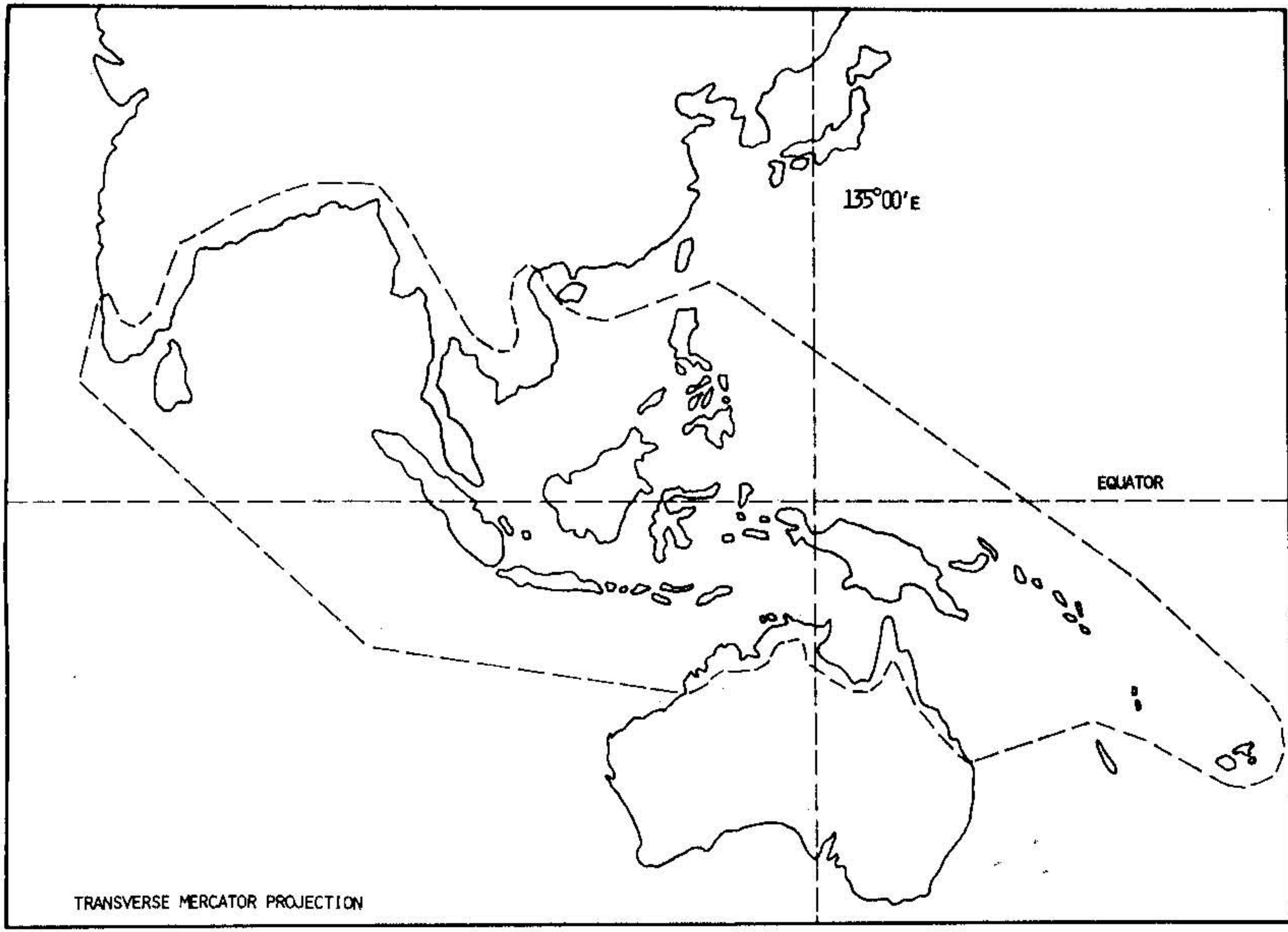

Figure 1. Former distribution of *Crocodylus porosus* (adapted from Neill 1971).

classification of habitat types found on the coastal rivers in the Northern Territory and we now give this, with some additional habitat types.

Lower Mangrove - This habitat is characterized by long sloping banks of soft mud, with mangrove species the only riverside vegetation. Such habitat is found in the downstream sections of all rivers. Salinity in these areas is between 20 and 35°/oo.

Floodplain - Floodplain is characterized by open plains, abutting the river, of the grasses *Ischaemum villosum* var. *australe*, *Imperata cylindrica* var. *major* and *Coelorrachis rottbellioides*, and/or the sedges *Cyperus* spp. and *Fimbristylis* spp. Small mangroves *Avicennia marina* and paperbarks *Melaleuca acaciodes* sometimes form a sparse line along the river edge. This habitat occurs in downstream sections of all rivers studied (salinity: 20-35°/oo) and is often associated with lower mangrove habitat.

Upper Mangrove - Upper mangrove is characterized by strand communities in floodplain or sparse mangrove areas. The communities are commonly composed of palms *Corypha elata*, ferns *Acrostichum speciosum*, and the vines *Derris trifoliata* and *Flagellaria indica*. River banks in this habitat may be steep with a substrate of firm mud. This habitat occurs in the upper reaches of the Tomkinson, Liverpool and Cadell Rivers (salinity: 0-20°/oo).

Freshwater Swamp - This is characterized by freshwater seepage. Swamps, with water depths ranging from 10 to 300 cm, commonly contain the melaleucas *M. dealbata*, *M. leucadendra*, *M. viridiflora*, the sedges *Baumea rubiginosa* and *Scirpus* sp., and water lilies *Nymphaea gigantea*.

Freshwater swamps often drain into the main river by way of small creeks. The area of swamp may drastically recede during the dry season.

Floodplain Billabongs - These are beside the river and fill from either abnormally high tides or wet season rains. They often contain brackish water and may dry out completely during the dry season.

Eucalypt Forest - This is characterized by the presence of steep earth banks, lined by sparse forest of *Eucalyptus miniata* and *E. tetradonta* with an understorey of the broad-leaved grasses *Heteropogon* spp., *Coelorrachis rottbellioides*, and *Themeda australis*. Few plants are found at water level and no mangroves are present. This habitat is found on the upper reaches of the Liverpool and Blyth Rivers (salinity: 0-5°/oo), for example.

Sand-Phragmites - This habitat, found, for example, on the upper reaches of the Liverpool River (salinity 0-5°/oo), is characterized by sandbanks. Abutting these are areas of *Phragmites karka*, *Acadia auriculiformes* and *Pandanus aquaticus*.

Exposed Shore Communities - This category is a catch-all for the many dry exposed habitats, often with sharp relief, found near the coast and including beaches, rocky foreshores, cliffs and rocky areas around creeks.

Webb (1977) gives a generalized description of the Liverpool River System, which exemplifies many characteristics of TYPE 1 rivers (see salinity classification below).

The river can be divided into tidal and non-tidal sections. The non-tidal section flows through the rocky Arnhem Land plateau for some 120 km. The river here is narrow, contains fresh, clear water and flows mainly on substrates of rock or sand. The river may expand into swamps, which are typically lined with *Pandanus*, paperbark (*Melaleuca* sp.) and eucalypt forest. By the end of the dry season, water flow may cease and the river can become a string of isolated water holes. Small numbers of *C. porosus* are found in this freshwater section of the river. Individuals are darker in color than those from the tidal section; some are black on the dorsal surface. This habitat is more typical of *C. johnstoni*, the freshwater crocodile; the interaction between the two species has not been studied in detail (but see Messel et al. 1978-1986, 1-3, 16, and Webb et al. 1983).

In the Liverpool River, the demarcation between tidal and non-tidal sections occurs at the edge of the escarpment. The banks of the tidal section are mainly mud. They are lined with either mangrove forest or floodplain grasses and sedges. There are two tidal cycles per day and tidal range is about 3 m. The water in the tidal section is usually saline and some 20 km upstream appears to be a drowned river valley; the river course fixed by geological structure. Further upstream, the river meanders through an extensive floodplain and there is continual erosion of one bank and deposition on the other.

During the wet season, the non-tidal section of the river receives the runoff from a large area of the escarpment. Water levels rise and there is usually widespread flooding of the tidal section and a flushing of saline water from the river. We have recorded essentially fresh water at the Liverpool River mouth in the wet season.

With the cessation of rain, tidal influence extends back up the river and a salt wedge gradually moves upstream. By the end of the dry season the water is brackish at the upper limit of tidal influence. Most *C. porosus* are in the tidal section of river.

The habitat types described are very much generalized. In other rivers, the proportion of one to the other may change considerably. For example, the tidal sections of the Woolen (Messel et al. 1978-1986, 9) and King Rivers (Messel et al. 1978-1986, 5) are drowned river valleys into which the upstream non-tidal sections drains directly, i.e., there is virtually no meandering flood plain river. In Andranangoo Creek (Messel et al. 1978-1986, 6) on Melville Island, there is no sharp demarcation between tidal and non-tidal. As one moves upstream the environment gradually changes from mangroves and mud to *Pandanus* and paperbark. In addition, large areas of the bank are composed of freshwater swamps. In rivers like the Glyde (Messel et al. 1978-1986, 9, 18) the tidal section peters out in a massive area of freshwater swamp (the Arafura Swamp), into which flows a freshwater river, the Goyder. This latter river resembles the upstream freshwater billabongs of the Liverpool River. In the Mary River, the cessation of wet season rains, and subsequent drying, leaves large closed flooded plain billabongs and only a very minor flowing creek. In the Buckingham River (Messel et al. 1978-1986, 10), the demarcation between tidal and non-tidal sections of the river is sharp, a large cliff face.

SALINITY

Analysis of the number, distribution and size structure of crocodiles sighted during the general surveys of northern Australian tidal systems indicates that one of the most important parameters characterizing a tidal waterway is its salinity profile. The profile and habitat type image one another and appear to largely determine the suitability or otherwise of the tidal waterway for breeding, nest and rearing. We roughly classified the tidal rivers and creeks on the northern Arnhem Land coastline into three different types of waterways. This classification plays a critical role in the unraveling of the dynamics of populations of *C. porosus* (especially see Messel et al. 1978-1986, 5, 9-11) and is given by:

TYPE 1 - Tidal river systems meandering through coastal floodplains and having a heavy freshwater input during the wet season. The freshwater inflow decreases but remains sufficient, as the dry season progresses, to prevent the salinity upstream (though progressing upstream gradually) from rising above the sea water values measured at the mouth of the system. Such systems usually have good to excellent nesting habitat and could be expected to have good recruitment potential. The Goomadeer River System was classified as such a system (Messel et al. 1978-1986, 5).

TYPE 3 - Tidal waterways which also have a heavy freshwater input during the height of the wet season, but in which the freshwater input drops rapidly with the onset of the dry season. These waterways, which usually have short surveyable lengths and often direct openings to the sea, are typified by salinities which during the dry season are above those measured at their mouths and which increase with increasing distance upstream - they are hypersaline and become increasingly so as the dry season progresses. Nesting habitat in such systems is minimal or non-existent. Recruitment potential is also usually low or non-existent. All Night Creek (Messel et al. 1978-1986, 5) is an example of such a system; most of the coastal creeks surveyed on the southern coast of the Gulf of Carpentaria also fall into this category (Messel et al. 1978-1986, 13).

TYPE 2 - Tidal systems which fall somewhere between TYPE 1 and TYPE 3 above and which tend to show hypersaline characteristics as the dry season progresses. Such systems usually have good to poor nesting habitat and equivalent recruitment potential depending upon how close they are to TYPE 1 or 3 above. The King River (Messel et al. 1978-1986, 5) and Dongau Creek on Melville Island (Messel et al. 1978-1986, 6) are examples of such systems.

It will be seen that each of these three system types has its own characteristic type of salinity variation, both in respect of time of year and distance upstream, and that the salinity characteristics largely determine the nature of the system. Figure 2 shows typical dry season salinity profiles for the three system types. The salinity profile of a system may be said to be its own unique signature. A large river system may have multiple signatures, one for its mainstream and different signatures for its creeks and subcreeks.

CLIMATE

Rainfall - The climate shows two distinct seasons. The 'wet' season (November to April) is associated with the north-west monsoon. The 'dry' season (May to October) is a period of infrequent or no rain. It results from a more northerly extension of anticyclonic weather patterns across the Australian continent during the winter months. During the 'dry' season, south-east trade winds of up to 30 knots are prevalent over the study area.

As an example of climatic variations over a year, we give some data for the Blyth-Cadell study area (Messel et al. 1978-1986, 1) where the most extensive population studies have been carried out. Mean annual precipitation is 1,141 mm at Maningrida and 1,143 mm at Milingimbi. Seasonal rainfall distribution and number of raindays per month are shown in Fig. 3.

A heavy build up of cumulus cloud occurs in October before the monsoon arrives. During the wet season, the rivers often flood for periods of up to several weeks. Peak flooding usually occurs between January and March.

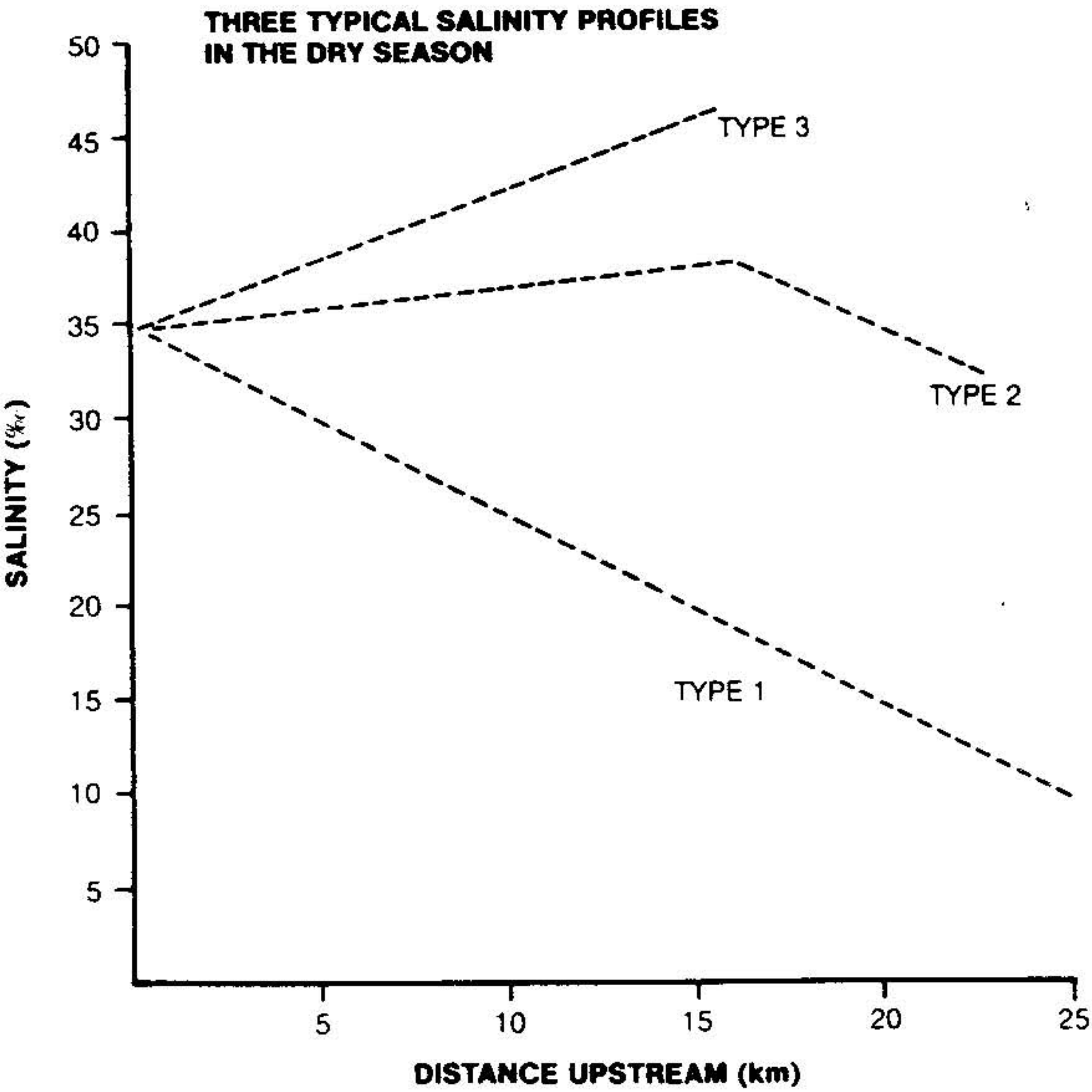

Figure 2. Typical dry season salinity profiles for the three types of tidal systems occurring in the classification scheme described in the text.

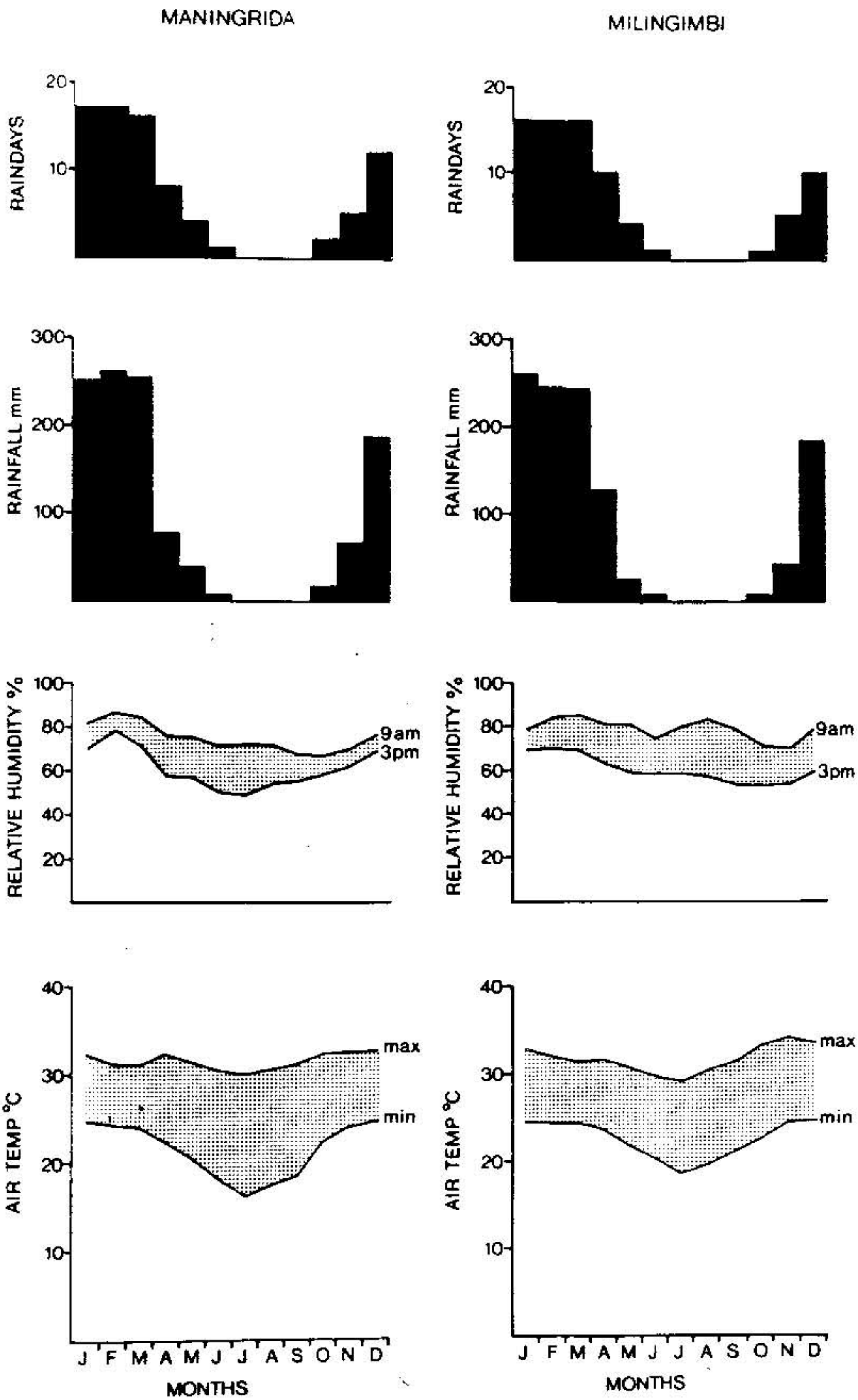

Figure 3. Mean annual number of rainy days, rainfall regimes, mean relative humidity and mean maximum and minimum temperatures at Maningrida and Milingimbi meteorological stations, which are adjacent to the study area.

Temperature and Humidity - Seasonal fluctuations in relative humidity and mean maximum and minimum monthly temperatures for weather stations at Maningrida and Milingimbi are also illustrated in Fig. 3. In the study area, temperatures remain high throughout the year. High rainfall and heavy cloud, common during the 'wet' season, produce high humidity and lessen extremes of temperature.

Twenty-four Hour Temperature Measurements - Twenty-four hour temperature profiles of the air (1 m above ground), water and substrate (exposed mud 1-2 cm depth) were measured 32 km upstream from the mouth of the Blyth River (in an area having the highest density of *C. porosus*). Temperatures were recorded at hourly intervals during four seasons (Figs. 4-6; note that substrate temperatures are not shown).

During the wet season, the water temperatures remain constant, 30±1°C. During the dry season, water temperatures steadily fall until they reach about 25°C during June and July (however, water temperatures as low as 21.9°C were recorded at km 45 in July 1976), begin to rise again and slowly approach 26°C in September and 29°C in October. Water temperatures slightly lag air temperatures. Air and substrate temperatures also showed diurnal and seasonal changes. Night temperatures down to 12.7°C were recorded during the dry season.

Considerable variation in both air and water temperatures may occur over a few days. On 14 June, 1976 (Fig. 4), air and water temperatures fluctuated between 20-28°C and 25-26°C, respectively. By June 21, after a cold snap, air temperatures had fallen to between 13-24°C, while the temperature of the water had dropped to around 24°C. Similar fluctuations can be seen on the temperature profiles for 22 and 25 September, 1976. The large differences after midnight between air and water temperatures can give rise to heavy fog on the upstream portions of the rivers.

NESTING

C. porosus deposit their eggs in a mound nest which may be constructed from a variety of vegetable debris, with varying proportions of mud, dirt or even sand. The vegetable debris, including leaf litter, rushes, roots, sticks, reeds, grasses, often living green materials as well as dead. Floodplain nests are usually constructed principally of the grass *Ischaemum australe* var. *villosum*, if available. The feet and tail are used to scrape up vegetation and the mouth is also used. The nest is compacted and takes one to several nights to construct. Vegetation and soil from an area up to 70 m^2 is raked together. On completion the nest often has distinct tail groove across the top. Typical dimensions of a nest are 0.5 m high, and 1.6 m in diameter.

Nest sites are typically selected close to permanent water. With the exception of nests constructed in large or small freshwater swamps, off from the downstream high salinity sections of the waterways, or on upstream swamps and/or billabongs, all the other nests appear to be constructed on those sections of the waterway which are brackish by June or July, with salinities around 1 to 10 parts per thousand. These sections are of course completely fresh during the wet season.

It is not clear why there are no nests on the downstream mouth sections of tidal rivers. Nests in swamps have the greatest chance of survival and swamps must be considered optimal habitat for nesting.

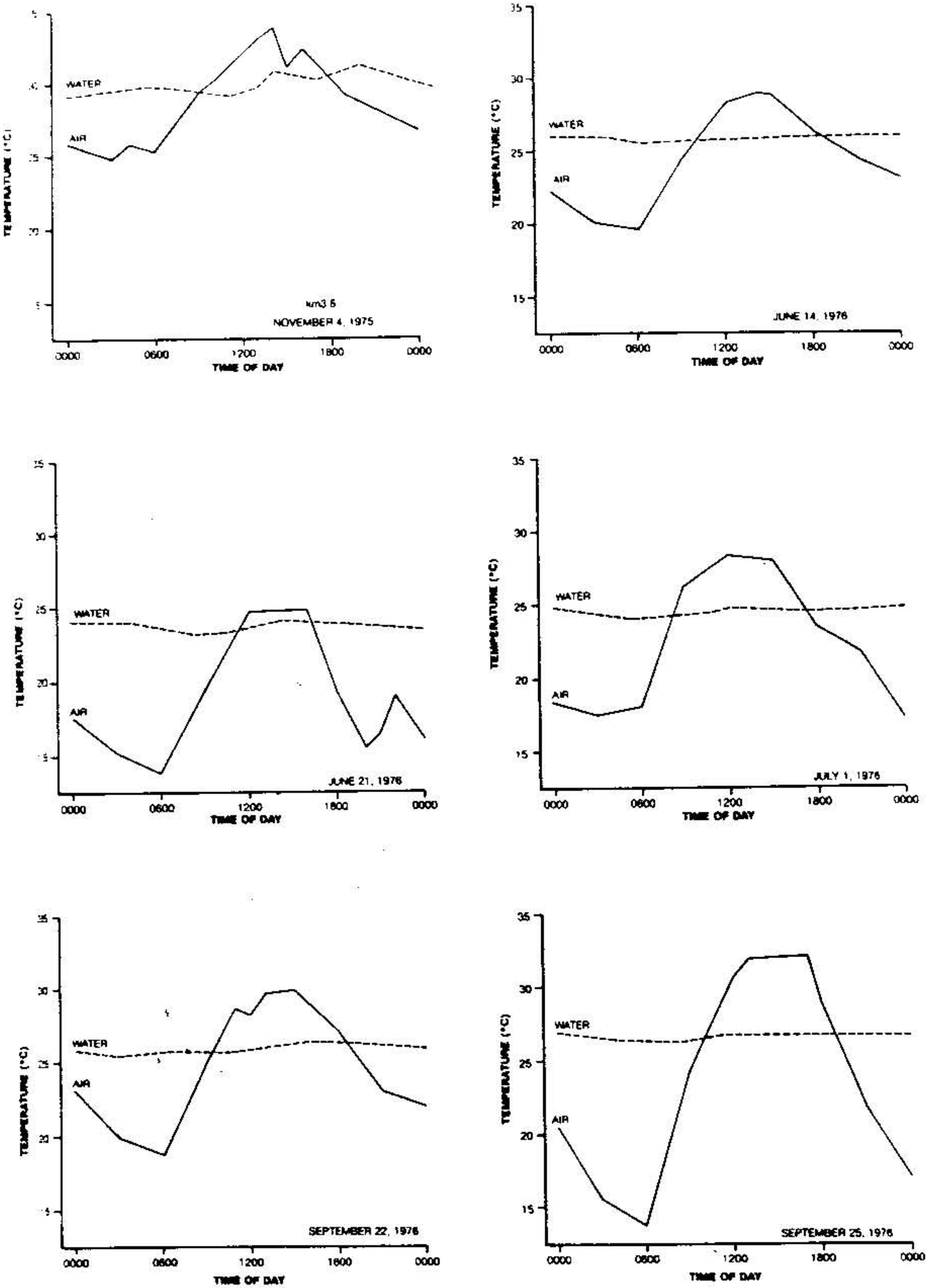

Figure 4. Twenty-four hour temperature profiles of the air (1 m above ground level) and water. Temperatures were recorded at hourly intervals. All measurements were taken at km 32 upstream on the Blyth River (except November profiles which were taken at km 3.6) during 1975 and 1976.

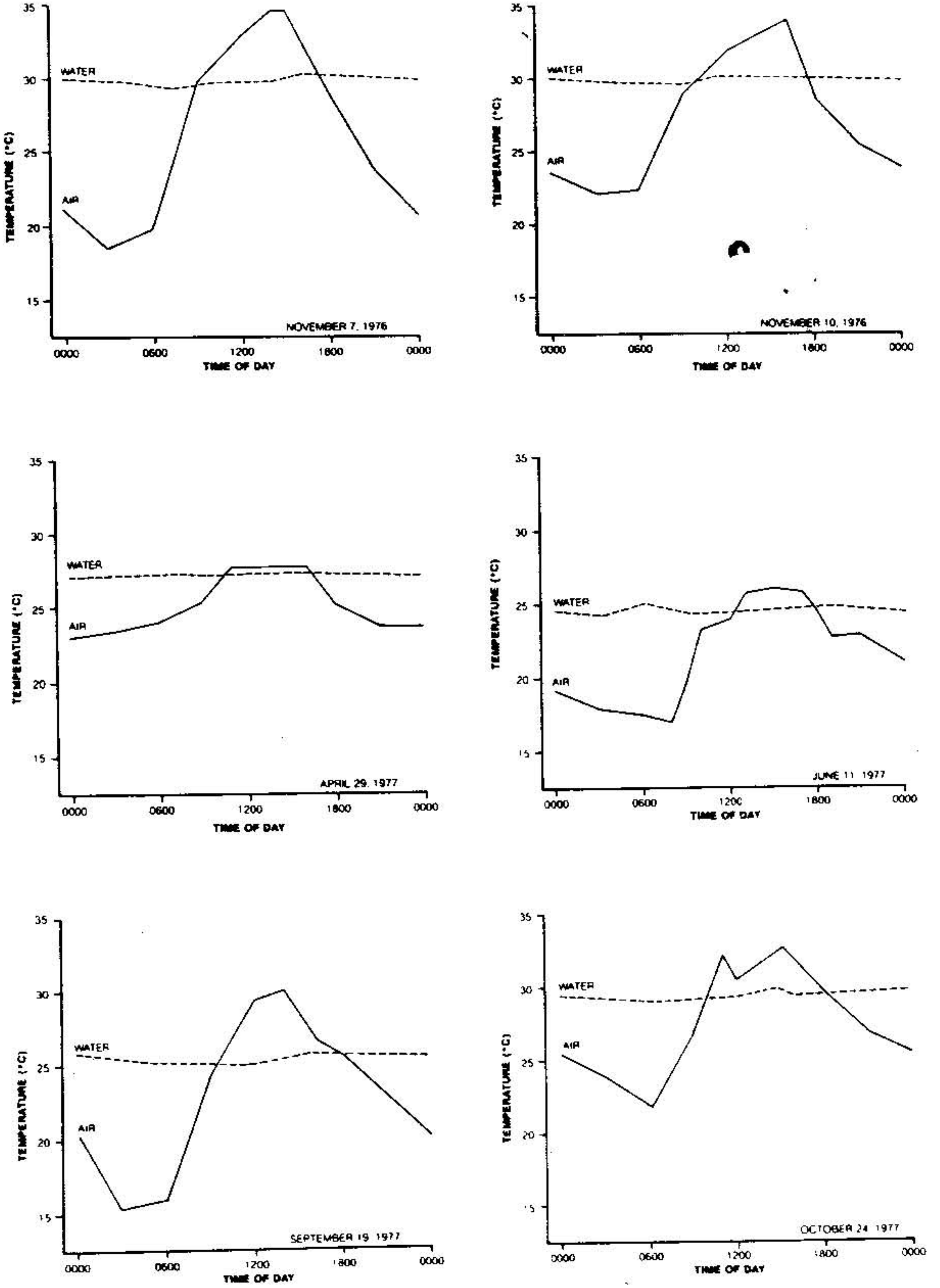

Figure 5. Twenty-four hour temperature profiles of the air (1 m above ground level) and water. Temperatures were recorded at hourly intervals. All measurements were taken at km 32 upstream on the Blyth River during 1976 and 1977.

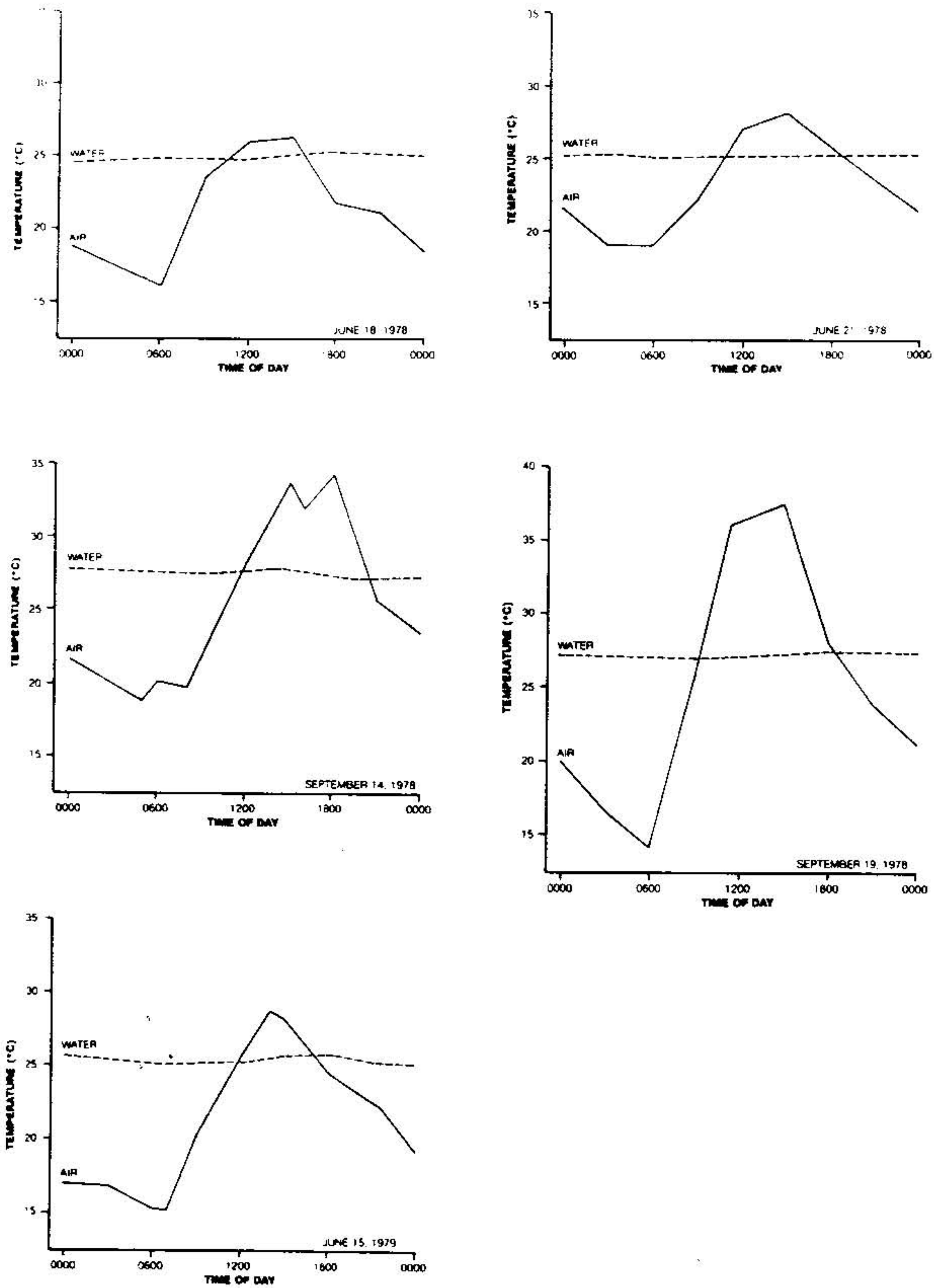

Figure 6. Twenty-four hour temperature profiles of the air (1 m above ground level) and water. Temperatures were recorded at hourly intervals. All measurements were taken at km 32 upstream on the Blyth River during 1978 and 1979.

Webb et al. (1977) describe a number of nests in the Liverpool-Tomkinson area. Nests were built in open grassplain with no shade or protection, beneath small shrubs with only little protection from the sun or wind, beneath dense shrubs and in forests and swamps where they were almost continually shaded and protected from wind, or on one side of a forest where they were completely shaded during some part of the day and either protected or exposed to prevailing winds. Most nests are built on a rich, black, floodplain soil. Riverside nests are not found in mangrove forests. Most are on concave banks where the river comes close to or abutts the adjacent floodplain, or on the floodplain behind the mangroves. One was located on sandy soil in the upper reaches of the river and the remainder were in swamps. A considerable part of most nests was soil, the vegetation being mixed with wet mud during construction. The adult sometimes packed mud onto the nest after the eggs had been laid. Nests in swamps were on a peat-like tangle of roots and debris which formed the swamp floor. This substrate is spongy and the nests were built against, or close to, large trees (usually *Melaleuca* sp.), the roots of which provided a stable foundation.

Associated with most non-swamp nests are a number of wallows; the adult will often lie in these. On occasion the female can be seen lying over the nest. Female *C. porosus* in the wild do not appear, in northern Australia, to defend their nests against approaching humans and usually go straight to the river when approached.

Egg laying probably takes place soon after the completion of the nest. Eggs are deposited in a cavity within the central area of the nest mound. The eggs are laid in rapid succession, the crocodile often using her rear legs to guide them into the chamber. No egg layering is apparent. On completion of egg laying, the opening to the nest cavity is covered over and packed down. The egg cavity is usually deep, with a distance of about 20 cm between the top of the nest and the top of the eggs. Nests without eggs are not uncommon and are not understood. Some of these nests are small with no permanent wallow, whereas others are complete and in all respects resemble nests with eggs. Some may be found adjacent to nests with eggs, suggesting that they are some type of "test" nest. Others are not associated with nests containing eggs. The more likely explanations are:

1. They are made by adolescent *C. porosus*, i.e., "practice" nests

2. They are false starts where conditions at the site were not suitable for completion or changes in weather stopped nest construction.

3. They were intended for eggs and abandoned because of human or other disturbance.

Two unusual nests were found on the Liverpool River (Messel, pers. obs.). The first nest was constructed of grasses and sand only and the eggs were deposited just below the surface, on the side of the nest. Some of the eggs were showing. About a kilometer further upstream a second strange nest was discovered. Rather than constructing a mound, this female had dug and deposited her eggs in a chamber in the black soft soil. Only a small amount of grass was piled over the chamber.

C. porosus eggs are hard-shelled, white and develop an opaque ring of heavily clacified shell around the middle of the long axis of the egg if the embryo is alive. This provides the embryo with its vital supply of calcium. Egg numbers average around 50, with typical weight, length and width of 110 g, 8 cm and 5 cm respectively. Some nests, however, contain tiny eggs, averaging around 65 g. Small females may build small nests and lay small eggs.

C. porosus nesting is essentially a wet season activity, possibly triggered by rising temperatures, however, late nesting in the March-April period, after the peak of wet season flooding, is common. Courtship and mating begin in the late dry season (September to November) and probably occur throughout the wet season; the time between mating and egg laying may be four-six weeks. Nest construction and egg-laying may occur between November and May, with the peaks being in the January-February and March-April periods. The latest nest we have found was laid down sometime in June. The incubation period is temperature dependent and averages around 90 days. Internal nest temperature vary diurnally (Webb et al. 1977), with mean daily temperatures varying from 27°C to 33°C, depending on what time of year the nest is constructed. Nesting still incubating at the beginning of the dry season have lower temperatures. Temperature of incubation influences the proportion of males hatching: the higher the temperature the higher the proportion of males.

The female apparently remains near and guards the nest for much of the incubation period and will repair any damage. The female does not attend the nest continually for the entire incubation period, but frequently leaves it for short intervals. She assists the hatchlings by opening the nest (which sometimes has a hard-baked exterior), probing with the snout and digging with fore and hind limbs, in response to their calling within (a high pitched nasal "gn- arr"). The hatchlings use the caruncle, a protruberance on the end of the end of the nose, to slice their way out of the egg.

At least some adult *C. porosus* remain in the water with grouped hatchlings (a creche) for up to and possibly more than two months but creche formation is apparently the exception rather than the rule in many rivers of northern Australia (Messel et al. 1978-1986, 1:332), and may vary with river type and parental age. In 1979, we found seven creches on the Peter John River (Messel et al. 1978-1986, 11:34) and only two on the Goromuru (Messel et al. 1978-1986, 11:11). Could it be that the young females do not provide parental care and only do so gradually, as they get older? Since the badly depleted *C. porosus* population in northern Australia would have a majority of young parents this might account for the lack of creche formation in many cases. Age dependent parental behavior has not been reported before and would be difficult to explain. However, to date no alternative explanation has been found. (Parental care could also depend on the population density, with more care occurring at higher densities.) The breeding age for males might be a minimum of 12 years, and for females, 10 years, though females as young as 7 years have nested on farms apparently (Grigg pers. comm.).

Magnusson (1978) reports some experiments on hatchling vocalization and concludes that there is little doubt that hatchling calls group hatchlings in field. He suggests that, in the absence of an attending adult, dispersal of hatchlings may be an advantage.

A high proportion of nests are lost due to various factors. The main losses are due to flooding of nests, with subsequent drowning of the embryos. In some areas up to 90% of nests can be destroyed by flooding. Predation on *C. porosus* eggs does not appear to be significant. Monitor lizards appear to be the main predator, with wild pigs also occasionally destroying nests and eating eggs, as do native rats. Aboriginals still also take eggs as a traditional part of their diet. Birds take a toll of just-hatched hatchings making their way to the water.

A fully successful nest may be defined as one in which each of the 50 eggs produce one hatchling in the river at hatchling time. Nests may be successful to varying degrees because of many different causes; some of the eggs may be broken, others destroyed by predators; eggs may not be fertile or the nest may be inundated, killing various fractions of the embryos, depending upon the flood level. Undoubtedly flooding causes the greatest full or partial loss of nests. However, the fraction which are lost in this fashion various from year to year and from one river to another.

On river systems (Messel et al. 1978-1986, 2-4, 12, 13 and 16) where it is sometimes possible to estimate the minimum number of nests from which the hatchlings were derived, the loss factor, from eggs in the nest to hatchlings in the river, appears to be in excess of 90%. It is at this stage of the recruitment cycle where the major losses appear to occur. Once hatchlings are in the river, losses appear much less drastic: some 29% over the mid-dry season, followed by a further loss of some 31% over the ensuing nine months (Table 8.4.1, Messel et al. 1978-1986, 1).

Cannibalism of hatchlings is also another factor that could be important (Messel et al. 1978-1986, 14:43), and would be density dependent. One thing is certain, however, and that is that major flooding leads to the catastrophic loss of nests and in those years hatchling recruitment can only come from freshwater swamp nests and late March-April riverside nests. Were it not for the long nesting period, from early November to mid April, it is unlikely that *C. porosus* would have survived for long on the northern Arnhem Land coastline. In areas such as Papua New Guinea with much more extensive swamp habitat, the situation is different.

The proportion of adult female population that nest annually is poorly known. There is evidence to suggest that some females do not nest each year (Messel et al. 1978-1986, 18:122-124). There is also some evidence that a small proportion of wild females may nest twice in any one season (Webb et al. 1983) and this had already been suggested by Messel et al. (1978-1986, 18:122). Could it be that food supply is the proximal factor involved and that it is the condition factor of the females which determines whether she nests once or twice annually, or not at all, and when the egg laying occurs?

There are still a great many questions to be answered on nesting and undoubtedly these include the hardest ones. On the Blyth-Cadell and Liverpool-Tomkinson River Systems, which have been studied for more than ten years, there are a number of puzzling questions (Messel et al. 1978-1986, 1, 7, 18). For example, in the early to mid-seventies most hatchling recruitment occurred on the Liverpool; since 1976 most has occurred on the Tomkinson. The habitat has not altered and both rivers appear to have almost the same number of large animals. Further, a relatively dry wet season, with little or no flooding is not invariably followed by heavy hatchling recruitment (see our Chapter on Population Dynamics of *C. porosus*).

Webb et al. (1983) examine nesting in a perennial, somewhat elevated, freshwater swamp connected to a meandering tidal floodplain river and in perennial floodplain river channels where floating mats of vegetation overlie freshwater. Nests are constructed on the floating mats. Considerable attention is paid in that paper to embryo mortality and its causes, as well as to the detailed structure of the vegetation.

Habitat required for nesting by *C. porosus* has been described by Magnusson (1978, 1980a) and he has also discussed mortality of eggs (1982) and creche formation (1980b).

FEEDING

A study of the food items taken by 289 hatchlings and small crocodiles has been made by Taylor (1979), who developed a method of removing stomach contents from these crocodiles without sacrificing the animals (Taylor et al. 1978). Her studies indicate that the food items of hatchlings and small crocodiles predominantly consist of crustacea (crabs and shrimps) with smaller proportions of spiders and vertebrates. She also found that crocodiles >4' in length ate significantly more birds and mammals than crocodiles <4'. She suggests that the diet of *C. porosus* reflects the local availability of prey - an apparent exception was the absence of fish and fiddler crabs in the diet of *C. porosus* from habitats where these animals are abundant.

Her suggested explanation for the surprising absence of fish in the diet of hatchlings and small crocodiles is that in most instances, these size classes are not sufficiently agile to capture surface fish.

Observations on the Blyth-Cadell system (Messel et al. 1978-1986, 1:Chapter 7) showed fish being taken by juveniles and many attempts being made to catch them. Most of Taylor's animals were <1.0 m in length and most of the Blyth-Cadell observations were for animals 1.0-1.2 m in length. Undoubtedly *C. porosus* becomes more adept with age at catching fish. The typical way for crocodiles up to 4-5' to catch prey was by snapping sideways or by 'arch-lunge' feeding. In the arch-lunge method the crocodile arches its body and then lunges straight forward at considerable speed.

Larger juveniles (>1.2 m) take an increasing number of vertebrate prey. In the river, birds and mammals are not as abundant as crabs and prawns, and must be specifically hunted. The behavior associated with hunting has been observed a number of times and is the same as sometimes reported during attacks on man (Webb et al. 1978).

The crocodile sights or hears a disturbance from a distance and move towards it on the surface until it appears to sight the prey. It then orients its head toward it, dives and swims underwater to where the prey was. The head usually emerges just in front of the prey. If the prey is a bird moving along the edge of the bank, the crocodiles emerge where the prey was when the crocodile dived, i.e., they do not seem to be able to anticipate lateral movement of the prey.

Frequently, the prey escapes when the head emerges, however, if it does not, the crocodile either lunges forward with the jaws agape or snaps sidewise.

A common method for capturing small fish, employed by *C. porosus* 3-6' in length, was often observed for a 3-4' individual living directly across from the research vessel at km 32 on the Blyth River (Messel et al. 1978-1986, 1:453). The crocodile swam within inches of the banks, against the running tide, so that fish passed between it and the bank. The tail was used to block the passage of the fish, and would curl quickly inwards towards the bank, the head would swing simultaneously towards the bank and snap at the fish. Usually, several attempts are made before a successful capture. On other occasions, the crocodile simply swam along the bank against the tide, with its mouth open and snapped at fish as they ran into it.

Adults appear to show opportunistic selectivity in their feeding habits. The normally attack anything over a given minimum size. The types of prey found or reported in adult stomachs are birds, snakes, lizards, turtles, fish, large crabs, other crocodiles, wallabies, buffalo, cattle, and virtually any mammal which comes near the water's edge. Flying foxes are reputed to be a favorite delicacy and we have often found crocodiles in the mangroves beneath flying fox colonies (Messel et al. 1978-1986, 2:color plate 2.17, (5:60). Large crocodiles may be cannibalistic and hatchlings and small juveniles have been found in their stomachs (Messel et al. 1978-1986, 14:43).

C. porosus also appear to have a predilection for magpie geese (Messel et al. 1978-1986, 1:Chapter 6, 6). In Appendix A1.3 of Messel et al. (1978-1986, 1) some opportunistic observations on crocodile feeding are described. A 6-7' crocodile was observed to leap out of the water and catch a mullet; a 3-4 m crocodile was observed to catch and kill a 1 m shark. Other items that have been observed being taken include eels, mangrove snakes and cormorants.

reflects the local availability of prey - an apparent exception was the absence of fish and fiddler crabs in the diet of *C. porosus* from habitats where these animals are abundant.

Her suggested explanation for the surprising absence of fish in the diet of hatchlings and small crocodiles is that in most instances, these size classes are not sufficiently agile to capture surface fish.

Observations on the Blyth-Cadell system (Messel et al. 1978-1986, 1:Chapter 7) showed fish being taken by juveniles and many attempts being made to catch them. Most of Taylor's animals were <1.0 m in length and most of the Blyth-Cadell observations were for animals 1.0-1.2 m in length. Undoubtedly *C. porosus* becomes more adept with age at catching fish. The typical way for crocodiles up to 4-5' to catch prey was by snapping sideways or by 'arch-lunge' feeding. In the arch-lunge method the crocodile arches its body and then lunges straight forward at considerable speed.

Larger juveniles (>1.2 m) take an increasing number of vertebrate prey. In the river, birds and mammals are not as abundant as crabs and prawns, and must be specifically hunted. The behavior associated with hunting has been observed a number of times and is the same as sometimes reported during attacks on man (Webb et al. 1978).

The crocodile sights or hears a disturbance from a distance and move towards it on the surface until it appears to sight the prey. It then orients its head toward it, dives and swims underwater to where the prey was. The head usually emerges just in front of the prey. If the prey is a bird moving along the edge of the bank, the crocodiles emerge where the prey was when the crocodile dived, i.e., they do not seem to be able to anticipate lateral movement of the prey.

Frequently, the prey escapes when the head emerges, however, if it does not, the crocodile either lunges forward with the jaws agape or snaps sidewise.

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the freshwater region of the river, typified by the fringing riverside vegetation, the number of crocodiles sighted drops drastically. This is the normal situation for TYPE 1 rivers. However, if there is extensive swamp adjoining the upper reaches, the density may in fact increase. Examples of such rivers are the Glyde and the South Alligator. Where there are extensive swamp areas there is major movements between the swamp and tidal river (Messel et al. 1978-1986, 4, 14, 18, 19); Jenkins and Forbes 1985) as the dry season progresses.

The distribution on short TYPE 3 systems is usually even. In the Chapter on Population Status and Conversation we will give detailed information on the densities on animals on the various waterway TYPES.

Not many small crocodiles are seen in the wide open mouth sections of rivers where there is rough water and wave action. They appear to dislike rough water.

SALINITY TOLERANCE

During the course of the crocodile survey program of the University of Sydney many observations of *C. porosus* in water considerably more saline than seawater have been made. The highest reading to date is 78°/oo, where a (4-5') *C. porosus* was sighted (Messel et al. 1978-1986, 18:140). Messel et al. (1978-1986, 1:Section 7.3) give details of many more observations of crocodiles of all sizes, including hatchlings, in hypersaline waters. These field observations indicate that *C. porosus* are able to tolerate very high salinities but probably for short periods only. The discovery of lingual salt glands in *C. porosus* (Taplin and Grigg 1981) revealed the mechanism for removal of excess salt. It is, however, still unclear whether prolonged exposure to high salinities will increase mortality, especially in hatchlings. Messel et al. (1978-1986, 1:376) describe the observation of a number of hatchlings (n = 11) in salinities of up to 50°/oo, but a resurvey three weeks later showed only two (one in 50°/oo salinity). It is unknown whether the missing animals had died or moved out because of the hypersalinity. To test the tolerance of hatchlings to very high salinities, 20 hatchlings were captured on the Tomkinson River, measured, marked and released on Mungardobolo Creek at km 25.3 on July 19. Mungardobolo Creek drains into the Tomkinson and is highly hypersaline (Messel et al. 1978-1986, 7). During the general resurvey of the Liverpool System on October 19, no hatchlings were sighted. The thirteen non-hatchlings sighted were in low tide salinities varying from 38°/oo to 58°/oo. No hatchlings were sighted on the Liverpool and Tomkinson Rivers on either side of Mungardobolo Creek for several km. A further exhaustive search for hatchlings was made by Laurie Taplin (see below) in November. On the night of November 12, a female hatchling No. 1842 was recaptured at km 21.9 on the Tomkinson River. This meant that it had travelled a distance of 13.2 km from its release point. It was in excellent condition. It thus appears likely that of the 12 hatchlings, all except one were predated (most unlikely) or perished because of the high salinity. Our results differ from those of Magnusson (1978) who suggests that hatchling mortality is not affected by high salinities, however, it should be noted that his results were obtained on waters which were not hypersaline.

A mark-recapture study by Grigg et al. (1980) on the Tomkinson River showed little signs of distress in hatchlings that were in salt water for periods of up to 4 months. However, the salinity in their study area only varied from 25-34°/oo and so was not hypersaline.

Taplin (1982) characterizes *C. porosus* as not only a remarkably efficient osmoregulator but also the most euryhaline reptile known to date. At both ends of the salinity spectrum, *C. porosus* appears to depend on its food intake to compensate net water or sodium loss.

METHODS OF MOVEMENT

Methods of Locomotion - Webb (1977) gives a description of methods of movement used by *C. porosus*. There are four main ones; swimming, high walking, the belly run, and the gallop. All were recognized by Cott (1961) in his magnificent study of the Nile crocodile, *C. niloticus*.

When swimming, the front and rear legs are held beside the body, and the complete post-cranial body moves in successive undulations. In the water, crocodiles often drift with the legs hanging down and the tail gently sweeping from side to side. If disturbed, the region of the body behind the head may submerge and the hind feet are spread out. From this posture they can rapidly submerge, backwards.

In the high walk the body is held off the ground except for limbs and tail tip. The limbs move toward each other on one side, while they separate on the other. Crocodiles can "run" using the same basic high walk stance. The tracks of a high walking crocodile are distinctive.

The belly run or slide is typically used when moving from a bank into the water. Using gravity, and as Cott (1961) pointed out, "the polished ventral shields...like the undercarriage of the sleigh", they slide down the bank using the hind limbs to propel them. The tail sweeps from side to side as they move, and in soft mud, this is much like swimming; it leaves a characteristic track.

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