Paleosuchus

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In 1950 Federico Medem arrived in Colombia and set about studying the crocodilians of that country. By the time of his death in 1984 Fred Medem had contributed significantly to studies of all species of South American crocodilians (Medem 1981a, 1983). However, he will probably be best remembered for his pioneering work on the genus *Paleosuchus*. When I started studying *Paleosuchus* in 1979 the ground work had been laid and any basic information I could not find in his publications Fred provided in correspondence. This paper is largely a review of the literature, most of which was written by Federico Medem. It is unfortunate that Fred could not write it himself. I am also grateful to Andy Ross who provided much literature not available in Brasil. The work was financed by the Instituto Nacional de Pesquisas da Amazonia and by grant number 40.5055/83 from the Brazilian Conselho Nacional de Desenvolvimento Cientifico e Tecnologico to W. E. Magnusson.

NOMENCLATURE

Biochemical analyses (Densmore 1983) support the status of *Paleosuchus* as a distinct genus within the Alligatorinae. The problems associated with *Paleosuchus* nomenclature are complex and have been detailed by Mook and Mook (1940). However, since Medem's (1958) revision there has been almost universal acceptance of the names *Paleosuchus trigonatus* and *P. palpebrosus* for the two South American species of dwarf caimans. The only modern point of contention is the allocation of *Jacaretinga moschifer* Spix to synonymy with one of the species of *Paleosuchus*. The type specimen of *J. moschifer* was destroyed during World War II. However, the description of *J. moschifer* is accompanied by a figure of a crocodilian with a snout shape similar to that of *P. trigonatus*. Vaillant (1898) considered *J. moschifer* to be synonymous with *P. palpebrosus* based on the description which specifically mentions four rows of dorsal scutes between the hind legs. Medem (1958) considered *J. moschifer* to be a composite, the description based on *P. palpebrosus* and the figure based on a *P. trigonatus*, and so synonymized *J. moschifer* with *P. trigonatus*. The synonomy would not be important except that *J. moschifer* was described from Bahia, an area which has several confirmed reports of *P. trigonatus* (Magnusson 1987). For zoogeographic reasons I agree with Vaillant (1898) that *J. moschifer* is a synonym for *P. palpebrosus*. Also, Muller (1923), a specialist familiar with the species of *Paleosuchus*, identified and catalogued the type specimen as *P. palpebrosus*.

Medem (1983) considered Seba's plate 105, Figs. 3 and 4, of the specimen on which Schneider based his description of *P. trigonatus*, to represent the species we now call *P. palpebrosus* but did not suggest that the names of the two species be switched. In the interest of nomenclatural stability it may be necessary to designate a neotype for Schneider's *Crocodilus trigonatus*.

MORPHOLOGY

Species in the genus *Paleosuchus* are among the smallest of the Crocodilia. Medem (1981a) encountered male *P. trigonatus* up to 136 cm snout-vent length (SVL), however most adult males are in the size range 75-90 cm SVL. Females reach about 75 cm SVL. Few data are available for *P. palpebrosus* but it is generally considered that they mature at smaller sizes than *P. trigonatus*. Medem (1981a) records male *P. palpebrosus* up to 90 cm SVL and females up to 68 cm SVL. *Paleosuchus* tend to have short tails, at least in comparison to *Caiman crocodilus* (Vanzolin and Gomes 1979).

Distinctive features of the skull are the lack of distinct supratemporal fossae (small fossae are present in juvenile *P. trigonatus*), 8 teeth in the premaxilla, and the lack of an interorbital ridge. Three bones form a plate over the orbit and almost obscure it when the skull is viewed from above. The shape of the skull of *P. trigonatus* is that of a generalized crocodilian, but *P. palpebrosus* has a high smooth "dog-like" skull (Medem 1958, 1981a). Some individuals have body characteristics of *P. palpebrosus* but head shape and color of *P. trigonatus*. Medem (1970, 1981a) considered these to be hybrids. The best feature to distinguish between skulls of the two species is the relative size of the external mandibular foramen. In *P. trigonatus* the maximum width of the foramen (measured perpendicular to the long axis) is equal to or greater than the distance from the foramen to the inferior edge of the angular. The width of the external mandibular foramen is less than the distance from the foramen to the inferior edge of the angular in *P. palpebrosus*.

The skins of both species of *Paleosuchus* are heavily ossified, the bony osteoderms of the venter, dorsum and tail being so closely juxtaposed that the animal almost appears to be enclosed in a shell. Algae adhere to the skins of both species in captivity, and in some natural habitats (Medem 1958), giving the animals a green color. Medem (1981a) gives the sizes and meristics of individuals of each species collected in Colombia.

The eyes of *Paleosuchus* are a rich brown color. Medem (1981a) presents many color plates of each species. Adult *P. palpebrosus* have extensive dark pigment on the ventral surfaces and light-brown heads. Adult *P. trigonatus* have dark heads and generally lack pigment on the ventral surface. The dorsal surface of the head behind the eyes is light yellow in juveniles of each species (color photographs in Medem 1981a). Other aspects of coloration are variable and not very distinctive (Medem 1958).

The only other crocodilian genus with deep-brown eyes, heavily-armoured skin, heavily ossified palpebrals, and small adult size is the African crocodyline *Osteolaemus tetraspis*. Too little is known of the life histories of either genus to warrant speculation on the reasons for this morphological convergence but it may be significant that the distributions of both genera are centered on areas of tropical rainforest.

DISTRIBUTION

Paleosuchus trigonatus occurs throughout the Amazon and Orinoco drainage basins and the coastal rivers of the three Guianas. *P. palpebrosus* occurs over essentially the same range and extends south across the Brazilian shield to the Rio Parana and Rio Paraquay drainage basins. It also occurs in the Rio Sao Francisco drainage basin of the Brazilian states of Bahia and Minas Gerais. Medem (1983) gives detailed locality records. Two records for *P. trigonatus* (Aruana and Bahia) south of the Amazon Basin given by Medem (1983) are probably erroneous (Magnusson and Yamakoshi 1986). In Venezuela *P. trigonatus* is largely restricted to the southern, forested regions whereas *P. palpebrosus* occurs extensively over the northern "llanos" areas of the Rio Orinoco drainage (Gorzula 1987: Figs. 2 and 3).

Despite being sympatric over large areas, the two species of *Paleosuchus* are rarely syntopic. In water bodies in which they are found together one species is usually common and the other rare (Medem 1967, 1971a). The major habitat for *P. trigonatus* appears to be small forest streams (Medem 1967, Dixon et al. 1977, Magnusson 1985) and *P. palpebrosus* rarely occurs in that habitat. In the central Amazon Basin *P. palpebrosus* is found most commonly in inundation forests around the major rivers and lakes (Magnusson 1985). On the Brazilian shield, *P. palpebrosus* occurs in streams lined by gallery forests that run through savanna (Rebelo and Louzada 1984). Much of the confusion that surrounds the ecological distributions of the two species stems from the fact that it is difficult to work in small rainforest streams and gallery forest. Most observations (as distinct from occurrences) of *Paleosuchus* are made around large water bodies with easy access by boat. Individuals, especially large males and dispersing juveniles, are often found in such situations but to date there is no evidence that either species normally breeds around large water bodies. Large rivers and lakes are normally the major habitats for *C. crocodilus*, *Melanosuchus niger* and *Crocodylus intermedius*. Medem (1980) suggested that the occurrence of *Paleosuchus* in some habitats in Colombia increased after the larger, commercially more valuable species, had been eliminated by overhunting.

Much more work needs to be done on the ecological distributions of the species of *Paleosuchus*, especially *P. palpebrosus*, but care must be taken to evaluate habitats for the presence of both sexes, nests and juveniles. Spotlight surveys from a boat as are used for most other species of crocodilians are probably of little use for evaluating populations of *Paleosuchus*. Gorzula (1987) suggests that the water bodies in which *P. trigonatus* occurs are chemically distinct from those in which *C. crocodilus* occurs, so limnological variables may be useful for distinguishing habitats.

FOOD

As with other crocodilians, *Paleosuchus* species eat a variety of vertebrate and invertebrate prey. Medem (1981a) lists the stomach contents of *Paleosuchus* taken in a variety of habitats in Colombia, Vanzolini and Gomes (1979) give stomach contents of *P. trigonatus* taken in Brazil, and Ruesta (1981) describes the stomach contents of 3 *P. trigonatus* from Peru. Large males of both species occasionally eat other crocodilians (Medem 1981a).

In the central Amazon Basin *P. trigonatus* eats more terrestrial vertebrates than other crocodilians of similar size but *P. palpebrosus* eats similar foods (mainly invertebrates and fish) to *C. crocodilus* and *M. niger* in the same size range. Mammals and snakes are taken mainly by large *P. trigonatus* with fixed home ranges (Magnusson et al. 1987). The diet of *P. palpebrosus* in savanna gallery forest has not been studied.

REPRODUCTION

Medem (1981a), Dixon and Soini (1977), Ruesta (1981, 1982-83) and Magnusson et al. (1985) have described nests of *P. trigonatus*. Ruesta (1982-83) also described the embryos. The nests found by Ruesta and by Dixon and Soini in Peru were located 13 September and 14 August-30 November, respectively. The nest found by Medem in Colombia was located 13 February and had well developed embryos. Magnusson et al. (1985) found nests in the Manaus area between August and January. Egg laying apparently occurs at the end of the dry season and hatching at the beginning of the wet season. In the Manaus area *P. trigonatus* frequently make their nests beside or on top of termite mounds which elevate the temperatures of the eggs above that which they would otherwise attain (Magnusson et al. 1985). Medem (1981a) and Ruesta (1982-83) give egg dimensions. *P. trigonatus* has been bred in the Cincinnati Zoo (Jardine 1981).

Medem (1971b) recorded a nest of *P. palpebrosus* found in gallery forest in Colombia 1 November 1967, which hatched in December. Another nest found in the same area, but in a slightly more exposed site, had recently laid eggs 8 August 1970. That nest had a temperature of 31°C at 22cm depth. A third nest was located among four small trees on an elevated mound of earth formed by dry canals, 3km from a permanent canal, in August 1978 (Medem 1981a). Nest and egg dimensions of the three nests are given by Medem (1981a). Rebelo and Louzada (1984) found hatchlings near a nest in June-July in the Reserva Biologica Aguas Emendadas on the Brazilian Shield but the age of the nest could not be determined. Marc Hero (pers. comm.) encountered hatchling *P. palpebrosus* 13.2 cm and 14.2 cm SVL in the Rio Negro in October 1985, indicating nesting in the early dry season. The limited data coupled with the great climatic and geographical variation within the range of *P. palpebrosus* makes generalizations about its nesting season(s) presently inadvisable.

Medem (1981a) reports in detail the captive reproduction of a female that he considered to be a hybrid between *P. palpebrosus* and *P. trigonatus*. The female was mated by a *P. palpebrosus* and laid her eggs 27 September 1977. *P. palpebrosus* has also been bred in the Rio Grande Zoo, Albuquerque (A. Dale Belcher, pers. comm.).

Medem (1971b, 1981a) gives incubation periods of 90-92 and 147 days for *P. palpebrosus* eggs incubated artificially at variable temperatures. Ruesta (1982-83) reported incomplete incubation of *P. trigonatus* eggs after 3 months but the eggs had been moved and the final incubation temperature was not given. Jardine (1981) reported an incubation period of 114-118 days for eggs of *P. trigonatus* incubated artificially at 29-31°C. The data in Figure 1 indicate that the normal incubation period of *P. trigonatus* in the Manaus area is in excess of 100 days. This is longer than the incubation periods reported for all other alligatorines and most other crocodilians (Magnusson 1979).

PARASITES, DISEASES AND PREDATORS

Nothing is known of th effects of parasites, diseases and predators on populations of *Paleosuchus*. Magnusson (1985) reports variation in the frequency of parasitism by nematodes and leeches in different habitats in Amazonia and Medem (1981b) lists internal parasites found in
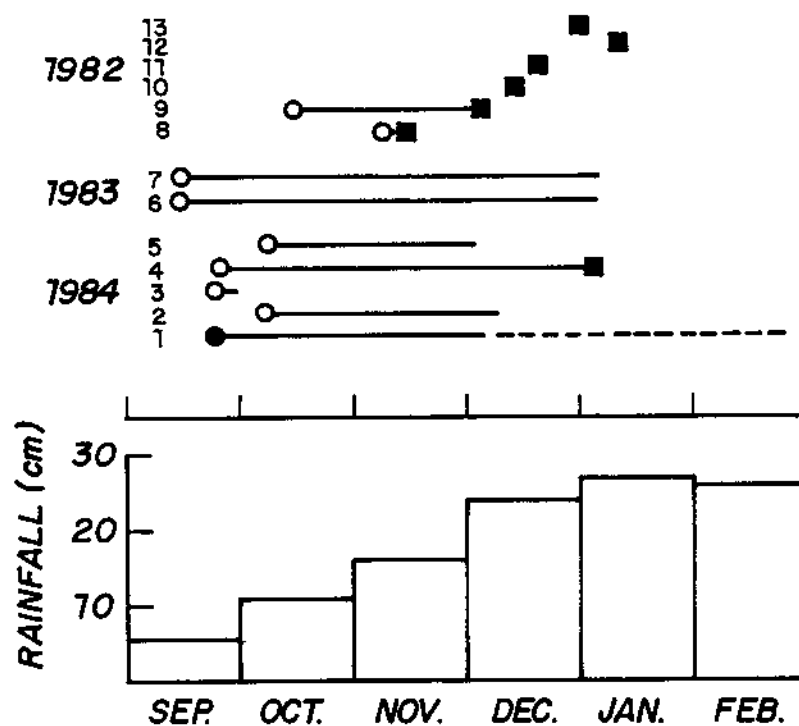
Figure 1. Dates of laying (solid circles), hatchling (solid squares), first encountering (open circles), and periods with incubating eggs (lines), for 13 nests in the Manaus area. The dates of death of eggs in nest #1 are not known and the period of uncertainly is indicated by the broken line. Rainfall records are means (1910-1975) for the city of Manaus.

Paleosuchus in Colombia. Medem (1981a, 1981b) reports attacks by tabanid flies on animals restrained on shore near the banks of rivers during daylight hours.

There are no reports of diseases in wild *Paleosuchus* and the only confirmed predators of *Paleosuchus* are man, anacondas (*Eunectes murinus*) and other crocodilians (Medem 1983). However, jaguars (*Panthera onca*) regularly eat *C. crocodilus* (Medem 1981a) and other reptiles (Louise Emmons, pers. comm.). There is no reason to believe that they do not also eat *Paleosuchus*. The only large *P. trigonatus* (approx. 65 cm SVL) that I have found dead was eaten by a large cat (*P. onca* or *Felis concolor*). It is likely that the cat killed the *P. trigonatus* as, apart from a conspecific, there are no other predators in the area that are likely to be capable of killing a large *P. trigonatus* close to water.

Most of the nests of *P. trigonatus* I studied in 1983 and 1984 were destroyed by predators. However, I believe the high rate of predation may be related to interference with nests while measuring temperatures. None of the nests studied in 1982, which were all discovered late in incubation, suffered predation. Ruesta (1981) and Medem (1983) list probable nest predators of South American crocodilians but, apart from humans, no predators have been caught in the act of robbing *Paleosuchus* nests.

BEHAVIOR

Little is known of the behavior of either species of *Paleosuchus* and they are not good candidates for behavioral research as they are much more shy in the presence of humans than most crocodilians. My coworkers and I have caught one female *P. trigonatus* several times in a shallow stream in front of a nest with incubating eggs, and tracks in front of another nest indicate that a female was in attendance. We have never been attacked when opening nests but have noted altered behavior by females associated with hatchlings. Twice females have left their refuges and approached us when we were catching hatchlings near nests and on one occasion a female, which was accompanied by a hatchling group and that had been noosed around the back legs, chased us out of the stream. We have not observed aggressive behavior towards humans by *Paleosuchus* in any other situation. Medem (1981a) describes aggressive behavior by a captive female *Paleosuchus* defending a nest and Gorzula (1984) describes having his inflatable boat sunk by a *P. trigonatus* which responded to human initiations of hatchling *C. crocodilus* calls.

All successful nests in my study area were opened by a crocodilian and females with hatchling groups were found in front of four recently opened nests. One nest, constructed in the home range of an adult male but far from the normal area of activity of any female, was found recently opened and the hatchling group was accompanied by the adult male. No female was found in the area despite intensive searching. A female (64 cm SVL) had been caught at that site the preceding August but no female had been seen there before or after so it seems likely that the male opened the nest and released the young. Eggs in some nests in the Manaus area are encased in hard termite workings by the end of incubation (Magnusson et al. 1985). Nest opening by an adult is probably essential for successful hatching of those eggs. More detailed observations will probably show *Paleosuchus* to have the same range of nest-guarding, nest-opening and hatching-defense behaviors found in other crocodilians.

After heavy rain *P. trigonatus* are often found in rapids or small waterfalls; sitting perpendicular to the current with their mouths open, the lower jaw submerged and the upper jaw above water level. I assume that they are foraging, but I have no evidence of what they catch with this technique.

SUGGESTIONS FOR FURTHER RESEARCH

Much remains to learn about the ecologies of both species of *Paleosuchus*. It is obvious that the habitats of each differ, and that the habitats of both are different from those of other sympatric crocodilians but just which differences are critical remains conjecture. Reasons for habitat segregation could include competition, predation, and behavioral and physiological adaptations. To differentiate the effects of these factors would require large scale experiments, though areas in which sympatric species have been eliminated by overhunting could serve as unplanned manipulations.

P. trigonatus may differ from other crocodilians in its thermal biology because temperatures in its main habitat are moderate, relatively invariant, and opportunities to bask are limited. Zoo animals could serve for the study of the effects of temperature on digestion and metabolic rate.

Field studies will have to focus on populations rather than presence/absence data as has been the pattern in the past. Presence/absence data have raised some interesting questions but to date have been of limited use in providing answers. My as yet unpublished studies indicate that *P. trigonatus* have small home ranges (of the order of 500-1000m small stream) and, if the same proves true for *P. palpebrosus*, long term studies of population dynamics, reproduction and habitat use could be done on marked populations, simply and at low cost. Comparative studies of populations of *P. palpebrosus* living on the high, cold plains of the Brazilian shield, flooded forests of the Amazon system and the lowland floodplains of the Orinoco system would be particularly interesting. Small implanted transmitters could overcome many of the problems associated with difficult habitats and the wariness of the species. Basic data on diet are lacking for *P. palpebrosus* over most of its range and most of the data on the diet of *P. trigonatus* are from a few localities. Stomach contents could be collected by non-destructive means (Taylor et al. 1978) in parallel with other studies.

Schmidt commented in 1928(:212) "It is one of the curiosities of zoological collecting that so little is known of the habits and distribution of these species (*Paleosuchus*)". Sixty years later we know only a little more of their distributions and we have advanced very little in studies of their habits. They remain "one of the most interesting problems in South American zoology" (Schmidt 1928:212).

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GROWTH OF *Crocodylus porosus* IN THE WILD

IN NORTHERN AUSTRALIA

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INTRODUCTION

The main data on growth in the wild of *Crocodylus porosus* in this chapter come from three extended experiments within the former Sydney University--Northern Territory Government Joint Crocodile Research Project. All three have been reported on separately previously, but our aim in this review is to look at the data as a whole, and reanalyze it to obtain the most information possible on aspects of growth of *C. porosus*. The first experiment involved a capture-recapture study of 254 individuals on the Liverpool-Tomkinson River System (Monograph 7); a multiple regression model was fitted to this date (Webb et al. 1978) to derive growth curves and to examine variables affecting growth. Eight animals first captured between 1973 and 1975 were recaptured in 1983; some of them having been captured two times previously. These data also provided valuable information (Chapter 2 Monograph 18). The second experiment was carried out by Magnusson (1978, and several papers) and he studied by capture-recapture techniques the growth of *C. porosus* up to 133 days, again by fitting growth curves. The third experiment (Chapter 8, Monograph 1) involved the capture of hatchlings on the Blyth-Cadell River System (some 30 km to the east of the Liverpool-Tomkinson System) in 1978 and recaptures in following years.

Throughout this chapter we shall be referring to Monograph 1, which is but one of a series of 19 published by Pergamon Press between 1979 and 1986 (Messel et al. 1979-1986) and reporting on the lengthy *C. porosus* studies by Messel and his collaborators. We restrict ourselves to growth of *C. porosus* only. In Chapter 2 of Monograph 18, on which the present chapter is based, we compared these growth rates with those of other crocodilians. In seeking to understand the growth rates presented in this chapter, we are unfortunately lacking quantitative data on an important piece of information--the food availability (or, at least, the relative food availability) on the rivers considered at different times of the year, in different years and on any differences in food availability on different rivers. The ability of crocodilians to survive in a very low growth situation may be illustrated with an example given by Deraniyagala (1939). He quotes the case of two hatchling *C. porosus* (hatching total length around 30 cm), one of which was kept in a tub and the other in a small natural pond (with access to a wild diet). The animal in the tub died after 2 years at a length of only 35 cm, whereas the one in the pond had attained a length of about a meter after only 10 months. An example of the effect of feeding on growth may be taken from our own data. A hatchling captured at SVL 16.4 cm on the downstream Liverpool was recaptured after 3 months on the Tomkinson. Its SVL had changed by only 0.3 cm and weight by only 5 g, which is essentially no growth over the period. This animal had a skewed jaw which presumably interfered considerably with its ability to catch food items; it was very thin on second capture. Other

examples of very low growth over 3 months of the dry season were seen on the upstream Blyth (see Part 1). The differences in growth between Deraniyagala's two animals were probably due to a number of factors, the availability of a proper diet possibly being a major one. However. given that the animals can survive for so long in an essentially no growth situation, it is clear that attempts to interpret variations of growth amongst wild populations are fraught with difficulties, especially when so many necessary data are either unavailable or very difficult to obtain. The results in this Chapter obtained from recaptures over lengthy periods can be suggestive only. and there is need for smaller scale experiments to examine particular points.

To avoid constant repetition, all growth rates referred to in this Chapter are snout-vent length (abbreviated SVL) rates. Units of growth, if not explicitly stated, are cm/day. For conversion between head length (HL) and snout-vent length (SVL), we have used the same equations as used by Webb et al. (1978:388). Other conversions (e.g., SVL to total length, TL) may be obtained from Webb and Messel (1978) who also gave references to other morphometric work on *C. porosus*. All uncertainties quoted are standard deviations (n-1 method). Differences between means are tested by using the t-test.

PART 1. EMBRYONIC GROWTH AND POST-HATCHING GROWTH UP TO 133 DAYS

1.1 Embryonic Growth

Estimates of growth rates for embryonic *C. porosus* may be obtained from data given by Deraniyagala (1939) for animals in Sri Lanka and by Magnusson and Taylor (1980) for animals in Arnhem Land, northern Australia. The data are inadequate, but we have tried to look at the limited available data in a number of ways. The results are not claimed to be any more than indications of embryonic growth rates. The egg sizes reported by Deraniyagala are consistent with the egg sizes reported by Webb et al. (1977); for 22 nests they report mean egg lengths ranging from 7.2 cm to 8.1 cm, and Deraniyagala's nests I, II, and III have mean egg lengths of 7.4 cm, 7.9 cm, and 8.3 cm. The sizes of hatchlings are also consistent (see Table 1). In fact, the mean HL of 17 animals in Table LVIII of Deraniyagala is 4.8 ± 0.2 cm, to be compared with 4.6 cm (no error limit given) as the mean for 5 nests given by Webb et al. (1978). (However, there can apparently be great variation in egg and hatchling sizes; results from Edward River crocodile farm in north Queensland, Australia, appear to show that small females yield small eggs and small hatchlings (G. Grigg, pers. comm.).

We shall now examine the available data on embryonic growth and derive some estimates for their growth rates. These can only be indications, however, because the length of incubation can vary greatly, from some 80 to 120 days. Nests laid late in the dry season develop more slowly because of the cooler temperatures, and there.are indications from field observations that some late nests may not hatch at all. Detailed studies are required for embryonic growth under different temperature regimes in the field.

Deraniyagala gives the following records for embryos from Nest II (days are estimated days after laying, allowing 97 days for incubation; he suggests, however, that the incubation was by no means normal).

Days	37	48	60	97
Total length (cm)	8.1	11.9	17.0	29.4 ± 0.5
	n = 1	n = 1	n = 1	n = 4

Table 1. Examples of sizes on hatching of *C. porosus* from Arnhem Land, northern Australia (Liverpool-Tomkinson Rivers System) and Sri Lanka (Deraniyagala 1939).

Nest	Sample	SVL	Length	Weight	Age Processed
Myeeli 1 Removed from nest after hatching 4.3.76	48	14.1 ± 0.3	30.0 ± 0.7	83.0 ± 3.4	~ 2 days
Myeeli 2 Removed from nest after hatching 16.2.76	46	13.6 ± 0.5	29.6 ± 0.6	74.5 ± 4.1	~ 2 days
Myeeli 3 Removed from nest after hatching 18.4.76	50	13.8 ± 0.3	29.9 ± 0.5 (49 anmls)	69.6 ± 3.5	~ 2 days
Liverpool km 47.5 Artificial nest 17.3.76	15	13.7 ± 0.7 (14 anmls)	29.6 ± 1.2	81.2 ± 5.7	~ 2 days
Atlas Creek Artificial nest hatched[1] 15.2.77	26	14.9 ± 0.3	32.0 ± 0.7	82.8 ± 2.7	~ 6 days
Billabong Morngarrie Creek Removed from nest after hatching 13.4.76	11	13.4 ± 0.5	28.8 ± 1.1	59.2 ± 6.0	~ 1 day
Liverpool B22 Artificial nest hatched 30.4.76	26	14.1 ± 0.4	29.9 ± 0.6	63.2 ± 7.6	11-13 days
Tomkinson B48 Artificial nest hatched 30.4.76-10.5.76	8	13.6 ± 0.3	29.1 ± 0.5	59.8 ± 6.5	1-10 days
Tomkinson km 68.5 Artificial nest hatched 19.2.77	9	14.4 ± 0.3	30.8 ± 0.7	73.1 ± 1.5	~ 7 days
T12 Tomkinson km 53.9 between 4-9.6.74	29	14.9 ± 0.2	31.7 ± 0.5	92.7 ± 4.2	~ 7 days
T13 Tomkinson km 59.7 between 4-9.6.74	14	14.0 ± 0.2	29.9 ± 0.5	87.4 ± 4.5	~ 7 days

Table 1. cont.

Nest	Sample	SVL	Length	Weight	Age Processed
T14 Tomkinson km 65.1 between 21-28.6.74	9	14.5 ± 0.2	31.0 ± 0.5	82.8 ± 2.8	~ 7 days
Deraniyagala Nest I Artificial	11	--	30.1 ± 1.0	90.2 ± 6.1	0
Deraniyagala Nest II Artificial	4	--	29.4 ± 0.5	78.8 ± 6.3	0
Deraniyagala Nest IV Artificial	5	14.6 ± 0.2	30.4 ± 0.3	79.4 ± 3.6	0
Liverpool 1975 hatched May 4 Artificial	23	13.5 ± 0.6	28.3 ± 1.4	64.7 ± 4.8	7 days

[1]. The description "artificial nest" means that the eggs were removed from a natural nest and incubated in an artificial nest.

This shows a TL growth rate for the 37 days before hatching of 0.34 cm/day, which gives an SVL rate of 0.17 cm/day (using an approximate conversion factor of 2); Nest III gives 0.15 cm/day for 37 days before hatching. Deraniyagala states that his animals were incubated at temperatures which fluctuated daily between 27 and 30°C.

From Table 1 of Magnusson and Taylor (1980) we may also obtain some estimates for embryonic growth rates. They give measurements for two series of embryos taken from two different nests; the Series I nest was incubated at a mean 2.5°C lower than that of Series II (28.5°C against 31.0°C). For the Series I animals one obtains, from the 51st to 86th day, an SVL growth rate of 0.15 cm/day and for the Series II animals an SVL growth rate, from the 49th to 86th day, of 0.155 cm/day. To obtain these results we have used a conversion factor of 4.01 between snout-vent and head length rates, since fitting of the four pairs of snout-vent and head length values in their Table I to a straight line gives SVL = 4.01 HL - 3.7, with coefficient of determination 0.991. If we regress the total length against head length for all the animals in Table LVIII of Deraniyagala, then we obtain TL = 8.37 HL - 10.53 (coefficient of determination 0.97). If we use the conversion factor 0.48 given in Appendix I of Webb and Messel (1978) for converting between the snout-vent length and total length (for their smallest class of animals; they do not consider embryos), then we obtain a conversion factor between snout-vent length growth rate and head length growth rate of 4.02.

When comparing Deraniyagala's results with those of Magnusson and Taylor, one must bear in mind possible variations in incubation period discussed already and differences in temperature.

Magnusson and Taylor give an HL (Series II) of 3.74 cm at 86 days, whereas Deraniyagala (using his ages) has animals of 80 days with HL of 4.2 cm. Plotting of Deraniyagala's head length

measurements against age for Nest II gives a good fit to a straight line between 26 and 81 days (8 points, coefficient of determination = 0.99), with an SVL growth rate of 0.20 cm/day (using 4.01 to convert) compared with 0.155 cm/day for the Series II animals. If the Series I head lengths are plotted against age, a good fit to a straight line is again obtained between 9 and 86 days (8 points, coefficient of determination 0.995; the 28 day value is omitted) with an average SVL growth of 0.17 cm/day. Taking the Nest II and III growths over the last 37 days, one obtains from the head lengths an SVL rate of 0.13 cm/day (somewhat less than that obtained from the total length change), indicating that there may have been a slow-down in growth near hatching time for these two nests (though the data are perhaps too limited to draw such a conclusion). If one looks at Nest I and calculates the average SVL growth over the last 25 days, it is 0.15 cm/day, comparable with the Nest II and Nest III rates over the last 37 days. Thus, an SVL growth rate of between 0.15 and 0.20 cm/day covers the range of results, with the various uncertainties mentioned previously, for the 80 or so days before hatching occurs.

Webb et al. (1983) present some further data on development of *C. porosus* embryos, giving equations relating age to snout-vent length and head length (both expressed as ratios of egg length) for a 30°C incubation. Taking a mean egg length of 8.13 cm as given for their sample, the data in their Table 1 indicates SVL growth rate of 0.18 cm/day (62- 82 days) using the SVL coefficients and 0.27 cm/day (36-62 days) using the head length coefficients (and converting as previously).

1.2 Hatchling Growth up to 133 Days

Magnusson (1978) carried out a study on hatchling growth up to an age of 133 days by means of capture-recapture methods. He has presented (Magnusson and Taylor 1981) a mean growth rate for these animals during the wet season (months) for their first 80 days, obtaining an SVL rate of 0.09 cm/day. Since each animal in his study was individually marked and some were captured up to five times, much might be learned by examining the individual growth records. This will also allow examination of variations of initial growth between animals from different nests. Nests are identified in Table 1.

In Table 2 we give the individual growth records for the three animals that were captured four or more times; all came from the Myeeli nest. We also present in records A to H, in Table 3, SVL growth records over different periods for animals from various nests. The identification numbers of each crocodile are given so that progress of particular crocodiles can be followed. The best record is for the animals from the Myeeli I swamp (records A, F, G). Comparison of the growth from 0-37 days and from 0-96 days shows little difference in average rate, despite the 0-96 day period, including 40 days of dry season growth (of course, very early in the dry season; there is no sharp transition from wet season to dry season conditions). The 0-65 day average is higher than the shorter and longer period average, as is also shown for the three individuals in Table 2, all of whom show an increased rate of growth from their 37th-65th day. Animal 1403 also shows a slightly higher rate of growth from its 0th-65th day than from 0th-35th day.

The highest rates of growth (record C) are the 0-53 day growths of animals hatched at the base and released at km 23.4 on the Tomkinson River. The average growth rate is 0.126 ± 0.021, with the highest rate being that of 1415 at 0.158 cm/day, almost double the rate of the slowest growing animal in this group. This high growth occurs at the end of the wet season. Record E shows growth rates for these animals from their 53rd to 82nd day, and the rates for 1404, 1406, and 1407 have dropped considerably. The growth over this period is all in the dry season.

The lowest average rates of growth are from a group of animals that were raised at the base and then released into the Liverpool River at km 47.3. The growth record D is from mid-May to mid-June and so is an all dry season growth rate. These animals may be compared with those in record C, whose wet season growth over a corresponding age span is up to four times higher.

Webb et al. (1977) gave results for three nests (T12, T13, T14) on the Tomkinson River, all of which hatched in June 1974. The initial sizes for the surviving hatchlings from these nests are given in Table 1. (It should be noted that all the standard errors in this reference were calculated incorrectly and are generally too small.) Mean daily SVL growth rates of the hatchlings from these nests were 0.06, 0.05 and 0.05 cm/day, respectively, for periods of 69, 63, and 52 days. These growth rates are all in the dry season (all periods ending mid-August) and may be compared with records, C, D, and F. The dry season growth rate over the same age interval is again considerably less than the wet season one. Magnusson and Taylor (1981) also compared the wet season growth rate of hatchlings with these dry season rates and found that they were significantly higher.

Additional information on early growth may be obtained from data on recaptures of some of the animals from the Liverpool 1975 nest (see Table 1). Five of these animals were recaught after spending 18-21 days in the wild and their SVL mean growth rate was 0.086 ± 0.021 cm/day (period of growth from 6th to 26th day). Three other animals recaught after spending from their 6th to 70th day in the field showed an average growth rate of 0.058 cm/day. The growth period for these animals begins in mid-May and so is all dry season growth. The initial growth rates up to the 26th day are comparable with the purely wet season early growth rates.

The growth rates of Record C (mean 0.126 cm/day) are not far below those that we have obtained for embryonic growth rates and perhaps represent an upper limit to the initial growth rate of C. porosus.

1.3 Blyth-Cadell Hatchling Study

Further information on early growth of C. porosus may be obtained from our capture-recapture study on the Blyth-Cadell Rivers System. A large number of hatchlings of various ages were captured in mid-June 1978 and recaptured in late September 1978. The results (Monograph 1, Chapter 8) show that the mean rate of growth of all hatchlings over the 3-month period (all dry season) was 0.030 ± 0.013 cm/day. Because this sample includes hatchlings of various initial ages, care should be exercised when comparing this with the most comparable previous results, those for the Tomkinson T12, T13, and T14 nests of 1974 discussed in the previous section.

Growth rates on the Cadell and Blyth rivers are almost the same during the dry season. Males in September 1978 were bigger than females. There was an indication that male hatchlings grow slightly faster than female hatchlings during the dry season.

Results on hatchling movement suggest that hatchlings move preferably to certain mid-sections of the Blyth River, and hence it was important to check whether hatchlings remaining on particular subsections of the river showed differing BWT gains. If they did, then the movement might be interpreted in terms of the hatchlings seeking a more adequate food supply. One of the problems faced in this consideration is that of small sample number. By examining the rates of new weight to old weight, we found that there were no significant differences between growth on different sections of the river, over a period of nine months which included the wet season. However over 3 months of the dry season the brackish midsection of the Blyth showed significantly higher mean body weight gains than the upstream freshwater sections. The differences are probably related to food supply.

Table 2. Capture histories of three hatchlings from the Liverpool-Tomkinson Rivers System. All hatched from a natural nest on March 4, 1976.

Animal 1360

Age (days)	0		37		65		96
SVL (cm)	13.8		16.5		19.1		21.0
Rate (cm/day)		0.073		0.093		0.061	

Animal 1370

Age	0		19		37		65		96		131
SVL	14.1		15.3		17.2		20.5		21.9		22.5
Rate		0.063		0.106		0.118		0.045		0.017	

Animal 1394

Age	0		35		65		94
SVL	14.7		17.5		20.1		21.0
Rate		0.080		0.087		0.031	

In his thesis Magnusson (1978) fits a curve to records of animals up to 133 days old. He found that a parabola gave a better fit to the data than a straight line and that the growth curve also predicted a rate of 0.031 cm/day at 120 days (well into the dry season).

The largest growth rate over the 3-month dry season period on the Blyth was for an animal that went from 19.0 to 24.7 SVL, a rate of 0.061 cm/day. As described in Chapter 8, Monograph 1, growth on the freshwater section of the Blyth was particularly slow. Several animals only gained between 0.4 cm and 0.7 cm in the period, corresponding to growth rates ranging from 0.004 to 0.008 cm/day. Examination of Magnusson's growth records over dry season periods shows that animal 1370 grew only 0.6 cm from mid-June to mid-July (0.017 cm/day).

Record D of Table 3 shows a mean dry season growth rate (0.039 cm/day) for young animals consonant with that found on the Blyth-Cadell System (0.03 cm/day). Animal 1370 shows a mean rate from its 65th to 131st day of 0.030 cm/day and animal 139a has the same rate from its 65th to 94th day.

To examine further the relationship between growth rate and SVL, the change in SVL over the 3-month dry season period was regressed against the initial SVL, for animals (both male and female) that remained on the km20-35 section of the Blyth River (we have selected this section to omit the slow growth freshwater sections). The slope was 0.20 (standard error 0.1), showing a slight upward trend of growth rate with size, but the coefficient of determination was only 0.08 so one should treat the result with care. From Magnusson's results for the wet season one might have expected a clear downward trend in hatchling growth with increasing initial SVL (and hence increasing age), though we did note previously some evidence for an increase in growth with age for some of Magnusson's animals up to 60 days. The possible discrepancy here could perhaps be understandable in the following way. During the wet season food availability is higher than during the dry and is not a restrictive factor on growth. Under the harsher conditions of the dry season,

Table 3. SVL growth rates of animals from some of the nests in Table 1 for various periods measured in days after hatching.

RECORD A	0-(35-37) days		RECORD E	53-82 days
	Myeeli 1 Nest			Liverpool km 47.5 Nest
				Released on Tomkinson
1360	0.073			
1362	0.071		1404	0.083
1367	0.074		1406	0.072
1370	0.084		1407	0.041
1389	0.083		1413	0.038
1394	0.080		Mean	0.058 ± 0.022
1403	0.094		All dry season growth	
Mean	0.080 ± 0.008			
All wet season growth				

RECORD B	0-(37-39) days		RECORD F	0-96 days
	Myeeli 2 nest			Myeeli 1 Nest
1316	0.085		1360	0.075
1344	0.095		1364	0.074
1348	0.122		1370	0.081
Mean	0.100 ± 0.019		1391	0.083
All wet season growth			1394	0.067
			Mean	0.076 ± 0.006
RECORD C	0-53 days		40 days are dry season	
	Liverpool km 47.5 Nest			
	Released on Tomkinson			
1404	0.126			
1405	0.125		RECORD G	0-65 days
1406	0.132			Myeeli 1 Nest
1407	0.109		1358	0.080
1410	0.138		1360	0.0815
1414	0.081		1370	0.098
1415	0.158		1394	0.083
1416	0.132		1396	0.102
1418	0.134		1403	0.098
Mean	0.126 ± 0.021		Mean	0.090 ± 0.010
Almost all wet season growth			Almost all wet season growth	

RECORD D	13-52 days			
	Liverpool B22 Nest			
1486	0.029		RECORD H	0-82 days
1492	0.047			Liverpool km 47.5 Nest
1506	0.026			Released on Tomkinson
1514	0.028		1404	0.111
1510	0.053		1406	0.111
1517	0.053		1407	0.085
Mean	0.039 ± 0.013		Mean	0.102 ± 0.015
All dry season growth			Almost all wet season growth	

Table 4. Examples of growth on the Liverpool-Tomkinson Rivers System over intervals which are mainly in the dry season[a].

Initial size	Sex	Mean SVL growth (cm/day)	Interval (days)
1. H	F	0.050	146 (17)
2. 2-3'	M	0.054	152 (51)
3. 3-4'	M	0.0355	124 (30)
4. 3-4'	M	0.0357	255 (145)
5. H	F	0.038	124 (30)
6. 2-3'	M	0.028	118 (36)
7. H	M	0.054	263 (49)
8. 2-3'	M	0.032	174 (41)
9. H	M	0.0527	387 (151)
		0.0552	270 (116)
		0.047	117 (35)

a. The number of wet season days in the interval is shown in parentheses.

however, food accessibility may be greater for larger animals. In this way animals that are larger at the start of the dry season may be able to cope better in terms of food sources and so grow faster. Further, an analysis of weights in June of animals that survived to September and those that did not showed that the initial weights of survivors was significantly higher.

PART 2   COMPARISON OF GROWTH IN THE WET AND DRY SEASON

2.1 Introduction

In northern Australia the year is divided into distinct wet and dry seasons (Chapter 3. Monograph 1). As has already been stated by several authors (Magnusson 1978, Chapter 8- Monograph 1, Webb et al. 1978), there are considerable differences between the growth rates of C. porosus over the wet season and over the dry season. It is suggested in Section 8.5.4 of Monograph 1 and by Webb et al. (1978) that increased abundance of food sources is the main reason for higher growth during the wet season, in contrast with the view of Magnusson (1978) who suggests that temperature and/or salinity are the major factors involved.

Our purpose here is to review the previous data and present some further data. The discussion is also necessary as a prelude to later sections. In Parts 1.2 and 1.3 we have already mentioned the influence of wet and dry season on early growth of hatchlings. Ideally one would like to have a continuous series of measurements, at say one monthly intervals, for a series of animals living in the wild over a number of years. Unfortunately such data would he very difficult,

if not impossible, to obtain. To work on the rivers during the wet season is very difficult and recapturing animals over successive months would become increasingly difficult due to increasing wariness. For these reasons the main data available comprise capture-recapture records over periods normally involving a mixture of wet and dry season periods.

Another factor to be borne in mind in looking at data which extends over a number of years is that conditions relevant to growth may well vary from year to year. For example, we may have a particularly heavy wet season one year and a particularly dry one the following year. The availability of food could well be different during the two wet seasons and during the following dry seasons. The 1978-1979 wet season was a particularly dry one and growth rates between mid-1978 and mid-1979 obtained on the Blyth-Cadell Rivers System (Chapter 8, Monograph 1) could be less than normal on those rivers. Availability of various food species may also vary over the years and on different rivers in different ways. With all these varying factors affecting interpretation of differences between wet and dry season growth rates of animals in the wild, one must take results on a particular river at a particular period as a guide only. In the following we have attempted to obtain estimates of wet and dry season growth rates by careful examination of capture-recapture records for animals over the period 1973-1980 on the Liverpool-Tomkinson and Blyth- Cadell Rivers Systems. The approach to wet-dry season growth in Webb et al. (1978) has certain flaws which are discussed in detail in Section 2.4, page 39, Monograph 18.

2.2 Examples from the Liverpool-Tomkinson System

Examples illustrating dry and wet season growth may be gleaned from the capture-recapture records on the Liverpool-Tomkinson System. They are presented in Table 4 and we shall discuss some of these.

The simplest description of growth over an interval (ΔT, days) involving both wet season (ΔT_W) and dry season (ΔT_D) periods is to assume linear growth (at different rates) over the two periods. Let a (cm/day) and b (om/day) be the growth rates over the wet and dry season respectively. The change in SVL (ΔSVL, cm) over ΔT is given by ΔSVL $= a \, \Delta T_W + b \, \Delta T_D$. Such a model has of course a very artificial sharpness in the boundary between the two seasons. Following Webb et al. (1978) we take the wet season as extending from December to April (151 days) and the dry from May to November (214 days). Days 1-120 and 334-365 are wet season and days 121-333 are dry season. The coefficients a and b will also depend on the age of the crocodile. To illustrate this approach we take the example of animal 9 in Table 4 that was captured three times on the Liverpool-Tomkinson system over the period of approximately one year. Over a period of 387 days from mid-dry season (day 180) to mid-dry season (day 202) the growth rate was 0.0527 cm/day. From day 85 to day 202 the growth rate was 0.047 cm/day. Use of these results gives a = 0.091 cm/day and b = 0.028 cm/day when substituted into the equation above. This is the only example (besides the animals of Tomkinson nests T12, T13, T14 to be discussed shortly) we have on the Liverpool-Tomkinson System of an animal caught three times within approximately a year and so allowing calculation of a and b as above.

If an assumption is made about the magnitude of b then estimates of a may be made. These estimates can be a rough guide only, especially when one recalls the artificiality of a sharp boundary between the wet and dry season and that the growth rate probably varies over the wet season and over the dry season. However, by assuming various values for b, a range of values for a may be obtained. Consider for example animal 2 from Table 4 and taking b = 0.03, we obtain a = 0.10. Any lower value for b would give a higher value for a and vice-versa. Taking b = 0.05 gives a = 0.06. This animal is of 79 cm length initially, in the middle of its second dry season, and a rate of growth of

0.10 cm/day over the initial part of the following wet season would be a rate comparable to that of Magnusson's under 80 day old animals during the wet season (Part 1).

The group of hatchlings from the Tomkinson nests T12, T13, T14 (see Part 1.2) gives rates of growth over approximately 2 months of the dry season and then over the next year (see Part 3.2). These mean rates are both about 0.06 cm/day. This example is out of line with the rest of the data and the reason for this is not clear. Possibly there was a higher food supply on the relevant section of the Tomkinson that year than is usual during the dry season.

2.3 The Blyth-Cadell Study

The Blyth-Cadell capture-recapture study initiated in 1978 (Chapter 8, Monograph 1) was specifically designed to throw light on the question of wet and dry season growth rates. Hatchlings were initially captured in June, then again in September (giving a dry season growth rate) and then again in the following June. On the Blyth River the overall average dry season rate was 0.030, from September to the following June it was 0.053, and from June to June 0.048. Calculation of a wet season growth rate as in Part 2.2 gives a rate of 0.073 if we use the June to June rate and 0.070 if we use the September to June rate. Similar calculations for the Cadell results lead to rates of 0.084 in both cases. In this we have assumed, of course, that the average rate over the dry season period outside the June to September interval is also 0.030 in both the first and second year. If it is in fact lower (as appears likely) then the mean rate over the wet season will be larger.

It had been planned to obtain a growth rate over the animals' second dry season by recapturing in October 1979, but extraordinary circumstances (Chapter 8, Monograph 1) meant that only 4 growth records could be obtained for this. The rates over some 4 months of the second dry season were 0.014, 0.015, 0.005 (males) and 0.008 (female) (Table 8.5.8, Monograph 1), with overall mean 0.010. The sample is so small that it is hard to conclude much but we may perhaps take the figure of 0.010 as an estimate of dry season growth rate in the second year, on the Blyth-Cadell Rivers, indicating decreasing growth rate with age (Chapter 8, Monograph 1). This figure is lower than the 0.03 used in the calculations of wet season rates above. If one uses the 0.010 in the above calculation for all dry season days in the second year, one obtains wet season rates of 0.079 on the Blyth and 0.091 on the Cadell. Given that the growth rate probably declines with the progress of the dry season and with age, we may take the wet season growth rate as being in the range 0.07 to 0.10, which again is comparable with the initial wet season growth of Magnusson's hatchlings.

In October 1980, 11 animals were recaptured on the Cadell River. These will be discussed in more detail in Part 4 (Table 11). However, they do throw some further light on differences between wet and dry season growth rates. Nine of the animals were recaptured in June 1979 and so we may calculate for them an average growth rate over a 480-day period which includes 151 days of wet season; all these animals were at least one year old in June 1979. For the 6 males the average growth rate was 0.0195 ± 0.0042 cm/day (range, 0.012-0.023) and for the 3 females it was 0.0137 ± 0.0021 om/day (0.012-0.016). For the males, if we allow no growth at all over the dry season component of the 480-day interval, we obtain a wet season growth rate of 0.064 cm/day. If we take the figure of 0.010 cm/day that we have just obtained from the June 1979-October 1979 captures, the wet season growth rate becomes 0.042 cm/day. For the females, the same calculations give rates of 0.045 and 0.023 cm/day. The sample size is of course small but the results appear to indicate, especially if we allow a second and third dry season growth rate of 0.01 cm/day, that the growth rate for both males and females over their second complete wet season is considerably less than over their first complete wet season. Further discussion of wet and dry season growth rates

Table 5. Sizes of male and female crocodiles at various ages as predicted by equations (5) and (6) of Webb et al. 1978[1].

	Ages (years)	HL (cm)	SVL (cm)	TL (cm)	In feet	Annual rate (SVL; cm/day)
MALE	0	4.6	13.2	28.0	11"	
	0.5	8.0	25.3	52.9	1'9"	0.062
	1.0	11.0	36.0	75.0	2'6"	
	1.5	13.7	45.3	94.1	3'1"	0.048
	2.0	16.0	53.6	111.1	3'8"	
	2.5	18.1	60.9	126.1	4'2"	0.038
	3.0	19.9	67.3	139.2	4'7"	
	3.5	21.5	72.9	150.7	4'11"	0.029
	4.0	22.9	77.8	160.7	5'3"	
FEMALE	0	4.6	13.2	28.0	11"	
	0.5	7.8	24.6	51.5	1'8"	0.058
	1.0	10.6	34.5	71.9	2'4"	
	1.5	13.0	43.1	90.0	2'11"	0.044
	2.0	15.2	50.5	104.9	3'5"	
	2.5	17.0	57.0	118.0	3'10"	0.033
	3.0	18.6	62.5	129.0	4'3"	
	3.5	19.9	67.4	138.9	4'7"	0.025
	4.0	21.1	71.6	147.3	4'10"	

[1]. HL denotes head length, SVL denotes snout-vent length and TL denotes total length. The total length was calculated from the snout-vent length using equations from Appendix 2 of Webb and Messel 1978. The annual growth rates are also shown. For consistency with Webb et al. 1978 we have in this Table taken 13.2 cm as the SVL on hatching rather than 13.9 cm which was used in Part 3.4. The figure of 13.2 cm is obtained from HL using the equations on page 388 of Webb et al. 1978, as are all SVLs in this Table.

Table 6. Mean SVL growth rates of hatchlings for the period from June, 1978 to June, 1979 on the Blyth Cadell and Blyth-Cadell Rivers. Abstracted from Table 8.5.7, Monograph 1.

	Blyth		Cadell		Blyth-Cadell	
	Rate	n	Rate	n	Rate	n
All hatchlings	0.0483 ± 0.0065	46	0.0530 ± 0.0033	9	0.0484 ± 0.0063	61
Males	0.0502 ± 0.0046	33	0.0530 ± 0.0059	3	0.0495 ± 0.0052	41
Females	0.0432 ± 0.0079	13	0.0530 ± 0.0017	6	0.0461 ± 0.0079	20

Table 7. Possible SVL (cm) of hatchling hatched on February 1 for two different sets of growth rates (see text, part 3.4).

Day number	Feb. 1 32	Mar. 21 80	Apr. 30 120	Jun. 9 160	Jul. 19 200	Aug. 28 240	Oct. 7 280	Nov. 16 320
Upper Rate	13.9	18.7	22.7	24.7	26.7	28.7	30.7	32.7
Lower Rate	13.9	16.8	19.2	20.4	21.6	22.8	24.0	25.2

Parts 3 and 4. It is interesting to speculate what the growth rates of *C. porosus* in the wild might be in areas such as Papua New Guinea or Borneo where one does not have such a marked dry-wet season difference as in northern Australia. In the absence of a harsh dry season, considerably higher annual growth rates than described here might be expected, especially for smaller animals.

PART 3 GROWTH OF *C. porosus* OVER THE FIRST YEAR

In order to allow comparison of growth rates on different rivers over the first year of life, we have calculated growth rates for animals that remained on the Liverpool River and those that remained on the Tomkinson River over their first year. This will also allow comparison with the rates (Chapter 8. Monograph 1) already obtained for the Blyth and Cadell rivers. These rates may also be compared with those given by the growth curve (Table 5) and obtained in a much less direct fashion (Webb et al. 1978).

3.1 Liverpool Hatchlings

Twenty-three hatchlings (including 12 males and 11 females) were captured in the mid-dry season of 1973 and recaught one year later. The overall mean growth rate for these animals was 0.054 ± 0.006 (range 0.043-0.069). For the males it was 0.056 ± 0.006 (range 0.097-0.069), for the females 0.050 ± 0.005 (range 0.043-0.058). Nine hatchlings were similarly recaptured over the 1974-1975 period. The overall average for these animals was 0.054 ± 0.008 (6 males, 3 females). The mean growth rates over the two periods are identical. The largest growth rate for an animal in the later period was for a male whose rate was 0.074, the snout-vent length increasing from 20.1 to 46.4 cm. The lowest growth was for a female, 0.045 cm/day; its snout-vent length changing from 20.5 to 37.3 cm. Taking all 32 animals, the growth rate was 0.054 ± 0.007 cm/day (0.056 ± 0.007 for males, 0.050 ± 0.005 for females). The interval between recaptures ranged between 340 and 370 days with most being within the range 350-365 days.

To investigate whether there were any differences in growth rates along the river (salinity gradient), the animals were grouped into various intervals between km 20 and km 60 (non-freshwater section). The sample is admittedly small, but there was no indication of any differences in the hatchling mean growth over a year dependent on their position on the brackish section of the river. Most of the animals were caught within a kilometer or so of their first capture positions and one may assume that they spent most of the year along the same stretch of river. These results are consistent with those of Webb et al. (1978), who found position along the brackish sections of the river to be an unimportant variable. The results are also consistent with those obtained for the Blyth River where there appeared to be no difference in growth over the full year between the brackish and freshwater sections (though there was over the three months of dry season growth). Magnusson (1978) and Magnusson and Taylor (1981) also found no dependence of growth on salinity in a somewhat limited salinity regime.

3.2 Tomkinson Hatchlings

In Part 1.2 we referred to the initial growth rates of animals from the three nests T12, T13, T14 on the Tomkinson in June 1974. Twenty-two of these animals were recaught in July 1975, and their average growth rate over a period of some 340 days from mid-August of 1974 was 0.060 ± 0.005. This rate is about the same as their initial growth rate over some two months in the 1974 dry season, and does not show the usual decline from the initial growth rate that was observed with

animals that spent their initial growth period in the wet season. Of this sample, 12 were males (0.061 ± 0.005; range 0.054-0.074) and 10 were females (0.0585 ± 0.0040; range 0.052-0.063), and there thus was no significant difference in the male-female growth rates, though the female rate was, as usual, lower. The mean interval between captures was some 340 days. Twenty-one other animals were captured in mid-dry season of 1973 and recaptured some 340 days later in 1974. The average growth rate was 0.054 ± 0.009 cm/day (8 males, 0.063 ± 0.0071, range 0.052-0.071; 13 females, 0.049 ± 0.005; range 0.038- 0.056). The female growth rates of the 1973-1974 season are lower than those of the 1974-1975 season. This difference is in fact significant at the 0.01% level. Since the male rates over the same two years are much the same, it is hard to understand this difference.

The growth rates for hatchlings on the Liverpool-Tomkinson system calculated in this direct fashion are in good agreement with those predicted by the growth curve (Table 5).

3.3 Growth Over the First Year on Different Rivers

In Chapter 8 of Monograph 1 it was shown that growth over the first year was somewhat higher on the Cadell River than on the Blyth River, into which it runs about 20 km from the mouth of the Blyth. The sample on the Cadell was only small however. The Liverpool-Tomkinson Rivers System lies some 30 km to the west of the Blyth-Cadell Rivers System and the Tomkinson runs into the Liverpool about 20 km from its mouth (Monograph 15). By the end of the dry season the Cadell is slightly brackish at the upstream limit of navigation by survey boat, whereas the Blyth is fresh; likewise the Tomkinson is slightly brackish, whereas the Liverpool is fresh at the upstream level (see Monographs 1 and 7 for full details on the salinity regimes of these rivers). The two river systems are thus somewhat similar, the Blyth corresponding to the Liverpool and the Cadell to the Tomkinson. Now that we have obtained separate growth rates for the Liverpool and Tomkinson we can make some comparisons of growth rates.

Because most of the intervals for the Tomkinson recaptures are about 340 days compared with 350-360 days for the Liverpool and Blyth-Cadell recaptures, there is a slight upward bias (due to a higher percentage of wet season) in the Tomkinson rates. This may be corrected by using the two-rate model discussed in Part 2. Taking a dry season growth rate of 0.030 cm/day, one finds that the Tomkinson rates for 360 days are some 2% lower than the rates over the 340 days given in Part 3.2. It is these corrected rates for the Tomkinson which we use in our comparisons.

Because of the small sample size for the growth over the first year on the Cadell, we shall not include the Cadell in the comparisons here; as we have already said, the rates of growth on the Cadell were higher than on the Blyth. The mean yearly rates on the Blyth were 0.050 ± 0.005 (n = 33) for males and 0.043 ± 0.008 (n = 13) for females (Table 8.5.7, Monograph 1). The various rates are collected in Table 6.

The male growth rates on the Liverpool and Tomkinson rivers are not significantly different. The female rates are significantly different (at 0.1% level) if we use the 1973-1974 results for the Tomkinson but are not different if we use the 1974-1975 results for the Tomkinson.

Comparisons of the male rates on the Tomkinson with those on the Blyth give results that are highly significant (at 0.0001% level). Comparison of the rates for females on the Blyth and Tomkinson shows that the 1974-1975 rates are highly significantly different (at the 0.01% level), but the 1973-1974 rates are not.

Comparisons of male rates on the Liverpool with those on the Blyth show the difference to be significant at the 0.1% level. The female rates also differ significantly at the 1% level.

The results clearly indicate higher growth in the first year on the Liverpool and Tomkinson rivers than on the Blyth. In fact, the largest growth rate on the Blyth was 0.060 cm/day, for a male, which is about the mean male growth rate on the Tomkinson (the rates on the Liverpool-Tomkinson system are also mostly higher than on the Cadell, though the numbers in the Cadell sample are only small). There is also a strong indication that males grow better on the Tomkinson than on the Liverpool; for females the picture is complicated by the disparity between the 1973-1974 and 1974-1975 growth rates.

3.4 Range of Sizes Amongst Hatchling Captures and Ambiguities

Besides the capture-recapture records, we also have available many hundreds of single captures and much may be learned from the size structure of the population at a given time of year. In this section we shall use all available information to consider the range of size that a hatchling may assume during its first dry season. Because of the possibility of errors in measurement, we only take examples of size and growth that are paralleled by at least one other animal. These sizes may then be correlated with the growth rates we have been considering and the possible times of hatching.

Nesting of *C. porosus* in northern Australia (Webb et al. 1977; Magnusson 1978) is stated to take place between November and May, during the wet season. Incubation periods vary between 80 and 100 days. Normally, though during the dry season hatching can take much longer (or as mentioned in Part 1, it may not even occur at all) because the temperature is lower. If a nest is laid on the earliest possible date, say 1 November, then the eggs could be expected to hatch around 1 February. If laid at the end of May they would probably hatch no sooner than 1 September. R. Jenkins (pers. comm.) has found a riverside nest in the Alligator River region which was laid down in August. This is exceptionally early (or late) and we will use the November date in our discussions. It is unknown whether any eggs from such an August nest would hatch.

We first consider animals hatching early in the year. Animal 1406 (record H, Table 3) hatched on 19 March with an SVL of 14.5 cm and by June 9 had an SVL of 23.6 cm. If we assume that an animal with comparably high growth rate had hatched on 1 February with an SVL of 13.9 cm, we may make some calculations of the range of maximum sizes possible over the year. The figure of 13.9 has been adopted for the SVL on hatching, since the mean of the means in Table 1 for hatchlings $\leq$ 2 days old is 13.9 $\pm$ 0.43. Considering first the upper range of growth, we take a mean growth to the end of the wet season (30 April) of 0.1 om/day. One hatchling, captured on day 205 (24 July) and recaptured on day 351 (17 December), had a mean growth of 0.05 cm/day (the SVL going from 23.0 to 30.3 cm). We may thus take 0.05 cm/day as a possible rate over the dry season, leading to the predicted lengths shown in Table 7. Taking a lower rate for growth during the wet season of 0.06 cm/day and during the dry of 0.03 cm/day we obtain the lower growth rate shown in Table 7.

Examination of our capture-recapture records reveals the following examples. An animal (Blyth River) caught on 22 June (day 173) had an SVL of 25.1 cm. A group of animals was captured on the Blyth River around the end of October (day 300) with SVLs ranging from 29 to 31.5 cm, in agreement with the upper size suggested from an animal born near 1 February. Animals were caught on the Goromuru River in 1975, around day 280, with an SVL of 31.1 and 31.5 cm. In late September (day 269) 1978, an animal was caught on the Cadell River with an SVL

of 28.0 cm; an animal with the same SVL was caught in late August on the Tomkinson River. Another animal with an SVL of 18.5 cm on day 112 (late April) had an SVL of 32.7 cm by day 10 of the next year. If we allow an initial growth rate of 0.1 om/day, then this animal hatched in early March. With this same sort of growth and a hatching in early February, it seems we could have an animal with an SVL of 33 cm by the end of November. After examining late hatchling growth we shall look again at the question of maximum hatchling sizes late in the dry season.

We now consider the lower size range of hatchlings later in the dry season and attempt to relate this to the latest possible times of hatching. Amongst the Blyth-Cadell captures of late October 1974 (around day 300), there were 3 hatchlings captured on the upstream Blyth River (around km 42) with SVLs of 16.0, 16.5, and 16.5 cm. Some other animals in the range of 17.0-18.5 cm were also captured at this time. During the September 1978 captures on the same river system, the smallest animal caught had an SVL of 17.1 cm. So in 1974 one had animals 1 cm (SVL) shorter one month later. As we have discussed earlier, some very low growth rates occurred over the June-September period on the upstream Blyth in 1978 (see Chapter 8, Monograph 1). If we assume that the mean initial rate of growth of the late October 1974 hatchlings was 0.06 cm/day (i.e., the same as the initial rate for the Tomkinson T12, T13, and T14 nests) and that their initial SVL was 14.0 cm, then a 16.5 cm SVL corresponds to an age of about 40 days, and with a normal incubation period of 90 days we obtain a date of mid-June for the laying of the nest, which would be a late nest. A longer than normal incubation period (as would be highly likely during the colder dry season months) and a lower growth rate would of course push the date further back. Pushing laying back to the end of April (the end of the wet season) and assuming 90 day incubation, we would obtain an age of 90 days for the 16.0 cm hatchling, corresponding to a mean growth rate of 0.02 cm/day, a growth rate that seems possible after examination of the Blyth-Cadell capture-recapture data.

An animal that had an SVL of 16.0 cm in late October and grew at the average rate of 0.05 om/day over the next year would by the following October have an SVL of 34.3 cm, at a rate of 0.04 cm/day It would have an SVL of 30.6 om. Thus there could be an overlap in sizes in the late dry season of animals born early that same year or born late in the dry season of the previous year. It is possible that in our assignment of animals to the hatchling class for calculating the Liverpool and Tomkinson growth rates we have erred, in that the animal is actually in its second dry season. Such cases, and there would only be a few, would have the effect of lowering the mean growth rate since growth over the second year of life is slower (see later).

Another way of comparing growth on the two river systems is to compare the sizes of the animals in the second year, in mid-dry season. On the Blyth-Cadell System the largest recapture had an SVL of 42.0 cm, with several others over 40 cm. Examination of the Liverpool-Tomkinson data reveals several animals in mid-July with snout-vent lengths around 46 cm, and numbers between 42 cm and 46 cm. It is also interesting to note that one of the Blyth October 1979 captures, 1753, which had an SVL of 41.8 cm in June, had only 42.5 cm in October. These observations again indicate a higher growth rate on the Liverpool-Tomkinson system.

PART 4 GROWTH OF SMALL (3-6', 0.9-1.8 m) *C. porosus*

In this part we re-examine the growth records for animals after their first year on the river and up to the fourth year. This main purpose again is to look for differences between different rivers. For animals larger than 2-3' (0.6- 0.9 m) it is impossible in some cases to be certain of an animal's age, and this uncertainty increases with age. However, amongst the capture-recapture records on the Liverpool-Tomkinson System there are a number of triple captures where animals

were caught in three successive years, and in these cases we know much more about the age of the animal. These triple captures of animals in the wild provide very valuable data, and we have tried to make full use of them.

4.1 Growth from Second to Third Year on the Liverpool-Tomkinson System

The capture-recapture records show 13 animals that spent their second year on the Liverpool River. The SVL growth rates for these initially 2-3' animals from mid-dry season to mid-dry season are:

All animals: 0.038 ± 0.007 (n = 13, range 0.029-0.050); Males: 0.039 ± 0.007 (n = 7, range 0.031-0.050); Females: 0.036 ± 0.006 (n = 6, range 0.029-0.044).

As expected the growth rate for males is higher than that for females, though not significantly.

There were 34 animals that spent their second year on the Tomkinson River from mid-dry season to mid-dry season and were initially 2-3' animals. The growth rates for these animals were:

All animals: 0.045 ± 0.006 (n = 34, range 0.034-0.059); Males: 0.045 ± 0.007 (n = 8, range 0.038-0.054); Females: 0.045 ± 0.006 (n = 26, range 0.034-0.059).

Interestingly, the male and female rates on the Tomkinson are identical. The hatchling growth rates for males and females over the one year period 1974-1975 were also very close.

The average time interval between these Tomkinson recaptures is only 340 days, somewhat short of the average full year interval between the Liverpool recaptures. To enable a comparison of these rates, we may correct the Tomkinson rates by assuming a two rate growth over the year (see Part 2.2). If we assume a rate of growth of 0.02 cm/day (the mean of 0.03 for the first dry season and 0.01 for the second dry season, see Part 2.3) during the dry season component, then we can calculate that the rate 0.045, over 340 days, represents a rate of 0.043 over 365 days. We may take then the corrected Tomkinson annual rates as:

All animals: 0.043 ± 0.006 (n=34); Males: 0.044 ± 0.007 (n = 8); Females: 0.043 ± 0.006 (n = 26).

The male rates are not significantly different between the Liverpool and the Tomkinson; the female rates are significantly different at almost the 1% level. From the equations in the growth paper (see caption of Table 5) we can calculate the mean rate of growth of animals from 1.5 to 2.5 years to compare with the directly calculated rates above, 0.043 (males) and 0.038 (females).

4.2 Growth from the Third to Fourth Year on the Liverpool-Tomkinson System

Examination of the capture-recapture records reveals 21 cases of animals that are likely to be going from their third year to their fourth year (mid-dry season to mid-dry season). Some are definite cases because they are triple captures; in a few cases the initial sizes may be a little large (the two largest animals we have included had SVLs of 58.8 cm and 60 cm). The mean SVL growth rates were:

All animals: 0.0316 ± 0.0072 (n = 21, range 0.018-0.047); Males: 0.0337 ± 0.0049 (n = 5, range 0.026-0.038); Females: 0.0309 ± 0.0078 (n = 16, range 0.018-0.047).

The time Interval for these rates is (365 ± 25) days.

Six of the females on the Tomkinson included above are triple captures that we definitely know are going from their third to fourth year. The mean rate for these (over approximately 340 days) is 0.028 ± 0.010 (range 0.018- 0.047). Thus the male growth rate is higher, but not significantly.

Unfortunately the numbers of animals which spent the year on one particular river are insufficient to allow any comparison of the Liverpool and Tomkinson growth rates. The equations from Webb et al. (1978) predict the following values for growth rates from 2.5 to 3.5 years: 0.033 (males) and 0.028 (females).

4.3 Two Year Growth Rates from First to Third Year on the Liverpool-Tomkinson System

By selecting from triple captures and 2 year spaced captures we can obtain a mean SVL rate of growth from the hatchling to the 3-4' (0.9-1.2 m) stage over a 2-year period from mid-dry season to mid-dry season. There are 19 such cases from the whole Liverpool-Tomkinson system, with the interval between recaptures varying between 675 and 740 days. The mean growth rates over the approximately 2-year interval are:

All animals: 0.044 ± 0.007 (n = 19, range 0.034-0.056); Males: 0.046 ± 0.006 (n = 11, range 0.034-0.056); Females: 0.042 ± 0.007 (n = 8, range 0.034-0.052).

These rates may be compared with those calculated using the equations of Webb et al. (1978), calculating from age 0.5- 2.5 years; 0.049 cm/day for males and 0.044 cm/day for females. The rates predicted are in good agreement with the directly calculated rates. In Table 8 we give the individual records of growth of the 11 triple captures included in the above. It will be seen that the growth rate over the second year is on average only 60% of that over the first year.

From the 19 two-year spaced captures we can abstract some information on relative growths on the Liverpool and Tomkinson rivers. The samples are very small unfortunately, but the results are in support of earlier results indicating a higher growth rate on the Tomkinson. For male animals on the Liverpool, the mean growth rate was 0.0434 ± 0.0021 (n = 5, range 0.041-0.046). On the Tomkinson there were 2 males with mean 0.0528 (0.0499, 0.0557). For females on the Liverpool, the mean rate was 0.0362 ± 0.0018 (n = 4, range 0.0343-0.0384). On the Tomkinson it was 0.0489 ± 0.0026 (n = 3, range 0.0473-0.0519). Interpretation of these differences is complicated by the fact that the Liverpool capture intervals ranged from 718 to 739 days, whereas the Tomkinson intervals ranged from 675 to 703 days. As we shall now show, even when this is compensated for, the strong indication is still that the growth rate is higher on the Tomkinson. We again use the simple model from Part 2.2. We take a two year growth, allowing 0.08 over the wet season and 0.02 over the dry season. Over 730 days (302 wet, 428 dry) this gives a mean rate of 0.045. Over 675 days. with 55 fewer dry season days, we get a rate of 0.047, so the shorter interval has little effect on the average rate.

4.4 Growth from Second to Fourth Year on the Liverpool-Tomkinson System

By selecting from triple captures and 2 year spaced captures we can obtain a mean SVL rate of growth from the 2-3' (0.6-0.9 m) stage on the Liverpool-Tomkinson system. The interval between captures varies from 666 days to 730 days, with the majority of intervals being around 680 days. The mean growth rates are:

All animals: 0.0368 ± 0.0063 (n = 21, range 0.025-0.047). Males: 0.0380 ± 0.0076 (n = 9, range 0.025-0.047). Females: 0.0358 ± 0.0053 (n = 12, range 0.028-0.046).

Unfortunately the samples are too small to permit any conclusions about differences between Liverpool and Tomkinson growth rates, the majority of the animals being from the Tomkinson River.

In Table 9 we give the individual histories of the triple captures included in the above animals. The equations in Webb et al. (1978) give rates of 0.038 for males and 0.033 for females for growth from 1.5 to 3.5 years. The male-female differences are not significant, though as usual the male rate is higher.

Table 8. Capture histories of animals caught on the Liverpool-Tomkinson System in their first year and recaptured in their second and third years[1].

Number	Sex	Initial SVL	1st year rate	SVL	2nd year rate	Final SVL
15	M	25.4	0.047	42.4	0.022	50.7
30	M	25.0	0.059	46.0	0.027	56.1
94	M	23.0	0.062	44.5	0.031	55.9
95	F	21.0	0.054	40.0	0.017	46.2
98	F	24.0	0.043	39.0	0.034	51.6
103	M	22.5	0.053	41.0	0.032	53.0
184	M	23.0	0.059	43.2	0.042	57.7
232	F	20.0	0.053	38.2	0.042	52.7
270	M	22.0	0.061	42.9	0.039	56.3
349	F	29.0	0.056	48.1	0.038	60.9
351	M	21.5	0.070	45.1	0.042	59.1

[1]. The rates of SVL growth are also given (the intervals between captures vary between 337 and 371 days).

4.5 Growth Rates of Animals up to 6' (1.8 m)--Liverpool-Tomkinson System

In Table 10 we present some interesting growth records for animals up to 6' (1.8 m) in length. The ages of most of these animals is uncertain to within a year. We shall now comment on some of these growth records.

Animal 37 exhibits a very high growth rate for a non- hatchling over a 2-year period, going from a total length of 1.0 m to 1.81 m over the period. Because of a toe abnormality noted on both captures, there is no question that this was the same animal both times. Its mean growth rate over 2 years matches that of many hatchlings in their first year. This animal could conceivably be 1.5 years old on first capture and so had reached 1.8 m (6') at age 3.5 years. Animal 291 exhibits a growth rate that is not much lower. The two males 451 and 517 exhibit a mean growth of 0.030 om/day over what is probably their fourth year of growth (from age 3.5 to 4.5). Animals 124, 176, 177, and 195 have very similar mean growth rates of around 0.036 cm/day over a 2-year period which possibly is from their third to fifth year on the river (age 2.5 to 4.5 years). So at 4.5 years they have an SVL of 80 cm, which is in agreement with the growth curve.

4.6 Blyth October 1980 Recaptures

In October 1980 11 animals (7 males, 4 females) were recaptured of the original animals of 1978; the animals were very difficult to approach and this was all that could be caught in the time available. Summary histories of the animals are given in Table 11. Since all these animals had been captured in September 1978 we can calculate 2 year SVL growth rates. For all animals it is 0.032 ± 0.005 cm/day; for the males, 0.033 ± 0.004 om/day, and for the females, 0.029 ± 0.06 cm/day. The largest rate was 0.040 cm/day for a male, and the lowest 0.022 cm/day for a female. These rates may be compared with those for animals for which we calculated 2-year growth rates in Section 4.3. The rates are less than those on the Liverpool-Tomkinson system. The male rates differ at the 0.01% level and the female rates at the 1% level.

Though the sample of animals on the Blyth-Cadell is much smaller than for the Liverpool-Tomkinson, it is interesting, by looking at individual examples, to compare the extremes of growth on the Liverpool-Tomkinson and Blyth-Cadell rivers systems. The largest animals captured (1617 and 1817) on the Blyth-Cadell system in October 1980 had an SVL of 50 cm. Within a month or so, their ages may be estimated at 32 months. Two very comparable animals from the Liverpool-Tomkinson system (1 male, 1 female) of similar age had SVLs of around 63 cm, and there are many examples of animals of the same age with SVLs between 57 and 60 cm. The smallest male captured (1631) on the Blyth-Cadell system had an SVL of 43 cm and total length 87 cm, so it has not reached the 3-4' category yet. This animal is at least 28 months old and may be compared with an animal from the T14 1974 Tomkinson Nest which had the same SVL at some 13 months (both animals were hatched around June-July). Again we see that the growth rate, on average, appears to be greater on the Liverpool-Tomkinson system than on the Blyth-Cadell system and that, as we have already discussed, the confident attribution of an age to a given animal more than a year old is impossible, especially if the animals are from different systems. In October 1981 we managed to recapture one of the 1978 hatchlings, a female, and at the age of at least 42 months, its SVL was only 49 cm. Use of the growth curve (Fig. 3) in Webb et al. (1978) would give an SVL of 67 cm at 42 months. Some discussion of these animals recaptured on the Blyth-Cadell in October 1980 has already been given in Part 2.3.

Table 9. Capture histories of animals caught on the Liverpool-Tomkinson System in their second year and recaptured in their third and fourth years[1].

Number	Sex	Initial SVL	1st year rate	SVL	2nd year rate	Final SVL
35	M	42.5	0.0431	58.7	0.0264	68.2
40	F	39.0	0.0368	52.1	0.0195	59.3
92	F	36.0	0.0429	51.0	0.0249	60.2
262	F	36.0	0.0436	50.9	0.0252	59.4
301	M	39.0	0.0376	52.0	0.0338	63.5
317	F	37.5	0.040	50.9	0.0251	59.2
318	F	36.0	0.0418	50.0	0.0240	58.2
321	F	36.5	0.0445	51.4	0.0466	67.4
322	F	31.0	0.0533	48.9	0.0297	59.0
355	F	36.5	0.0524	54.2	0.0184	60.4

[1]. The rates of SVL growth are also given (the intervals between captures average around 340 days, with 378 the longest interval and 335 the shortest).

Table 10. Growth records for animals up to 6' (1.8m) in length on their final capture. All animals are from the Liverpool-Tomkinson System.

No.	Sex	Initial SVL	Final SVL	Rate	Period (days)
37	M	49.0	87.1	0.0518	736
110	F	52.0	77.5	0.0351	727
124	M	55.0	80.7	0.0365	704
165	M	64.0	77.4	0.0388	345
176	M	58.0	82.8	0.0356	696
177	M	56.0	81.3	0.0364	696
195	M	48.0	74.4	0.0380	695
291	M	46.5	78.6	0.0467	687
451	M	65.0	75.3	0.0300	343
517	M	72.5	82.1	0.0291	330

Table 11. Growth histories for 11 hatchlings first captured in June or September, 1978 and recaptured in October, 1980 on the Blyth-Cadell Rivers System. Rates are cm/day.

	Sex	Capture	SVL	Rate	Capture	SVL	Rate	Capture	SVL
1617	M	June 78	23.1	0.033	Sept 78	26.2	0.048	June 79	38.8
		--	--	0.023	Oct. 80	50.0			
1626	F	June 78	21.0	0.045	Sept. 78	25.2	0.022	Oct. 80	41.5
1631	M	June 78	20.1	0.012	Sept. 78	21.2	0.048	June 79	34.0
		--	--	0.019	Oct. 80	43.0			
1644	M	June 78	17.4	0.006	Sept. 78	18.0	0.072	June 79	37.0
		--	--	0.023	Oct. 80	48.0			
1656	M	June 78	18.7	0.016	Sept. 78	20.2	0.057	June 79	35.4
		--	--	0.022	Oct. 80	46.0			
1687	M	June 78	20.0	0.034	Sept. 78	23.2	0.029	Oct. 80	45.0
1758	F	June 78	19.5	0.024	Sept. 78	21.7	0.066	June 79	39.0
		--	--	0.012	Oct. 80	45.0			
1773	F	June 78	18.4	0.020	Sept. 78	20.3	0.068	June 79	38.2
		--	--	0.016	Oct. 80	46.0			
1816	M	Sept. 78	17.1	0.007	June 79	37.2	0.012	Oct. 80	43.0
1817	M	Sept. 78	26.5	0.057	June 79	41.5	0.018	Oct. 80	50.0
1818	F	Sept. 78	24.8	0.054	June 79	39.0	0.013	Oct. 80	45.0

PART 5 GROWTH OF LARGE ANIMALS

In October-November of 1980 and 1981 a number of animals caught originally between 1973 and 1976 on the Liverpool-Tomkinson system were recaptured, providing valuable information on the growth of *C. porosus* after the third year, i.e., for the ages where the data were very limited before. In Table 12 we give the capture histories of these animals and also the average rate of SVL growth between first and last capture. In Table 13 we give the size at the end of each year calculated using the growth curves in Webb et al. (1978); for large animals we have used the 65 cm maximum head length curve for males, and the 51 cm maximum head length curve for females; we have also calculated the yearly growth rates.

It may be seen in Table 12 that for males, 0.025 cm/day seems to be about the average growth rate over the first seven or so years of life (491, 382, 454, 1418, 1059). From Table 13 and assuming an initial SVL of 13.9 cm (see Part 3.4), we see that the growth curve of Webb et al. (1978) predicts an average SVL growth rate of 0.037 cm/day over the first seven years; a figure which is too high when compared with the specific examples. Both animals 491 and 454 are from the June 1974 Tomkinson nests and so are known to be 7.2 years old. Use of the growth curve for large males (the 65 cm case) would predict that their SVL should be around 110 cm which is much higher than these two examples and also than that of 382, about a year younger.

Animal 251 merits attention. Between its first two captures, about a year apart, its growth rate was 0.030 cm/day. Over the next six years, between the 1974 and the 1981 captures, It averaged 0.021 cm/day. According to the growth curve, an animal with an SVL of 65 cm should be some 3 years old, and so by October 1981 animal 251 should be some 10 years old, with an SVL of 126 cm (53 om case) or 131 cm (65 cm) case instead of the 122.0 cm found. The 65 cm case also predicts, between the 4th and 10th year, an average growth rate of 0.024 cm/day, which is fairly close to the observed value of 0.021 cm/day.

The two females recaptured in 1980 and 1981 (438 and 148) also deserve comment. Animal 438 has an SVL of 77.4 cm at an age of some 6.5 years, again somewhat less than that predicted by the growth curves. Animal 148 may be taken as approximately 2.5 years old on first capture (according to the growth curve) and so has an SVL of 110 om at age approximately 10 years in good agreement with the 51 cm curve for females.

Animal 1418, one of Magnusson's 1976 hatchlings, at 5.5 years, has an SVL of 69 cm, which by the growth curve should be the SVL of a 3 year old. However, as we have seen in Part 4.3, there are examples of animals that show growths up to their third year in line with that predicted by the growth curve.

Animals 176 and 177 (see Table 10) both males from the Liverpool, have SVLs of about 58 cm in July 1973 and about 83 cm in June 1975. It is easily within reason that these animals hatched in June 1971, and thus at the age of 48 months have SVLs slightly larger than that of 491 which is some 88 months old. (One wonders if possibly 1978-1981 was not such a good period for growth. Since we are comparing the Blyth-Cadell and Liverpool-Tomkinson systems for different years, it is possible the years on the Blyth-Cadell were bad ones for growth. However, the comparisons of the Liverpool and the Tomkinson in Parts 3 and 4 are over the same years and there are differences.)

Some other individual growth records for larger animals over the period 1973-1976 may also be examined. One female (359) changed from an SVL of 80.0 to 107.0 cm over a 22 month period, giving the high average rate of 0.040 cm/day (calculation from the head length change gives an

Table 12. Capture histories of animals recaught on the Liverpool-Tomkinson Rivers System in October, 1980 and October, 1981[1].

Animal	Sex	Capture Date	SVL (cm)	Capture Date	SVL (cm)	Capture Date	SVL (cm)	Rate (cm/day)
491	M	17.8.74	15.5	26. 7.75	38.3	23.10.81	82.0	0.025
251	M	16.8.74	65.0	25. 7.75	75.3	13.10.81	122.0	0.022
382	M	29.6.74	18.4	21. 5.75	38.8	1.11.80	86.0	0.029
438	F	2.8.74	22.4	1.11.80	77.4	--	--	0.024
454	M	16.8.74	18.9	24. 7.75	39.6	6.10.81	90.9	0.028
1418	M	17.3.76	14.9	11. 5.76	22.0	8.10.81	69.2	0.027
148	F	20.8.73	60.0	27. 8.74	72.1	22.10.81	110.0	0.017
1059	M	23.7.75	20.5	8.10.81	77.5	--	--	0.025

a. The rate shown is that between the initial and final capture.

Table 13. Growth of large crocodiles calculated using the equations of Table 1 of Webb et al. (1)[a].

	Age (years)	HL (cm)	SVL (cm)	TL (cm)	TL (feet)	Growth rate
MALE	4.0	23.1	78.5	162.2	5'4"	0.028
	5.0	26.0	88.8	183.3	6'0"	0.026
	6.0	28.7	98.4	203.0	6'8"	0.0245
	7.0	31.2	107.3	221.2	7'3"	0.023
	8.0	33.6	115.7	238.4	7'10"	0.021
	9.0	35.8	123.4	254.2	8'4"	0.020
	10.0	37.8	130.6	269.0	8'10"	0.018
	11.0	39.7	137.3	282.7	9'3"	
FEMALE	4.0	21.1	71.6	147.3	4'10"	0.0215
	5.0	23.4	79.5	163.2	5'4"	0.020
	6.0	25.4	86.8	177.9	5'10"	0.018
	7.0	27.3	93.5	191.3	6'3"	0.017
	8.0	29.1	99.7	203.8	6'8"	0.016
	9.0	30.7	105.5	215.5	7'1"	0.015
	10.0	32.2	110.8	226.1	7'5"	0.014
	11.0	33.6	115.8	236.2	7'9"	

a. For males we have taken the 65 cm maximum head length case; for females the 51 cm case. The annual growth rate (SVL, cm/day) is also shown. See Table 5 for symbols.

SVL rate of 0.037 cm/day). This is a very high rate for a large animal, especially a female. Another female (1070) grew from an SVL of 103 to 114 cm (0.024 cm/day) over a 460-day period; another (401) grew from 107 to 114 cm over a year (0.019 cm/day). The growth of two large males (called A and B) has already been detailed in Webb et al. (1978). Another record of a large male is that of 365, which changed in SVL from 149 to 160 cm over a 282-day period, giving a rate of 0.039 cm/day (however calculation from the head length change gives an SVL rate of 0.027 cm/day and shows that care must be taken in interpreting SVLs derived from HLs, especially for big animals).

In Table 14, we show the capture histories of 8 animals recaught in October 1983, of animals first caught in the period 1973-1975. Since the growth rate slows with age and the growth rates in Table 13 are obtained by averages over a longer period (9-10 years in most cases) than those in Table 12 (7-8 years in most cases), we would expect the rates in Table 13 to be somewhat lower. This appears to be the case, though the sample is of course very small. We shall now comment on some individual cases of particular interest.

Animal 931 was 3.44 m long on initial capture and weighed 163 kg. On recapture some 8 years later its length was 3.54 m and its weight was 154 kg. With such a large animal measurement uncertainty can be large, but it is clear that the animal has hardly grown over the 8-year period. The weight loss is perhaps attributable to the fact that the initial capture was in July, reasonably early in the dry season, whereas the recapture was at the end of October, near the end of the dry season. The food supply appears to be better over the wet season, and one would expect the animal's condition to be lower at the end of the dry season than at the start. A further complicating factor is that the 1981-1982 and 1982-1983 wet seasons were "dry" ones, and there may have been less than the usual supply of food. Generally speaking, it does appear that some large animals appear to stop growing, whereas others continue to grow.

Animals 131 and 318 are both females and show dramatically the variation in growth rates that can occur and that were emphasized. The brands on both these animals were clear and unambiguous. Female 131 was caught as a hatchling in 1973 and recaught in October 1983 with a length of 2.52 m and a weight of 57.2 kg. Female 318 was caught as a 2-3' animal in 1973; most likely it was a late hatchling in 1972 but it may have been an early hatchling in 1973. On recapture 318 was 1.87 m in length and 19.1 kg in weight; its weight was one-third that of 131. Seeing the two animals side by side it was hard to believe that 318 was the older animal. Female 131 looked in very fine condition, whereas 318 was in poor condition; of course, it is possible 318 was diseased in some way.

Worrell (1964) presents information about a large *C. porosus* kept in a zoo. The animal was approximately 2 m originally and for 6 years grew at an SVL rate of 0.040 cm/day (at apparently a uniform rate) and then slowed, averaging only 0.010 cm/day over the following 16 years. The latter growth rate is hard to interpret as the animal may have stopped growing at some stage. However, the rate of 0.040 cm/day from approximately its fifth to eleventh year is high. The animal of course is in a state of captivity and is presumably always well fed; however, the figure indicates a possible growth rate for a large animal, one that is higher than most of our observations in the wild. At an age of approximately 27 years the animal was about 4.9 m in length. Animal 251 is 2.4 m, with an age of probably 10 years, in comparison with this captive animal which was 3.7 m at about 12 years. We also have the cases A and B of Webb et al. (1978), one of which showed no appreciable growth over 3.3 years and another (B) which averaged 0.011 cm/day over 2.3 years (very similar to Worrell's rate over 16 years). This animal (of total length 4.0 m, 13 feet) was estimated as 20-24 years old.

Table 14. Capture histories of animals recaught on the Liverpool-Tomkinson Rivers System in October, 1983. The growth rate shown is that between the initial and final captures.

Animal	Sex	Capture Date	SVL (cm)	Capture Date	SVL (cm)	Capture Date	SVL (cm)	Rate (cm/day)
184	M	23.8.73	23.0	17. 7.75	57.7	28.10.83	105.0	0.022
				Also recaptured 2.8.74 with SVL of 43.2				
331	M	17.9.73	39.0	15. 7.75	62.9	25.10.83	111.0	0.020
517	M	29.8.74	72.5	25. 7.75	82.1	29.10.83	127.5	0.016
931	M	28.5.75	171.0	19.10.83	180.0	--	--	0.003
131	F	19.8.73	27.0	23. 7.75	63.5	25.10.83	126.5	0.027
318	F	16.9.73	36.0	24. 7.75	58.2	24.10.83	93.5	0.016
				Also recaptured 17.8.74 with SVL of 50.0				
1049	F	21.7.75	20.5	27.12.75	24.0	20.10.83	90.0	0.023
246	F	4.9.73	23.0	20.10.83	106.0	--	--	0.022

In Webb et al. (1978), there is a discussion of typical maximum sizes reached by *C. porosus* on different rivers. For males, they estimate (from hunters' reports) 4.2-5.0 m and for females, 3.2-3.7 m (though some male specimens are known to exceed 6.0 m). Cott (1961) in discussing the maximum size of *C. niloticus* quotes (also from shooters' reports) 4.0 to 4.6 m as the average for large crocodiles shot in an area in Central Africa, with specimens up to 6 m. In other areas animals up to 6.5 meters have been taken. Webb and Messel (1978) report a reliable measurement of a *C. porosus* specimen of at least 6.15 m, and less reliable reports give lengths over 8 m. The typical maximum size reached by *C. niloticus* and *C. porosus* do not appear to be all that different. From his data, Cott takes it as evident that the maximum size attained by *C. niloticus* differs widely according to locality, in agreement with the general opinion amongst hunters (quoted by Webb et al. 1978) that the typical maximum size of *C. porosus* males varies in different river systems and regions. This would fit in with our results for early growth, which appear to indicate differences between river systems. However in attempting to draw inferences about differences of growth of larger animals on different rivers, one must always remember that the animals can and do move between river systems.

ACKNOWLEDGEMENTS

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STATUS AND CONSERVATION OF *Crocodylus porosus* IN AUSTRALIA

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Following very severe exploitation for the skin trade during the 1950's and 1960's, the Australian population of *Crocodylus porosus* was very severely depleted by the start of the 1970's (Bustard 1970, Messel pers. obs.). A total import-export ban on crocodile skins and products by the Federal Government in 1972 effectively ended the period of intensive exploitation, though this had already happened in many areas due to numbers being too low for economic exploitation.

In 1971 the University of Sydney Crocodile Research Group commenced its study of *C. porosus* in northern Australia. The results of this lengthy and extensive study have appeared in numerous publications covering the physiology, nesting, growth, movement, mortality and population structure and status of *C. porosus* over much of the northern Australian coastline.

An important aspect of this work has been the development of systematic survey methods to enable the numbers of *C. porosus* on the tidal waterways to be estimated and the carrying out of surveys using these methods over a period of years to monitor the changes in the population. (A full description of the survey methods used and of the Project's aims may be found in Chapters 1 and 2, Monograph 1, Messel et al. 1979-1986). In this chapter we only summarize the results of some ten years of night-time crocodile surveys, involving well over 70,000 km of river travel, and discuss the results.

During the period 1975-1979, using a research vessel as a floating base, some 100 tidal systems (Fig. 1, and Figs. 1 to 9, Chapter 9, Monograph 1) were surveyed systematically and many of these were surveyed more than once. In the Northern Territory 3,998 km of tidal waterways were surveyed; in Western Australia 527 km and in Queensland 643 km. The detailed results of the study and the analyses of these results appeared in a series of 19 Monographs (Messel et al. 1979-1986) and 2 Western Australian Reports (Messel et al. 1977, Burbidge and Messel 1979) and a series of specialist papers. Intensive population surveys and studies were continued during 1980, 1981, 1982 and 1983 on some 330 km of tidal waterways centered on the Liverpool-Tomkinson and Blyth-Cadell Rivers Systems in northern Arnhem Land and on some 59.3 km of associated alternative habitat. These relatively undisturbed waterways constituted our population dynamics and status monitoring systems. In addition Ngandadauda Creek and the Glyde River with its associated Arafura Swamp were resurveyed twice in 1983. During June-July 1984 we resurveyed the 861.2 km of tidal waterways in Van Diemen Gulf which includes the Adelaide and Alligator Region River Systems and the Cobourg Complex. In September-October 1985 the major tidal waterways of the southern Gulf of Carpentaria were resurveyed. All these latter surveys are analyzed in great detail in Monographs 18 and 19 (Messel et al. 1979-1986) and were described in the population dynamics chapter.
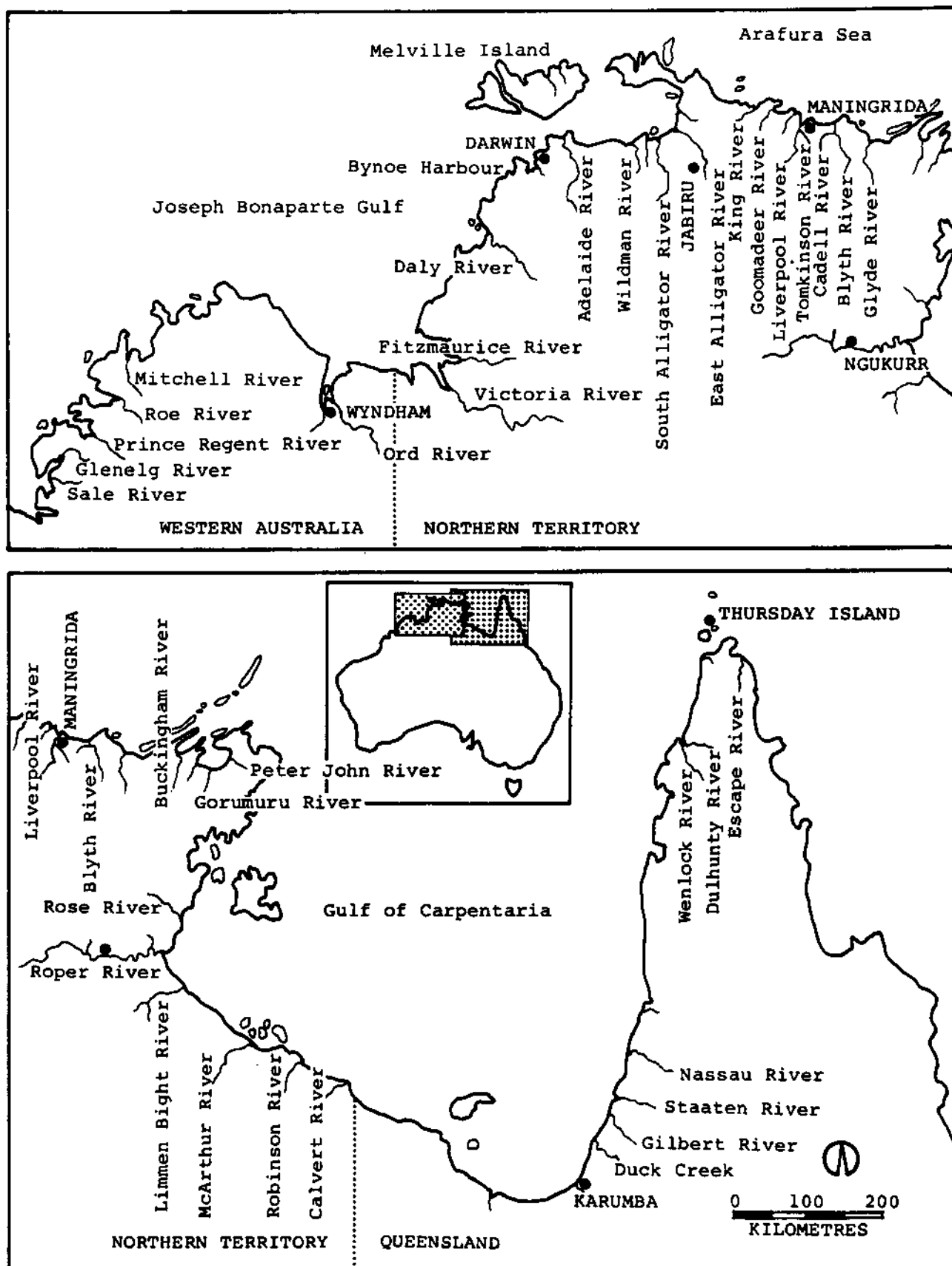
Figure 1. Area map, northern Australia, showing locations of some of the rivers surveyed.

The results of our surveys and studies have allowed a picture of *C. porosus* population dynamics in northern Australia to be developed and this picture was presented in some detail in our chapter on population dynamics. It enables us to account in a consistent fashion for the results of the surveys and to predict results to be expected on future surveys. The results also enable us to make an assessment of the overall status of *C. porosus* in northern Australia, and of the prospects for recovery of the population. Management implications of the results and population model are discussed also. The presentation here is necessarily very much abbreviated and the reader is referred to the 19 Monographs and 2 Reports for a wealth of supportive detail.

STUDY AREA AND METHODS

Study Area - Figures 1 to 9 in Chapter 9, Monograph 1, enable the locations of all waterways surveyed to be ascertained. The approximately 100 waterways surveyed extend from the Sale River (124°36'E, 15°58'S) at the top of Cape York Peninsula in Queensland. The only major area of coastal *C. porosus* habitat inadequately sampled is the eastern coast of Cape York Peninsular. The waterways of the Northern Territory have been most thoroughly surveyed, most of them having been surveyed at least twice. Each of the Monographs (except 15) deals with the waterways of a particular area and, besides the results of crocodile counts, gives details of salinity and temperature profiles, tidal patterns, ranges and delays and fringing riverside vegetation. Color photographs in each Monograph illustrate the nature of the waterways. Detailed river work maps (of all waterways surveyed) with mileages are collated in Monograph 15 and show channels and navigational hazards such as rock bars and sand and mud bars. Figures 1-6 in our Population Dynamics Chapter in the current volume show the monitored area, the Alligator Rivers Region and the Adelaide River in more detail.

Survey Methods - The methods used for surveying tidal river systems and their crocodile populations are described by Messel (1977), Messel et al. (1978) (also see for full details, Chapter 2, 4, 5 of Monograph 1). Particularly, it should be noted that these methods do not necessarily apply to non-tidal systems or swamp habitats.

Night-time spotlight counts are normally conducted from two modified 5.5 m work boats, each with three or four staff members. A 3.5 m dinghy with a 9.9 HP motor is used for surveys of upstream areas, billabongs and small coastal creeks. The staff members include a spotter, driver and recorder/navigator.

Crocodiles can be located as the tapetum of their eyes reflects light and appears as a red glow in the beam of the spotlight. Counts can proceed when the tide leaves 60 cm or more of exposed bank (Plate 2.1, 1, Monograph 1) on the sections to be surveyed. This means surveys must normally be carried out within 2-3 hours of low tide, depending upon the tidal pattern. Most crocodiles are spotted in the shallow water at the edge of the river; surveying when ≥ 60 cm of bank is exposed assures that a minimal number are missed because of screening by vegetation.

The location (± 100 m) of each crocodile spotted is recorded. Whenever possible, the animal is approached to within 6 m and its size is estimated by an experienced observer, who also notes its situation on the bank or in the water. Measurements are also made, at 5 km intervals, of air and water temperatures, salinity and light level.

The survey methods outlined yield a distribution of crocodile numbers and size classes for the tidal system. The question then is: what relation do these numbers have to the actual number of crocodiles on the system? The Blyth River calibration survey study was initiated in 1976 to gain

some insight into this difficult question (Messel 1977 and Monograph 1). Two 10 km calibration sections were surveyed 204 times.

It was shown in Monograph 1 that, providing surveys are made when EB $\geq$ 60 cm, in the manner indicated, there is no statistically significant variation in the fraction of crocodiles counted on surveys made during any time of the night and no significant variation between surveys made on incoming or outgoing tides. It was further shown that there is no consistent statistically significant variation between surveys carried out during different periods of the dry season.

In Monograph 1, it was also shown that the estimate for the actual number of crocodiles present on the river is approximated by the expression (aN $\pm$ b N), where N is the number of crocodiles sighted on a single survey (N to be > 10) and the coefficients 'a' (the inverse of the average fraction of crocodiles counted) and 'b' have different values for the various size classes, and b includes the confidence level factor. Values of a and b are given in the accompanying Table. For instance, for non-hatchlings the implication is that 95% of observations would fall in the interval (1.64N $\pm$ 2.01 N) and 99% of the observations in the interval (1.64N $\pm$ 2.64 N). For simplicity of interpretation, a difference between two counts will be called significant at the 95% (99%) level if the two counts do not overlap at their 95% (99%) confidence limits. These coefficients were derived on the basis that the counts were well described by the binomial distribution. Full details may be found in Chapter 5 of Monograph 1.

Size Classes	95% Confidence Level		99% Confidence Level	
	a	b	a	b
Hatchlings	1.59	1.89	1.59	2.49
Small (2-6')	1.49	1.68	1.49	2.21
Hatchlings plus small	1.52	1.73	1.52	2.28
Non-hatchlings	1.64	2.01	1.64	2.64
All crocodiles	1.59	1.89	1.59	2.49

RESULTS

The picture of the dynamics of C. porosus that has emerged from our studies and which is presented in our earlier chapter on population dynamics, shows that when discussing population increases or decreases, it is usually essential to consider not only results for individual waterways, but also those for broad groups of tidal waterways. We were able to show in Monographs 1, and 9 to 11, that a decrease in crocodile numbers in a TYPE 1 tidal waterway need not necessarily imply that the population of C. porosus is decreasing. The decrease may only imply that a fraction of the sub-adult C. porosus has been excluded from the system by breeding adults. Furthermore, the surviving fraction of the excluded sub-adults could give rise to a increase in population numbers in adjacent TYPE 2 and TYPE 3 waterways, and they could in due course return to the TYPE 1 system. Because C. porosus is known to travel long distances (Webb and Messel 1978), it is necessary first to consider small geographic subgroups and then larger groupings of tidal waterways covering broader geographic areas, if one is to appreciate the overall changes occurring in the populations of C. porosus. The tidal waterways considered in each Monograph normally form a natural geographic subgroup and these often contain a mixture of TYPE 1, TYPE 2 and TYPE 3 systems. For instance those in Arnhem, Buckingham and Castlereagh Bays form such subgroups. In particular it should be realized that repeated surveys of just one part of a waterway can be very limited value because of

seasonal adjustments that occur in the distribution of animals on a complete waterway, as well as movements in and out of the waterway.

In Table 1 we present the following results up to the end of 1979 for each survey of the tidal waterways of the Northern Territory, Western Australia and Queensland: the number of *C. porosus* sighted within each size class, the midstream distance surveyed, density of non-hatchlings sighted and the 95% confidence level for the estimate of the actual number of non-hatchlings present. Also shown is the broad classification of tidal waterway TYPE as determined by the salinity signature of the waterway. It usually does not include the often differing TYPES of the waterway's sidecreeks; the dominant TYPE only is normally given. All crocodiles whose size class could not be determined positively (the EO, EO > 6' and EO > 6' classes) have been lumped together and shown in the EO size class. When it is necessary to allocate these crocodiles to various size classes, it is probably best to use the scheme outlined in Table 3 in the Population Dynamics Chapter.

Our results for the tidal waterways of the Northern Territory are presented in the same sequence as the Monographs. We then group and sum the results for the latest survey of each waterway, according to TYPE 1 (and waterway whose TYPE has a "1" in it), TYPE 2-3 (any waterway whose TYPE has a "2" but not a "1" in it) and TYPE 3. The summing of these three then yields the overall results for the Northern Territory. The percentage which each size class constitutes of the total number of *C. porosus* sighted is also shown. Next, we present the overall results for subgroups of waterways, grouped according to geographic proximity. Wherever possible, we show results for the 1975 and 1979 surveys so that increases or otherwise in population size for the geographic areas concerned may be examined. Finally the latest surveys (up to the end of 1979) of the tidal waterways of the Northern Territory are gathered and summed for the four large geographic areas:

1. Gulf of Carpentaria, which covers tidal waterways from the Queensland border of Gove (Figs. 5 to 7 Chapter 9, Monograph 1).
2. North Arnhem Land, which covers the tidal systems from the Burungbirinung River in the east to the King River in the west (Fig. 5 Chapter 9, Monograph 1).
3. Darwin eastward to the Cobourg Peninsula including Melville Island waterways (Fig. 4 Chapter 9, Monograph 1).
4. Darwin westward, from Port Darwin to the Victoria River near the Western Australian Border (Figs. 2 and 3 Chapter 9, Monograph 1).

The total number of *C. porosus* sighted, to the end of 1979, on the 3,997.6 midstream km of tidal waterways surveyed in the Northern Territory was 5,472, of which 1,293 were hatchlings. Since only some 50% of hatchlings survive from June of their first year to June of the next (Table 8.4.1, Monograph 1), they should not be included in any estimate of the viable population. We therefore usually give densities and estimates for the actual number of crocodiles present for the non-hatchling classes only. On this basis the overall density of th 4,179 non-hatchling crocodiles sighted is 1.0/km and the 95% confidence levels for the estimate of the number present is 6,724-6,984. This figure and corrections made to it for waterways which were not surveyed is discussed later, as are the results for Queensland and Western Australia.

The density figure of 1.0/km is of very limited value, for the density of non-hatchlings sighted in TYPE 1 and non-TYPE 1 systems is quite different. On the 2,175.5 km of TYPE 1 tidal waterways surveyed, the density of the (4,491-1,197 =) 3,294 non-hatchlings sighted was 1.5/km whereas on the TYPE 2.3 and TYPE 3 systems it was 0.5/km and 0.4/km respectively.

The size class structure of the crocodilians sighted in the TYPE 1, 2 and 3 systems also varies (Table 1). However, it should be cautioned that there can be considerable overlap and merging between the system TYPES. For instance large TYPE 1 tidal waterways such as the Adelaide and Liverpool River systems contain TYPE 2 to TYPE 3 systems as well. If these were subtracted from the systems, the difference would be further exaggerated. Table 1 also shows the percentage which each size class constitutes of the total number of crocodiles sighted. Thus in TYPE 1 systems some 27% of the crocodiles sighted are hatchlings, whereas in TYPE 2-3 systems this figure falls to 14% and in TYPE 3 systems down to 4%, showing a much decreased hatchling recruitment in non-TYPE 1 systems. In TYPE 3 systems the percentage of crocodiles in the hatchling, (2-3') and (3-4') size classes combined is some 11% whereas in TYPE 1 systems it is at least 52%. On the other hand the percentage of crocodiles in the $\geq$ (4-5') size classes is some 39% in TYPE 1 systems and 73% in TYPE 3 systems. These percentages do not take into account the EO class which amounts to 10%, 16% and 16% for TYPE 1, TYPE 2-3 and TYPE 3 systems respectively. However since large crocodiles are usually more wary than small ones (Webb and Messel 1979), any correction would tend to exaggerate further the differences between the TYPE 1 and non-TYPE 1 systems. It is likely that the difference between the figure of 10% for the EO size class in TYPE 1 systems and 16% for non-TYPE 1 systems is accounted for by the fact that there is a higher fraction of large crocodiles in non-TYPE 1 systems than in TYPE 1 systems. These results for size class structure indicate the utility and importance of our classification of waterways.

In Tables 1A and 1B of the Population Dynamics Chapter we give in the same format the results of surveys since 1979 in the monitored area, and in the Alligator Rivers Region and the Adelaide River. Table 2 of this Chapter gives the results for the resurveys of the waterways of the Gulf of Carpentaria carried out in 1985. For convenience, the earlier results for these latter systems are repeated in Table 2.

POPULATION STATUS

<u>1979 Estimate for the Northern Territory</u> - On the basis of the surveys carried out up to and including 1979 we estimated in Monograph 1, Chapter 9, the total population of *C. porosus* in northern Australia. We now reproduce that estimate and the basis for it.

Of the 3,997.6 midstream km of tidal waterways surveyed in the Northern Territory in 1979, 54% (2,175.5 km) were TYPE 2-3 and 22% (883.7 km) were TYPE 3 systems. In making corrections for tidal waterways not surveyed, one should use the density appropriate to the waterway TYPE, because as we saw in the Results section the densities are quite different between the different TYPES.

Our estimate of the surveyable distances of tidal waterways not surveyed systematically in the Northern Territory is as follows:

	km
Melville and Bathurst Islands	330
Western Australian border to Gove	280
Gulf of Carpentaria	50
	660

Since practically all of these waterways are non-TYPE 1 systems, many being difficult to enter, and also since we had a very large sample of non-TYPE 1 waterways, it was thought not worthwhile endeavoring to survey them. During 1972 one of the authors (HM) had surveyed most of the

waterways on Melville and Bathurst Islands which were omitted thereafter, and it was found than that these waterways contained even fewer *C. porosus* than those tidal waterways on Melville Island chosen for more intensive study (Monograph 6).

The shores of the coastline amounting to some 3,200 km were not surveyed either for a number of reasons. First there is the risk to life involved in trying to do so; secondly, on each occasion that we have surveyed long sections of bays and inlets at considerable cost and danger, we have sighted either no or only sporadic *C. porosus*. Though the density of *C. porosus* along the shores of the coastline may have been greater in bygone days, it is almost negligible at present and must be considerably less than 0.1/km (see Monograph 9). The reasons for this are probably many. The more important are that there are so few *C. porosus* and that they appear to dislike waves intensely (see Appendix A 1.2 of Monograph 1; wave action on the northern Australian coastline is high during much of the dry season). There is also little vegetation to provide cover along the long stretches of sandy and rocky foreshores.

In each tidal waterway surveyed, the survey boats proceeded as far upstream as depth of water would permit. In the case of non-TYPE 1 systems this constituted a much higher fraction of the overall waterway than in the case of TYPE 1 systems which have more extensive drainage courses. In most instances in non-TYPE 1 systems, the extreme upstream sections have no water in them near low tide and thus their omission yields almost negligible error in the estimate for the actual number of *C. porosus* present on the system. The case of TYPE 1 waterways is more complex, for here the waterway courses may have non-navigable (by survey boat) freshwater sections greater in length then the surveyed sections. These are usually beyond the tidal limit and often consist of intermittent waterholes with intervening sections which are dry during the dry season. *C. porosus* is known to inhabit the freshwater sections but its density is small. On these sections of the waterways *C. johnstoni* appears to be the main species (Monographs 2, 3, 12, 13 and 16). The Roper River is an example of such a river system, as are the McArthur, Adelaide, Alligators, Prince Regent, Mitchell, Ord and Victoria River systems. A pointed out in Chapter 6 of Monograph 1, in our discussion of the distributional pattern of *C. porosus*, the number of *C. porosus* sighted int he freshwater section of the Blyth River falls quickly and drastically as one proceeds further upstream. The same phenomenon was discussed again at some length in Monographs 10 and 12, where it was cautioned that care must be taken when comparing non-hatchling *C. porosus* densities of one waterway with another. By including long freshwater sections one can bring down the density figure to very low values. For instance on the Roper River we found a non-hatchling density of 1.14/km. The density of the 20 non-hatchlings sighted on the 68.5 km of freshwater sections above km 85 was only 0.3.km. During the calibration surveys on the Blyth River, the average density of non-hatchlings sighted on the first purely freshwater (km 40-45) section was only 1.1/km compared to at least 2.7/km for the whole river system. The density falls rapidly as one proceeds upstream of km 45. On the basis of the above discussion, one could perhaps add some 1,000 km of TYPE 1 river distance to the 2,175.5 km surveyed, but the density of *C. porosus* on these unknown sections is unlikely to be more than 0.2/km. During 1972 we systematically surveyed waterhole after waterhole on the sections of the Goyder River upstream of the Goyder crossing and sighted only 2 *C. porosus*. The Goyder River runs into the Arafura Swamp which is known to be one of the few large remaining freshwater swamp areas in northern Australia.

The relatively few freshwater swamps both large and small in the Northern Territory are known to contain populations of *C. porosus*, but these have not been inventoried systematically and the present extent of the populations in them remains unknown. However, from the many casual observations already made, we believe it is likely to prove to be considerably less than 20% of the population sighted in tidal river systems.

On the basis of the above and with due reservations being made, our generous estimate for the number of sightings of non-hatchling *C. porosus* in the Northern Territory which were omitted from our tidal river survey is:

Unsurveyed tidal waterways (660 km x 0.5/km)	330
Unsurveyed freshwater sections of TYPE 1 systems (1,000 km x 0.2/km)	200
Unsurveyed foreshores of coastline (3,200 km x 0.05/km)	160
Freshwater swamps, taking 20% of the number sighted in tidal systems	<u>836</u>
	1,526

If one applies the same confidence limits for these 1,526 non-hatchlings as we have for our surveys (this procedure for the assumed 836 non-hatchlings in freshwater swamps is dubious, but is as valid an assumption as any other at present!) then there could be between 2,424 and 2,582 non-hatchlings additional to the 6,724-6984 derived from the surveys. Thus using (4,179 + 1,526 =) 5,705 non-hatchlings, there could be between 9,204 and 9,508 non-hatchling *C. porosus* in the Northern Territory as of October, 1979. We feel it would require unrealistic assumptions to carry this figure much above 10,000. We even retain some doubts about the maximum figure of 10,000; it may well be a substantial overestimate. On the other hand, we do feel that our estimate of 6,724 to 6,984 is a reliable lower one for the actual number of non-hatchling *C. porosus*, for this figure is based upon careful and systematic observations made over a period of almost 5 years and some 50,000 km of waterway travel.

Western Australia in 1978 - Tidal river systems in the Kimberley were chosen for survey by the Department of Fisheries and Wildlife, Western Australia (Messel et al. 1977, Bürbidge and Messel 1979). It is believed that the majority of the large Kimberley tidal waterways were surveyed; the only significant areas not surveyed are the Walcott Inlet-Secure Bay area and the West Arm of the Cambridge Gulf, with their associated rivers and creeks. It is also believed that small populations occur in such areas as the mouth of the Drysdale River. Commonly, small coastal rivers and creeks in the Kimberley have short surveyable tidal sections which are terminated by rocky ledges and often by waterfalls.

We believe that we examined more than half of the better *C. porosus* habitat in the Kimberley. In the 527.3 km surveyed, 898 crocodiles were sighted of which 227 were hatchlings. The 671 non-hatchlings yield a density of 1.3/km and the estimate for the actual number of non-hatchlings present, at the 95% confidence level, is 1,048-1,152. Assuming that the number of non-hatchlings which would be sighted in the areas not surveyed is also 671 we obtain lower limits of 2,127-2,275 for the number of non-hatchlings remaining in the Kimberley as of July 1978. One can extend this estimate (of say 2,500) almost without limit if one cares to make what we feel would be unreasonable assumptions.

Queensland in 1979 - A sample of four major tidal waterways on the west coast of southern Cape York Peninsula, which were known to have contained some of the best populations of *C. porosus* during the 1950's and 1960's, was chosen by the Queensland National Parks and Wildlife Service for survey. In addition the Port Musgrave area, containing what is believed to be the best remaining tidal waterway habitat for *C. porosus* in Queensland, and the Escape River on northeastern Cape York Peninsula, were also chosen for survey. As seen in Table 1, the results for the Port Musgrave area and the other areas were quite different. Whereas the non- hatchling density was 1.8/km for the 241.0 midstream km surveyed on the Port Musgrave waterways, the non-

hatchling density for the groups of waterways on south-western Cape York Peninsula (359.7 km) was only 0.4/km surveyed) is 0.9/km and the estimate at the 95% confidence level for the actual number of non-hatchlings present is 945-1,043.

What estimate can one make for the number of non-hatchling *C. porosus* in overall northern Queensland? The lengths of the remaining waterways on the maps look large, but most of the rivers have relatively short navigable sections. Without carrying out further surveys one can only make a broad estimate; it would be surprising if non-hatchling *C. porosus* densities on them were as high as the 0.4/km we found for the southern waterways surveyed. Erring on the generous side, we estimate that there are probably a further 2,400 km of waterways not surveyed. Using a non-hatchling density of 0.4/km this would yield a further 960 crocodiles which would be sighted. On this basis, the estimate at the 95% confidence level for the actual number of non-hatchling crocodiles present, using the (606 + 960 =) 1,566 value, is 2,488 to 2,648 or say 3,000. However, without further surveys one is unable to substantiate this number.

Northern Australia in 1979 - We now have estimates for the populations of non-hatchling *C. porosus* in the Northern Territory, the Kimberley of Western Australia and northern Queensland. However only the figures for the tidal waterways surveyed may be deemed to be reliable; the remainder are probably upper limits and may be over-estimated considerably. With this warning in mind our upper estimates for the non-hatchling *C. porosus* populations were:

Northern Territory	10,000
The Kimberley	2,500
Northern Queensland	3,000

15,500.

'Dry Wet' Seasons in estimating population status - 'Dry wet' seasons play a very important role in the dynamics of *C. porosus* populations, and it was the continuing of the surveys after 1979, in the monitoring area, that allowed us to unravel this as we described in our Population Dynamics Chapter--see Tables 1A and 1B of the same Chapter. By a 'dry wet' we mean a west season which has considerably less than the usual amount of rainfall and thus does not give rise to extensive flooding of the tidal upstream sections of the waterways. The wet season of 1978-1979 was an exceptionally dry one and those of 1981-1982 and 1982-1983 were also dry ones. As is evident from the Tables, there was in 1979 an increase in the number of sightings in the tidal waterways, right across the Northern Territory. At the time we interpreted this increase as a sign of the expected recovery of the population. Now, however, we believe this interpretation may have been too optimistic. To account for the results in our monitoring area, the only reasonable explanation we are able to give, which is in accord with the observations made during the 1979, 1982 and 1983 surveys following 'dry wet' seasons, is that the Arafura Swamp is acting both as a breeding system (during normal wet season periods) and as a rearing stockyard of varying extent, for sub-adult crocodiles from Arnhem Bay in the east to the King River in the west. The Blyth-Cadell System is a very important component of this. During a severe 'dry wet' season as in 1978-1979, the water levels in small and large swamps fall drastically and crocodiles inhabiting these have no choice but to leave. They can only return to the tidal waterways, both TYPE 1 and non-TYPE 1, and this they do--as they did in 1979 and 1982. Many animals frequenting the alternative freshwater habitat must have come from TYPE 1 tidal breeding systems and hence, as the swamps dry, some of the sub-adult animals probably return to the tidal system from whence they originally came, the others apparently have to frequent non-TYPE 1 tidal systems--even though temporarily--until they can go back to the swamp rearing stockyard or a TYPE 1 system. Some of the returning large animals appear successful in establishing a territory for themselves (and perhaps a few of the 3-6' animals also); the others appear to be excluded yet again-- and specially the 3-6' and sub-adult large

animals--on the commencement of the breeding season. When the next 'dry wet' arrives [if there has been the usual wet season(s)], large and sometimes 3-6' animals again are excluded from the swamps and the degree of the process must depend upon just how 'dry' the wet season is--upon how much the swamp water levels fall. The whole process is superimposed upon the normal exclusion and re-entry of animals which takes place in usual years and which accounts for most of the sub-adults sighted in non-TYPE 1 systems. Thus, whether 'dry wet' seasons are the proximal factor involved or not, they are certainly associated with the major influxes of large and sometimes 3-6' animals sighted on the tidal waterways during surveys made in June-July, after a 'dry wet'. Thus 'dry wets' appear to play a very important role in the dynamics of *C. porosus* populations.

As we have said, the influxes of large and sometimes small animals in 1979 were in fact a general phenomenon on the tidal waterways of the Northern Territory (Table 1). It was especially marked on the waterways of the Alligator Region (on the Wildman, for example, 21 large animals were sighted in September, 1978 and 56 were sighted in August, 1979). Both these systems have fairly extensive associated freshwater complexes. Increases also occurred on non-TYPE 1 systems with little associated freshwater complexes, for example on the TYPE 3 waterways of the Milingimbi Complex the number of animals $\geq$ 4-5' increased from 29 to 63 between 1975 and 1979. In the latter cases the animals could only have come from further afield (in the Milingimbi case, from the Arafura Swamp via the Glyde River). A very interesting exception to the general pattern was the waterways of Arnhem Bay. There was no increase in the number of large animals sighted between 1975 and 1979, and this could be connected with the relative lack of swamp associated with this whole area and the somewhat wetter climate there.

1985 Update - Our estimate of 15,500 for 1979 was based, as discussed earlier, on counts carried out in a year when most crocodiles were concentrated into the tidal waterways. Our allowance for the numbers in the relatively scarce swamp areas was very likely too generous; it is hard to know with certainly as systematic and reliable surveying of such freshwater habitat has not been carried out extensively and usually requires methods quite different from those applicable on tidal waterways. In October, 1983 we surveyed the largest remaining open body of water in the Arafura Swamp (the old Arafura billabong) and sighted 70 animals including 32 $\geq$6', concentrated into its 2 km. Taking into account the few remaining open water billabongs and low water level in the swamp, we estimated 400 as a generous upper limit to the number of crocodiles in the swamp at that time.

Our results in the monitored area between 1979 and 1983 (see Tables 1A and 1B of the Chapter on Population Dynamics and the "Overview" paper in Monograph 18) gave no reason for modifying the 1979 estimate by much to obtain the 1983 population.

Though there appears to have been no sustained significant increase in the number of non-hatchling crocodiles sighted on the tidal waterways of the Maningrida area since our surveys started in 1974, the size structure of the animals sighted appears to have been changing slowly. Notwithstanding substantial fluctuations, the ratios of small (2-6') to large ($\geq$6'), and 3-6' to large animals was decreasing on the Blyth-Cadell, may have been decreasing on the Liverpool-Tomkinson and was decreasing overall on the tidal waterways of the Maningrida monitoring area. Thus there was some indication of the commencement of a slow recovery phase.

In the case of the tidal waterways of the Alligator Region and the Adelaide River System, we were able to show (Population Dynamics Chapter), as expected from the model, an important and apparently continuing recovery was underway; that the Adelaide River System was recovering faster than the rivers of the Alligator Region. The tidal waterways in the Alligator Region indicate the potential for recovery , at a rate equal to or even better than that found for the Adelaide System.. However, at present too many crocodiles are being killed in fishing nets so the potential

cannot be realized until the commercial net fishing for barramundi is halted in these rivers, all of which are in Australia's Kakadu National Park. Restoration of habitat after eradication of the feral water buffalo will also aid the full recovery of the population (both in the Alligator Region and the Adelaide River). The Adelaide however does not have the protection of being in a national park.

The present results for the 787 km of tidal waterways resurveyed in the southern Gulf of Carpentaria (Table 2) shows that the C. porosus population in this area remains as severely depleted today as it was in 1979. There has been no significant change in this population, however there is some hint, from the smaller numbers sighted in the TYPE 3 creeks, that it is dropping even lower. There can be little hope for these populations in the southern Gulf if barramundi netting in the area is not severely curtailed. Even the C. porosus population in the Roper River System is in great danger, if netting is allowed to continue well upstream--to the km 61.5 point. This ensures that the major fraction of the C. porosus population in the System is within the netting limit (see Fig. 12.31 Monograph 12). If the Roper System is depleted then there will be little hope for the long term survival of the remnant C. porosus population in the other tidal systems in the southern Gulf of Carpentaria, such as the Limmen, Towns, Yiwapa and Nayarnpi nearby. These systems depend to a large degree on animals excluded from the Roper System. They cannot rely on animals excluded from the large McArthur System, for it is already as depleted as they are.

During the past three dry seasons we have resurveyed some 2,111 km of tidal waterways in the Northern Territory as follows:

		km
1983	Northern Arnhem Land, Maningrida area	462.9
1984	Alligator Region - Adelaide River Systems and Cobourg Complex	861.2
1985	southern Gulf of Carpentaria	787.0
		2,111.1

This constitutes more than 50% of the some 4,000 km of tidal waterways surveyed to the end of 1979 in the Northern Territory.

On the basis of the data we have gathered on our resurveys between 1979 and 1983, and during 1983, 1984 and 1985, we can now update our 1980 estimate for the non-hatchling C. porosus population in the Northern Territory (Chapter 9 Monograph 1). Keep in mind that such a large portion of the hatchlings are lost each year that they are not a good indicator of population trends. Hatchling numbers may increase dramatically during the hatchling season and decrease during the rest of the year; they are also very variable from year to year. If a census were taken later in the year after many hatchlings have been lost, the same population would be smaller. This is why crocodilian monitoring programmes all over the world, e.g., North America, India, Africa, focus on non-hatchlings. Our 1980 estimate was 10,000 non-hatchlings and allowing for the recovery of the population on the Adelaide and Alligator Rivers we found in 1984, we feel that estimate might be increased by up to 20 percent, perhaps to a figure of some 12,000 non-hatchlings now. One cannot be more precise about such an estimate.

The probability of the *C. porosus* populations in the Kimberley of Western Australia recovering over a period of several decades is fair, especially in the George Water, St. George Basin, Roe-Hunter and Ord River waterways where barramundi net fishing in the rivers is minimal and there is no destruction of nesting habitat by feral water buffaloes. We will be resurveying areas in Western Australia in 1986.

The same cannot be said for most of the tidal waterways in northern Queensland, especially in the light of our resurveys of the southern Gulf of Carpentaria. In these, the density of *C. porosus* is probably already at dangerously low levels and recruitment is minimal. Barramundi net fishing which is allowed in the rivers is not only quickly exhausting the rapidly dwindling barramundi resource but is drowning a substantial fraction of the few remaining large *C. porosus*. It is likely that, with the exception of the Port Musgrave area, the population of *C. porosus* in northern Queensland is still falling and is well on the road to exhaustion.

MANAGEMENT OF THE *C. porosus* POPULATION

What are the management implications of our results? We are not management authorities, but are aware that a multitude of factors--some of them political--must be taken into consideration. For example, for reasons based on public safety, Australian society could decide that all waterways utilized for business and/or pleasure or which had settlements near them, should be cleared of *C. porosus* and the *C. porosus* should be allowed to exist and perhaps recover, only in a number of designated parks and/or reserves used for scientific and/or tourism purposes (we have suggested some suitable areas in Chapter 9, Monograph 1, p. 439). Such a decision would result in the removal of *C. porosus* from many of the waterways in northern Australia and could have far reaching ecological consequences, many of which probably could not be foreseen beforehand. Based on examples from elsewhere in the world, we know that the removal of a predator from the top of a complex food chain cannot occur without some major consequences. The Australian people would have to decide whether the unhindered enjoyment of the waterways of northern Australia is worth the risk of possibly disastrous consequences to the whole ecology of the waterways. The fishing industry is one group that readily springs to mind as a possible sufferer.

Or it might be decided to encourage the establishment of a commercial *C. porosus* skin industry based upon the wild population. Since some 70% of the 3-6' animals are lost--and these are the most valuable ones commercially--one is tempted to believe that their removal beforehand would yield a valuable resource without harming it. But one must proceed with extreme caution before embarking upon such an enterprise. Undoubtedly the exclusion and/or loss of some 80% of the 3-6' animals is an integral part of the vital process of sorting out the successful from the less successful, or sorting out the stronger and more dominant component of the population. Removing a given fraction of the population might very well remove the stronger component and thus over the long term set the population on a declining course. We simply do not know. On page 15 of Monograph 1, we proposed in 1981 a critical experiment to test the effect of removing a given fraction of the (3-6') *C. porosus* population and proposed that some 25 to 40% of the (3-6') animals be removed annually for a period of 4 to 5 years from the downstream sections of the Adelaide River to see what effect if any this had upon the population in that river. For the experiment to be meaningful, one had to monitor the population changes on another set of control tidal waterways in which the *C. porosus* population remained untouched. The University of Sydney financed the costly monitoring of a control group of waterways for 4 years and this work has now been completed successfully. Though the proposed experiment had very important ramifications for the management and ranching of the *C. porosus* resource, no financial support had been forthcoming, from relevant authorities, for the other half of it. The original opportunity has been

lost, but the experiment still must be done (though at much greater cost) so that important management decisions can be made on an adequate data base.

We have already mentioned two very important factors affecting any possible *C. porosus* recovery, that can be influenced by correct management. The first of these is prevention of further destruction to habitat by the feral water buffalo and a program to allow recovery of already damaged habitat. The second factor is the continuing loss by drowning in fishermen's nets of hundreds of large crocodiles per year (see Monograph 1:437-438). Some of these nets are set legally. Our results show that over 80% of the 3-6' animals are excluded from many TYPE 1 waterways and that this exclusion also involves large animals; that there is great and continuing movement of these animals into and out of the river systems. Allowance of net fishing in or at the mouths of rivers, specially the TYPE 1 waterways is certain to remove an important component of the large animals and could well ensure that the population in those waterways never recovers or even declines. For instance, we believe that the decrease in the number of large animals sighted on the West Alligator and Wildman Rivers shown in Table 9 of the Population Dynamics Chapter is probably due to the continuing heavy commercial net fishing in those rivers. The total lack of any recovery over six and a half years in the waterways of the southern Gulf of Carpentaria, described earlier, is also undoubtedly due to continuing net fishing.

Undoubtedly economic and political considerations are involved in arriving at a reasonable compromise in relation to the matter of commercial net fishing in tidal waterways. We have no desire whatever to become involved in argumentation about it. At the very minimum it is suggested that all net fishing be definitely phased out over a period of two years in rivers included in national parks (it is still legal to set nets in the tidal waterways of Kakadu National Park). The continued loss of very valuable large crocodiles in the quest for the rapidly dwindling barramundi resource should be stopped.

Crocodile farming should be encouraged and removal of eggs from the wild from nests which are known to be flooded during the January-March period might be considered on certain selected tidal waterways. Early November nests or March-April late nests must not be robbed. Because of the heavy losses of hatchlings and 3-6' animals, we feel that release of such animals into TYPE 1 systems, except in cases of very depleted systems, is purely cosmetic and a waste of effort. If restocking is to be considered then TYPE 2-3 or TYPE 3 systems and freshwater complexes should be uses, and only ≥4' size classes should be released. Even then, many uncertainties remain about the success of such a restocking policy.

ACKNOWLEDGEMENTS

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Table 1. Number of *C. porosus* sighted within size class on tidal waterways of the Northern Territory, Western Australia and Queensland during night-time spotlight surveys[a].

System	Date	Total	Numbers in size class								Kilometers surveyed	Density	95% levels	Type
			H	2-3	3-4	4-5	5-6	6-7	>7	E.O.				
BLYTH-CADELL						MONOGRAPH 1								
	Oct. 74	387	89	81	147	58	6	2		4	91.9	3.2	454- 524	1
	Nov. 75	353	50	106	81	72	23	4	2	15	94.9	3.2	462- 532	
	Sept. 76	348	82	63	104	46	14	7	6	26	92.0	2.9	403- 469	
	Nov. 76	307	61	61	103	47	10	4	2	19	92.0	2.7	371- 435	
	Apr. 77	327	72	70	108	48	10	2	4	13	92.0	2.8	386- 450	
	May 77	333	88	60	94	55	13	4	1	18	92.0	2.7	370- 432	
	June 77	365	108	36	102	69	13	10	3	24	90.5	2.8	389- 453	
	Sept. 77	386	105	45	132	47	17	4	4	32	90.5	3.1	427- 495	
	Oct. 77	360	112	68	83	47	18	8	3	21	90.5	2.7	375- 439	
	June 78	432	173	65	81	67	15	6	4	21	90.5	2.9	393- 457	
	Sept. 78	399	155	60	79	56	18	8	6	17	90.5	2.7	369- 431	
	June 79	465	123	91	93	59	31	16	26	26	94.5	3.6	524- 598	
VICTORIA						MONOGRAPH 2								
FITZMAURICE	Aug. 78	139	13	8	21	22	26	8	13	28	229.1	0.6	184- 230	1
	Aug. 78	79	9	5	13	25	6	4	11	6	146.6	0.5	98- 132	1
ADELAIDE						MONOGRAPH 3								
	July 77	417	48	24	88	116	47	35	33	26	226.3	1.6	566- 644	1
	Sept. 78	381	62	24	71	90	43	33	32	26	221.0	1.4	487- 559	
	Sept. 79	374	53	8	46	75	58	47	64	23	231.6	1.4	490- 562	
DALY	Aug. 78	115	5	7	16	25	21	11	18	12	90.0	1.2	159- 201	1
MOYLE	Aug. 78	16			1	4	2	1	2	6	10.0	1.6	18- 34	1
MURGENELLA						MONOGRAPH 4 (14)								
	Oct. 77	95	1	1	8	33	13	6	18	15	45.9	2.0	135- 173	1
	June 78	173	48	16	4	17	24	23	30	11	44.9	2.8	183- 227	
	Aug. 79	198	47	24	12	22	24	27	26	16	45.6	3.3	223- 273	

Table 1. cont.

System	Date	Total	H	Numbers in size class 2-3	3-4	4-5	5-6	6-7	>7	E.O.	Kilometers surveyed	Density	95% levels	Type
EAST ALLIGATOR	Oct. 77	318	53	18	37	57	41	40	34	38	114.9	2.3	402- 468	1
	June 78	329	39	14	63	51	42	31	51	38	118.9	2.4	442- 510	
	Aug. 79	393	53	30	44	58	28	58	64	58	119.2	2.9	521- 595	
SOUTH ALLIGATOR	Oct. 77	142	6	3	12	24	24	25	31	26	113.8	1.2	209- 257	1
	July 78	157	4	1	4	14	43	24	38	25	113.2	1.3	223- 273	
	Aug. 79	164	9	2	4	12	24	31	51	37	114.0	1.4	237- 287	
WEST ALLIGATOR	Oct. 77	83	9	2	14	14	15	10	10	9	42.2	1.8	104- 138	1
	July 78	85	23	5	12	9	13	10	6	7	40.4	1.5	86- 118	
	Aug. 79	96	12	9	13	14	7	12	14	15	42.2	2.0	120- 156	
WILDMAN	Sept. 78	118	53	16	6	8	10	9	7	9	33.5	1.9	91- 123	1
	Aug. 79	155	21	34	15	14	7	17	31	16	33.5	4.0	197- 243	
GOOMADEER	Aug. 75	46		27	7	5	4			3	45.3	1.0	61- 89	1
	Sept. 76	52	18	5	8	5	1	3	3	9	45.3	0.8	44- 68	
	June 77	50	2	9	13	10	6	2	1	7	45.3	1.1	65- 83	
	July 79	90	29	14	7	14	10	6	1	9	45.3	1.4	84- 116	
KING	Aug. 75	17	3	3	3	2			4	2	52.0	0.3	15- 31	2
	Aug. 76	37	12	8	7	1	1	1	4	3	52.0	0.5	31- 51	
	June 77	38	18	4	5	5	1		1	4	48.7	0.4	24- 42	
	July 79	48	3		11	10	9	2	5	8	48.5	0.9	61- 87	
MAJARIE	Aug. 75	12	1	1	2	2	1	1		2	20.1	0.5	11- 25	3
	Aug. 76	7			3					4	20.1	0.4	7	
	July 79	18			1	7	4	1	3	2	24.1	0.7	21- 39	
WURUGOIJ	Aug. 75	4					2		2		16.4	0.2	4	3
	Aug. 76	1								1	16.4	0.1	1	
	July 79	9				3	1		4	1	16.4	0.5	9	
ALL NIGHT	Aug. 75	3					2		1		9.1	0.3	3	3
	Aug. 76	0									9.1	0.0	0	
	July 79	6		1				1		4	9.1	0.6	6	

MONOGRAPH 5

Table 1. cont.

System	Date	Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
				2-3	3-4	4-5	5-6	6-7	>7					
MONOGRAPH 6														
ANDRANANGOO	June 75	40	14	2	5	6			2	11	47.8	0.5	33- 53	1
	Nov. 75	17	7	1	4		1	2	2	7	47.8	0.4	20- 36	
	Aug. 76	41	7	1	8	10	3	3	1	8	47.8	0.7	44- 68	
	June 77	43	7	1	5	9	4		3	14	47.8	0.8	47- 71	
	Oct. 79	56	4	1	3	9	7	6	10	16	48.4	1.1	71- 99	
DONGAU	Oct. 72	15	2	2		3			8		22.4	0.6	14- 28	2-3
	July 75	10	4			1	4		1		22.4	0.3	6	
	Nov. 75	2				2					22.4	0.1	2	
	Aug. 76	17	3	2	3		1	1	5	2	22.4	0.6	15- 31	
	June 77	17	5	1	3	3	1	1	3		22.4	0.5	13- 27	
	Oct. 79	15				3	3	2	5	2	22.4	0.7	17- 33	
JOHNSTON MAINSTREAM	Oct. 72	4							4	4	30.0	0.1	4	2-3
	June 77	17					3	3	7	4	30.0	0.6	20- 36	
	Oct. 79	14				1	4	4	1	4	36.3	0.4	15- 31	
OVERALL JOHNSTON	Oct. 79	20			2	1	5	5	2	5	89.8	0.2	24- 42	2-3
BATH	Oct. 72	0									15.0	0.0	0	
	July 75	0									12.0	0.0	0	
TINGANOO	Oct. 79	5		1		1	1		1	1	14.5	0.3	5	
	Oct. 72	0			(however, 2 large slides seen)							14.5	0.0	0	
	July 75	1					1				14.5	0.1	1	
	Nov. 75	0									14.5	0.0	0	
	Aug. 76	1							1		14.5	0.1	1	
	Oct. 79	6				1	2	1	1	1	14.5	0.4	6	
MONOGRAPH 7														
LIVERPOOL-TOMKINSON	July 76	228	19	39	56	27	13	13	3	68	152.2	1.4	314- 372	1
	May 77	245	40	6	51	59	30	13	5	41	145.1	1.4	307- 365	
	Oct. 77	228	56	7	39	62	24	9	1	30	123.4	1.4	256- 308	

Table 1. cont.

System	Date	Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
				2-3	3-4	4-5	5-6	6-7	>7					
LIVERPOOL- TOMKINSON	Sept. 78	233	37	18	37	65	19	14	8	35	141.4	1.4	293- 349	
	July 79	515	289	11	39	43	34	29	20	50	150.0	1.5	341- 401	
	Oct. 79	355	161	16	36	37	29	17	23	36	141.1	1.4	290- 346	2
NUNGBULGARRI	Aug. 75	29		4	11	3		1		10	15.0	1.9	37- 59	1
	July 76	15	2		3	5	1	1		3	13.6	1.0	14- 28	2
	June 77	14	2	2		6	1	1		2	13.6	0.9	13- 27	2
	July 79	35	10		4	4	6	5	2	4	14.8	1.7	31- 51	1
MONOGRAPH 8														
ROSE	Oct. 78	7				2		3		2	23.5	0.3	7	1
MUNTAK	Oct. 78	3				1				2	6.7	0.4	3	2
HART	Oct. 78	4				1				3	7.5	0.5	4	2
WALKER	Oct. 78	15	1		4	2	1	2	1	4	24.4	0.6	15- 31	1
KOOLATONG	Oct. 78	5					1	2	1	1	11.0	0.5	5	1
MONOGRAPH 9														
BENNETT	Sept. 75	3			1	1		1			17.6	0.2	3	3
	June 79	10			1	1	3	2	3		53.0	0.2	10- 22	
DARBITLA	Aug. 75	13		1		5	3	2	1	1	34.8	0.4	14- 28	2-3
	June 79	19		2		2	3		3	9	35.7	0.5	22- 40	
DJIGAGILA	Sept. 75	8				5	1	2			23.0	0.4	8	3
	June 79	23	1	1	1	2	6	3	4	5	25.0	0.9	27- 45	
DJABURA	Sept. 75	3	1			2					21.6	0.1	3	3
	June 79	14	3		1	7	2			1	25.7	0.5	14- 28	
NGANDADAUDA	Sept. 75	19			5	1	3	2	1	4	22.6	0.7	18- 34	3
	June 79	21		2	2	3	3	2	4	5	23.9	0.9	25- 43	
WOOLEN	Sept. 75	31	5	2	5	3	3	3	4	6	80.4	0.3	33- 53	2
	July 79	57	14	3	6	10		2	6	6	102.5	0.4	58- 84	
GLYDE	Sept. 75	28			3	6		3	4	12	45.9	0.6	35- 57	1
	July 79	100	36	9	10	9	10	6	6	14	45.9	1.4	89- 121	

Table 1. cont.

System	Date	Total	H	2-3	3-4	4-5	5-6	6-7	>7	E.O.	Kilometers surveyed	Density	95% levels	Type
CADELL CREEKS														
	Sept. 75	4			(not used)	1	1			1	7.0	0.6	4	3
HUTCHINSON	Sept. 75	25	6	1	3	4	1	3		1	58.3	0.3	22-40	3 & mini 1
	July 79	56	10	5	5	9	13	6	2	9	78.5	0.6	61-89	
KALARWOI	Sept. 75	82	38	3	17	3	4		1	1	38.9	1.1	59-85	1 & 2-3
	June 79	132	45	15	16	19	11	16	4	11	40.1	2.2	124-162	
BUCKINGHAM	Sept. 75	100	10	7	8	14	8	1	7	14	31.1	2.9	129-167	2
	June 79	101	16	42	24	17	9	8	3	16	35.3	2.4	120-158	
WARAWURUWOI	Oct. 75	18		7	3	5	4	1	4	2	28.8	0.6	21-39	3
	June 79	34		1	1	4	3	7	2	10	37.0	0.9	44-68	
KURALA	Oct. 75	16			3	5	2	1	9	3	27.8	0.6	18-34	3
	June 79	26				6	7	3	2	4	36.4	0.7	33-53	
SLIPPERY	Oct. 75	9			2	1	2	1	6	3	11.0	0.8	9	3
	June 79	20		2	5	7	2	4			10.7	1.9	24-42	
MONOGRAPH 11														
BURUNGBIRINUNG	Oct. 75	13	9	2	7	8	2	3		5	13.0	0.3	4	2
	May 79	37	3	8	17	23	3	3	4	2	11.7	2.9	44-68	
PETER JOHN	Oct. 75	142	27	58	48	21	7	5	3	16	41.5	2.8	167-211	1
	May 79	300	136	60	19	10	11	1	3	1	42.1	3.9	243-295	
CATO	Oct. 75	108	59	6	19	5	9	1	4	5	23.5	2.1	66-94	1
	May 79	89	34	19		7	3	1	1		23.0	2.4	75-105	
DARWARUNGA	Oct. 75	15	1	1	4	10	1	2	2	7	47.8	0.3	17-33	2-3
	May 79	34		1	6	25	5	2	4	9	45.0	0.7	42-66	
HABGOOD R.	Oct. 75	101	13	24	14	23	10	3	2	7	22.0	4.0	125-163	1
	May 79	111	23	15	23		15			2	22.1	4.0	125-163	
HABGOOD CK.	Oct. 75	6			1	2	1			1	4.4	1.4	6	3
	May 79	4				3					3.4	1.2	4	
BARALMINAR	Oct. 75	15			1	6	4	1			25.2	0.6	17-33	2-3
	June 79	30		5	5	13	4	3	3	5	26.4	1.1	38-60	

Table 1. cont.

System	Date	Total	H	Numbers in size class 2-3	3-4	4-5	5-6	6-7	>7	E.O.	Kilometers surveyed	Density	95% levels	Type
GOBALPA	Oct. 75	15	2		3	6	2	1		1	19.3	0.7	14- 28	2-3
	June 79	17			3	5	3	2	4		21.3	0.8	20- 36	
GOROMURU	Oct. 75	299	128	95	37	14	7	6	6	6	44.3	3.9	254- 306	1
	June 79	410	134	58	139	31	10	5	7	26	48.0	5.8	420- 486	
MONOGRAPH 12														
LIMMEN BIGHT	May 79	19	1	1		3	8	3	2	1	127.3	0.1	21- 39	2
TOWNS	May 79	55	28	1	6	7	7	2	3	1	57.2	0.5	34- 54	2
ROPER	May 79	430	126	67	41	86	39	34	26	20	262.8	1.2	477- 549	1
YIWAPA	May 79	9	4				2	3			14.6	0.6	9	3
MANGKURDUR-RUNGKU	May 79	2					2				6.5	0.3	2	3
MONOGRAPH 12														
CALVART	Apr. 79	2					1	1			38.4	0.1	2	2
EINSTEIN	Apr. 79	1								1	6.6	0.2	1	3
MAXWELL	Apr. 79	0									2.0	0.0	0	3
SCHRODINGER/ FERMI	Apr. 79	1							1		2.0	0.5	1	3
ROBINSON	Apr. 79	0									35.9	0.0	0	2
FAT FELLOWS	May 79	1				1					11.0	0.1	1	3
GALILEO	May 79	0									8.0	0.0	0	3
ARCHIMEDES	May 79	3				1	1	1		1	6.4	0.5	3	3
PLANCK	May 79	1				1					15.1	0.1	1	3
WEARYAN	May 79	4	2			1	1				34.4	0.1	4	2
FARADAY/DAVY	May 79	1				1					10.5	0.1	1	3
COULOMB	May 79	0									13.3	0.0	0	3
McARTHUR	May 79	28			2	3	6	4	5	8	232.6	0.1	35- 57	1
MONOGRAPH 14														
SALTWATER	Aug. 79	29		1	1	6	4	6	9	2	14.1	2.1	37- 59	3

Table 1. cont.

System	Date	Total	Numbers in size class								Kilometers surveyed	Density	95% levels	Type
			H	2-3	3-4	4-5	5-6	6-7	>7	E.O.				
MINIMINI	Aug. 79	11			1	4	3	1	2		43.8	0.3	11- 25	3
MIDDLE ARM	Aug. 79	6				3	2	1			28.5	0.2	6	3
IWALG	Aug. 79	10				3	1	2	2	2	53.5	0.2	10- 22	3
ARM A	Aug. 79	5				3		1		1	26.7	0.2	5	3
ARM B	Aug. 79	3				1		1	1		15.0	0.2	3	3
ARM C	Aug. 79	7				3	1	1		2	29.3	0.2	7	3
ARM D	Aug. 79	9				1		3	2	3	19.8	0.5	9	3
ILAMARYI	Aug. 79	16			1	3	4	3	3	3	44.4	0.4	18- 34	3
MONOGRAPH 17														
PORT DARWIN	Sept. 79	80	4	8	6	8	8	9	16	21	148.6	0.5	107- 143	2-3
PORT PATTERSON	Sept. 79	10			1	1	2	2	1	3	59.9	0.2	10- 22	3
PORT HARBOUR	Sept. 79	24	2	1	1	4	4		9	3	109.5	0.2	27- 45	3
LATEST SURVEY ONLY														
Total TYPE 1		4491	1197	478	629	597	392	353	413	432	2175.5	1.5	5287-5517	1
% of total			27	11	14	13	9	8	9	10	54			
Total TYPE 2-3		591	82	32	80	105	79	54	62	97	938.4	0.5	790- 880	2-3
% of total			14	5	14	18	13	9	10	16	23			
Total TYPE 3		390	14	8	20	88	72	61	64	63	883.7	0.4	578- 656	3
% of total			4	2	5	23	18	16	16	16	22			
Overall total		5472	1293	518	729	790	543	468	539	592	3997.6	1.0	6724-6984	1 to 3
% of total			24	9	13	14	10	9	10	11				
MONOGRAPHS 4 & 14														
ALLIGATOR REGION	77	638	63	21	71	128	93	81	93	88	316.8	1.8	895- 991	1
EXCL. WILDMAN	78	744	116	38	83	91	122	88	125	81	317.4	2.0	980-1080	
	79	851	116	64	73	106	83	128	155	126	321.0	2.3	1151-1259	
ALLIGATOR REGION	78	862	169	54	89	99	132	97	132	90	350.9	2.0	1084-1190	1
	79	1006	137	98	88	120	90	145	186	142	354.5	2.4	1366-1484	

Table 1. cont.

System	Date	Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
				2-3	3-4	4-5	5-6	6-7	>7					
MONOGRAPH 14														
COBOURG COMPLEX & SALTWATER	79	96		1	2	27	15	19	19	13	275.1	0.3	137- 177	3
ALLIGATOR REGION COBOURG COMPLEX & SALTWATER	79	1102	137	99	90	147	105	164	205	155	629.6	1.5	1521-1645	1 & 3
MONOGRAPH 6														
ANDRANANGOO, DONGAU & TINGANOO MELVILLE I.	75	51	18	2	5	7	5	3	11		84.7	0.4	42- 66	1 to 3
	79	77	4	1	3	13	12	9	16	19	85.3	0.9	103- 137	
	79	102	4	2	5	16	18	14	19	25	189.6	0.5	141- 181	
MONOGRAPH 5 & 7														
NUNGBULGARRI TO KING	75	111	4	35	23	15	8	3	6	17	162.2	0.7	154- 196	1 to 3
	79	206	42	15	23	35	31	17	15	28	158.2	1.0	243- 295	
MONOGRAPH 1, 5 & 7														
BLYTH TO KING BUT USING LIVERPOOL '76 FOR '75	75	712	73	180	162	116	46	13	11	111	416.0	1.5	997-1099	1 to 3
	79	1186	454	117	155	137	96	62	61	104	402.7	1.8	1146-1254	
MONOGRAPH 9														
CASTLEREAGH BAY & HUTCHINSON STR.	75	130	14	11	19	27	9	12	14	24	304.2	0.4	168- 212	1 to 3
	79	300	62	17	25	43	42	29	33	49	390.2	0.6	359- 421	
MONOGRAPH 10														
BUCKINGHAM & ULUNDURWI BAYS	75	225	48	58	33	28	20	4	11	23	137.6	1.3	263- 317	1 to 3
	79	313	61	16	46	53	32	38	26	41	159.5	1.6	381- 455	

Table 1. cont.

System	Date	Total	Numbers in size class							E.O.	Kilometers surveyed	Density	95% levels	Type
			H	2-3	3-4	4-5	5-6	6-7	>7					
ARNHEM BAY							MONOGRAPH 11							
	75	714	238	187	96	93	43	15	21	21	241.0	2.0	737- 825	1 to 3
	79	1032	331	161	250	119	54	23	22	72	243.0	2.9	1097-1203	
NORTH ARNHEM LAND TO KING							MONOGRAPH 1, 5, 7 TO 11							
	75	1781	373	436	310	264	118	44	57	179	1098.8	1.3	2234-2384	1 to 3
	79	2831	908	311	476	352	224	152	142	266	1195.4	1.6	3066-3242	
GULF SOUTH COAST							MONOGRAPH 12 & 13							
	79	116	31	2	8	16	24	12	11	12	600.7	0.1	120- 158	1 to 3
GULF SOUTH COAST EXCL. TOWNS	79	61	3	1	2	9	17	10	8	11	543.5	0.1	80- 110	1 to 3
ROPER SYSTEM & COASTAL CREEKS	79	450	126	67	41	90	43	37	26	20	283.9	1.1	495- 567	1 to 3
GULF WEST COAST							MONOGRAPH 8							
	78	34	1		4	6	2	7	2	12	73.1	0.5	42- 56	1 to 2
TOTALS														
GULF OF CARPENTARIA	78, 79	600	158	69	53	112	69	56	39	44	957.7	0.5	683- 767	1 to 3
NORTH ARNHEM LAND	79	2831	908	311	476	352	224	152	142	266	1159.4	1.6	3066-3242	1 to 3
DARWIN EASTWARD TO COBOURG INCL. MELVILLE	79	1578	194	109	141	237	181	225	288	203	1050.8	1.3	2195-2345	1 to 3
DARWIN WESTWARD	78, 79	463	33	29	59	89	69	35	70	79	793.7	0.5	663- 747	1 to 3
NORTHERN TERRITORY	78, 79	5472	1293	518	729	790	543	468	539	592	3997.6	1.0	6724-6984	1 to 3

Table 1. cont.

System	Date	Total	H	2-3	3-4	4-5	5-6	6-7	>7	E.O.	Kilometers surveyed	Density	95% levels	Type
						Numbers in size class								
WESTERN AUSTRALIA - Reports 24 & 34														
LAWLEY	July 77	44	13	1	4	6	8	5	3	4	37.0	0.8	40- 62	2
MITCHELL	July 77	50	8	1	9	12	8	3	6	3	47.7	0.9	56- 82	1
ROE	July 77	176	52	40	27	22	14	8	6	7	68.6	1.8	181- 225	1
HUNTER	July 77	47	11	7	5	10	6	4	2	2	39.3	0.9	47- 71	2
ST. GEORGE											(estimate)			
BASIN ARMS	July 77	72	10	1	2	18	10	15	13	3	36.0?	1.7	86- 118	2 to 3
PRINCE REGENT	July 77	74	15	4	25	12	8	5	1	4	58.6	1.0	82- 112	1
GEORGE WATER														
& GLENELG	July 78	213	73	33	26	33	18	12	12	6	96.3	1.4	206- 254	1 to 3
											(estimate)			
ST. GEORGE														
BASIN ARMS	July 78	97	25	3	1	13	12	14	25	4	72.0?	1.0	101- 135	2 to 3
PRINCE REGENT	July 78	92	31	11	17	11	8	6	6	2	68.0	0.9	84- 116	1
ORD	July 78	179	14	17	39	50	19	11	8	21	98.4	1.7	245- 297	1
TOTAL LATEST														
SURVEYS		898	227	113	128	157	93	63	68	49	527.3	1.3	1048-1152	1 to 3
% OF TOTAL			25	13	14	17	10	7	8	5				
QUEENSLAND - MONOGRAPH 16														
NASSAU	Apr. 79	103	4	27	30	23	7	5	3	4	146.3	0.7	142- 182	1
STAATEN	Apr. 79	20		6	3	2	2	3	3	1	74.5	0.3	24- 42	1
GILBERT	Apr. 79	8				1	3	1		3	65.2	0.1	8	1-3
DUCK	Apr. 79	27		2	5	5	3	6	4	2	73.7	0.4	34- 54	1-3
TOTAL		158	4	35	38	31	15	15	10	10	359.7	0.4	228- 278	1 to 3
WENLOCK	Nov. 79	311	83	67	65	44	8	8	4	32	103.7	2.2	344- 404	1
DUCIE	Nov. 79	201	28	52	48	40	16	3	2	12	109.9	1.6	258- 310	1
DULCIE	Nov. 79	1					1				3.5	0.3	1	1
PALM	Nov. 79	9	1		2	1	1			4	6.0	1.3	8	1
NAMALETA	Nov. 79	14		1		7			1	5	17.9	0.8	15- 31	3

Table 1. cont.

System	Date	Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
				2-3	3-4	4-5	5-6	6-7	>7					
PORT MUSGRAVE	Nov. 79	536	112	120	115	92	26	11	7	53	241.0	1.8	654- 736	1 & 3
ESCAPE	Nov. 79	31	3			5	6	2	7	8	42.0	0.7	35- 57	1
TOTAL QUEENSLAND	79	725	119	155	153	128	47	28	24	71	642.7	0.9	945-1043	1 & 3
& OF TOTAL			16	21	21	18	6	4	3	10				

a The midstream distance surveyed and density of non-hatchling crocodiles sighted on it is shown, as are the 95% confidence limits for the estimate of the actual number of non-hatchlings present. The TYPE classification of each waterway is given also (see text).

Table 2. Number of *C. porosus* sighted within each size class on tidal waterways of the southern Gulf of Carpentaria during night-time spotlight surveys carried out during 1979 and 1985.

System		H	2-3	3-4	4-5	5-6	6-7	>7	EO			95% Levels	TYPE
					Numbers in size class								
MONOGRAPH 12													
Limmen Bight													
May 79	19	1	1		3	8	3	2	1	127.3	0.1	21- 39	2
Oct. 85	31[a]	2	1				4	7	17[a]	127.3	0.2	37- 59	
Towns													
May 79	55	28	1	6	7	7	2	3	1	57.2	0.5	34- 54	2
Oct. 85	28		1	1	5	9	2	7	3	57.2	0.5	35- 57	
Nayarnpi													
Oct. 85	5							2	3	17.9	0.3	5	3
Roper													
May 79	439	126	67	41	86	39	34	26	20	262.8	1.2	477-549	1
Sept. 85	405	44	134	43	52	31	34	37	30	262.8	1.4	554-630	
Yiwapa													
May 79	9				4	2	3			14.6	0.6	9	3
Sept. 85	5				1		1		3	14.6	0.3	5	
Mangkurdurrungku													
May 79	2					2				6.5	0.3	2	3
Sept. 85	0									6.5	0	0	
MONOGRAPH 13													
Wearyan													
May 79	4	2				1	1			34.4	0.1	4	2
Sept. 84	5			1			1		3	34.4	0.1	5	
Fat Fellows													
May 79	1			1						11.0	0.1	1	3
Sept. 85	1							1		11.0	0.1	1	
Galileo													
May 79	0									8.0	0	0	3
Sept. 85	0									8.0	0	0	
Archimedes													
May 79	3					1	1		1	6.4	0.5	3	3
Sept. 85	0									6.4	0	0	
Faraday/Davy													
May 79	1				1					26.2	0.04	1	3
Sept. 85										26.2	0	0	
McArthur													
May 79	28			2	3	6	4	5	8	232.6	0.1	35- 57	1
Sept. 85	48	2	14	1	3	1	5	9	13	232.6	0.2	61- 89	

[a] Treat with caution as this number probably includes *C. johnstoni*.

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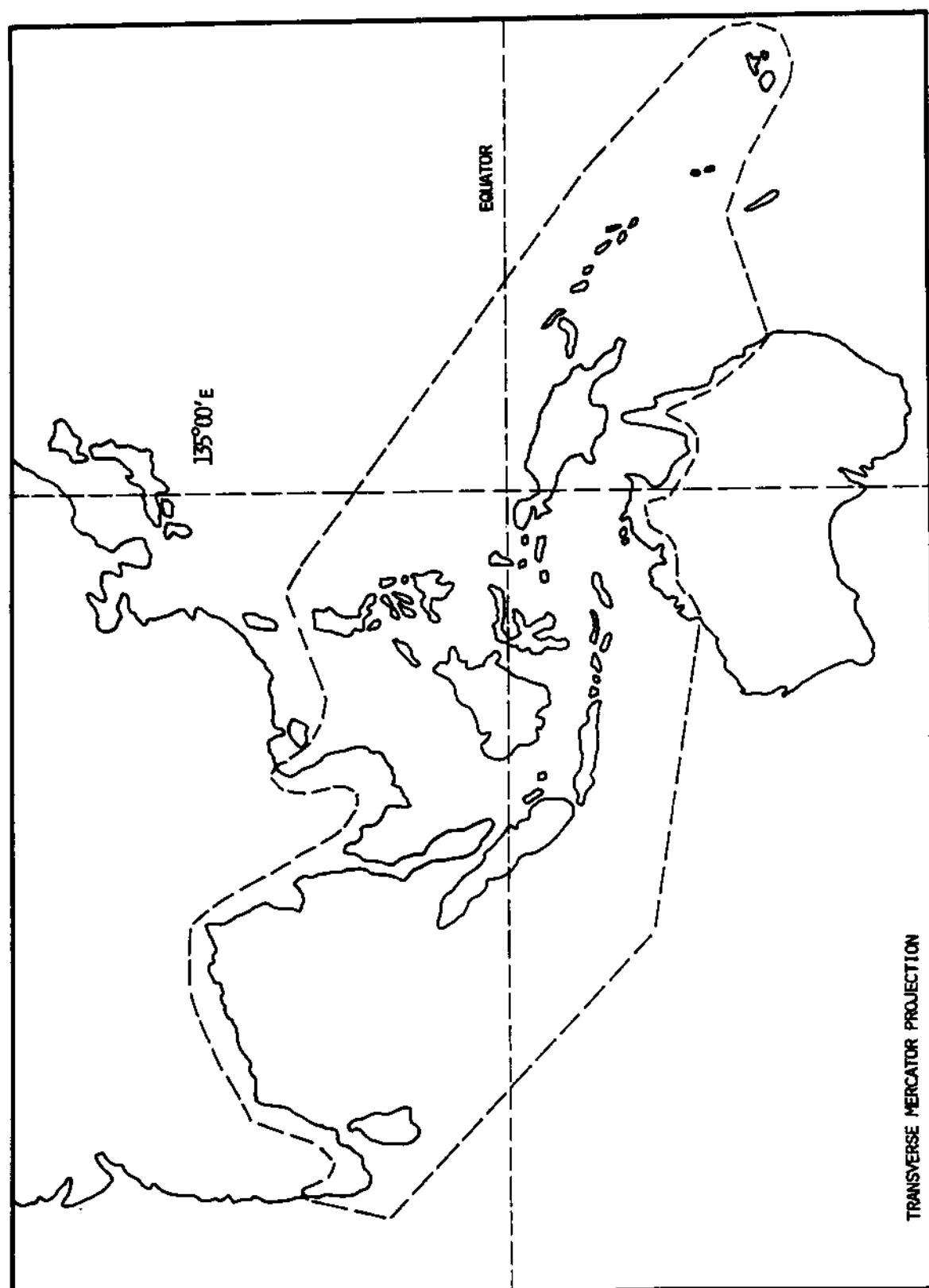
Figure 1. Former distribution of *Crocodylus porosus* (adapted from Neill 1971).

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.
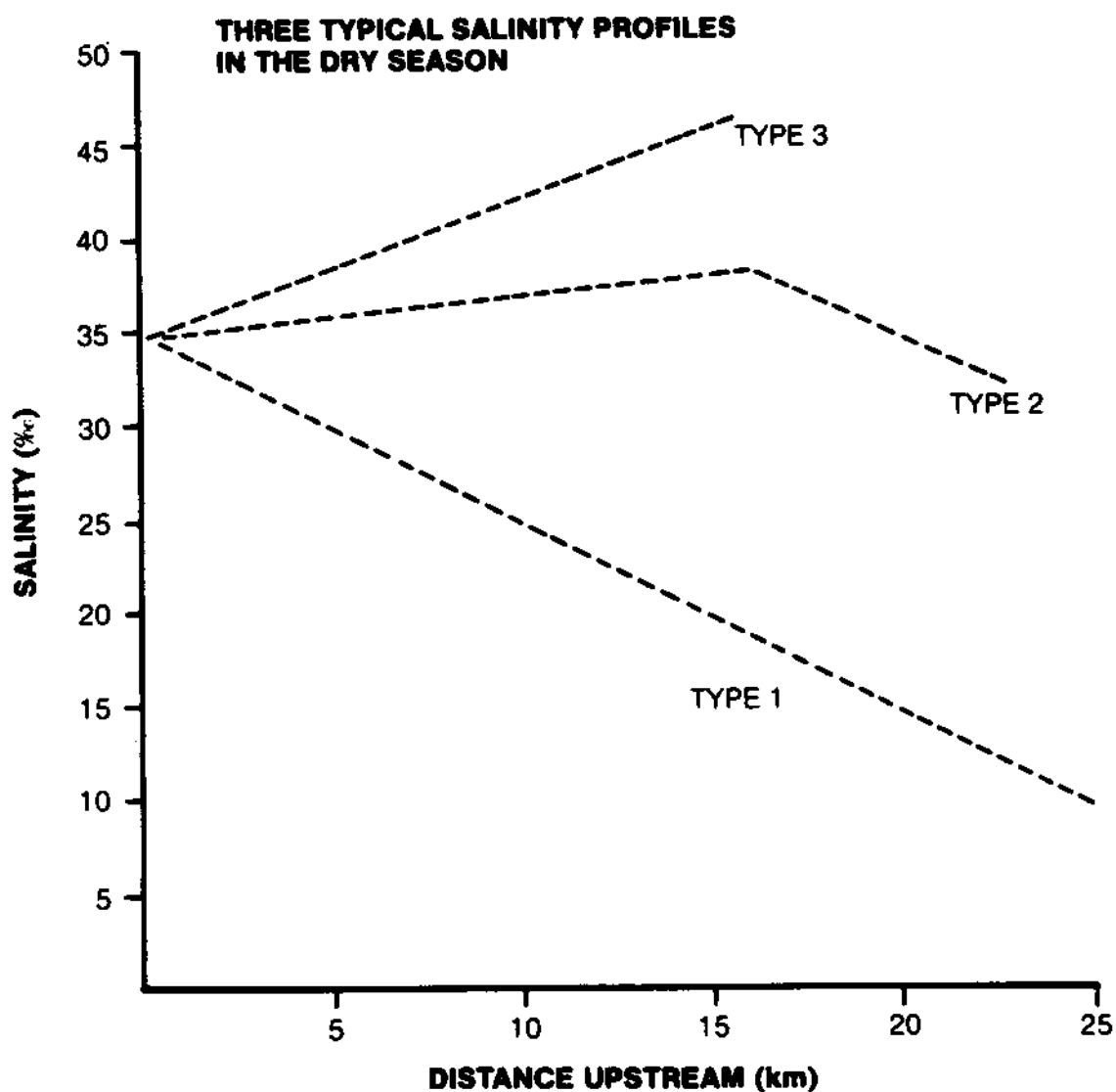
Figure 2. Typical dry season salinity profiles for the three types of tidal systems occurring in the classification scheme described in the text.
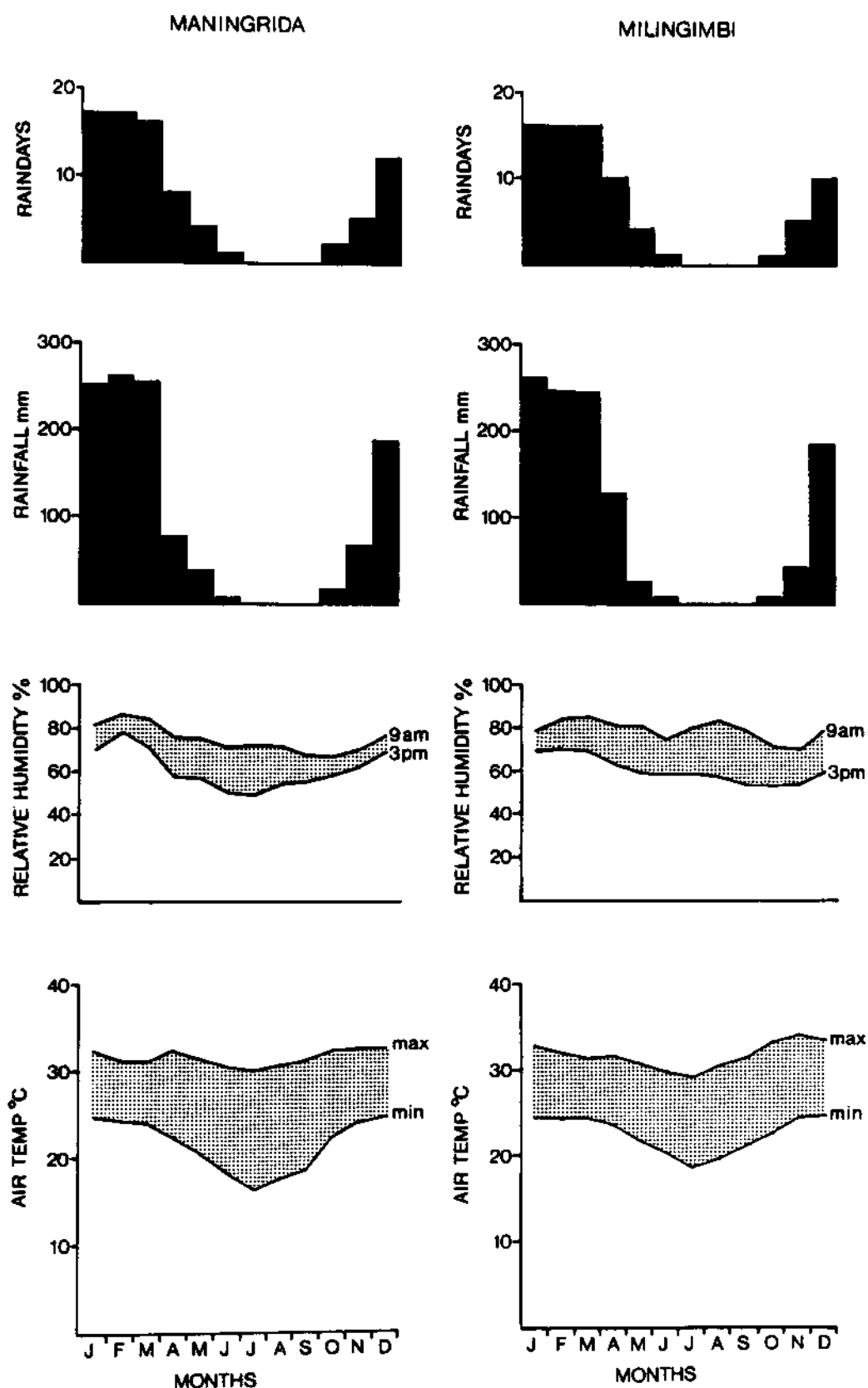
Figure 3. Mean annual number of rainy days, rainfall regimes, mean relative humidity and mean maximum and minimum temperatures at Maningrida and Milingimbi meteorological stations, which are adjacent to the study area.

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, $30 \pm 1°C$. 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.
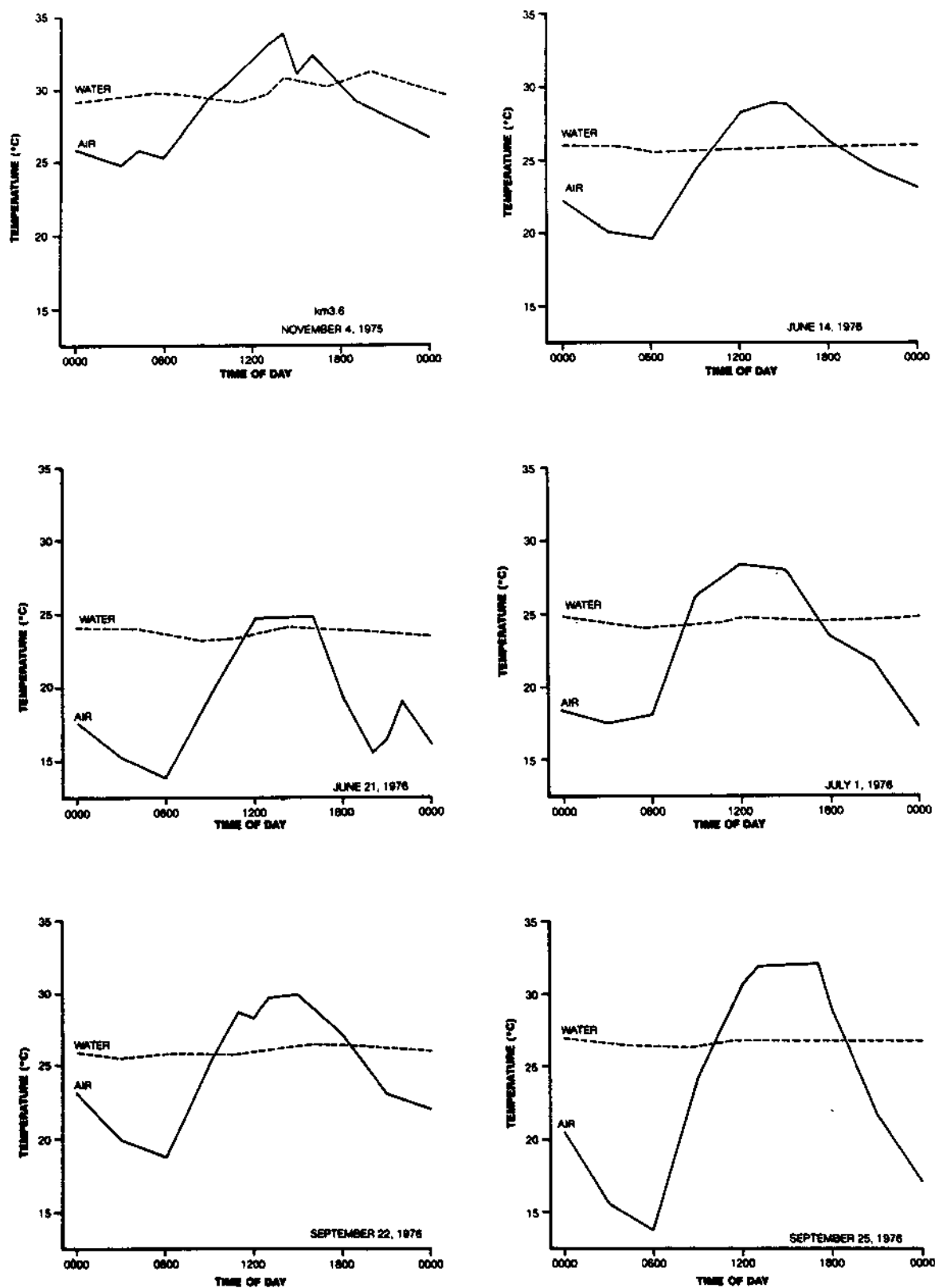
Figure 4. Twenty-four hour temperature profiles of the air (1 m above ground level) and water. Temperatures were recorded at hourly intervals. All measurements were taken at km 32 upstream on the Blyth River (except November profiles which were taken at km 3.6) during 1975 and 1976.
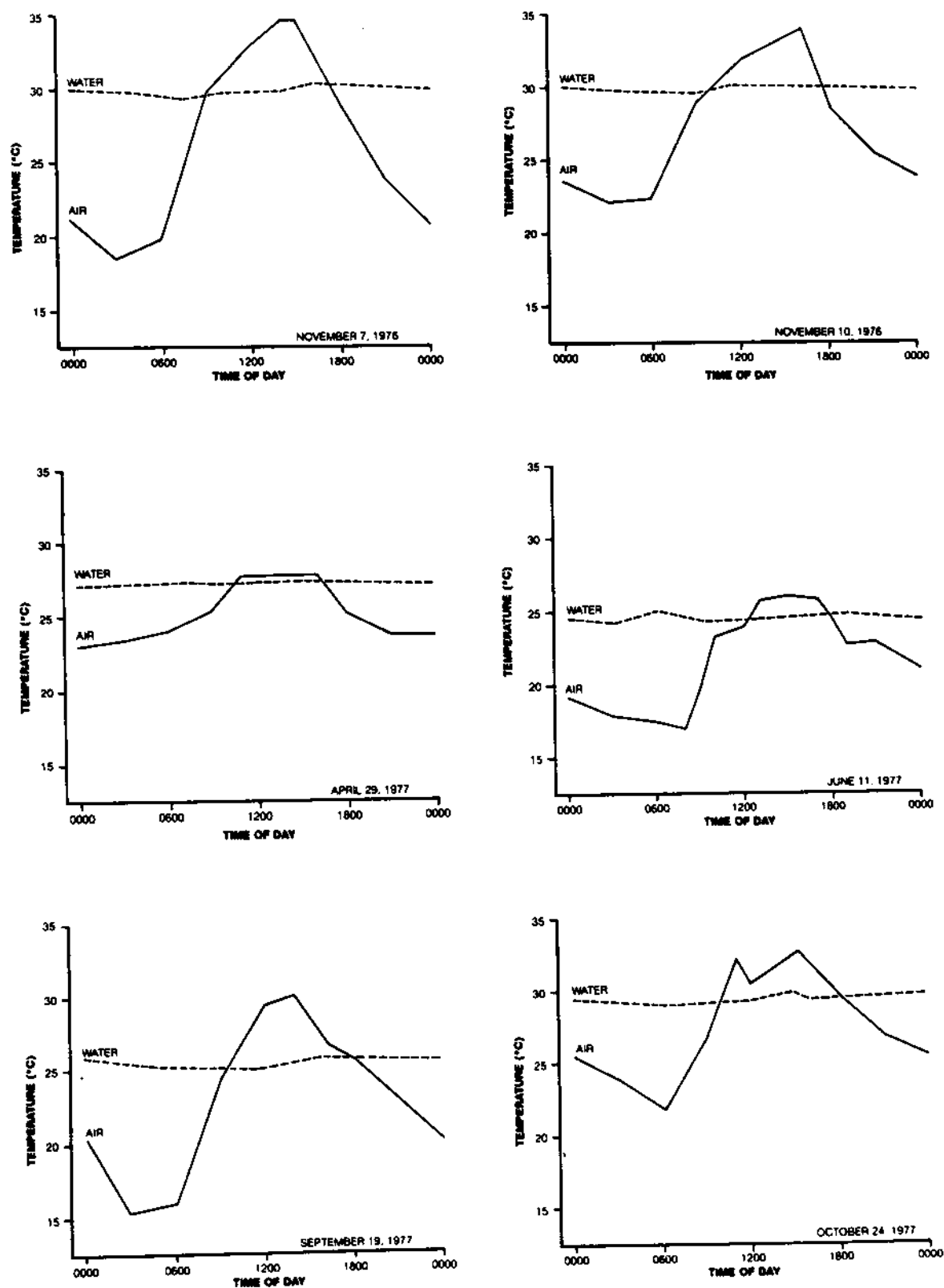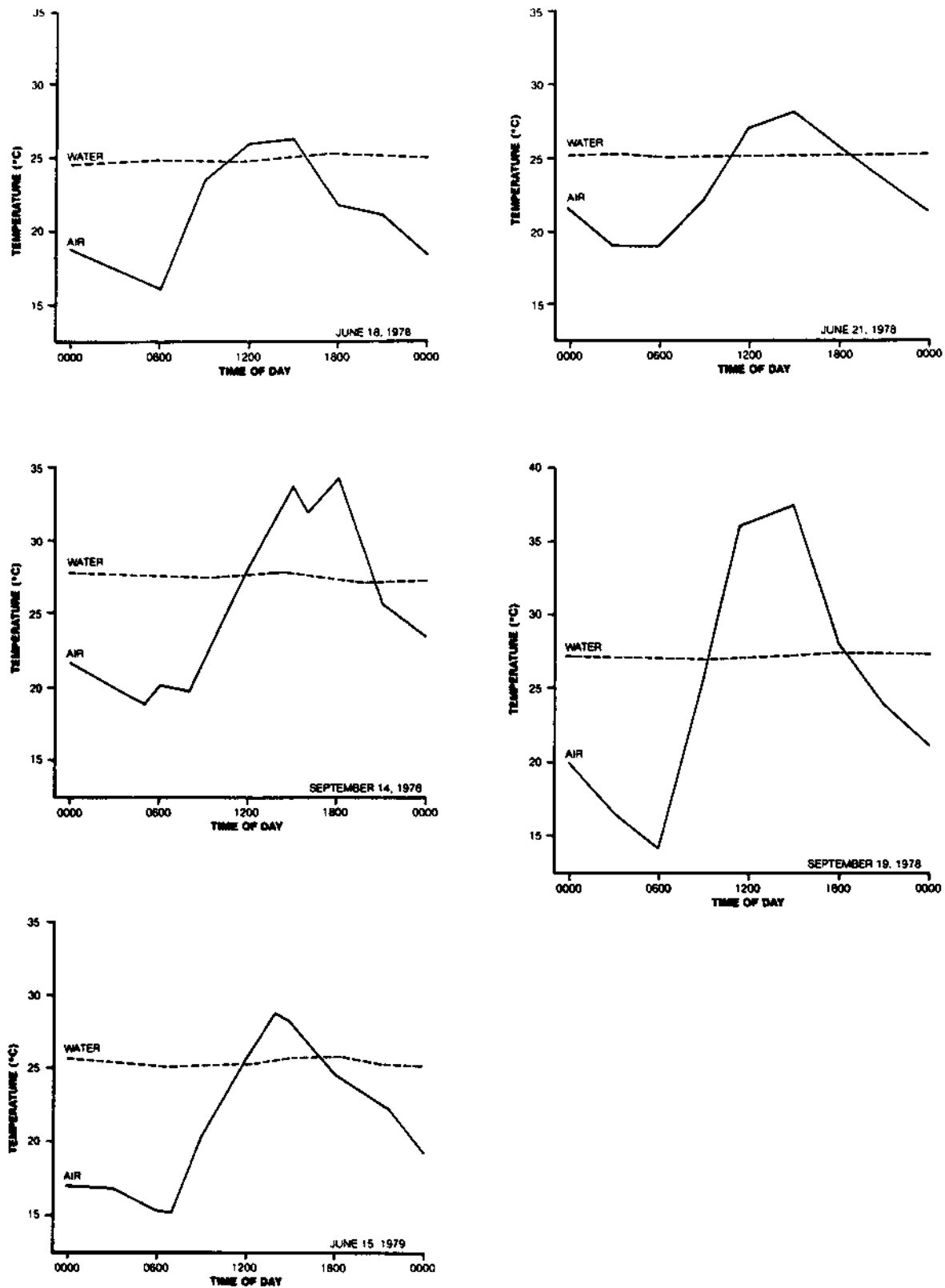
Figure 5. Twenty-four hour temperature profiles of the air (1 m above ground level) and water. Temperatures were recorded at hourly intervals. All measurements were taken at km 32 upstream on the Blyth River during 1976 and 1977.

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.

Feeding was observed to occur during the day and at night, the crocodiles feeding when food was available, on both rising and falling tides.

Extensive night-time observations of feeding during surveys of crocodile numbers led to no obvious relationships between environmental variables and feeding. There was an indication that, on the sections where growth appeared to be slower, there was more activity directed towards catching food items. On these same sections the percentage of small crocodiles sighted feeding is twice that of hatchlings, probably indicating only that small crocodiles require more of the small food items such as prawns.

DISTRIBUTION OF ANIMALS

Movement of animals will be discussed also in the chapter on *C. porosus* population dynamics. Here we characterize briefly typical distributions of *C. porosus* on tidal waters. Each monograph in the series by Messel et al. (1978-1986) includes histograms of the distribution of night-time sightings along the waterway, for each size class.

Webb and Messel (1978) discussed the distributional pattern of crocodiles on the Blyth-Cadell Rivers System in a preliminary fashion and referred to the near normal (bell-shaped) distributional pattern of hatchlings and 2-3' crocodiles around the nest sites. They also referred to the further downstream movement, relative to the nesting site, of the 3-4' and 4-5' sized crocodiles and concluded that there were many factors which could presumably affect movement and dispersal patterns of both adult and juvenile *C. porosus*. The results obtained from the Blyth-Cadell study (Messel et al. 1978-1986, 1:Chapter 6) demonstrate that those crocodiles which do remain in the river system are distributed along it in a quite definite fashion. The position of the peak of the distribution (mean distance upstream) varies for each size class and is roughly inversely proportional to size: the mean distance upstream of the hatchling peak is greater than that for 2-3' sized crocodiles; in turn, the mean distance upstream of 2-3' sized crocodiles is greater than that for 3-4' crocodiles. The peak is still quite distinct for the 4-5' size class but is not so evident for the 5-6' size class and specially not for larger crocodiles, which appear to be more evenly distributed along the river.

As we show incontrovertibly in our chapter on *C. porosus* population dynamics, some 80% of crocodiles in the sub-adult classes are lost from the Blyth-Cadell Rivers System. We also show that the same occurs in other TYPE 1 river systems (Messel et al. 1978-1986, 10-12). On this basis, the distributional pattern of crocodiles in size classes $\geq$ (2-3') is more readily understood. The gradual shifting of the distributional peak downstream, of crocodiles in the 2- 4', 4-5' and 5-6' size classes, may be understood, at least in part, on the basis of these crocodiles being on their way out of the river system, as they are forced gradually downstream by the large crocodiles, which are more evenly distributed along the river system. The long distance movers of Webb and Messel (1978) are also easily explained; they are presumably largely (but not solely) that fraction of the respective size classes, which are forced to leave the river - hence the increasing number of long distance movers with increasing size of sub-adults.

Food supply and salinity, which appear to be closely related, undoubtedly also play a role, for, as Taylor (1979) has shown, the diet of *C. porosus* changes as the animal increases in size. Whether or not food supply and/or salinity are the proximal factors involved, it is a fact that the peak of the distributional curve appears to be centered around the brackish sections of the river, especially in the changeover zone from salt to fresh water. On the Blyth River, this occurs on the km 30-35 section. Normal end of the dry season salinities on this section are close to 10°/oo. As soon as one reaches

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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A MODEL FOR THE POPULATION DYNAMICS OF *Crocodylus porosus* IN NORTHERN AUSTRALIA

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INTRODUCTION

In our chapter on the population status of *Crocodylus porosus* in northern Australia we describe the survey methods used in monitoring the populations and describe briefly the history of the surveys. More than 100 tidal river and creek systems were surveyed at least once between 1974 and 1979. In some cases the surveys have been continued over a period of ten years.

Intensive population surveys and studies were continued during 1980-1983 on some 330 km of tidal waterways (Figs. 1-3) centered on the Liverpool-Tomkinson and Blyth-Cadell Rivers Systems in northern Arnhem Land and on some 59.3 km of associated alternative habitat. These relatively undisturbed waterways constituted our population dynamics and status monitoring systems. In addition Ngandadauda Creek and the Glyde River with its associated Arafura Swamp were resurveyed twice in 1983 (Figs. 1, 4-5). All these latter surveys are analyzed in great detail in Messel et al. (1979-1984, 18).

The results of our survey and studies have allowed a picture of *C. porosus* population dynamics in northern Australia to be developed, and this picture is presented in some detail. It enables us to account in a consistent fashion for the results of the surveys and to predict results to be expected on future surveys.

One implication of the picture was that recovery of the crocodile population should occur more rapidly in areas where the TYPE 1 rivers (see Point 1 in the population model) have closely associated extensive freshwater complexes. One of the best such areas remaining in northern Australia is the Alligator Region, where there is the largest concentration of TYPE 1 *C. porosus* systems in northern Australia. For this reason the waterways of the Alligator Region and the Adelaide River were resurveyed in July 1984.

The Adelaide, East Alligator South Alligator, West Alligator, and Wildman River Systems and Murgenella Creek-- all TYPE 1 systems (Fig. 6)--were first systematically surveyed in 1977 (the Wildman in 1978) and then resurveyed in 1978 and again in 1979. Just to the north of the Alligator Region, the largest assemblage of TYPE 3 waterways in northern Australia--the Cobourg Complex consisting of the Ilamaryi and Minimini Complexes and Saltwater Creek--were surveyed for the first time in 1979 (Fig. 6). Our results and discussions of the surveys were presented in Messel et al. (1979-1984, 1, 3, 18) for the Adelaide River System and Messel et al. (1979-1984, 1, 4, 14) for the Alligator Region River Systems and the Cobourg Complex. Detailed descriptions of the waterways were given in those citations also and full work maps in Messel et al. (1979-
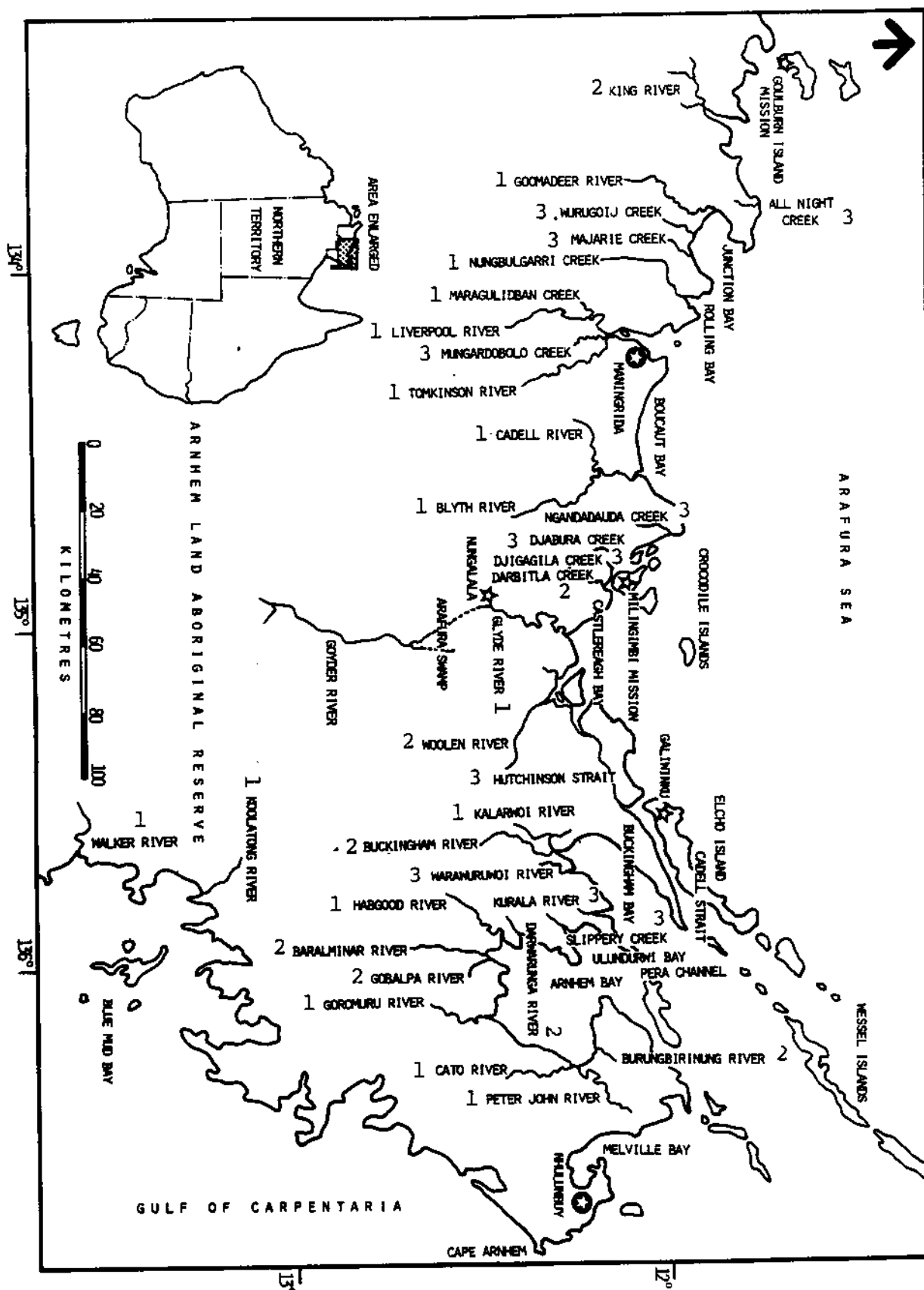
Figure 1.   General area map showing the waterways of the monitored area, with their TYPE classifications.

Figure 2. The Liverpool-Tomkinson Rivers.
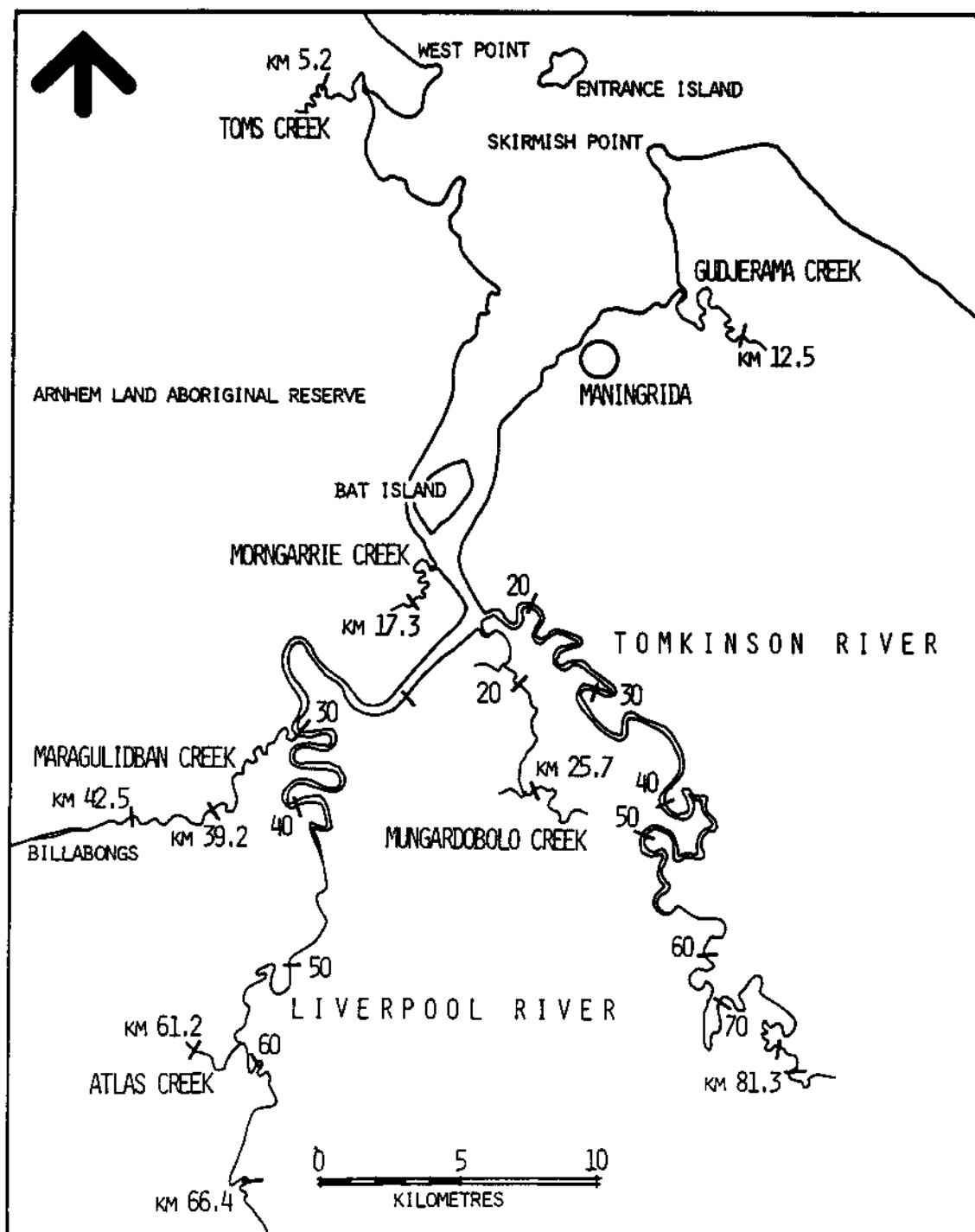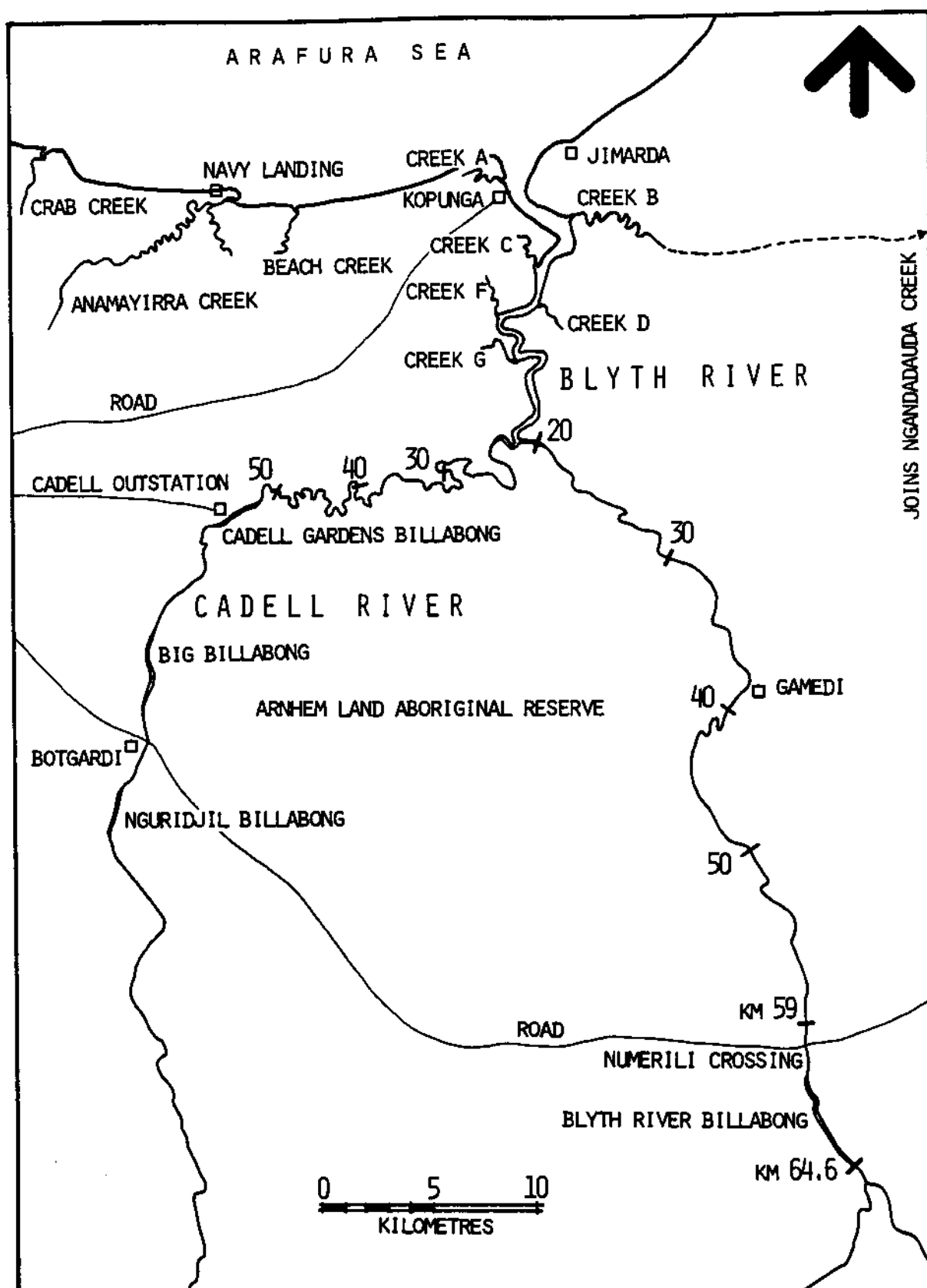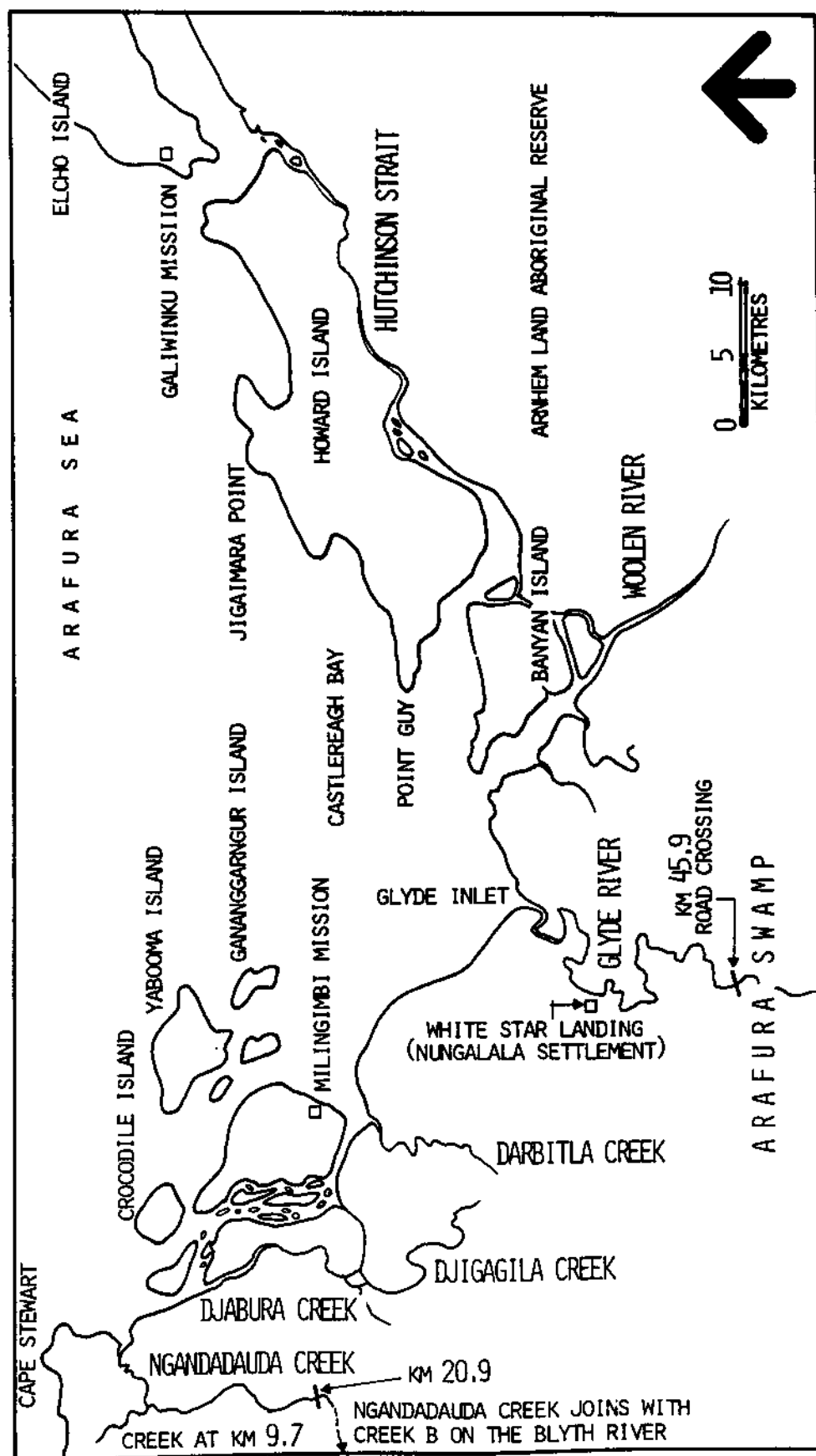
Figure 3. The Blyth-Cadell Rivers.

Figure 4.   General area map showing the tidal waterways of the Milingimbi Complex and Castlereagh Bay.
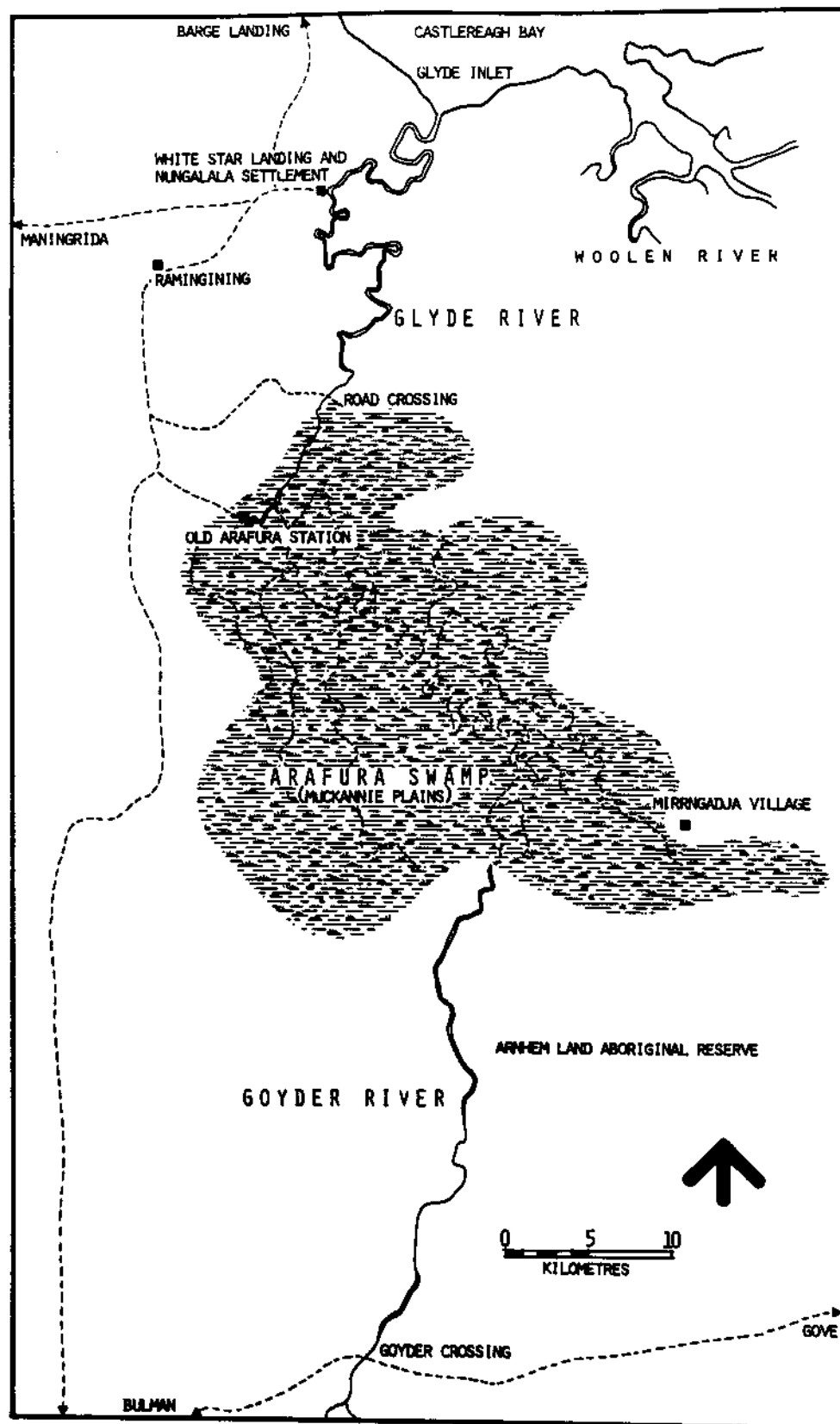
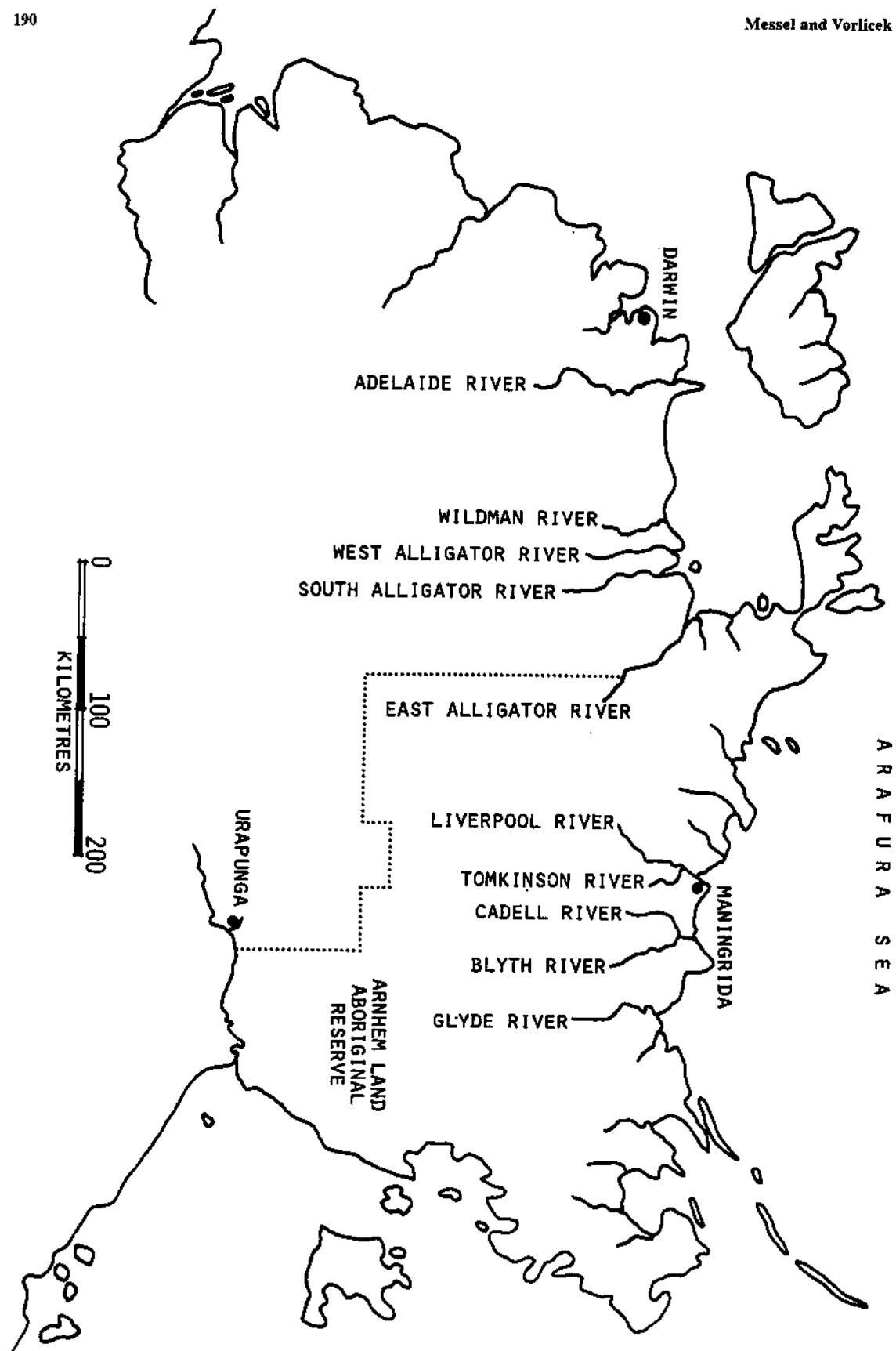**Figure 5. The Glyde-Arafura and Goyder Areas.**

Figure 6. General area map showing rivers and creeks on the Cobourg Peninsula and the Alligator Region. The dotted area shows the Cobourg Mangrove Complex which is one of the largest in Australia.

1984, 15). The results and analysis of the July 1984 surveys is presented in detail in Messel et al. (1979-1984, 19).

Our approach in this chapter is to present the model we have developed and describe how the results obtained In the Maningrida monitored area and Alligator Rivers Region fit the model. This of course is a somewhat circular process, since the model was derived partly from consideration of these results. Other evidence is also presented to support the basic ideas of the model.

We believe that the construction of a mathematical model of *C. porosus* population dynamics would be premature at this stage. There are far too many uncertainties in values for basic biological parameters to allow a sensible predictive model. Examples of such uncertainties include: percentage of mature females in a given population; percentage of mature females nesting; variability in nesting in different years and different rivers; detailed understanding of territorial requirements and so on.

RESULTS

As we describe in our chapter on population status, when discussing population changes it is essential to consider results for broad groups of waterways as well as those for individual waterways. In Table 1A we present results for each survey of the tidal waterways of the monitored area from 1974 to 1983. The table is in our standard format, which is described in the Results section of the chapter on Population Status, and the reader should refer to this.

In Table 1B we present the results for all surveys carried out in the Alligator Region, Cobourg Complex, and Adelaide River, in the same form as Table 1A. Tables 2 and 3 are obtained using Table 1A, and highlight a number of salient features of the data for the Blyth-Cadell and Liverpool-Tomkinson Rivers Systems. In Tables 4 and 5 we show summary results for the number of crocodiles sighted in the hatchling, small (3-6'), and large size classes during the general night-time surveys of the major components of the Blyth-Cadell and Liverpool-Tomkinson Rivers Systems. The more important size classes are the 3-6'), large, and $>3'$. Interpretation of small and non-hatchling numbers can be distorted temporarily because of variations arising from the input of 2-3' animals after a heavy hatchling recruitment year. This variation appears to soon disappear once the animals reach the $>3-4'$ size classes.

Table 6 gives summary results in the different size classes for the waterways of Rolling and Junction Bays. Table 7 does likewise for each of the major components of our monitoring area and for their combined total. Table 8 gives the results for the surveys of the main alternative *C. porosus* habitats associated with the monitored area. The reader is asked to spend a few minutes looking down the columns in Tables 4 to 7 before proceeding. Table 9 for the Alligator Region and Adelaide River Systems has been obtained using Table 1B and presents the results in similar form to Tables 2 and 3, with the sightings grouped into important size classes.

We draw attention to two important points when considering and comparing the results shown in the Tables. The first relates to the matter of errors in size class estimation. We discussed this matter in some detail in Messel et al. (1979-1984, 1:80, 335, 389 and 18:117) and refer the reader to these. The second matter concerns the importance of comparing results for equivalent survey seasons; that is, breeding versus breeding and non-breeding versus non-breeding periods whenever possible (Messel et al. 1979-1984, 18:124-125). For example, October-November surveys should, if possible, be compared with other October-November surveys and not June-July

Table 1A. Number of *C. porosus* sighted within each size class on tidal waterways of the 330 km of control systems in the Maningrida area of northern Arnhem Land and on Ngandadauda Creek and the Glyde River draining the Arafura Swamp, during night-time spotlight surveys[1,2].

System	Date	Total	H	2-3	3-4	Numbers in size class 4-5	5-6	6-7	>7	E.O.	Kilometers surveyed	Density	95% levels	Type
BLYTH-CADELL						*MONOGRAPH 1*								
	Oct. 74	387	89	81	147	58	6	2	4	4	91.9	3.2	454- 524	1
	Nov. 75	353	50	106	81	72	23	4	2	15	94.9	3.2	462- 532	
	Sept. 76	348	82	63	104	46	14	7	6	26	92.0	2.9	403- 469	
	Nov. 76	307	61	61	103	47	10	4	2	19	92.0	2.7	371- 435	
	Apr. 77	327	72	70	108	48	10	2	4	13	92.0	2.8	386- 450	
	May 77	333	88	60	94	55	13	4	1	18	92.0	2.7	370- 432	
	June 77	365	108	36	102	69	13	10	3	24	90.5	2.8	389- 453	
	Sept. 77	386	105	45	132	47	17	4	4	32	90.5	3.1	427- 495	
	Oct. 77	360	112	68	83	47	18	8	3	21	90.5	2.7	375- 439	
	June 78	432	173	65	81	67	15	6	4	21	90.5	2.9	393- 457	
	Sept. 78	399	155	60	79	56	18	8	6	17	90.5	2.7	369- 431	
	June 79	465	123	91	93	59	31	16	26	26	94.5	3.6	524- 598	
	Oct. 80	400	119	89	71	48	22	9	4	38	92.9	3.0	427- 495	
	July 81	366	76	86	84	43	24	11	9	33	90.1	3.2	442- 510	
	Oct. 81	315	72	77	60	32	20	16	7	31	89.9	2.7	367- 430	
	June 82	408	136	42	59	49	31	22	20	49	91.9	3.0	413- 479	
	Nov. 82	347	111	43	66	46	28	15	10	28	92.5	2.6	356- 418	
	July 83	465	157	98	61	48	30	19	9	43	91.8	3.4	470- 540	
	Oct. 83	354	73	95	69	45	24	11	10	27	92.8	3.0	427- 495	
GOOMADEER						*MONOGRAPH 5*								1
	Aug. 75	46		27	7	5	4			3	45.3	1.0	61- 89	
	Sept. 76	52	18	5	8	5	1	3	3	9	45.3	0.8	44- 68	
	June 77	50	2	9	13	10	6	2	1	7	45.3	1.1	65- 83	
	July 79	90	29	14	7	14	10	6	1	9	45.3	1.4	84- 116	
	June 81c	43	6	5(3)	11(3)	8(1)	4	3	1	5	45.0	0.8	49- 73	
	Oct. 81	45	17	3	13	6	1			5	45.0	0.6	35- 47	
	June 82	61	18	5	12	5	2	4	4	11	45.3	0.9	58- 84	
	Oct. 82	54	9	7	9	11	5	4	3	6	45.3	1.0	61- 87	
	June 83	63	24	5	6	8	3	3	4	10	45.3	0.9	51- 77	
	Oct. 83	73	33	8	5	8	5	4	3	7	45.3	0.9	53- 79	
MARJARIE														3
	Aug. 75	12	1	1	2	2	1	1	2	2	20.1	0.5	11- 25	
	Aug. 76	7			3					4	20.1	0.4	7	
	July 79	18			1	7	4	1	3	2	24.1	0.7	21- 39	
	June 81	19			2	2	4	2	3	6	21.1	0.9	22- 40	

Table 1A. cont.

System	Date	Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
				2-3	3-4	4-5	5-6	6-7	>7					
MARJARIE														
	Oct. 81	17			3	4	2	1		7	22.0	0.8	20- 36	
	June 82	17	2	1	1	2	2	1	3	5	23.8	0.6	17- 33	
	Oct. 82	12				4	5	1	1	1	23.3	0.5	13- 27	
	June 83	24	4		4	4	5	2		5	24.1	0.8	24- 42	
	Oct. 83	19		1	4	1	6	3	1	3	24.1	0.8	22- 40	
WURUGOIJ														
	Aug. 75	4				3	1				16.4	0.2	4	3
	Aug. 76	1								1	16.4	0.1	1	
	July 79	9					2	2	4	1	16.4	0.5	9	
	June 81	6			1	1	1	1	1	1	16.4	0.5	6	
	Oct. 81	8			1	1	3			1	16.4	0.5	8	
	June 82	7					2		2	2	16.2	0.4	7	
	Oct. 82	8	1			2	2	1	1	3	16.4	0.4	7	
	June 83	6				1	2	1		1	16.4	0.4	6	
	Oct. 83	11		1	2	3	1	2		3	16.4	0.7	11- 25	
LIVERPOOL-TOMKINSON								MONOGRAPH 7						
	July 76	228	19	39	56	27	13	3	3	68	152.2	1.4	314- 372	1
	May 77	245	40	6	51	59	30	13	5	41	145.1	1.4	307- 365	
	Oct. 77	228	56	7	39	62	24	9	1	30	123.4	1.4	256- 308	
	Sept. 78	233	37	18	37	65	19	14	8	35	141.4	1.4	293- 349	
	Oct. 79	335	161	16	36	37	29	17	23	36	141.1	1.4	290- 346	
	July 79	515	289	11	39	43	34	29	20	50	150.0	1.5	341- 401	
	Oct. 80	295	71	51	37	32	29	12	14	49	140.6	1.6	337- 397	
	July 81	256	26	52	48	29	23	15	15	48	140.6	1.6	347- 407	
	Oct. 81	254	34	33	50	34	23	14	14	52	141.1	1.6	331- 391	
	June 82	467	193	29	64	50	37	23	17	54	141.1	1.9	416- 482	
	Oct. 82	384	144	16	48	51	25	21	17	62	141.1	1.7	363- 425	
	July 82	432	121	83	64	56	32	17	15	44	141.1	2.2	475- 466	
	Oct. 83	327	63	77	47	39	34	8	14	45	141.1	1.9	400- 466	
NUNGBULGARRI														
	Aug. 75	29		4	11	3		1		10	15.0	1.9	37- 59	1
	July 76	15	2		3	5	1	1		3	13.6	1.0	14- 28	
	June 77	14	2	2		6	1	1		2	13.6	0.9	13- 27	
	July 79	35	10		4	4	6	5	12	4	14.8	1.7	31- 51	
	June 81	27	2	4	10	4	1	1	1	6	14.8	1.7	31- 51	
	Oct. 81	25		2	12	4	2			5	14.8	1.7	31- 51	
	June 82	23		2	8	4	3	1	1	4	14.8	1.6	28- 48	
	Oct. 82	29		1	9	8	2	2	4	3	14.4	2.0	37- 59	

Table 1A. cont.

System	Date	Total		Numbers in size class								Kilometers surveyed	Density	95% levels	Type
			H	2-3	3-4	4-5	5-6	6-7	>7	E.O.				
							MONOGRAPH 9								
NUNGBULGARRI	June 83	55	34	2	6	5	5			3	14.4	1.5	25- 43	
	Oct. 83	38	15	1	5	4	6	1	1	5	14.4	1.6	28- 48	
NGANDADAUDA	Sept. 75	19	3	2	5	1	1	2	1	4	22.6	0.7	18- 34	3
	June 79	21			2	3	3	4	4	5	23.9	0.9	25- 43	
	June 83	30			2	5	7	1	2	13	23.6	1.3	38- 60	
	Oct. 83	21				5	8	4	2	2	23.6	0.9	25- 43	
GLYDE	Sept. 75	28	36	9	3	6	2	1	4	12	45.9	0.6	35- 57	1
	July 79	100	5	9	10	9	10	6	6	14	45.9	1.4	89- 121	
	July 83	118			35	16	8	6	10	29	45.9	2.5	164- 206	
	Oct. 83	91		3	22	12	11	5	11	27	45.9	2.0	130- 168	

1. The midstream distance surveyed and density of non-hatchling crocodiles sighted on each waterway is shown, as are the 95% confidence limits for the estimate of the actual number of non-hatchlings present. The TYPE classification of each waterway is given also.

2. The 1976 results for the Liverpool-Tomkinson given here differ by 20 from those in Table 9.2.1 (Monograph 1) because these animals are now included in the upstream Tomkinson (km 73.7-80.1) on Table 8.

3. Numbers in brackets give numbers of crocodiles removed by Biology researchers before survey.

Table 1B. Number of C. porosus sighted within each size class on tidal waterways of Van Diemen Gulf, during night-time spotlight surveys carried out between 1977 and 1984.

System	Date	Total	Numbers in size class							E.O.	Kilometers surveyed	Density	95% levels	Type
			H	2-3	3-4	4-5	5-6	6-7	>7					
ADELAIDE							MONOGRAPH 3							
	July 77	417	48	24	88	116	47	35	33	26	226.3	1.6	556- 644	1
	Sept. 78	381	62	24	71	90	43	33	32	26	221.0	1.4	487- 559	
	Sept. 79	374	53	8	46	75	58	47	64	23	231.6	1.4	490- 562	
	July 84	602	60	36	105	79	64	78	120	60	231.6	2.3	842- 936	
MURGENELLA							MONOGRAPH 4 (14)							
	Oct. 77	95	1	1	8	33	13	6	18	15	45.9	2.0	135- 173	1
	June 78	173	48	16	4	17	24	23	30	11	44.9	2.8	183- 227	
	Aug. 79	198	47	24	12	22	24	27	26	16	45.6	3.3	223- 273	
	July 84	236	7	17	61	28	21	31	57	14	45.6	5.0	346- 406	
EAST ALLIGATOR	Oct. 77	318	53	18	37	57	41	40	34	38	114.9	2.3	402- 468	1
	June 78	329	39	14	63	51	42	31	51	38	118.9	2.4	442- 510	
	Aug. 79	393	53	30	44	58	28	58	64	58	119.2	2.9	521- 595	
	July 84	411	22	51	72	35	24	47	60	100	119.2	3.3	598- 678	
SOUTH ALLIGATOR	Oct. 77	142		12	12	24	24	25	31	26	113.8	1.2	209- 257	1
	July 78	157	6	3	4	14	43	24	38	25	113.2	1.3	223- 273	
	Aug. 79	164	4	1	4	12	24	31	51	37	114.0	1.4	237- 287	
	July 84	279	39	15	17	18	25	38	91	36	114.0	2.1	363- 425	
WEST ALLIGATOR	Oct. 77	83	9	2	14	14	15	10	10	9	42.2	1.8	104- 138	1
	July 78	85	23	5	12	9	13	10	6	7	40.4	1.5	86- 118	
	Aug. 79	96	12	9	13	14	7	12	14	15	42.2	2.0	120- 156	
	June 84	120	17	2	33	21	18	6	12	11	42.2	2.4	149- 189	
WILDMAN	Sept. 78	118	53	16	6	8	10	9	7	9	33.5	1.9	91- 123	1
	Aug. 79	155	21	34	15	14	7	17	31	16	33.5	4.0	197- 243	
	June 84	226	26	60	46	20	23	24	13	14	33.5	6.0	300- 356	
ALLIGATOR REG. EXCL. WILDMAN	Oct. 77	638	63	21	71	128	93	81	93	88	316.8	1.8	895- 991	1
	June 78	744	116	38	83	91	122	88	125	81	317.4	2.0	980- 1080	
	Aug. 79	851	116	64	73	106	83	128	155	126	321.0	2.3	1151-1259	
	July 84	1046	85	85	183	102	88	122	220	161	321.0	3.0	1514-1638	

Table 1B. cont.

System	Date	Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
				2-3	3-4	4-5	5-6	6-7	>7					
ALLIGATOR REG.	June	862	169	54	89	99	132	97	132	90	350.9	2.0	1084-1190	1
WITH WILDMAN	Aug.	1006	137	98	88	120	90	145	186	142	354.5	2.4	1366-1484	
	July	1272	111	145	229	122	111	146	233	175	354.5	3.3	1836-1972	
SALTWATER	Aug.	29	6	1	1		4	6	9	2	14.1	2.1	37- 59	3
	July	25			4	3	3	1	6	2	14.1	1.3	22- 40	
MINIMINI	Aug.	11			1	4	3	1	2		43.8	0.3	11- 25	3
	July	9					2	3	1	3	43.8	0.2	9	
MIDDLE ARM	Aug.	6			1	1	2	1	1		28.5	0.2	6	3
	July	10				3	2	3	1	1	28.5	0.4	10- 22	
IWALG	Aug.	10				1	3	2	2	2	53.5	0.2	10- 22	3
	July	25			3	3	6	5	5	3	53.5	0.5	31- 51	
MINIMINI COMPLEX	Aug.	27			1	10	6	4	4	2	125.8	0.2	34- 54	
	July	44			4	4	12	10	7	7	125.8	0.3	59- 85	
ARM A	Aug.	5				3		1		1	26.7	0.2	5	3
	July	9					1	4	4		26.7	0.3	9	
ARM B	Aug.	3				1		1	1		15.0	0.2	3	3
	July	4				1		1	3		15.0	0.3	4	
ARM C	Aug.	7				3	1	1		2	29.3	0.2	7	3
	July	5				2	1	1		1	29.3	0.2	5	
ARM D	Aug.	9				1		3	2	3	19.8	0.5	9	3
	July	7				1	1	1	2	2	19.8	0.4	7	
ILAMARYI	Aug.	16				3	4	3	3	3	44.4	0.4	18- 34	3
	July	7				1	1	1	2	2	44.4	0.2	7	
ILAMARYI COMPLEX	Aug.	40				11	5	9	6	9	135.2	0.3	53- 79	3
	July	32				4	2	7	14	5	135.2	0.2	41- 63	
COBOURG COMP.	Aug.	67			1	21	11	13	10	11	261.0	0.3	94- 126	3
	July	76			4	8	14	17	21	12	261.0	0.3	107- 143	
COBOURG COMP. & SALTWATER	Aug.	96			2	27	15	19	19	13	275.1	0.3	137- 177	3
	July	101	6	1	8	11	17	18	27	14	275.1	0.3	136- 176	

Table 1B. cont.

System	Date		Total	H	Numbers in size class						E.O.	Kilometers surveyed	Density	95% levels	Type
					2-3	3-4	4-5	5-6	6-7	>7					
ALLIGATOR REG. +COBOURG COMP. & SALTWATER	Aug.	79	1102	137	99	90	147	105	164	205	155	629.6	1.5	1521-1645	1 & 3
	July	84	1373	117	145	237	133	128	164	260	189	629.6	2.0	1989-2131	
ADELAIDE + ALLIGATOR REG. EXCL. WILDMAN	July & Oct.	77	1055	111	45	159	244	140	116	126	114	543.1	1.7	1486-1610	1
	Sept. & June	78	1125	178	62	154	181	165	121	157	107	538.4	1.8	1491-1615	
	Sept. & Aug.	79	1225	169	72	119	181	141	175	219	149	552.6	1.9	1667-1797	
	July	84	1648	145	121	288	181	152	200	340	221	552.6	2.7	2387-2543	
ADELAIDE + ALLIGATOR REGION INCL. WILDMAN	Sept. & June	78	1243	231	78	160	189	175	130	164	116	571.9	1.8	1596-1724	1
	Sept. & Aug.	79	1380	190	106	134	195	148	192	250	165	586.1	2.0	1883-2021	
	July	84	1874	171	181	334	201	175	224	353	235	586.1	2.9	2710-2876	
ABOVE + COBOURG COMP. & SALTWATER	Sept. & Aug.	79	1476	190	107	136	222	163	211	269	178	861.2	1.5	2037-2181	1 & 3
	July	84	1975	177	181	342	212	192	242	380	249	861.2	2.1	2864-3034	

Table 2A. Blyth-Cadell Rivers System. Table for the Blyth-Cadell Rivers System showing various size class groupings[a].

Survey		Total	H	2-5 ft	≥5 ft	2-6 ft (S)	≥6ft (L)	3-6 ft (M)	S:L	M:L
26 Oct.	74	387	89	286	12	292	6	211	48.7	35.2
1 Nov.	75	353	50	263	40	289	14	183	20.6	13.1
Major flooding										
23 Sept.	76	348	82	221	45	240	26	177	9.2	6.8
4 Nov.	76	307	61	217	29	230	16	169	14.4	10.6
11 Apr.	77	327	72	230	25	242	13	172	18.6	13.2
3 May	77	333	88	215	30	231	14	171	16.5	12.2
8 June	77	365	108	215	42	232	25	196	9.3	7.8
16 Sept.	77	386	105	234	47	257	24	212	10.7	8.8
23 Oct.	77	360	112	204	44	226	22	158	10.3	7.2
10 June	78	432	173	219	40	238	21	173	11.3	8.2
12 Sept.	78	399	155	200	44	221	23	161	9.6	7.0
No flooding - driest wet on record										
10 June	79	465	123	251	91	287	55	196	5.2	3.6
4 Oct.	80	400	119	220	61	249	32	160	7.8	5.0
Heavy flooding										
9 July	81	366	76	223	67	253	37	167	6.8	4.5
19 Oct.	81	315	72	179	64	204	39	127	5.2	3.3
Dry wet - minor flooding only										
25 June	82	408	136	166	106	205	67	163	3.1	2.4
6 Nov.	82	347	111	164	72	197	39	154	5.1	3.9
Dry wet - minor flooding only										
15 July	83	465	157	221	87	258	50	160	5.2	3.2
26 Oct.	83	354	73	217	64	246	35	151	7.0	4.3

[a] The 2-3', 3-4' and 4-5 size classes are grouped together (2-5') and the size classes above those in another group (≥5'). We have also grouped the crocodiles sighted into small (2-6'), medium (3-6') and large (≥6'). Also shown are the ratios small/large and medium/large. This Table was obtained by using the data given in Table 1. See caption to Table 3 for division of the EO crocodiles among the various size classes.

Table 2B Liverpool-Tomkinson Rivers System. Equivalent Table for the overall Liverpool-Tomkinson Rivers System[a].

Survey		Total	H	2-5 ft	≥5 ft	2-6 ft (S)	≥6 ft (L)	3-6 ft (M)	S:L	M:L
Major flooding										
18 July	76	228	19	144	65	169	40	130	4.2	3.3
25 May	77	245	40	129	76	166	39	160	4.3	4.1
27 Oct.	77	228	56	118	54	147	25	140	5.9	5.6
27 Sept.	78	233	37	131	65	156	40	138	3.9	3.5
No flooding - driest wet on record										
16 July	79	515	289	109	117	152	74	141	2.1	1.9
19 Oct.	79	355	161	101	93	136	58	120	2.3	2.1
15 Oct.	80	295	71	136	88	173	51	122	3.4	2.4
Heavy flooding										
2 July	81	256	26	145	85	176	54	124	3.3	2.3
5 Oct.	81	254	34	134	86	166	54	133	3.1	2.5
Dry wet - minor flooding only										
12 June	82	467	193	161	113	207	67	178	3.1	2.7
16 Oct.	82	384	144	135	105	171	69	155	2.5	2.2
Dry wet - minor flooding only										
1 July	83	432	121	217	94	257	54	174	4.8	3.2
13 Oct.	83	327	63	177	87	219	45	142	4.9	3.2

[a] Note that the 1976 survey shows 68 (EO) crocodiles sighted and 34 of these were taken to be large. This is probably too high a figure for the large animals. An intensive recapture programme was carried out in 1975 thus making many more animals more wary then normal. Most of the animals involved in the recapture programme were small. It is thus likely that the true ratios for 1976 are somewhat higher than those shown.

Table 3A. Summary Table showing for each suvey of the overall Blyth-Cadell Rivers System the number of crocodiles in the size classes indicated[a].

Survey Date		Total	H	$\geq$2 ft	$\geq$3 ft	$\geq$4 ft	$\geq$5 ft	$\geq$6 ft	$\geq$7 ft	Kilometers Surveyed	Density
26 Oct.	74	387	89	298	217	70	12	6	4	91.9	3.24
1 Nov.	75	353	50	303	197	114	40	14	7	94.9	3.19
Major flooding											
23 Sept.	76	348	82	266	203	95	45	26	15	92.0	2.89
4 Nov.	76	307	61	246	185	79	29	16	6	92.0	2.67
11 Apr.	77	327	72	255	185	75	25	13	9	92.0	2.77
3 May	77	333	88	245	185	88	30	14	7	92.0	2.66
8 June	77	365	108	257	221	115	42	25	11	90.5	2.84
16 Sept.	77	386	105	281	236	99	47	24	15	90.5	3.10
23 Oct.	77	360	112	248	180	94	44	22	10	90.5	2.74
10 June	78	432	173	259	194	110	40	21	11	90.5	2.86
12 Sept.	78	399	155	244	184	103	44	23	12	90.5	2.70
No flooding - driest wet on record											
10 June	79	465	123	342	251	154	91	55	35	94.5	3.62
4 Oct.	80	400	119	281	192	115	61	32	17	92.9	3.02
Heavy flooding											
9 July	81	366	76	290	204	115	67	37	20	90.1	3.22
19 Oct.	81	315	72	243	166	101	64	39	18	89.2	2.70
Dry wet - minor flooding only											
25 June	82	408	136	272	230	163	106	67	37	91.9	2.96
6 Nov.	82	347	111	236	193	123	72	39	19	92.5	2.55
Dry wet - minor flooding only											
15 July	83	465	157	308	210	142	87	50	24	91.8	3.36
26 Oct.	83	354	73	281	186	113	64	35	19	92.8	3.03

[a] The EO (eye reflection only was seen) classes have been added together in each survey and 50% of these have been distributed equally among the 3-4', 4-5' and 5-6' size classes; the remaining 50% have been distributed to the $\geq$6 size classes with 1/3 being allocated to the 6-7' size class and 2/3 to size class $\geq$7. This weights the distribution heavily in favor of large crocodiles, which are known to normally be the most wary. When the EO is an odd number, the bias is also given to the large size classes. For 1974, all EO crocodiles were put in the $\geq$7 size class.

Table 3B. Equivalent Table for Liverpool-Tomkinson System.

Survey Date		Total	H	≥2 ft	≥3 ft	≥4 ft	≥5 ft	≥6 ft	≥7 ft	Kilometres Surveyed	Density
						Major Flooding					
18 July	76	228	19	209	170	103	65	40	26	152.5	1.37
25 May	77	245	40	205	199	142	76	39	19	145.1	1.41
27 Oct.	77	228	56	172	165	121	54	25	11	123.4	1.39
27 Sept.	78	233	37	196	178	136	65	40	20	141.4	1.39
					No flooding - driest wet on record						
16 July	79	515	289	226	215	168	117	74	37	150.0	1.51
19 Oct.	79	355	161	194	178	136	93	58	35	141.1	1.38
15 Oct.	80	295	71	224	173	128	88	51	31	140.6	1.59
						Heavy flooding					
2 July	81	256	26	230	178	122	85	54	31	140.6	1.64
5 Oct.	81	254	34	220	187	129	86	54	32	141.1	1.56
					Dry wet - minor flooding only						
12 June	82	467	193	274	245	172	113	67	35	141.1	1.94
16 Oct.	82	384	144	240	224	166	105	69	38	141.1	1.70
					Dry wet - minor flooding only						
1 July	83	432	121	311	228	157	94	54	30	141.1	2.20
13 Oct.	83	327	63	264	187	133	87	45	29	141.1	1.87

Table 4. Sightings on the three major components of the Blyth-Cadell Rivers System[a].

Survey Date	Blyth Mainstream				Blyth Sidecreeks				Cadell				Totals		
	H	S	M	L	H	S	M	L	H	S	M	L	S	M	L
26 Oct. 74	41	207	151	6	1	3	3	0	47	82	57	0	292	211	6
1 Nov. 75	41	177	120	11	3	11	7	2	6	101	56	1	289	183	14
Major flooding															
23 Sept. 76	48	159	108	14	2	16	14	5	32	65	55	7	240	177	26
4 Nov. 76	40	142	108	10	3	16	13	1	18	72	48	5	230	169	16
11 Apr. 77	65	142	104	6	3	17	14	3	4	83	54	4	242	172	13
3 May 77	74	144	111	10	0	15	15	3	14	72	45	1	231	171	14
8 June 77	88	129	107	19	2	23	20	4	18	80	69	2	232	196	25
16 Sept. 77	75	164	139	19	2	18	15	2	28	75	58	3	257	212	24
23 Oct. 77	76	136	94	14	3	15	11	2	33	75	53	6	226	158	22
10 June 78	136	148	99	14	1	21	18	4	36	69	56	3	238	173	21
4 Oct. 80	86	171	106	40	1	15	14	9	37	101	76	6	287	196	55
Heavy flooding															
9 July 81	48	144	97	27	2	25	22	3	26	84	48	7	253	167	37
19 Oct. 81	37	127	75	28	3	13	12	2	32	64	40	9	204	127	39
Dry wet - minor flooding only															
25 June 82	84	118	94	41	1	14	13	6	51	73	56	20[b]	205	163	67[b]
6 Nov. 82	55	116	93	26[b]	0	9	9	3	56	71	51	11[b]	197	154	39
Dry wet - minor flooding															
15 July 83	146	127	84	35[b]	2	10	10	2	9	121	66	13	258	160	50[b]
26 Oct. 83	70	140	84	23	0	10	10	2[b]	3	96	57	10	246	151	35[b]

a The table shows the number of *C. porosus* sighted within the hatchling, small 2-6', medium 3-6' and large ≥ 6 size classes on the three major components of the Blyth-Cadell Rivers System: Blyth mainstream, Blyth sidecreeks and Cadell River; 49.8, 12.5 and 29.7 km respectively.

b Bias to large.

Table 5. Sightings on the three major components of the Liverpool-Tomkinson Rivers System[a]

Survey Date	Liverpool Mainstream				Liverpool Sidecreeks				Tomkinson				Totals			
	H	S	M	L	H	S	M	L	H	S	M	L	H	S	M	L
	Major flooding															
18 July 76	11	64	51	14	4	27	22	7[b]	4	77	56	20[b]	19	169	130	40[b]
25 May 77	13	67	64	12	4	28	27	7[b]	23	71	69	20	40	166	160	39[b]
27 Oct. 77	23	77	73	13[b]	5	20	20	4*	28	49	46	9[b]	56	147	140	25[b]
27 Sept. 78	13	69	63	21	7	20	17	5	17	67	58	14[b]	37	156	138	40[b]
	No flooding - driest wet on record															
16 July 79	24	63	59	29	5	24	20	21	260	65	62	24	289	152	141	74
19 Oct. 79	17	63	51	32	2	21	20	5	142	52	49	21	161	136	120	58
15 Oct. 80	28	61	51	25	17	25	23	7[b]	26	87	48	19	71	173	122	51[b]
	Heavy flooding															
2 July 81	8	75	47	23	1	23	18	8[b]	17	77	58	24[b]	26	176	124	54
5 Oct. 81	2	74	54	19	2	26	22	9[b]	30	65	57	27[b]	34	166	133	54
	Dry wet - minor flooding only															
12 June 82	7	66	59	30	8	36	34	10	178	105	85	27	193	207	178	67
16 Oct. 82	6	82	78	27[b]	3	32	28	18	135	56	48	25[b]	144	171	155	69
	Dry wet - minor flooding															
1 July 83	27	74	67	20	3	37	35	11[b]	91	145	71	24[b]	121	257	174	54
13 Oct. 83	21	70	64	19	2	28	25	9	40	121	53	17[b]	63	219	142	45[b]

a Number of *C. porosus* sighted within the hatchling, small 2-6', medium 3-6' and large ≥6 size classes on the three major components of the Liverpool-Tomkinson Rivers System: Liverpool mainstream, Liverpool sidecreeks and Tomkinson (normally 57.0, 27.4 and 56.7 km respectively, but distances can vary from year to year - see page 16, Monograph 7).
Note specially that during the 1977 and 1978 Tomkinson surveys, the river was surveyed to km 70 only and that a number of small and large crocodiles were thus not counted. Probably not more than 3 or 4 of each were thus omitted. Normally the Tomkinson is surveyed to km 73.7. Also see Table 8.
b Bias to large.

Table 6. Sighting on the waterways of Junction and Rolling Bays[a]

Survey Date	Goomadeer			Wurugoij			Majarie			Nungbulgarri			Totals					
	H	S	L	H	S	L	H	S	L	L	H	S	H	S	M	L	S/L	M/L
Aug. 75	–	44	2	–	4	–	1	7	–	4	–	23[b]	1	78[b]	46	12	6.5	3.8
Major flooding																		
July–Sept. 76	18	23	11	No survey	No survey		–	5	2	3	2	1–	2	38	33	17	2.2	1.9
June 77	2	41	7				10	2	4	9	51	40					5.7[c]	4.4[c]
No flooding – driest wet on record																		
July 79	29	49	12	–	2	7	–	13	5	9	10	16	39	80	66	33	2.4	2.0
Heavy flooding																		
June 81	6	30(7)[d]	7	–	3	3	–	11	8	4	2	21	8	65(7)[d]	56(4)[d]	22	3.0	2.5
Oct. 81	17	25	3	–	7	1	–	12	5	3	–	22	17	66	60	12	5.5	5.0
Dry wet – minor flooding only																		
June 82	18	29	14	–	3	4	2	8	7	4	–	19	20	59	51	29	2.0	1.8
Oct. 82	9	35	10	1	4	3	–	9	3	8	–	21	10	69	61	24	2.9	2.5
Dry wet – minor flooding only																		
June 83	24	27	12	–	4	2	4	15	5	2	34	19	62	65	57	21	3.1	2.7
Oct. 83	33	29	11	–	7	4	–	13	6	5	15	18	48	67	57	26	2.6	2.2

[a] The table shows the number of C. porosus sighted within the hatchling (H), small (S) and large (L) size classes on the tidal waterways of Junction and Rolling Bays, which are within the Maningrida monitoring area. Also shown is the number of medium crocodiles and the ratios of small to large and medium to large for the overall systems.

[b] This relatively high number may have resulted from animals leaving the Liverpool System after our intensive catching effort on it during the period of 1973-1975. See page 75, Monograph 7.

[c] Wurugoij and Marjarie Creeks were not surveyed resulting in the omission of a few small and large animals. Hence the value of S/L and M/L are probably slightly TOO HIGH.

[d] Numbers in brackets give number of crocodiles removed by Biology researchers before survey.

Table 7. Sightings within the Maningrida monitoring area[a].

Survey Date	Blyth-Cadell System				Liverpool-Tomkinson System				Rolling & Junction Bays				(Total)				>3'	S/L	M/L
	H	S	M	L	H	S	M	L	H	S	M	L	H	S	M	L			
Aug./Nov. 75	50	289	183	14	Data unusable				Data unusable				46	12		78			
Major flooding																			
July/Sept. 76	82	240	177	26	19	169	130	40[c]	20	38	33	17	121	447	340	83	423[d]	5.4	4.1[d]
May/June 77	108	232	196	25	40	166	160	39	4	51	40	9	152	449	396	73	469[d]	6.1[d]	5.4[d]
October 77	112	226	158	22	56	147	140	25	No surveys				168	373	298	47	345	7.9[e]	6.3[e]
September 78	155	221	161	23	37	156	138	40	No surveys				192	377	299	63	362	6.0[e]	4.7[e]
No flooding - driest wet on record																			
June/July 79	123	287	196	55	289	152	141	74	39	80	66	33	451	519	403	162	565	3.2[e]	2.5
October 80	119	249	160	32	71	173	122	51	No surveys				190	422	282	83	365	5.1[e]	3.4[e]
Heavy flooding																			
June/July 81	76	253	167	37	26	176	124	54	8	67(7)[b]	56(4)[b]	22	110	494(7)[b]	347(4)[b]	113	460	4.4	3.1
October 81	72	204	127	39	34	166	132	54	17	66	60	12	123	436	320	105	425	4.2	3.0
Dry wet - minor flooding																			
June/July 82	136	205	163	67	193	207	178	67	20	59	51	29	349	471	392	163	555	2.9	2.4
Oct./Nov. 82	111	197	154	39	144	171	155	69	10	61	24	24	265	429	333	132	465	3.3	2.5
Dry wet - minor flooding																			
June/July 83	157	258	160	50	121	257	174	54	62	65	57	21	340	580	391	125	516	4.6	3.1
October 83	73	246	151	35	63	219	142	45	48	67	57	26	184	532	350	106	456	5.0	3.3

[a] The table shows the number of *C. porosus* sighted within the hatchling, small (2-3'), medium (3-6') and large (>6') size classes on the major component tidal systems within the Maningrida monitoring area. Also shown is the ratio of small to large and medium to large crocodiles and the total number of medium plus large animals (that is animals >3).

[b] Numbers in brackets give numbers of crocodiles removed by Biology researchers before survey.

[c] See caption to Table 2B for the Liverpool-Tomkinson.

[d] See Table 6, footnote c.

[e] Because the four waterways of Rolling and Junction Bays were not surveyed in October 1977, September 1978 and October 1980 the totals for those surveys are TOO LOW. Inspection of the results for immediately preceding and succeeding surveys indicates that the totals for the three missing cases are too low by a MAXIMUM of 40(H), 80(S), 66(M), 33(L) and 99(>3'). The ratios shown for these surveys are thus probably TOO HIGH.

Table 8. Sightings on alternative habitats[a].

Habitat	Kilometers Surveyed	Oct.-Nov 1981			July-July 1982			Oct.-Nov. 1982			June-July 1983			October 1983		
		H	S	L	H	S	L	H	S	L	H	S	L	H	S	L
Liverpool River	6.4	No survey			No survey			5	3	—	5	1	—	1	4	—
Maragulidban Ck.	4.9	No survey			—	1	—	1	1	—	1	—	—	—	1	—
Tomkinson River km 73.7 - 81.3	7.6	11 (July 1976 to km 80.1)	9	—	18	14	—	11	13	2	18_1	9	—	8	9	—
Tom's Creek	8.9	1 (July 1979)	2	—	No survey			—	—	5	1	—	2_1	2	—	—
Crab Creek	3.0	—	2	—	No survey			1	—	—	2	—	1	1	—	—
Anamayirra Creek	7.3	No survey			7	—	9	5	—	10	6	—	5	3	—	—
Beach Creek	2.2	No survey			3	—	3	—	—	6	1	—	2	—	—	—
Blyth R. + Billabong km 49.8 - 64.6	13.2	1	2_2	—	1	1	3	5	7_2	7	1	4_2	1	—	8_4	4
Cadell Gardens Billabong	2.0	1 (Oct. 1980)	3	—	No survey			No survey			1	—	2	1	—	—
Cadell Big	4.0	No survey			3	—	2	No survey			3	—	—	3	—	—

[a] The table shows the number of *C. porosus* sighted within the hatchling, small and large size classes on the main alternative habitats of the Blyth-Cadell and Liverpool-Tomkinson Rivers Systems, such as various fresh and saltwater complexes and the extreme upstream sections of the Systems.

The results for these 59.3 km of waterways are not included in Tables 1 to 7. The first seven habitats listed appear to provide alternative habitat largely for animals from the Liverpool-Tomkinson and Rolling and Junction Bay Systems. Subscripts show the number of 2-3' animals included.

Table 9. Sightings on waterways of Van Dieman Gulf[a].

Survey		Totals	Hatchlings	(2-3')	(3-6')	Large (≥6)	3-6' / Large
ADELAIDE							
July	77	417	48	24	264	81	3.26
Sept.	78	381	62	24	217	78	2.78
Sept.	79	374	53	8	190	123	1.54
July	84	602	60	36	278	228	1.22
MURGENELLA							
Oct.	77	95	1	1	61	32	1.91
June	78	173	48	16	50	59	0.85
Aug.	79	198	47	24	66	61	1.08
July	84	236	7	17	117	95	1.23
EAST ALLIGATOR							
Oct.	77	318	53	18	154	93	1.66
June	78	329	39	14	175	101	1.73
Aug.	79	393	53	30	159	151	1.05
July	84	411	22	51	181	157	1.15
SOUTH ALLIGATOR							
Oct.	77	142	--	--	73	69	1.06
June	78	157	6	3	73	75	0.97
Aug.	79	164	4	1	58	101	0.57
July	84	279	39	15	78	147	0.53
WEST ALLIGATOR							
Oct.	77	83	9	2	47	25	1.88
June	78	85	23	5	37	20	1.85
Aug.	79	96	12	9	41	34	1.21
June	84	120	17	2	77	24	3.21
WILDMAN							
Sept.	78	118	53	16	28	21	1.33
Aug.	79	155	21	34	44	56	0.79
June	84	226	26	60	96	44	2.18
ALLIGATOR REGION EXCL. WILDMAN							
Oct.	77	638	63	21	336	218	1.54
June	78	744	116	38	336	254	1.32
Aug.	79	851	116	64	325	346	0.94
July	84	1046	85	85	453	423	1.07
ALLIGATOR REGION WITH WILDMAN							
June	78	862	169	54	365	274	1.33
Aug.	79	1006	137	98	369	402	0.92
July	84	1272	111	145	549	467	1.18

Table 9. continued.

Survey		Totals	Hatchlings	(2-3')	(3-6')	Large (≥6)	3-6' / Large
SALWATER							
Aug.	79	29	--	1	12	16	0.75
July	84	25	6	--	11	8	1.38
MINIMINI							
Aug.	79	11	--	--	8	3	2.67
July	84	9	--	--	6	3	2.00
MIDDLE ARM							
Aug.	79	6	--	--	5	1	5.00
July	84	10	--	--	6	4	1.50
IWALG							
Aug.	79	10	--	--	5	5	1.00
July	84	25	--	--	13	12	1.08
MINIMINI COMPLEX							
Aug.	79	27	--	--	18	9	2.00
July	84	44	--	--	23	21	1.10
ARM A							
Aug.	79	5	--	--	3	2	1.50
July	84	9	--	--	1	8	0.13
ARM B							
Aug.	79	3	--	--	1	2	0.50
July	84	4	--	--	--	4	0.00
ARM C							
Aug.	79	7	--	--	5	2	2.50
July	84	5	--	--	2	3	0.67
ARM D							
Aug.	79	9	--	--	2	7	0.29
July	84	7	--	--	2	5	0.40
ILAMARYI							
Aug.	79	16	--	--	8	8	1.00
July	84	7	--	--	3	4	0.75
ILAMARYI COMPLEX							
Aug.	79	40	--	--	20	20	1.00
July	84	32	--	--	8	24	0.33
COBOURG COMPLEX							
Aug.	79	67	--	--	38	29	1.31
July	84	76	--	--	31	45	0.69

Table 9. continued.

Survey		Totals	Hatchlings	(2-3')	(3-6')	Large (≥6)	$\frac{3\text{-}6'}{\text{Large}}$
COBOURG COMPLEX & SALTWATER							
Aug.	79	96	--	1	50	45	1.11
July	84	101	6	--	43	52	0.83
ALLIGATOR REGION + COBOURG COMPLEX & SALTWATER							
Aug.	79	1102	137	99	419	447	0.94
July	84	1373	117	145	592	519	1.14
ADELAIDE + ALLIGATOR REGION EXCL. WILDMAN							
July & Oct.	77	1055	111	45	600	299	2.01
Sept. & June	78	1125	178	62	553	332	1.67
Sept. & Aug.	79	1225	169	72	515	469	1.10
July	84	1648	145	121	731	651	1.12
ADELAIDE + ALLIGATOR REGION WITH WILDMAN							
Sept. & June	78	1243	231	78	582	352	1.65
Sept. & Aug.	79	1380	190	106	559	525	1.06
July	84	1874	171	181	827	695	1.19
ABOVE + COBOURG COMPLEX & SALTWATER							
Sept. & Aug.	79	1476	190	107	610	569	1.07
July	84	1975	177	181	870	747	1.16

[a] This Table was prepared using the results given in Table 1B and groups the crocodiles sighted into the important size classes shown.

Table 10. Sightings in 1979 and 1983 for combined systems[a].

Survey	Total	H	Size Class Numbers						km EO	Surveyed	95%	Density Levels	TYPE
			2-3	3-4	4-5	5-6	6-7	>7					
June & July 1979	1253	487	125	156	139	100	69	66	111	414.9	1.8	1201-1312	1 & 3
July & July 1988	1199	345	198	180	145	92	49	40	150	411.5	2.1	1342-1459	

Survey	Totals	H	2-3	Large 3-6	$\frac{3\text{-}6}{\geq 6}$	Large
June & July 1979	1253	487	125	450	191	2.36
June & July 1983	1199	345	198	492	164	3.00

[a] The table shows combined results for the Blyth-Cadell and Liverpool-Tomkinson Rivers Systems, Goomadeer and Glyde Rivers, and Nungbulgarri, Majarie, Wurugoij and ngandadauda Creeks (obtained using Table 1A). The results are given first in the form of Table 1 and then in the form of Table 9 to facilitate comparisons. Note that the 1983 survey was made after the 'dry wet' of 1982-1983 and hence animals were again concentrated into the tidal waterways, but not to the same degree as in 1979 when surveys were carried out after the 'driest wet' on record.

ones. In the case of the 1984 June-July surveys of the tidal waterways in the Alligator Region, results can be most meaningfully compared with those for the June-July 1978 and August 1979 surveys rather than the October 1977 one. However, even in the case of the 1979 results, considerable caution must be used, for the 1978-1979 wet season was the driest on record and many of the animals that would have normally been in the associated freshwater complexes at the time of the survey were forced back into the tidal waterways (see Messel et al. 1979-1984:1, 4, 14, and specially 18 where this matter is discussed in detail). In the case of Murgenella Creek, the concentration appears to have taken place in 1978 (Messel et al. 1979-1984, 4:18 and 14:76).

A MODEL FOR THE DYNAMICS OF *C. porosus* POPULATIONS

As stated previously, the model which we have built up and have been refining (specially see Messel et al. 1979-1984[1 and 18]) as more data are obtained not only enables us to account in a consistent fashion for the vast store of field observations and results we have accumulated for some 100 tidal waterways in northern Australia, but also enables us to predict successfully results to be expected on future individual surveys. The model runs as follows:

1. The tidal waterways of northern Australia have been classified according to their salinity signatures into TYPE 1, TYPE 2, and TYPE 3 systems shown in Fig. 7 (see our chapter on ecology of *C. porosus* for more detail on this). TYPE 1 systems are the main breeding ones and non-TYPE 1 systems are usually poor or non-breeding systems. It is the TYPE 1 systems and the freshwater billabongs and semipermanent and permanent freshwater swamps associated with them which account for the major recruitment of *C. porosus*; the other systems contribute to a lesser degree and they must depend largely upon TYPE 1 systems and their associated freshwater complexes for the provision of their crocodiles. Non-TYPE 1 systems also sometimes have freshwater complexes associated with them but these are normally quite minor.

2. As indicated in Fig. 7, our results show that in TYPE 1 systems some 27% of the crocodiles sighted are hatchlings (of which some 50% are normally lost between June of one year and June of the next, Messel et al. 1979-1986, 1:394), whereas in TYPE 2-3 systems this figure falls to 14% and in TYPE 3 systems down to 4%, showing a much decreased hatchling recruitment in non-TYPE 1 systems. In TYPE 3 systems the percentage of crocodiles in the hatchling, 2-3', and 3-4' size classes combined is some 11% whereas in TYPE 1 systems it is at least 52%. On the other hand the percentage of crocodiles in the $\geq$4-5' size classes is some 39% in TYPE 1 systems and 73% on TYPE 3 systems. Some 79% of the non-hatchling crocodiles are sighted on TYPE 1 waterways and 21% on non-TYPE 1 waterways (Messel et al. 1979-1986, 1:419).

3. The relatively few large, and more frequent small freshwater billabongs and semipermanent and permanent freshwater swamps associated with tidal waterways are known to contain *C. porosus* but have not been inventoried systematically, except in a few cases. The accurate extent of their non-hatchling *C. porosus* populations is unknown. Based upon the fact that the number of large freshwater swamp areas, with substantial perennial water (normally bordering old river channels), in northern Australia is very limited--perhaps 400 km^2 maximum--and upon limited observations, we estimated that in 1979 the non-hatchling *C. porosus* population was less than 20% of the non-hatchling population sighted in tidal systems. We now believe that the 20% figure was an overestimate for 1979--an unusual year associated with one of the "driest wet" seasons on record.

4. It appears that the populating of non-TYPE 1 systems (hypersaline or partially hypersaline coastal and non-coastal waterways) results mostly from the exclusion of a large fraction of the sub-adult crocodiles from TYPE 1 systems and any freshwater complexes associated with them. Adult
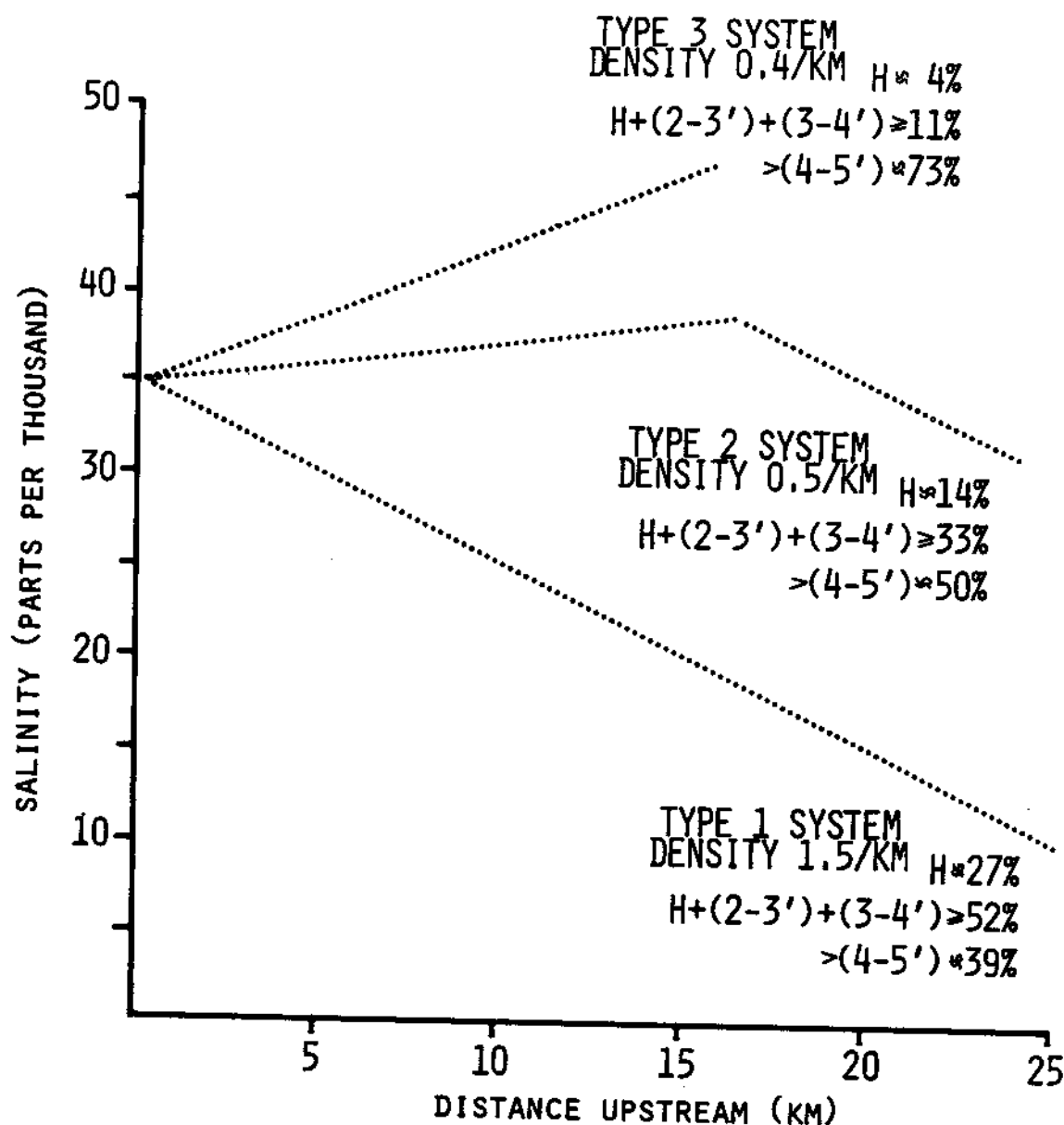
THREE TYPICAL SALINITY PROFILES IN THE DRY SEASON

Figure 7. Typical dry season salinity profiles for the three types of tidal river systems occurring in the model's classification scheme. In a TYPE 1 system the salinity decreases steadily as one progresses upstream from that of seawater measured at the mouth of the waterway (=35o/oo). In contrast, the salinity in a TYPE 3 system increases steadily as one progresses upstream. TYPE 2 systems fall somewhere between TYPE 1 and TYPE 3 systems and tend to show hypersaline tendencies as the dry season progresses. As shown above, the non-hatchling density and size structure of the crocodiles sighted in the three kinds of systems differ strikingly.

crocodiles appear generally to tolerate hatchlings, 2- 3', and sometimes even 3-4' sized crocodiles in their vicinity (hut not always--they sometimes eat them, Messel et al. 1979-1986, 14:43, or kill them, [1]:334), but not larger crocodiles. Thus once a crocodile reaches the 3-4' and 4-5' size classes, it is likely to be challenged increasingly not only by crocodiles near or in its own size class (Messel et al. 1979-1986, 1:454-458) but by crocodiles in the larger size classes and to be excluded from the area it was able to occupy when it was smaller. A very dynamic situation prevails with both adults and sub-adults being forced to move between various components of a system and between systems. Crocodile interactions or aggressiveness between crocodiles in all size classes increases around October--during the breeding season (Messel et al. 1979-1986, 1:445 and 18:109) and exclusions, if any, normally occur around this period. A substantial fraction (-80%) of the sub-adults, mostly in the 3-6' size classes but also including immature larger crocodiles, are eventually excluded from the river proper or are predated upon by larger crocodiles.

5. Of those crocodiles that have been excluded, some may take refuge in freshwater swamp areas and billabongs associated with the waterway from which they were excluded or in the waterways' non-TYPE 1 creeks if it has any. Others may travel along the coast until by chance they find a non-TYPE 1 or another TYPE 1 waterway, however in this latter case they may again be excluded from it; others may go out to sea and possibly perish, perhaps because of lack of food, as they are largely shallow water on edge feeders, or they may be taken by sharks. Those finding non-TYPE 1 systems, or associated freshwater complexes frequent these areas, which act as rearing stockyards, for varying periods, until they reach sexual maturity, at which time they endeavor to return to a TYPE 1 breeding system. Since a large fraction of the crocodiles sighted in non-TYPE 1 systems must be derived from TYPE 1 systems and their associated freshwater complexes, they are, as seen in (2) above, predominantly sub-adults in the $\geq 3'$ size classes or just mature adults (Messel et al. 1979-1986, 1:431). Both sub-adults and just mature adults might attempt to return and be forced out of the system many times before finally being successful in establishing a territory in a TYPE 1 system or in its associated freshwater complex. Crocodiles may have a homing instinct (this important point requires further study) and even though a fraction of crocodiles may finally return to and remain in a TYPE 1 system or in its associated freshwater complex, the overall sub-adult numbers missing-- presumed dead--remain high and appear to be at least 60-70%.

6. Normally, the freshwater complexes (swamps and/or billabongs) associated with tidal systems, are found at the terminal sections of small and large creeks running into the main waterway, or at the terminal sections of the mainstream(s). Though this alternative habitat is usually very limited in extent, sporadic (and sometimes extensive yearly) nesting does take place on it. There are, however, several fairly extensive freshwater complexes associated with TYPE 1 tidal systems and these are important as they may act both as rearing stockyards and as breeding systems, just as the TYPE 1 waterway does itself. Examples of these are the Glyde River with the Arafura Swamp (Messel et al. 1979-1986, 9), the Alligator Region Rivers with their wetlands (Messel et al. 1979-1986, 4, 14), and the Daly, Finniss, Reynolds, and Moyle rivers with their wetlands (Messel et al. 1979-1986, 2). Not only can the loss factor, which appears to occur during the exclusion stage, be expected to be lower for movements into and out of swamp areas associated with a TYPE 1 waterway than for movement into and out of coastal non-TYPE 1 systems, but the loss of nests due to flooding can also be expected to be less. We have observed nests made of floating grass cane mats in the Daly River Aboriginal Reserve area. Thus recovery of the C. porosus population on TYPE 1 tidal waterways, with substantial associated freshwater complexes, can be expected to be faster than on other systems (Messel et al. 1979-1986, 1:445, 14:98 and also see important results for the 1984 resurvey of Alligator Region and Adelaide River systems appearing in 19 and discussed here later).

7. Because of the -80% exclusion and at least 60-70% losses of sub-adult crocodiles as they proceed toward sexual maturity, there appears to have been no significant sustained increase in the

non-hatchling *C. porosus* population on the some 500 km of tidal waterways monitored in the Maningrida area of northern Australia since the commencement of our systematic surveys in 1974, a period of ten years (Messel et al. 1979-1986, 18). With the exception of the Glyde River, these waterways have only minor freshwater complexes associated with them.

8. Though there appears to have been no sustained significant increase in the number of non-hatchling crocodiles sighted on the tidal waterways of the Maningrida area since our surveys started in 1974, the size structure of the animals sighted appears to have been changing slowly. Notwithstanding substantial fluctuations, the ratios of small (2-6') to large ($\geq$6'), and 3-6' to large animals was decreasing on the Blyth-Cadell, may have been decreasing on the Liverpool-Tomkinson and was decreasing overall on the tidal waterways of the Maningrida monitoring area. Thus there was some indication of the commencement of a slow recovery phase.

9. For the 861 km of tidal waterways of the Alligator Region, with their substantial freshwater complexes, and the Adelaide River System, there was strong evidence, as of July 1984, that an important and sustained recovery was underway (as predicted in 6 above).

10. Though there are wide fluctuations, specially after "dry wet" seasons when the animals are concentrated into the tidal waterways, it appears that as the number of large crocodiles in a tidal waterway increases, there is a tendency for the number of sub-adults in the 3-6' size classes to decrease or only increase marginally. Thus the total number of 3-6' and large animals sighted appears generally to be holding steady or only increasing slowly. This density dependent behavior has an important bearing on the rate of population growth and on the size structure of the population.

11. When a steady state is reached in a "recovered" population, the ratio of 3-6' to large animals might be considerably less than one.

12. An important and remarkable fact becomes evident if one excludes the 3-4' size class and focuses on the 4-5' and 5-6' size classes only. Regardless of how large the recruitment may be, the number of animals sighted in the 4- 5' and 5-6' size classes seems to remain essentially constant or only increases slowly. Thus a major bottleneck occurs for these size classes. It is as if there are a definite number of slots for these animals on a given river system and that the number of these slots only increases slowly--if at all (note specially the results for the Blyth-Cadell and Liverpool-Tomkinson waterways in Messel et al. 1979-1986, 1, 18 and the 1984 results for the Alligator Region and Adelaide River systems appearing in 19). The crocodiles themselves appear to be primarily responsible for the very heavy losses of =70 percent that occur in the process of trying to secure these slots or to increase them in number.

13. If one considers a group of 100 of the sub-adult crocodiles in a TYPE 1 tidal system without a substantial freshwater complex associated with it, one can expect some 80 to be excluded from it, at least 60-70 to end up missing--presumed dead--fewer than 15-20 to successfully establish territories on the system without having to leave it, and the remainder might eventually also return and establish a territory, specially after becoming sexually mature. The very nature of this matter is such as to preclude precise figures and they must be looked upon as broad estimates only, however detailed study of our results (Messel et al. 1979-1986, 18) now indicates that the missing--presumed dead figure is likely to be in excess of 70. For systems with substantial freshwater complexes associated with them, this figure is likely to be considerably less.

14. When there is an exclusion of sub-adult animals, mostly 3-6' in size but also including immature larger animals, this takes place mainly in the breeding season, normally commencing around September-October and apparently lasting throughout the wet season. Any influx of

animals, in the 3-6' and/or large size classes, appears to occur mainly in the early dry season and to be completed in the June-early September period, but in some years may be earlier.

15. After a single "dry wet" season there is a substantial influx of large and sometimes 3-6' animals, forced out of freshwater complexes, into the tidal waterways and these are sighted during June-July surveys. Surveys made in October-November of the same year, usually reveal a substantial decrease in the number of 3-6' and/or large animals sighted; however, the number of large animals sighted sometimes remains higher than previously seen and hence a number of the new large animals do not return from whence they came. These animals appear successful in establishing a territory on the waterway, and it could be the waterway from which they had originally been excluded. The "dry wet" variation in the number of animals sighted appears to be superimposed upon the variations normally found during surveys following usual wet seasons--which generally result in extensive flooding on the upstream sections of the tidal waterways. Hatchling recruitment on the tidal waterways is generally greatly enhanced during "dry wet" seasons but appears to be greatly reduced in major swamp habitat. The reverse appears to be true during normal or heavy wet seasons.

DISCUSSION

The Monitored Area

The results of our surveys in our monitored area centered on Maningrida have been essentially summarized in points 9 to 15 of our model and are discussed in detail in Messel et al. (1979-1986, 18).

In Fig. 8 we have plotted, using Table 8, the number of 3-6', large and their sum, 3-6' plus large, or $\geq 3'$ animals sighted on surveys over the past 8 years of the Liverpool-Tomkinson, Blyth-Cadell, and the 4 waterways of Rolling and Junction Bays. The waterways of Rolling and Junction Bays would not be surveyed every time the Blyth-Cadell and Liverpool-Tomkinson were, thus resulting in a number of incomplete totals. These cases are referred to in the caption of Table 7, and certain corrections are suggested. The number of large crocodiles sighted on the overall Systems during the surveys of 1976 was 83 and the number of 3-6' animals was 340. The number of both 3-6' and large crocodiles sighted then essentially held steady or even declined slightly until June-July 1979 when there was a dramatic jump following the "driest wet" on record of 1978- 1979. In Messel et al. (1979-1986, 18) we discuss in detail where these additional animals may have come from and show that the results are explicable on the basis of their being forced out of the Arafura Swamp which was being used both as a breeding system and a rearing stockyard. By the time of the June-July 1981 surveys the number of 3-6' animals sighted was back to almost the same figure as in 1976 (347 versus 340), whereas the number of large crocodiles remained at a higher level, 113 versus 83. Obviously a number of the returning large animals were being successful in establishing a territory for themselves, probably in the very waterways from which they had been excluded, but many of their less successful rivals were)joining the ranks of the missing--presumed dead in the process. Then came the two "dry wets" of 1981-1982 and 1982-1983. Again there was an influx, this time of 72 3-6' and 58 large animals: 392 3-6' and 163 large animals (amazingly the number for 1979 had been 162) were sighted. Again a substantial fraction of the increase, specially for large animals could only have been derived from animals excluded from the Arafura Swamp. In June of both 1979 and 1982, concentrations of large animals were sighted at the mouth of the Blyth River, showing that they were entering and leaving the System through the mouth. By the time or the June-July 1983 surveys the number of large animals sighted had dropped to 125
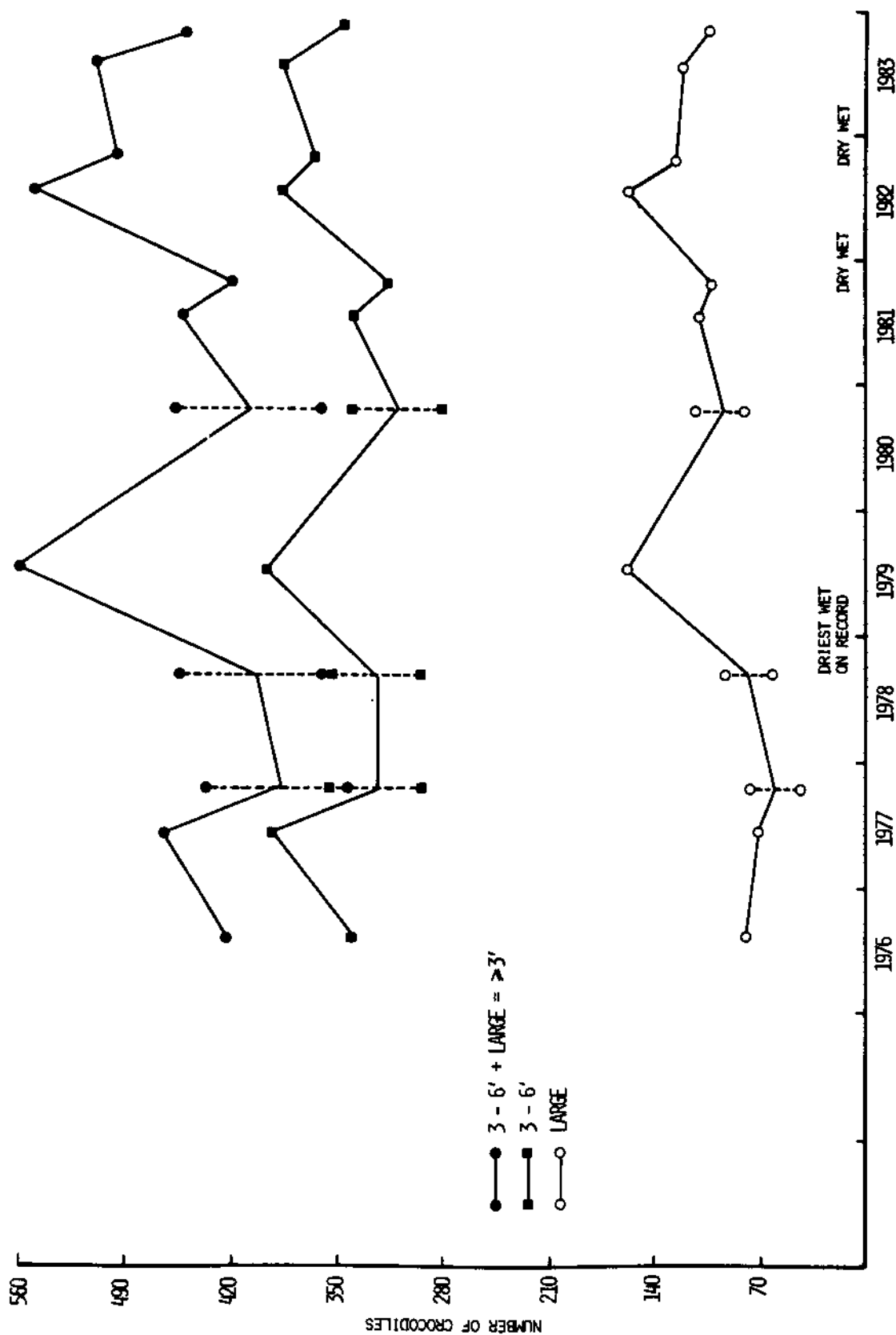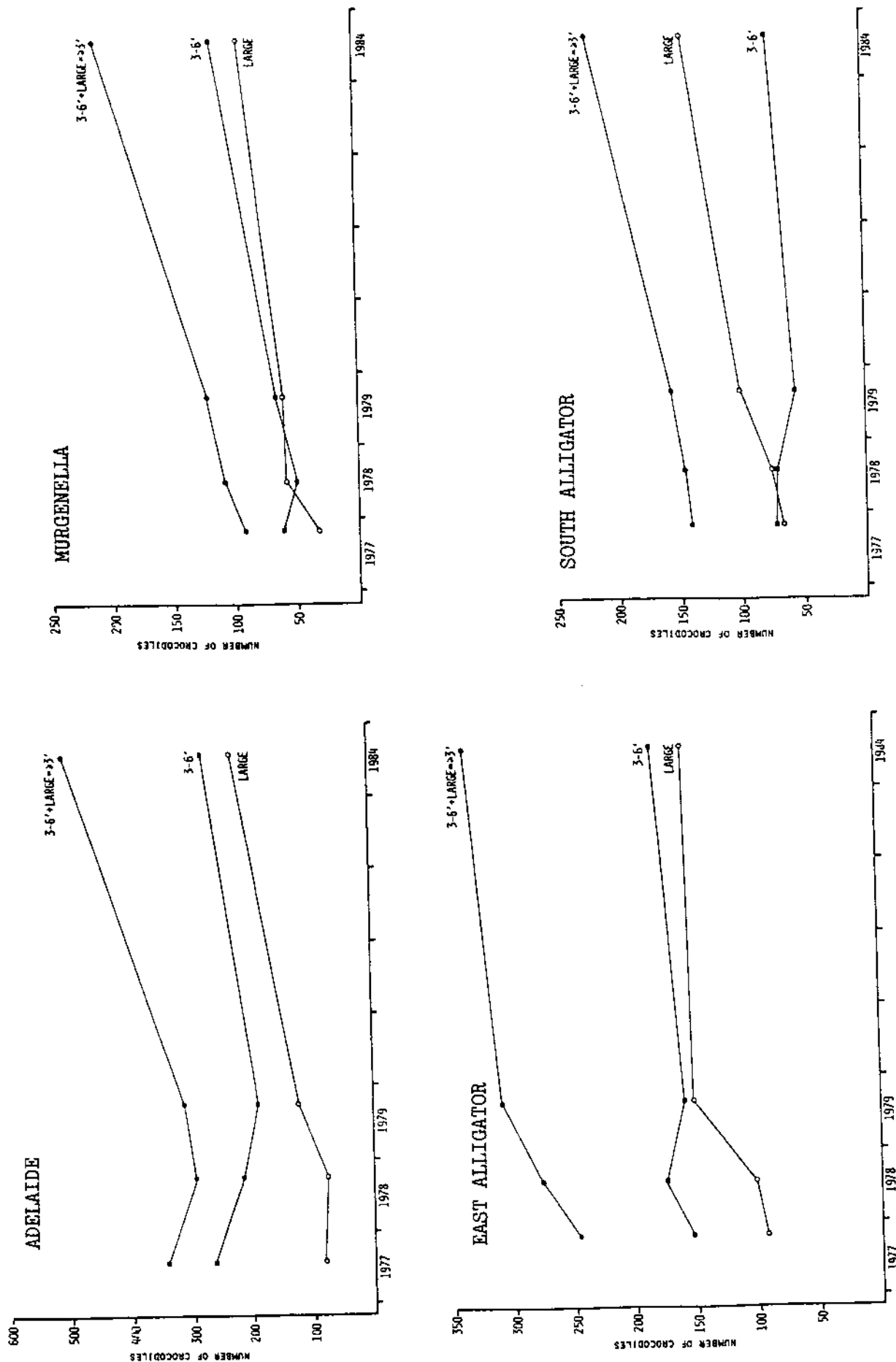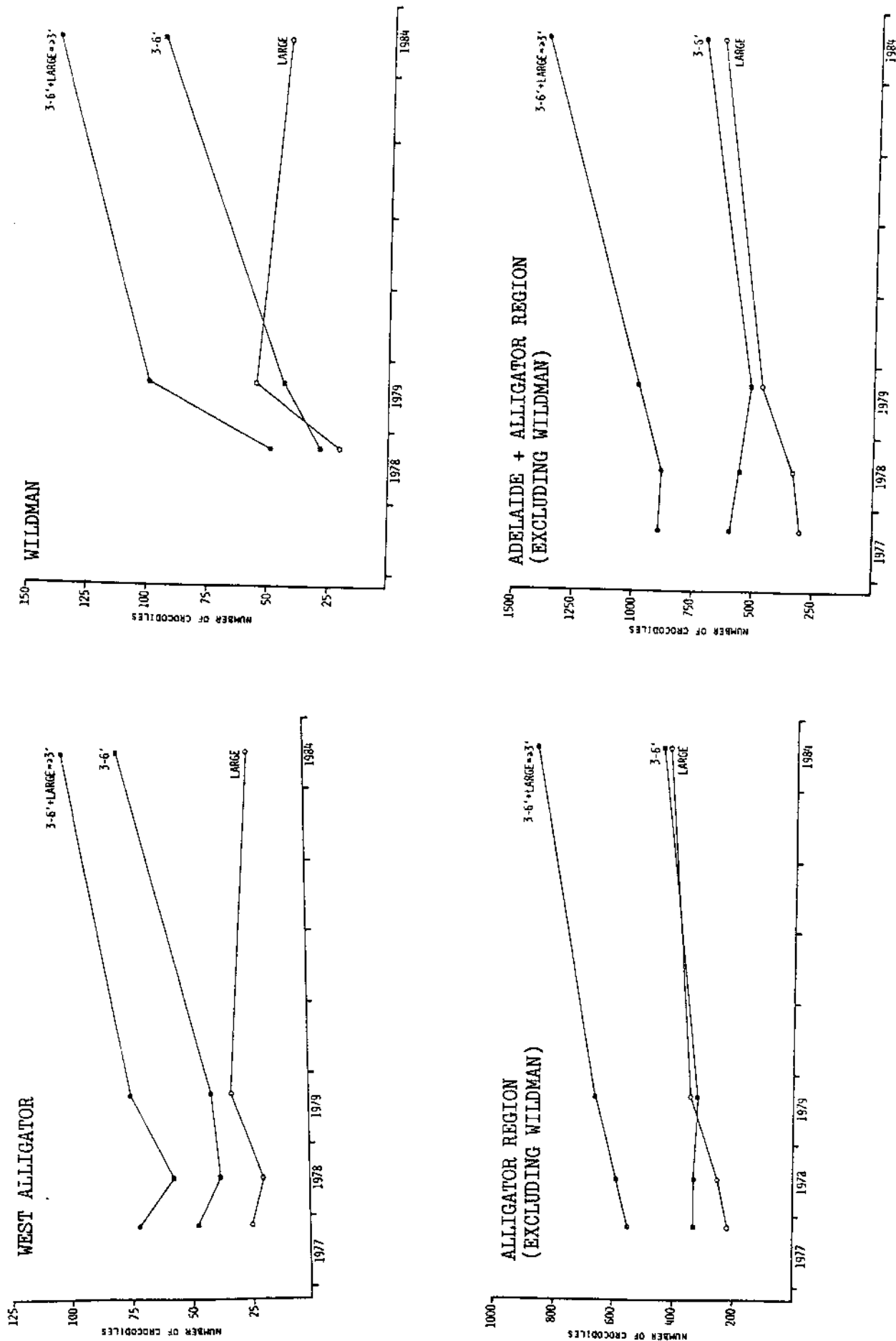
Figure 8. A plot of the number of 3-6', large ($\geq$6)' and their sum, 3-6' plus large or $\geq$3' animals for surveys carried out on the Liverpool-Tomkinson. Blyth-Cadell and Rolling and Junction Bays Rivers Systems during the eight years 1976 to 1983. For those years in which the waterways of Rolling and Junction Bays were not surveyed, we have plotted the numbers shown in Table 7 and the maximum figures also, but have drawn the line through the average value only.

whereas the number of (3-6') animals remained almost constant (392 versus 391). Then came the expected drop in numbers for the October 1983 survey when 350 3-6' and 106 large animals were spotted.

Obviously only a relatively small number of additional 3-6' animals may have been successful in establishing a territory for themselves during the 8 year period: it is as if there were a fairly definite number of slots or territories on the waterways for the 3-6' animals and the number and size of those slots can vary depending upon a complex set of factors of which food supply is one. Of course the 3-6' animals utilizing these in 1983 were not the same animals which filled those slots in 1976. Superimposed upon this is the increasingly aggressive behavior of the animals as the October-November period approaches and the more aggressive behavior of the large animals towards the 3- 6' ones during the breeding season.

The picture in the Maningrida area for the large animals is along the same lines. Comparing the surveys of July-September 1976 with those of June-July 1983 indicates that an additional (125 versus 83) 42 large animals had or were well on the way to establishing a territory for themselves. Study of Tables 4, 5, and 6 reveals that, as expected, those territories were in the TYPE 1 waterways. On the other hand, since only 106 large animals were sighted during the October 1983 survey, it is apparent that a number of large animals which held a territory in the July 1983 period could not do so once the breeding season commenced. Again one must realize that one is viewing a highly dynamic situation: a large animal may be successful in holding a territory for only a limited period. Even the largest animals may eventually be deposed by younger and more aggressive ones. This continual battle for the eventual right to breed is documented for many species. The losses involved during this process in the case of *C. porosus* are startlingly high, and this includes the large size classes.

A broad estimate for the minimum percentage of 3-6' crocodiles which are excluded and/or lost from the monitored area may be obtained by noting (Table 7) that 340 3-6' and 83 large animals were sighted during the July 1976 survey and that the July 1983 surveys revealed 125 large crocodiles only. Each of the 3-6' animals Of 1976 would, if they survived, be in the large size class by 1983 and hence the minimum percentage which have been excluded and/or lost (minimum because we have assumed that all the increase originated from the 340) by July 1983 is (340-42)/340 or 88%. Again if we assume that the 'dry wet' of 1981-1982 had concentrated back into our monitored waterways nearly all of the surviving large animals originally recruited there--and none originating from elsewhere--then 76% becomes the estimate for the missing--presumed dead--3-6' animals ((340- 80)/340 or 76%).

Obviously the exclusions and/or losses of animals in all size classes have to date nearly equalled the input. It should be stressed that the large size classes are included; that they also suffer substantial exclusion and/or losses for we know from our recapture work (see Messel et al. 1979-1986, 18) that some 3-6' animals do enter the large size class and yet the overall number of large animals sighted only increases marginally.

In order to eliminate the various possibilities as to where the large number of apparently missing crocodiles could be, we surveyed, in 1982 and 1983, all of the alternative habitat (such as small coastal creeks and billabongs) in the monitoring area that we could gain entry to, using boats, vehicles, and a helicopter. This was a very expensive and time-consuming exercise, but one we felt had to be done. The results given in Table 8 show that the alternative habitat does provide some important rearing stockyards for both large and small animals, but the number of animals involved is small compared to the hundreds missing (much more detail on the alternative habitat may be found in Messel et al. 1979-1986, 18). As pointed out previously, the Arafura Swamp appears to be the main haven of refuge for the excluded crocodiles.

RESULTS IN VAN DIEMEN GULF

In Tables 1B and 9 we have combined the results from 1977 to 1984 for the tidal waterways surveyed, from the Ilamaryi River in the Cobourg Peninsula to the Adelaide River in Adams Bay. The various combinations shown allow one to view the results from a number of different angles and to assess the recovery of *C. porosus* in this broad geographical area of northern Australia. In Figs. 9 and 10 we have plotted, using Table 9, the results of the Van Diemen Gulf surveys in the same manner as in Fig. 8 for the monitored area.

1. One point which stands out strongly for each of the combinations shown is the inflated number of animals sighted during the July 1984 survey in the 3-4' size class (Table 1B) and that this in turn has inflated the 3-6' size class number count (Figs. 9 and 10) and the 3-6'/large ratio (Table 9). These animals in the 3-4' size class are the result of the excellent breeding season during the "dry wet" of 1981-1982 and a large fraction of them are unlikely to enter the 4-5' and 5-6' size classes. Excluding such fluctuations, which appear to level out rather quickly, the number of 3-6' animals sighted normally remains fairly constant (see Table 2). However, as we have accumulated more and more data, it has become clear that it is the 4-5' and 5-6' size classes which provide most of the bottleneck and that the neck size appears to remain surprisingly constant for a given tidal system. This appears to be as true for the waterways of Van Diemen Gulf as for those in the monitored area.

2. Examining the results in Table 1B for the "Alligator Region plus Cobourg Complex and Saltwater"--629.6 km--shows that the number of 4-5' plus 5-6' animals sighted during the 1979 and 1984 surveys were 252 and 261 respectively. Interestingly the number of (6-7') animals positively identified was 164 on each survey.

For the "Adelaide plus Alligator Region with Wildman"-- 586.1 km--the 4-5' plus 5-6' counts for 1978, 1979, and 1984 were 364, 343, and 376 respectively. Considering the errors- -of up to one size class--which can easily arise in size class estimation, this is an amazing constancy.

If one then adds in the results for the Cobourg Complex and Saltwater, the 4-5' plus 5-6' counts for 1979 and 1984 become 385 and 404 respectively--again surprisingly constant for the 861.2 km of tidal waterways surveyed.

The same exercise may be carried out for the Blyth- Cadell and the Liverpool-Tomkinson River Systems, using Table 1A and again one finds a similar constancy in the number of 4-5' plus 5-6' animals sighted.

3. Though the number count for the 4-5' plus 5-6' size classes appears to remain closely constant from survey to equivalent survey, this is not the case for large animals. Once the animals have passed through the bottleneck, their numbers appear to continue to increase--in spite of various and continuing losses within their size classes as well (Table 9 and Figs. 9 and 10).

For the "Alligator Region plus Cobourg Complex and Saltwater"--629.6 km--the numbers of large animals sighted on the 1979 survey was 447 while the 1984 survey yielded 519 large animals.

For the "Adelaide plus Alligator Region with Wildman"-- 586.1 km--the number of large animals sighted during the 1978, 1979, and 1984 surveys was 352, 525, and 695 respectively. And if

Figure 9. A plot of the number of 3-6', large (≥ 6)' and their sum, 3-6' plus large or ≥ 3' animals for surveys carried out on the Adelaide River, Murgenella Creek, East Alligator River, and South Alligator River.

Figure 10. A plot of the number of 3-6', large (≥6') and their sum, 3-6' plus large or ≥3' animals for surveys carried out on the West Alligator River, the Wildman River, and the combined results for the Alligator Region (excluding the Wildman) and for the Adelaide River plus the Alligator Region (excluding the Wildman).

one adds in the Cobourg Complex and Saltwater Creek, then the number of large animals sighted on the 861.2 km of these tidal waterways during the 1979 and 1984 surveys is 569 and 747 respectively.

4. As already pointed out previously, the "dry wet" season of 1981-1982 apparently resulted in heavy hatchling recruitment and this in turn resulted in a high 3-4' animal count during the July 1984 survey. As has been shown during the course of our lengthy study on the Blyth-Cadell and Liverpool-Tomkinson Rivers Systems such fluctuations are soon smoothed out (Messel et al. 1979-1986, 1, 18 and Tables 1A and 2). The heavy 3-4' animal count in turn inflated the 3-6' count which in turn halted the decreasing 3-6'/large ratio (Table 9 and Figs. 9 to 10). Furthermore, the heavy losses of large animals through drowning in barramundi nets set in the tidal waterways of Kakadu National Park also leads to an artificially high ratio. Some idea of the impact of net fishing may be gained by comparing the results in Table 9 for Murgenella Creek, where net fishing is not allowed, and the West Alligator River, where it is allowed. If commercial net fishing was halted in the tidal waterways of the National Park, one could be confident that the ratio would continue to fall over the long term. However only repeated, careful, and systematic surveys of the overall waterways in the area can provide a long term check on this matter.

5. The density of non-hatchling crocodiles sighted during the 1984 resurvey increased in each of the systems and areas (Table 1B). For the overall 861.2 km of tidal waterways resurveyed, the increase was from 1.5/km for 1979 to 2.1 for 1984. This increase is significant statistically at >99% level of confidence and importantly the increase is not made up of increases in the 3-6' size classes (870 versus 610) only, but there was also a large increase in the number of large animals sighted (747 versus 569).

6. Along the waterways of the Alligator Region, there has been much destruction of riverine habitat by feral water buffalo. This is especially so for the South Alligator and accounts for the minimal hatchling recruitment. We believe that recruitment in the associated freshwater complexes must play an important role in the Alligator Region, especially for the South Alligator.

7. The total number of C. porosus sighted on the 261.0 km of waterways comprising the Cobourg Complex increased from 67 for the 1979 survey to 76 for the 1984 one. This increase is not statistically significant and the density figure for the Complex increased from 0.26/km to 0.29/km only.

Thus the present results support the view that a sustainable recovery in the C. porosus population is in progress in the Adelaide River System and In the tidal waterways of the Alligator Region. Furthermore this recovery is very much in accord with the predictions of our model. The recovery is much stronger than that found for the tidal waterways in the Maningrida area. In Table 10, we have combined data for 1979 and 1983 from Table 1A for the 411.5 km of tidal waterways monitored in the Maningrida area, which encompass the Coomadeer, Liverpool-Tomkinson, Blyth-Cadell, and Glyde Rivers Systems and various TYPE 3 creeks in the area, and presented these in the same form as the results shown in Tables 1A and 9. This then permits us to compare survey results for the monitored tidal waterways In the Maningrida area with those for the 861.2 km of waterways bordering Van Diemen Gulf. Comparing Tables 9 and 10 highlights immediately and strongly the difference between the regions. The explanation for the difference in recovery rates is straightforward. Whereas the freshwater complexes associated with the TYPE 1 waterways in the Maningrida area are scant, and hence most of the animals excluded from the tidal systems in the area had little choice but to leave the systems (and later endeavor to return or to be killed if they remained). In this process the losses in the 3-6' and large size classes are very high. On the other hand, in the Alligator Region, there are substantial freshwater complexes associated with the TYPE 1 tidal waterways and many of the excluded animals take refuge in these and they are used both as rearing stockyards and as breeding systems. In freshwater complexes there are many more

places for crocodiles to hide from other crocodiles than on a river with only two banks. The losses in this case could be expected to be lower (see points 5 and 6 of our model) and the recovery rate faster than on systems without associated freshwater complexes. For the overall waterways in the Alligator Region we found that the exclusion and/or loss factor varied between 47 and 82%. This latter high figure can probably be attributed largely to the loss of crocodiles through drowning in nets. Were it not for this, the figure would undoubtedly have been much lower and the recovery more spectacular.

For the Adelaide River System, two important factors appear to come into play. Though many of the former freshwater complexes associated with the System have been destroyed by feral water buffalo, the waterway has in addition an extensive (101.8 km) system of mostly TYPE 3 waterways on its downstream sections and hence when animals are excluded from the breeding sections they can take refuge in these without leaving the System. The exclusion and/or loss factor for the Adelaide System was only between 31 and 45%, compared to the 80 to 90% or more, for the waterways in the Maningrida area (Messel et al. 1979-1984, 18:127, 134, 155). The increase from only 81 large animals sighted on the Adelaide during the July 1977 survey to 228 large animals sighted on the July 1984 one is the consequence of these smaller losses. Given another decade or two of protection, the Adelaide System may begin approaching its former crocodile numbers.

An important implication of our results is that in much wetter climates than northern Australia, with much more extensive swamp areas (such as New Guinea, Malaysia, Thailand, Burma, for example) recovery could be expected to be faster, given enough animals to allow a recovery.

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APPENDIX--SUPPORTIVE EVIDENCE

In this appendix we summarize some of the data that provides additional support for our model. A full appreciation of course requires a complete reading of all the monographs and their analysis of individual systems (a somewhat daunting task admittedly!).

THE 1979 HATCHLING INPUT ON THE TOMKINSON

A spectacular illustration of the dramatic losses of small animals may be given by considering the fate of the very large hatchling input on the Tomkinson River in 1979. In June 1979, 289 hatchlings were sighted on the Liverpool-Tomkinson System; 260 of these were on the Tomkinson. There was an increase in the number of 3-6' animals on the Tomkinson from 62 in July 1979 to 85 in June 1982, which we believe was due to the return of some of the 1979 hatchlings to the mainstream from extreme upstream sections, because they were now in the size class to be excluded. By October many of these animals were gone from the system. In summary the number of 3-6' animals in the Liverpool-Tomkinson System was 120 in October 1979 and 142 in October 1983--the very large recruitment in 1979 had produced virtually no result.

RESULTS IN ARNHEM BAY

The waterways of Arnhem Bay (Messel et al. 1979-1984, 11) provide further evidence for the losses in the sub-adult size classes.

Arnhem Bay, because of the relatively narrow channel leading into it, is an enclosed system with three groups of waterways (Group 3 has the Goromuru River only). Each group has a major *C. porosus* breeding river in it, the Peter John, Habgood and Goromuru Rivers, which can supply *C. porosus* to adjacent waterways. Although we have no direct evidence, it would be surprising if there was no movement of *C. porosus* between the three groups.

We showed that there was a significant increase in the number of non-hatchling *C. porosus* sighted in the three groups of rivers from the October 1975 to the May-June 1979 surveys and hence that the population of *C. porosus* in Arnhem Bay is increasing (but see remarks on Arnhem Bay in Status Chapter). However, the increase is slow and there is strong evidence for continuing heavy losses (disappearance) in the transition from the 2-3', 3-4', and 4-5' size classes to the $\geq$5-6' size classes. Comparing the number of crocodiles in the 2-3', 3-4', and 4-5' size classes for the combined rivers of Arnhem Bay in October 1975 and the number in size classes $\geq$5-6' in May-June 1979 reveals that the loss (disappearance) of crocodiles in the transition from the 2- 3', 3-4', and 4-5' size classes to size classes $\geq$5-6' was some 88%.

There was no increase in large crocodiles sighted in Arnhem Bay in 1979, which is against the trend for most of the waterways surveyed in 1979. The reasons for this could be twofold: (a) the climate is wetter in the Arnhem Bay area; (b) there is only limited freshwater swamp.

DISTRIBUTION OF ANIMALS

In our ecology chapter we briefly discussed typical distributions of animals along a TYPE 1 waterway and how this fitted in with the idea of a movement of larger size classes downstream. Each system has of course its own peculiarities and we shall now give some examples, with references for the supportive details.

In 1979 we round for the overall Kalarwol River (Messel et al. 1979-1984, 10:28) that the losses of animals was considerably less than in other systems of similar type. The much lower percentage missing is undoubtedly connected with the fact that the Kalarwoi River has a TYPE 1 breeding, northern branch and a TYPE 2-TYPE 3 rearing stockyard adjoining it (the Kalarwoi mainstream). The subadult crocodiles displaced from the TYPE 1 breeding section need not travel out to sea (where a large fraction may perish) but can seek refuge in the adjoining TYPE 2-TYPE 3 mainstream. Since there is little or no breeding on this section, there is likely to be less competition between the sub-adult and adult size classes. The present result also provides additional evidence for the view that the high losses in the other TYPE 1 systems are associated with the sea movement of *C. porosus* from one system to another. A similar mechanism also applies for the Adelaide River, as we discussed in the results for Van Diemen Gulf.

The upstream section (km 73.7-81.3, Table 8) of the Tomkinson has a size class structure typical of a non-TYPE 1 system and appears to function as a refuge for larger animals excluded from the breeding sections of the river. The less desirable far upstream sections of the Liverpool and Blyth also appear to function in the same way, with higher numbers being sighted there in October surveys (excluded from main sections with onset of breeding season) than in June-July surveys (Messel et al. 1979-1984, 18:138).

The sighting of a different size class structure on each resurvey of TYPE 3 systems (but of course always mainly animals $>4'$) fits in with these systems being mainly inhabited by itinerant animals that move in and out of such systems.

Webb and Messel (1978) classified crocodiles into short and long distance movers. In terms of our model the long distance movers are simply the crocodiles unable to secure a territory and we also see why there is an increasing number of long distance movers with increasing size of sub-adults.

INJURIES, DEATHS, AND INTERACTIONS

During a daytime survey of the Tomkinson River in May 1975 a freshly killed 5' *C. porosus* was found at km 22 and was preserved. This animal had been captured, marked and released 2 years previously. The dead animal had a distinct pattern of crocodile teeth punctures and was presumably bitten to death by a larger crocodile. During the night-time survey of km 73.7-81.3 section of the Tomkinson River on 1 November 1982 (breeding season) a 7-8' freshly dead male *C. porosus* was found floating in the water at km 73. It appeared to be in excellent condition and had blood coming from its nostrils--it was probably killed by a blow from a larger crocodile.

On the survey of the Cadell River carried out on 6 November 1982, a 7-8' crocodile was sighted at km 45.9 (the breeding area) with a near leg that was almost completely torn off--obviously done by a larger crocodile.

A 14' animal found drowned in a fisherman's net on the Wildman River in August 1979 had the remains of three small crocodiles in its stomach--possible direct evidence of the cannibalism which we strongly suspect is a major factor in *C. porosus* population dynamics and density control. In July 1983 on the Glyde River, the lower half of an 8-9' crocodile was seen floating in the river. As we approached, the carcass was attacked by a 9-10' crocodile. Considering the concentration of large crocodiles in the Glyde at this time, it is quite likely that the dead animal had been killed by another and that we witnessed another case of cannibalism.

Webb and Messel (1977) found that there was no significant increase in injury frequency in size classes up to 4-5'; however, in size classes above this, injury frequency was high. This of course fits in completely with our model.

Appendix A1.4 of Messel et al. (1979-1984, 1) gives a number of examples of observations of territorial behavior and displays, including a detailed account of the interaction of two 3-4' crocodiles over several months in 1976. A single example will be given here.

At 1334 hrs at km 22, on the Blyth River, on 16 September 1978, a 7-8' crocodile was sighted basking on a gently sloping mud bank, near low tide. We were approaching it slowly in the survey boat in order to get a photograph. When the survey boat was some 30 meters away, the crocodile started to move towards the water. Suddenly a 6-7' crocodile rushed out of the water and chased the 7-8' one, snapping at its tail. The 7-8' crocodile raced along the mud bank in a semicircular path into the water, with the 6-7' crocodile still chasing it. By this time, the survey boat was only 2 to 3 meters away from the 6-7' crocodile, which had its back arched well out of the water. As we approached closer, the crocodile blew a thin stream of water from its nostrils into the air. We could see no sign of the 7-8' crocodile. The 6-7' specimen gradually submerged its back and just the head was left visible.

OBSERVATIONS OF CROCODILES IN MUD

During the night-time surveys many crocodiles have been observed buried in mud (Messel et al. 1979-1984, 1:Chapter 7). Often the mud is very thin and physiologically a crocodile in mud is like one in the water. In most instances only the eyes, cranial platform, and snout are showing. The phenomenon is also observed during daytime. After examining and dismissing salinity and temperature as the reasons, the only explanation for the behavior that we could think of was that of camouflage. Crocodiles bury themselves in mud to hide from other crocodiles and so escape territorial interactions. The same mechanism is the basic explanation of the observation of crocodiles on the bank (Messel et al. 1979-1984, 1:Chapter 7). We have often witnessed crocodiles being chased out on the bank at night by other crocodiles.

DISPERSAL OP HATCHLINGS

In June 1978 all hatchlings on the Blyth-Cadell System that could be caught were marked and released. They were systematically recaptured in September 1978 and again in June 1979 (Messel et al. 1979-1984, 1:Chapter 8). A few recaptures of the same animals were made in October 1979 (Messel et al. 1979-1984, 1:Chapter 8) and October 1980 (Messel et al. 1979-1984, 18:Chapter 5). The pattern that emerges is again that of some animals hardly moving at all and some moving large distances. Looking at the 11 recaptures in October 1980, 3 animals on the Cadell were recaptured within 200 meters of their initial capture as hatchlings. Long distance movement is

related to food supply hut the number of male long distance movers is very significantly greater than the number of female long distance movers. Could interactions be greater for males even at this early stage? The fact that the males had more tail injuries than females supports this view. Webb et al. (1978) and Magnusson (1978) give further results on hatchling dispersal.

RECAPTURES OF 1980, 1981 AND 1983

These recaptures on the Liverpool-Tomkinson System were of animals initially captured in 1973-1976. The details are given in Messel et al. (1979-1984, 18:63-65 and in our chapter on Growth of *C. porosus*. One female (131) stayed in the same area on the upstream Tomkinson for two years and some time after reaching 4' moved to the midsection of the Liverpool--this agrees with our model. A male (517) was captured at 5' size at km 19 on the Tomkinson; one year later it was at km 73 on the Tomkinson; eight years later it was back at km 18. This is suggestive of the animal being excluded to the non-breeding section of the Tomkinson and returning when large enough to establish a territory. Animal 184 (a male) was captured as a hatchling on Maragalidban Creek and recaught three more times over a period of 10 years; all captures were within 1 km or the initial capture. This animal is one of the 10-15% we believe manage to establish a territory in the area where they were born and never leave. Animals 382 and 1059 also hardly moved over a period of six years.

CONCENTRATION OF LARGE ANIMALS AT MOUTHS OF RIVERS

It is unusual to see concentrations of large (or small) animals near the mouth of rivers. We have seen it, however, on a few occasions, and these observations are understandable in terms of our picture of movement between the Arafura Swamp and the monitored area.

On the June 1979 survey, on the Blyth mainstream, the number of large animals sighted increased dramatically from 15 to 40 and from 23 to 55 for the overall Blyth-Cadell System. For us it was exciting to see so many large animals; they were mostly concentrated at the mouth region of the Blyth River and on the sidecreeks of the downstream section of the river. Where had these animals come from and were they coming into the river or leaving it? Since they were not sighted during the September 1978 survey, the evidence points to these animals trying to gain entrance to the waterway.

By October 1980 most of these additional large animals were gone again. We interpret this to mean large animals excluded from the Arafura Swamp after the dry wet of 1978-1979 were trying to enter the Blyth. Exactly the same phenomenon occurred in June 1982 after the dry wet of 1981-1982; 31 large *C. porosus* were sighted on the km 0-15 section of the Blyth River and its sidecreeks. By November 1982 the number of large *C. porosus* on the Blyth-Cadell System had dropped by 15 and the decrease occurred almost exclusively on the mouth section.

In July 1979, on the Glyde River, we observed 12 animals between km 0 and km 1.2 in size classes $\geq$4'. This was the first occasion we had seen such a concentration of *C. porosus* at a river mouth. These would be largely animals excluded from the Arafura Swamp and leaving the river or waiting to return. Because of this 1979 observation we were expecting a similar observation in July 1983 after the "dry wet" of 1981-1982, and so it turned out. Furthermore, there were 19 animals sighted on the km 0- 5 mouth section and the majority of these were large; 15 of the animals were sighted between km 0 and 2, strongly indicating that they were either entering or leaving the river

(in fact the October survey indicates they were entering the system). Three pairs of these large crocodiles were sighted interacting; that is, one was in the water directly facing one up on the bank. Further discussion may be found in Messel et al. (1979-1984, 18).

The large increase in the Milingimbi Complex (Messel et al. 1979-1984, 9) in 1979 also supports the idea of movement out of the Arafura Swamp via the Glyde River.

The idea of movement between the monitored area and the Glyde River is made more plausible by the sighting in 1976 in the Milingimbi Complex of a 12' male with a transmitter on its head that was originally caught at km 49 on the TomkInson one year earlier.

OBSERVATIONS WITH OTHER SPECIES

Cott (1961) remarked on the losses of small *C. niloticus* between the ages of about two and five years, crocodiles go into retreat in less desirable habitat and this cryptic behavior has probably been forced on them by the habit of cannibalism. Studies of *C. acutus* in Florida also indicate that a substantial fraction of sub-adult *C. acutus* remain unaccounted for (J. Kushlan, 5th Working meeting, Crocodile Specialist Group, 1980).

ECOLOGY OF THE AMERICAN CROCODILE, *CROCODYLUS ACUTUS*

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SPECIES IDENTIFICATION AND DISTRIBUTION

The American crocodile, *Crocodylus acutus*, is a large, relatively longirostrine crocodile widely distributed in the coastal regions of the northern neotropics. Although individuals have been reported historically to reach lengths of up to 6.25 m (Alvarez del Toro 1974) and 7.0 m (Schmidt 1924, Medem 1981), today *C. acutus* longer than 4 m are rare. The general morphological characteristics of the species have been described elsewhere (Mertens 1943, Brazaitis 1973), yet because of morphological similarities with two other species (*Crocodylus morletii* and *Crocodylus intermedius*), misidentifications of the species have not been uncommon, even among herpetologists. Frequent past confusion among these and other New World crocodilians has created nightmarish problems for nomenclatural review (Smith and Smith 1977).

Among all living crocodilians, *C. acutus* has the most reduced and irregular arrangement of dorsal osteoderms, usually with no more than 4 scutes in any of the 14-17 continuous precaudal scute rows (Ross and Mayer 1983). The American crocodile is also unique in the degree of development of a median preorbital elevation (MPE) on the snouts of adults and subadults (Brazaitis 1973, Alvarez del Toro 1974, Medem 1981). Although the size and shape of the MPE appears to vary somewhat geographically, and some preliminary evidence suggests that its size may be sexually dimorphic (pers. obs.), the MPE is a consistent and distinctive morphological feature among adults. Other species of crocodiles may have an MPE, but never as pronounced as in *C. acutus*. The combination of these two characteristics, irregular reduced dorsal scutes and the MPE, is sufficient to distinguish *C. acutus* from other crocodiles, with the possible exception of *C. moreletii* which has both characters developed to a slightly lesser degree. Morelet's crocodiles are best distinguished from *C. acutus* on the basis of ventrolateral scute intrusions on the base of the tail (Ross and Ross 1974).

The general distribution of the American crocodile includes both the Atlantic and Pacific coasts of southern Mexico, Central America, and northern South America, as well as the Caribbean islands of Cuba, Jamaica, Hispaniola and the southern tip of Florida, USA. The exact limits of the past and present mainland distribution of the species are somewhat confused due to a lack of systematic survey work, and the past misidentification of species. This is especially true for the Atlantic coast drainage. On the Mexican Gulf coast, *C. acutus* has definitely been recorded as far north as Cozumel Island (Field Museum of Natural History, FMNH 34563), Bahia de la Ascencion and Isla de Mujeres (Quintana Roo), and Laguna de Catemaco (Vera Cruz; Ross and Ross 1974). Literature accounts of *C. acutus* north of Vera Cruz on the Gulf coast appear to be based largely on misidentified *C. moreletii*.

The southernmost limit of *C. acutus* on the Atlantic coast of South America is similarly confused. Specimens of the American crocodile have been reported from the Paria Peninsula in Venezuela and on Trinidad, although the latter records probably represent vagrant animals (Medem 1983). Large crocodilians are known from the Orinoco delta region (F. Pannier, S. Gorzula, pers. comm.), but their specific identity is not known. Apparently, no members of the Crocodylidae are found south of the Orinoco delta.

The limits of the Pacific mainland distribution are better known due to the lack of congeners, and habitat limits to distribution. Crocodiles have been recorded from as far south as the Rio Tumbes and Rio Chira in northern Peru (Hofmann 1970, Medem 1983). In Mexico, the northwestern limit of crocodile distribution historically was the state of Sinaloa (Ross and Ross 1974, King et al. 1982).

The American crocodile reaches the northernmost limit of its range in Florida, USA. Although once found as far north as Lake Worth on the eastern coast of Florida, the current crocodile distribution now centers on Florida Bay. The present and past distribution of crocodiles in Florida are reviewed by Ogden (1978) and Kushlan and Mazzotti (1986).

Outside of its currently recognized range, *C. acutus* was also apparently found on the Bahamas (based on pre-Columbian fossils; King et al. 1982), and on the Cayman Islands, where specimens were collected as recently as 1939 (Grant 1940).

HABITAT RELATIONS

Macrohabitat

The American crocodile is typically found in freshwater or brackish water coastal habitats including, but not restricted to: the estuarine sections of rivers, coastal lagoons, and mangrove swamps (Alvarez del Toro 1974, Medem 1981). Although it is principally a coastal species, *C. acutus* is ecologically adaptable and is known to extend its distribution inland, especially along the courses of larger rivers and their associated wetlands habitat (Medem 1981). Individuals have been reported at altitudes of up to 610 m in Honduras (Schmidt 1924) and 1220 m in Mexico (Rio Tehuantepec: American Museum of Natural History, AMNH 100634). The species also inhabits landlocked lakes of varying salinities: freshwater (Schmidt 1924), brackish (Thorbjarnarson 1984, 1988), and hypersaline (Inchaustegui et al. 1980).

The American crocodile is regularly found on small offshore islands and atolls throughout its range. On many of these islands adult crocodiles can apparently exist without access to freshwater, although the presence of a freshwater source may be critical for the survival of hatchlings (see Temperature and Salinity Relations).

The adaptability of *C. acutus* in terms of habitat requirements extends to the use of disturbed, or man-made habitats. Although crocodiles are known to occupy man-made bodies of water in Venezuela (Embalse de Pueblo Viejo, Embalse de Tacarigua; Seijas 1986b), and Panama (Gatun Lake; Dugan et al. 1981, Rodda 1984), the most extensive use of disturbed habitats is in southern Florida. On Key Largo, crocodiles commonly occupy borrow pits and canals. Indeed, virtually all the nesting on Key Largo (which accounts for some 30% of the total nesting in Florida) is done on peat spoil banks created by dredging canals in mangrove areas (P. Moler, pers. comm.). A small population of crocodiles also inhabits the cooling canal system of the nuclear power plant at Turkey

Point. Nesting has occurred on several occasions in the spoil banks along the cooling canals (Gaby et al. 1985). Crocodiles are also known to occur in the cooling canal system of another power plant in Ft. Lauderdale (P. Moler, pers. comm.).

Microhabitat, Activity and Movements

Within the broad definition of *C. acutus* habitat outlined above, certain microhabitat features strongly influence the distribution of crocodiles in any given area. Crocodiles are principally inhabitants of shoreline habitats, preferring an amalgam of shallow and deep water areas, land for basking or nesting, and aquatic or semiaquatic vegetation for cover or increased habitat productivity. In addition to micro- environmental features, social factors play an important role in determining crocodile distribution. Crocodile size, population density, and population size-class structure all probably interact with environmental factors to define the overall pattern of habitat usage for any given population. Aside from these factors, the presence of humans or pattern of human activity may also modify crocodile habitat use. In most situations crocodiles are retiring and avoid areas frequented by humans. For instance, in Etang Saumatre, Haiti, a temporal habitat segregation was noted with crocodiles nocturnally entering areas used by people during the day (pers. obs.).

Because detailed information on many aspects of habitat selection is lacking, the following discussion centers on some of the more obvious factors that influence crocodile distribution and activity. This information is based primarily on work done on three crocodile populations: southern Florida; Etang Saumatre, Haiti; and Gatun Lake, Panama.

Hatchlings and Juveniles - Among nesting females (see following section) and recently hatched young, terrestrial habitat features are important in defining habitat requirements, as they determine where nesting can occur and the type of habitat into which the young are born. When nests are located adjacent to suitable habitat for hatchlings, the young may remain in the vicinity of the nest for several weeks, months, or even years (Alvarez del Toro 1974; Thorbjarnarson 1984, 1988; Rodda 1984).

In Florida, hatchling crocodiles frequently prefer to remain hidden in vegetation during the day, using such areas as mangrove prop roots, shoreline ledges or beach wrack for cover (Lang 1975b, Mazzotti 1983). In Panama, Rodda (1984) found 10 and 22 month old *C. acutus* along shorelines protected from waves and usually bordered by woody vegetation. In these areas the young crocodiles were frequently seen in floating mats of *Hydrilla*. In Etang Saumatre, Haiti, juvenile and hatchling crocodiles would spend most of the day hidden in root mats of *Conocarpus erectus* that grew in shallow water near the nesting beaches. At dusk, the crocodiles would leave their protected retreat sites and move to more open shoreline habitats or floating algae mats where they would forage (Thorbjarnarson 1984, 1988). Juvenile and hatchling crocodiles in Etang Saumatre were mostly sedentary. Of 10 recaptures, 8 were found at the original point of capture (mean interval 143 days). One juvenile dispersed 1.8 km over 339 days.

When the habitats adjacent to the nest are unsuitable for hatchlings, the neonates may disperse almost immediately. Factors which may cause dispersal are probably diverse, but are known to include wave exposure (Ogden 1978, Mazzotti 1983), and hypersaline aquatic environments (Inchaustegui and Ottenwalder pers. comm., pers. obs.). Mazzotti (1983) found hatchling *C. acutus* would disperse from wave exposed nest sites soon after hatching, moving up to 1.5 km from the nest in the following month. Lang (1975) and Ogden (1978), reported similar results from their studies in south Florida. Movements were either along the shore or inland into

protected, interior, shallow water habitats. In some cases hatchlings were noted to move overland for periods of up to 10 days without access to water (Mazzotti 1983). The general pattern of movements was away from exposed habitats and into sheltered mangrove lined creeks. Hatchlings from nests along creek sites dispersed less and tended to remain in the nest area for at least one year. Virtually all hatchling movements were nocturnal.

Rodda (1984) radio-tracked a group of 10 month old (N = 9), and 22 month old (N = 1) *C. acutus* along a sheltered shoreline in Gatun Lake, Panama. Census work in the area suggested that some of the crocodiles would remain near their nest for at least 22 months after hatching. Over a two-month period the radio-equipped crocodiles were found to remain within relatively restricted home ranges. The 10 month old crocodiles moved within an average of 330 m of shoreline, and spent approximately 80% of their time within a narrower core range of 200 m. The one 22 month old individual moved over 650 m of shoreline.

In the same study, Rodda (1984) examined a series of factors (water temperature, wind speed and direction, sun or moon visibility and altitude, moon phase, cloud cover, and water level) in relation to activity levels. Crocodiles were found to move significantly less during moonlit periods (no clouds, moon more than half full and $> 30^0$ from the horizon). A diurnal pattern of movements was found with activity showing a sharp increase just prior to dusk, then increasing steadily until 0300 h. A similar pattern was noted for the mean percentage of animals at the water's surface. Movements during the day (0900- 1700 h) were unusual.

Larger juvenile crocodiles (and subadults) may enter a dispersal phase and move much more than smaller individuals (see following section). Some juvenile crocodiles in southern Florida are known to disperse well away from their nest sites (P. Moler, pers. comm). One individual (84.5 cm TL) moved a minimum distance of 13.1 km over 18 months from its point of origin at the Turkey Point power station (Gaby et al. 1985).

Adults and Subadults - In southern Florida, Mazzotti (1983) reported that adult crocodiles spend most of their time in protected red mangrove (*Rhizophora mangle*) habitats. Over 75% of their observations of adults were in inland or protected coves characterized by deep water, often with undercut banks (see Burrows section) or overhung by mangrove prop roots. Some adults were also found to move to areas of high food availability such as active bird rookeries.

In Etang Saumatre, a brackish water lake in Haiti, adult and subadult crocodiles were found to be significantly more abundant in 5 of the 11 defined lakeshore habitat types (*Conocarpus* fringe, *Conocarpus* flats, *Salicornia* flats, submerged forest, and canal marsh), and were noted to avoid two habitats (rocky shore with medium and steep gradients (Thorbjarnarson 1984, 1988). Three principal environmental factors were considered to be important in determining habitat use: exposure to wave action, food availability and the presence of nesting habitat. The preference of certain habitats over others was attributed in part to the availability of suitable nesting beaches, or to food availability; an active heron rookery in the submerged forest, and the abundance of fish prey species in the *Conocarpus* flats. However, for all habitats the degree of wave exposure was apparently the overriding factor. Classifying lakeshore areas by the degree of wave exposure, crocodiles of all size classes were found in the highest density in protected areas (11.76/km) and in the lowest density in exposed areas (0.83/km) with an intermediate value for moderately exposed areas (7.79/km). A similar avoidance of wave action was noted in adjacent Lago Enriquillo (pers. obs.) and has been reported for *C. acutus* in Florida (P. Moler, pers. comm.), as well as for other crocodilians (Cott 1961, Graham 1968, Woodward and Marion 1978, Messel et al. 1981). Considering that the crocodile's respiratory and visual systems may be severely compromised by waves, avoidance of wave action is a very understandable feature of habitat preference and probably is a general attribute of habitat selection among all crocodilians.

A radio-telemetry study of adult crocodiles in Florida conducted by J. Kushlan and F. Mazzotti (Mazzotti 1983) determined that among 7 adult females (> 2.5 m TL) minimum activity areas averaged 89 ha, and demonstrated seasonal shifts in range associated with the nesting season. Main activity areas were located in protected creeks or ponds, but during the nesting season females would move to the more exposed nest sites in Florida Bay. This study and others have shown that habitat preference in adult females is strongly influenced by the availability of nesting habitat. Females demonstrate an increase in activity and movements during the breeding season (Gaby et al. 1985, Mazzotti 1983) which are often reflected in seasonal differences in habitat selection.

The two radio-equipped male crocodiles (2.3 m, 2.9 m TL) had larger activity areas (98 ha, 216 ha respectively) but did not enter the exposed Florida Bay to any significant degree. One male was noted to have a disjunct activity range occupying a river site, and interior ponds. One stay in the pond region coincided with the active nesting phase of a colony of wood storks (*Mycteria americana*; Mazzotti 1983).

Another type of seasonal activity shift was noted for *C. acutus* by Medem (1981) in freshwater riverine habitats in Colombia. Crocodiles were reported to leave the larger rivers during the wet season to avoid the swift currents and move into lagoons or other inundated areas adjacent to the main river course. Use of the main river channel was restricted primarily to the dry season.

Seasonal activity shifts associated with drought have also been commented on by various authors. Medem (1981) reports that *C. acutus* will bury itself in the mud for periods of up to 2-3 months, or remain in burrows (see below) when its normal habitat dries out. Similar accounts have been given by Varona (1980) for Cuba, Donoso Barros (1966) for Venezuela, and Casas and Guzman (1970) for Mexico.

No quantitative data exist describing daily variation in activity levels in adult or subadult *C. acutus*. Although most data suggest that hatchling and juvenile crocodiles are almost completely nocturnal, possibly to avoid diurnal predators such as raptors and wading birds, adult crocodiles are frequently active during daylight hours. Various behaviors, such as basking (Alvarez del Toro 1974), territorial defense and mating (Alvarez del Toro 1974, Garrick and Lang 1977, Inchaustegui et al. 1980) have been observed during the day. However, for adults as well as juveniles, foraging appears to be mainly a nocturnal activity (Alvarez del Toro 1974, pers. obs.).

Intermediate size-classes of *C. acutus* (large juveniles- subadults, 1.0-2.0 m total length) are frequently found in somewhat marginal habitats. Mazzotti (1983) noted that crocodiles in this size range were often found isolated from the adults and hatchlings and to be located in somewhat inaccessible areas. Gaby et al. (1981, 1985) observed a higher percentage of juveniles and subadult (27% of total) in hypersaline water than adults (5%). In Etang Saumatre subadult crocodiles were more likely to be found along exposed shorelines, and in fact one such marginal habitat (sand-grass-mud) was a statistically "preferred" habitat for subadults (Thorbjarnarson 1984, 1988). In coastal Haiti, juvenile and subadult crocodiles were more frequently reported from small, isolated patches of habitat away from breeding populations.

In the radio-telemetry study in Everglades National Park, Florida (Mazzotti 1983), the one subadult animal followed, a female, was found to move more than adults, and to have a larger minimal activity range (262 ha, 262 fixes), averaging 1.4 km between fixes. In Etang Saumatre, some subadults would also move considerable distances. One subadult male was found to have shifted entirely across the lake, a shoreline distance of 22 km, over a period of 306 days.

The dispersal phase of large juveniles and subadult crocodiles may be an integral part of the population dynamics of *C. acutus* and other crocodilians. The population model proposed by Messel et. al (1982) for *C. porosus* may have broad applicability to other species of crocodilians, especially *C. acutus* which is very similar in ecology to *C. porosus*. The data on habitat selection and movement that do exist for *C. acutus* seem to support the presence of dispersal and segregation phases of large juvenile and subadult crocodiles at a time when they may be coming into territorial conflict with adults.

Segregation of Size-Classes - In Florida, the spatial segregation of crocodiles by size-class has been observed in all three sub- populations. As noted above, Mazzotti (1983) reported intermediate-sized crocodiles were not frequently found together with hatchlings or adults. In the cooling canal system at Turkey Point, adult, subadult, and juvenile crocodiles were found in different habitats, with segregation taking place mostly with respect to water salinity (Gaby et al. 1981, 1985). A similar segregation has been noted among the crocodiles on Key Largo (P. Moler, pers. comm.) where physical habitat structure may play an important role. The spatial segregation of crocodiles by size-class may represent a difference in the physical habitat requirements of different sized crocodiles, or it may reflect social factors and agonistic encounters between size-classes as proposed in the Messel et al. (1982) model for *C. porosus*.

However, in other populations of *C. acutus* that have been studied, size-class segregation by habitat type is less clear-cut. In both Etang Saumatre and Lago Enriquillo, hatchling, juvenile, subadult and adult crocodiles were all found together in the same areas (Thorbjarnarson 1984, 1988). In these situations, an important regulatory factor determining the degree (or absence of) size-class segregation, may be population density. It may not be a spurious fact that size-class segregation has been noted in a population inhabiting coastal mangrove habitat in Florida, where population density was lower (see Population Ecology), and the available spectrum of habitats is greater. In the lacustrine crocodile populations on Hispaniola, greater crocodile densities and more limited habitat availability may result in a greater degree of size-class overlap in habitat usage. At the other extreme is the situation reported by Schmidt (1924) in Lago Ticamaya, Honduras, which had an extremely high crocodile density with a total lack of small juveniles. In this case the extremely high density may have triggered density-dependent population control measures which may have lead to the complete exclusion of smaller individuals from the main population body, or mortality via mechanisms such as cannibalism. Schmidt does report finding the remains of a 1.2-1.5 m crocodile in the stomach of a larger specimen, but under circumstances such as these cannibalism is difficult to distinguish from scavenging.

Temperature and Salinity Relations

Studies of the temperature relations of *C. acutus* have primarily involved hatchling (Mazzotti 1983) and juvenile (Lang 1979) crocodiles. Lang (1979) noted that under laboratory conditions the preferred body temperature of fasting *C. acutus* was similar at night (28.0° C) and during the day (27.9° C), but was slightly elevated following feeding (day 29.5° C, night 29.3° C). Testing for the upper limits of thermal tolerance in hatchlings, Mazzotti (1983) found observable signs of heat stress when cloacal temperatures exceeded 38° C.

Under field conditions, Mazzotti (1983) noted that hatchling *C. acutus* selected the coolest available microhabitats during the day, becoming active when surrounding temperatures dropped to within 1° C of the microhabitat temperature. The resulting pattern of activity indicates that hatchlings seek out the lowest available temperatures in order to avoid heat stress (Mazzotti 1983).

These data for hatchling *C. acutus* agree with the hypothesis of Lang (1975c) of *Crocodylus* as thermoconformers whose basic thermoregulatory strategy is to avoid rapid heating during the day.

No specific studies have examined the thermal relations of adult *C. acutus* but, in contrast to hatchlings, adults are well known to bask, especially during the morning or late afternoon hours. Basking is usually accomplished by hauling out on land, but in areas where suitable terrestrial habitat is not available, or a disturbing human presence is found, crocodiles will bask in a high emergent floating posture in the water (Alvarez del Toro 1974, Medem 1981, pers. obs.). Conversely, during the heat of the day adults are known to remain hidden in deep water (Alvarez del Toro 1974), or in cool, shaded aquatic situations (pers. obs.).

At times crocodiles will remain on land at night, and this behavior results in lowered body temperatures (Cott 1961, Graham 1968, Lang 1975c). In Lago Enriquillo and Etang Saumatre, this behavior was frequently noted in response to intense wave action (pers. obs.), but it may also occur in calm water areas. Crocodiles on land have also been observed gaping both during the day and at night, an action considered by various authors to be thermoregulatory in nature (Alvarez del Toro 1974, Loveridge 1984). Besides a temperature regulation function, gaping may also be used to dry out the mouth lining to control the growth of algae or fungi, or to desiccate aquatic ectoparasites (pers. obs.).

The salinity relations of *C. acutus* are of obvious importance as the species is frequently found in saline environments. A relatively large literature exists on the osmoregulation of *C. acutus* and other crocodilians.

Mazzotti (1983) found crocodiles in Everglades National Park occupied a wide range of salinities (0-35 parts per thousand (ppt)), with mean salinity values varying somewhat between size classes (adults 12.1 ppt, subadults 12.6 ppt, juveniles 20.1 ppt) and time of year (winter 12.4 ppt, spring 19.6 ppt, summer 17.3 ppt, and fall 15.1 ppt). The seasonal shift in mean salinity was associated with a population move towards the Florida Bay during the spring and the greater use of inland areas during the fall when freshwater discharge was at its highest. Average salinity for females (17.3 ppt) was higher than for males (10.8 ppt) and reflected to some degree the use of nesting sites in the higher salinity Florida Bay region.

Also in south Florida, Gaby et al (1985) reported finding crocodiles in salinities ranging from 0 to 40 ppt, and Dunson (1982) observed hatchlings in water up to 43 ppt. Gaby et al. (1985) also noted a size-class segregation by water salinity with adults more frequently observed in freshwater areas (38% of observations), as opposed to only 13% for juveniles and subadults. These two smaller size-classes had a greater tendency to be found in brackish (53%) or hypersaline water (27%). The mean water salinity for captured juveniles was 25.2 ppt.

In terms of osmoregulation, body size plays an extremely important role. Individuals larger than 200 g can fast in seawater for long periods without developing severe salt balance problems (Ellis 1981, Mazzotti 1983). Adult crocodiles, with a relatively small surface area to volume ratio, can presumably remain in saline water for extended periods. In Lago Enriquillo, crocodiles lived in water of up to 70-80 ppt for many years prior to the hurricanes of 1979 and 1980. However, in the same lake hatchling crocodiles would perish as a consequence of the hypersaline water unless they happened to disperse into one of the freshwater marsh areas that fringe the lake (Inchaustegui and Ottenwalder, pers. comm.).

The most crucial period for *C. acutus* in terms of osmoregulation is the first year or two of life. At small body sizes, a large surface area to volume ratio results in an increased capacity for water flux in relation to body mass. Hatchling crocodiles under laboratory conditions do not

maintain mass in full strength sea water (35 ppt), even when fed fish *ad lib* (Dunson 1970, Evans and Ellis 1977, Ellis 1981). However, field observations indicate that hatchlings not only tolerate salinities of up to 43 ppt, but under some circumstances grow extremely rapidly in hypersaline environments (Carney 1971, Gaby et al. 1981). An extra-renal salt excreting gland has been found in the tongue of *C. acutus* and all *Crocodylus* examined to date (Taplin and Grigg 1981). But under natural conditions of blood plasma salt levels, this extra renal excretory pathway apparently plays little or no osmoregulatory role in *C. acutus* (Dunson 1982). In the absence of major physiological adaptations for life in saline water, Mazzotti (1983) suggested that osmoregulation is accomplished primarily by behavioral means. The principal behavioral mechanism for maintaining water balance is probably drinking brackish water made available ephemerally by rains (Mazzotti 1983). Under laboratory conditions it was found that small *C. acutus* maintained in saline water will drink brackish water. Over a 10 day period, hatchlings were found to maintain mass in seawater (35 ppt) if provided with fish to eat, and placed in brackish water (4 ppt) for one day per week (Mazzotti 1983).

Burrows

The construction and use of burrows or dens by *C. acutus* has been widely observed and commented upon throughout the species range: Florida (Hornaday 1904, Dimock and Dimock 1908, Ogden 1979), Mexico (Casas and Guzman 1970, Alvarez del Toro 1974), Honduras (Schmidt 1924), Nicaragua (Camacho 1983), Colombia (Medem 1981), Venezuela (Donoso Barros 1966), Jamaica (L. Garrick, pers. comm.), Haiti and the Dominican Republic (pers. obs.). Burrows are used principally by adult crocodiles living in riverine habitats, although Medem (1981) also reports dens from lakes and mangrove swamps in Colombia. Other accounts of *C. acutus* from lacustrine habitats indicate that crocodiles do not dig burrows in these areas, perhaps because of a lack of suitable shorebank conditions or less seasonal variability in water levels (Etang Saumatre, Lago Enriquillo, pers. obs.; Lago Ticamaya, Schmidt 1924).

According to Medem (1981), burrow construction differs in relation to habitat type. Along rivers or in lakes, burrows are excavated in elevated banks and have from one to three entrances. In mangrove swamps they are usually found in the most elevated areas under the roots of mangroves or dead trees, or even in mounds of decomposing leaf litter. Varona (1980) reports that in Cuba, *C. acutus* burrows have an oval entrance, exposed at low tide, widening inwards. The burrow ascends and the roof of the terminal chamber is above the water level, sometimes even with "ventilation" holes to the surface. Crocodiles are reported to enter and leave the burrow head first so the terminal chamber needs to be large enough to allow the crocodile to turn around.

Burrows can be quite large. One burrow measured by Medem (1981) along the Rio Palenque in Colombia had two entrance tunnels (2.75 m, 5.80 m in length), one above the water, the other submerged, with a very large terminal chamber (8.5 m x 7.2 m). Ogden (1979) reported that in Florida crocodile burrows were often maintained near creek bank nest sites and were 3-9 m in length with entrances at or below the water line.

Burrows are probably used under various circumstances, as a refuge for resting and thermoregulation, an aestivation site for prolonged drought, or for protection from natural predators or man.

Habitat Relations with Other Crocodilians

Over its extensive range in the northern Neotropics, *C. acutus* overlaps, partially or entirely, the range of four (and possibly five) crocodilians: *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus rhombifer*, *C. moreletii* and possibly *C. intermedius*. The range of distribution overlap is: *Alligator*, southern Florida; *Caiman*, Caribbean drainage Honduras-Venezuela, Pacific drainage Oaxaca, Mexico-southern Ecuador; *C. rhombifer*, Cuba and the Isle of Pines; *C. moreletii*, Atlantic drainage southern Mexico-Guatemala; and *C. intermedius* possibly in the vicinity of the Orinoco delta. Indeed, on a macroscopic scale, the only parts of the range of *C. acutus* where it is not sympatric with another crocodilian are on the islands of Jamaica and Hispaniola, and in northwestern Mexico (Sinaloa-Guerrero).

Reports of ecological relations between *C. acutus* and other crocodilians are restricted primarily to habitat partitioning, and in some areas even this situation is confused. Where *C. acutus* is sympatric with another large, primarily freshwater species, it is generally restricted to brackish water habitats, and does not penetrate far into interior, freshwater areas (*Alligator* (Kushlan and Mazzotti 1986), *C. rhombifer* (Gundlach 1880; Barbour and Ramsden 1919; Varona 1966)), although the situation with *Alligator* is somewhat complicated by potential temperature limitations (Kushlan 1982). In Cuba, *C. rhombifer* is reportedly behaviorally dominant over even larger *C. acutus* in captivity (Varona 1966) and may actively exclude *C. acutus* from freshwater habitats. Although *C. acutus* ranges far up into freshwater rivers along the northern coasts of Colombia and Venezuela, it apparently never has been found far up into the Orinoco river, habitat of the large, freshwater *C. intermedius* (Medem 1981).

In regions where *C. acutus* is sympatric with a smaller crocodilian, habitat use normally includes a greater variety of freshwater environments. In Mexico, *C. acutus* ranges well upstream in many of the larger rivers, and also was frequently found in lakes (Alvarez del Toro 1974). In the same areas, the smaller species of crocodilians are found principally in small streams, or swampy, slow moving sections of rivers (*Caiman crocodilus*), or in small, turbid streams, swamps or swampy lakes (*C. moreletii*; Alvarez del Toro 1974). Similarly, in the Rio Atrato in Colombia, Medem (1981) noted a definite habitat segregation existed with *C. acutus* in the river and major tributaries, and *Caiman* confined to the surrounding swamps and smaller tributaries. A similar situation is presently found in eastern Honduras (pers. obs). In northern Venezuelan rivers, Seijas (1986b) found a broad overlap in the habitat usage between *C. acutus* and *Caiman crocodilus*. It was noted, however, that in areas where the two species were found together, the population levels of *Caiman* were considerably reduced. Other studies have also found that in the recent absence of *C. acutus*, other crocodilians have expanded into typical *C. acutus* coastal habitat: *C. moreletii* (Belize; Quintana Roo, Mexico; C. Abercrombie and M. Lazcano-Barrero, pers. comm.), *C. crocodilus* (Colombia, Medem 1981; Venezuela, Seijas 1986a). Medem (1981) and Seijas (1986a) have pointed out that in many instances, the ecological niche expansion of *Caiman* may be a direct result of the over-exploitation of the more commercially valuable *C. acutus* populations.

REPRODUCTIVE ECOLOGY

Territoriality, Courtship and Mating

Based on studies of captive crocodiles in Florida (Lang 1975a, Garrick and Lang 1977), and observations made on wild crocodiles in Mexico (Alvarez del Toro 1974) and the Dominican Republic (Inchaustegui, Ottenwalder, Robinson, pers. comm.) the breeding system of *C. acutus* is

polygynous. Adult males defend territories during the breeding season, excluding other males but permitting females to enter for courtship. Males are reported to interrupt the courtship activities of smaller neighboring males (S.Inchaustegui, J.A.Ottenwalder, D.Robinson, pers. comm.). Male territorial defense is composed of a series of stereotyped postures, frequently followed by actual or mock fighting. Territorial intruders are often approached in a head-emergent, tail-arched posture prior to fighting. Combat frequently includes lunges and chases. Following an aggressive encounter, dominant males commonly assume a raised "inflated posture" (Garrick and Lang 1977). Alvarez del Toro (1974) reported that, when encountering one another, territorial males would lift their snouts out of the water, snort loudly, and spurt water through their nostrils ("narial geysering" of Garrick and Lang 1977).

Indirect evidence of a polygynous mating system was also found in Etang Saumatre, Haiti (Thorbjarnarson 1984, 1988). Twenty-seven adult crocodiles were located in four distinct groups adjacent to the major nesting beaches one month prior to the peak oviposition period. The groups were well defined during the day, with a mean intergroup distance of 4.7 km, but at night would break up as individuals dispersed along the shoreline. These groups were inferred to be courtship assemblages, and contained one large male, and several smaller adults (presumably females but possibly including subdominant males). The male:female sex ratio of adult crocodiles captured in the same area shortly following the oviposition period was 1:3. At the same time, the corresponding sex ratio for another section of the lake, removed from the nesting beaches, was highly male biased (5 males:0 females) and indicated that a certain fraction of the adult male population may have been excluded from breeding.

Courtship and mating are exclusively aquatic activities. The main advertisement display of male C. acutus is a series of one to three headslaps (Garrick and Lang 1977). Courtship is usually initiated by the female, and typically consists of a somewhat stereotyped sequence of behaviors with females snout-lifting, swimming in slow circles around the male, or placing her head on the snout or back of the male. Males frequently respond to this activity by emitting a very low frequency sound, termed a sub-audible vibration (SAV) by Garrick and Lang (1977). The SAV is given from a typical "head-emergent tail-arched" posture, and causes the water on the males back to agitate upwards in what has been termed a "water dance" in alligators (Vliet 1987). Following the SAV are a further series of behaviors that include snout lifting and rubbing, bubbling, and temporary submergences. Copulation is done in shallow water and usually lasts several minutes (Lang 1975a, Garrick and Lang 1977).

The role of vocal signals in the establishment of territories, and courtship in C. acutus is not well understood. Garrick and Lang (1977) reported no bellowing in their study of captive individuals, but Herzog (1974) noted one instance of a captive C. acutus bellowing on land. Alvarez del Toro (1974) described bellowing in C. acutus in Mexico, noting that bellows are primarily heard during the early nighttime or morning hours, and were more frequent during the courtship season. The bellows are said to be answered by other males in the vicinity. A similar account is given by Medem (1981) for C. acutus, who also states that bellows can sometimes be heard in the afternoon, and are audible from afar.

Alvarez del Toro (1974) reported that females are territorial towards one another, but upon the approach of an adult male would snout lift and roar in an unusual fashion. Varona (1980) also indicated that in Cuba nesting females are territorial, and up to 5-6 may compete for one nest site. In other parts of its range, however, female C. acutus are apparently less territorial around the nest site and may nest colonially or in small groups: Florida (Kushlan 1982), Haiti (Thorbjarnarson 1984, 1988), Dominican Republic (pers. obs.).

Minimum Reproductive Size and Breeding Effort

The minimum reproductive size of male *C. acutus* is somewhat problematical as estimates must be based on size estimates of animals copulating (and producing fertile clutches), or anatomical examination. A further complication is that individuals may be physiologically mature, but excluded from breeding due to social factors.

Medem (1981) reported a captive 2.19 m total length (TL) male that mated with a 2.36 m TL female in Colombia. The resulting clutch, however, was infertile and suggests that the male was not yet sexually mature. The smallest reported lengths of mature males come from Etang Saumatre, Haiti, where two males captured adjacent to the nesting beaches during the breeding season, and assumed to be mature, were 2.82 m and 2.88 m TL (Thorbjarnarson 1984, 1988).

More data exist on the size of sexually mature females based on nesting individuals. Nevertheless, estimates vary considerably throughout the range of the species, suggesting that minimal size for reproduction needs to be treated as a population parameter, perhaps reflecting environmental or genetic differences in growth rates, and/or age at sexual maturity.

Alvarez del Toro (1974) reported never finding a reproductive female less than 2.8 m TL. Similarly, in Cuba, the reported minimum reproductive size of females is 2.7-3.0 m TL (Varona 1980). However, in other areas females are known to nest at much smaller sizes. Klein (1977) suggested 2.4 m TL as a minimum reproductive size for female *C. acutus* in eastern Honduras. In Etang Saumatre, females begin nesting at around 2.2-2.3 m TL, and never attain lengths over 2.5 m TL (Thorbjarnarson 1984, 1988). Based on the growth rates from recaptured individuals, the minimum reproductive age of females in Etang Saumatre is approximately 10 years. A similar minimum reproductive size in females was noted for nearby Lago Enriquillo (pers. obs.) as well as in Jamaica (L. Garrick, pers. comm.).

In Florida, Ogden (1978) estimated the total lengths of 8 *C. acutus* seen at nesting beaches was 3.9 m, 3.5 m, 3.1 m, 2.8 m (two nests), and 2.5 m (three nests; mean = 2.95 m). Also in Florida, Mazzotti (1983) estimated minimum nesting size to be 2.25 m TL, and captured 6 females at nests with total lengths of: 2.28 m, 2.47 m, 2.57 m, 2.59 m, 2.96 m, 3.08 m (mean = 2.66 m).

Estimates of breeding effort (the annual percentage of adult females that nest) have been made for two crocodile populations, Everglades National Park (Mazzotti 1983), and Etang Saumatre (Thorbjarnarson 1984, 1988). Both values were derived indirectly from estimates of the total adult female population size, and the known number of nests. The two populations had similar values: Florida 72%; Haiti 63.8%, and are comparable to published values for other populations: *A. mississippiensis*, 68.1% (although see Wilkinson (1984) for a much lower value); *C. niloticus*, 80% (Cott 1961); 67% (Blomberg et al. 1982); 87.6% (Graham 1968); 63% (Hutton 1984); and *C. johnsoni*, 90% (Webb et al. 1983).

Nest Site Selection

The American crocodile typically lays its eggs in a hole nest excavated into sand or soil near the waters edge. However, *C. acutus* appears to be one of the most adaptable of crocodilians in terms of nesting requirements and has been known to nest in a variety of situations. The use of soil or mangrove peat "mound" nests have been well documented in Florida (Campbell 1972,

Ogden 1978, Mazzotti 1983). Even more noteworthy are accounts that *C. acutus* will make small mound nests of scraped up vegetative litter. Under these circumstances the females are reported to dig a shallow hole into which the eggs are laid, then covered with leaf litter, grass or dead branches, forming a definite mound (although smaller in size than the nest mounds made by the sympatric *C. moreletii* and *Caiman crocodilus* (Alvarez del Toro 1974, Medem 1981). However, this behavior has not been well documented in the wild and probably plays an insignificant role in overall nesting ecology.

The ecological significance of hole versus mound nesting was discussed by Campbell (1972), who refuted the phylogenetic importance attributed to nesting mode described by Greer (1970, 1971). Campbell noted that mound nests are found most frequently in species that inhabit low-lying areas, swamps and marshes. He went on to speculate that individual differences in nest morphometry within a population may reflect the past nesting experience of specific females.

Perhaps of even greater important in defining nesting mode is the timing of nesting in relation to rainfall or water level variation. True mound nesters (e.g. the Alligatoridae) typically nest in the rainy season, frequently during peak water levels. Hole nesting crocodiles normally nest during periods of falling water levels (i.e. the dry season), with hatching taking place towards the beginning of the rainy season (see Timing of Nesting). However, with a hole nesting species such as *C. acutus*, the tendency to "mound" nests may be an adaptive response to nesting in low-lying areas where the probability of nest flooding is high (see Clutch Size, Fertility and Egg Mortality).

The following sections will provide accounts of nesting mode in two crocodile populations in very different habitats: the coastal lowlands of southern Florida, and the inland lakes of Hispaniola. The descriptions serve to highlight some of the variability in nest site selection.

South Florida - The principal nesting areas of *C. acutus* in southern Florida are found along creek banks, in exposed sandy beaches in Florida Bay, in man-made canal berms along the mangrove-lined bay side of Key Largo, and in the cooling canal system of the Turkey Point power plant (Ogden 1978, Mazzotti 1983, Gaby et al. 1985). Ogden (1978) noted a diversity of nesting sites in Florida Bay, but that all nests were located in well drained soil and had a deep water approach. Ogden classified nest sites into three major types which are, verbatim:

1. Open thickets of hardwood trees along the edges of 4 to 8 meter wide, deep water creeks with vertical, 0.5 to 1.0 m marl or muck banks.
2. Surrounded by varying amounts of hardwood shrubs and trees at the heads of narrow, shell-sand beaches.
3. In thickets of shrubby black mangrove (*Avicennia nitada*) behind marl banks rising 15 to 30 cm above water.

In Florida Bay two basic nest soil substrates are found: porous sand-shell soil, and marl; the latter having a very fine particle size and a high percentage of organic matter. The soil water content and resultant oxygen diffusion differ widely between the two soil types and play a significant role in determining egg physiology (Lutz and Dunbar-Cooper 1984; see Incubation and Nest Environment).

Ogden (1978) reported that 13 of 14 primary nest sites investigated had significant elevations (mounds) above the surrounding terrain. The elevations ranged from 9 to 65 cm (mean = 31 cm) and were apparently not correlated with location or soil type. Maximum diameters of nest mounds ranged from 1.0 m to 4.6 m (mean = 2.4 m, N = 14).

Eight of the 17 nests studied by Mazzotti (1983) in Florida Bay were classified as "mound" nests. During the course of this study subterranean flooding was found to be a major source of egg mortality. Under these circumstances mounding may be an adaptive feature reducing the probability of nest flooding (Mazzotti 1983: see Clutch Size, Fertility and Egg Mortality).

In five nests measured by Lutz and Dunbar-Cooper (1984), the mean depth to the top of the egg clutch was 33.5 cm. The corresponding depth to the bottom of the clutch averaged 51.0 cm.

Crocodile nests on Key Largo and Turkey Point are located in mangrove peat berms created during the construction of canals (Gaby et al. 1985, P. Moler, pers. comm.). The berms are generally elevated well above water level where the probability of nest flooding is usually minimal. On Key Largo the nests are normally situated in the open sun, although several nest sites are located under a low canopy of mangrove.

Hispaniola - The nesting biology of *C. acutus* has been studied in the Dominican Republic by Inchaustegui et al. (1980), and in Haiti by Thorbjarnarson (1984, 1988). The majority of the data from these studies deals with crocodiles in landlocked lakes: Lago Enriquillo in the Dominican Republic, and Etang Saumatre in Haiti.

Crocodile nests in Lago Enriquillo are located primarily in raised, sandy banks on two of the three largest islands in the lake. Additional nesting areas are found in several sandy to gravelly beaches situated around the lake's perimeter. Most nesting beaches are located in well drained sandy soils situated adjacent to calm water areas protected from the frequently intense surf that results from the easterly trade winds (6 of 7 major nesting beaches, pers. obs.). Courtship and mating were observed to take place in one of these calm-water refugia (Inchaustegui et al. 1980), and presumably a similar situation exists in the other areas. With a recent rise in lake level (about 5 m in 2 years following hurricanes in 1979 and 1980), crocodiles shifted nesting beaches as the old sites became inundated. However, in most areas nesting has continued in adjacent, higher, sites. The combination of suitable soil conditions with an adjacent calm-water refugium was sufficiently limiting as to lead to colonial nesting, with some beaches having 20-30 nests. All nests in Lago Enriquillo are hole-type nests.

In Etang Saumatre, which has no large islands, nesting is concentrated along 6.6 km of the uninhabited eastern lakeshore (Thorbjarnarson 1984, 1988). Nests are usually located in elevated sandy areas that were former lake shorelines, frequently on coralliferous limestone outcrops that extend down to the lakeshore. These areas provide a well drained nesting substrate, a deep water approach, and usually an adjacent calm-water refugium on the lee side of the limestone outcropping. Mean nest distance from the lakeshore was 27.5 m (range 7-47 m, N = 31) and height above the lake averaged 1.2 m (range 0.6-2.1 m, N = 31). Fifteen of 26 (57.7%) active crocodile nests were located in or adjacent to former charcoal making sites used in the past by local villagers. These charcoal sites provided a semi-open area in the surrounding thorn-scrub vegetation association, with a friable soil/charcoal fragment mixture. The use of former charcoal making sites for nesting has also been reported by Ottenwalder (pers. comm.) in the mangrove swamps of the Rio Massacre, Dominican Republic. However, in this situation the charcoal areas are raised mounds and represent the most elevated, well drained sites available.

In Etang Saumatre, nine physical parameters were measured at crocodile nest sites (Table 1). A stepwise discriminant analysis was performed among 15 null sites (chosen randomly, distance to lake fixed at 25 m), and 15 nest sites using 7 nest parameters (height above lake, soil moisture, percent shrub/tree canopy coverage, percent grass coverage, percent leaf litter coverage, height of woody vegetation, and distance to nearest tree). The analysis indicated that only soil moisture was important in distinguishing nest sites (mean 6.6% water by weight), from null sites (20.3% water; p

< 0.01). Percent shrub coverage was significantly higher at null sites (p < 0.05), but was correlated with soil moisture.

Nests in Etang Saumatre are hole-type nests with no mounding notable. The nest excavation is angled diagonally back into the soil. Mean perpendicular depth to eggs was: clutch top 24.1 cm (SD 4.7 cm, N = 13), and clutch bottom 37.9 cm (SD 4.3 cm, N = 12). Mean horizontal width of the egg chamber is 32.4 cm (SD 4.3 cm, N = 12). Because of a lower density of nesting females colonial nesting was not evident as it is in nearby Lago Enriquillo. The greatest number of nests found on any one beach was three.

Other Areas - Aspects of the nesting biology have also been noted in Jamaica (L. Garrick, pers. comm.), Cuba (Varona 1980), Mexico (Casas and Guzman 1970, Alvarez del Toro 1974), Panama (Breder 1946, Dugan et al. 1981), Honduras (Schmidt 1924, Klein 1977), Colombia, Venezuela and Ecuador (Medem 1981, 1983). These accounts support the generalization that *C. acutus* prefers to nest in sandy beaches, but is very adaptable and will nest in marginal areas such as gravel (Schmidt 1924, Alvarez del Toro 1974), wet, mucky soils (Varona 1980), wood chips (L. Garrick, pers. comm), or even make small, mound-type nests from vegetative matter (Alvarez del Toro 1974, Medem 1981, 1983).

Alvarez del Toro (1974) described a typical *C. acutus* nest in Chiapas, Mexico as being located in a sandy beach, beyond the bare sand fringe and usually near a shrub thicket. In Jamaica, Garrick (pers. comm.) noted that *C. acutus* nests were mounded, and found in sandy beaches located adjacent to mangrove swamps that provide habitat for the female. Along rivers, nests are positioned high up on banks in areas cleared by the female.

In Honduras, Schmidt (1924) found a crocodile nest in a gravel beach on an island in Lago Ticamaya, and Klein (1977) mentioned nests being located in sandy river bars. In Panama, *C. acutus* nests have been found in a clearing on a small forested island adjacent to Barro Colorado Island (Dugan et al. 1981), in a small lighthouse clearing in a forested mainland peninsula also near BCI (Rodda 1984), and in open, sandy river bars in the Rio Chucunague drainage (Breder 1946).

Table 1: Mean values of nine parameters for *C. acutus* nests in Etang Saumatre, Haiti. From Thorbjarnarson 1988.

Nest Parameter	Mean (SD)	Range	N
Distance to Lake (m)	27.5 (11.8)	7-47	31
Height above Lake (m)	1.2 (0.5)	0.6-2.1	31
Soil pH	6.2 (1.6)	5.2-7.1	15
Soil Moisture (% water)	6.6 (3.1)	3.4-14.3	12
Shrub/Tree Coverage (%)	30.1 (14.5)	10-60	29
Grass Coverage (%)	5.9 (5.8)	0-20	29
Leaf Litter Coverage (%)	18.4 (8.6)	10-30	29
Height of Vegetation (m)	3.4 (0.6)	2.0-4.5	27
Distance to Nearest Tree (m)	2.1 (1.1)	0.5-5.0	27

Nesting Behavior and Parental Care

Although Duval (1977) reports an interval of 84-107 days between observed copulation attempts and nesting in a captive situation, most reports from other captive and wild populations indicate that oviposition follows courtship activity by 1-2 months (Alvarez del Toro 1974, Garrick and Lang 1977, Varona 1980, Inchaustegui et al. 1980). Gravid females will begin visiting potential nest sites up to 4-6 weeks prior to laying (Ogden 1978, Thorbjarnarson 1984, 1988). These early visits are usually brief (less than one hour) and of irregular occurrence and provide the females with the opportunity to make shallow exploratory excavations. The nocturnal visits increase with frequency as the time for oviposition approaches, and egg laying usually follows several nights of more lengthy visits and increased digging activity (Ogden 1978). In Florida, digging is restricted to primary or secondary nest sites, usually found within 35 m of one another (Ogden 1978), but in Etang Saumatre, where more potential nest sites are available, excavations are frequently scattered among several sites (Thorbjarnarson 1984, 1988). Gravid females in both Lago Enriquillo and Etang Saumatre were noted to infrequently drop their eggs prematurely while walking along the beach searching for nest sites (both lakes), or even in the water (Lago Enriquillo). The etiology of this premature oviposition is unclear.

Nesting sites in Etang Saumatre are reused regularly. Forty-six percent of the nests located in 1984 were used the previous year, 15 % were used previous to 1983, and 39% were located in apparently new sites (Thorbjarnarson 1984, 1988). Similar to the situation in adjacent Lago Enriquillo, a rising lake level since 1980 has forced some crocodiles to seek new nesting sites.

Female C. acutus in Lago Enriquillo emerge from the water to nest shortly after dark (pers. obs.). One female was discovered in the final stages of egg laying at 2315h on 12 February 1982. Detailed behavioral observations of oviposition by a captive female were made in Isla Salamanca National Park, Colombia by Pachon, Ramirez and Moreno (cited in Medem 1981). Using her hind legs the female dug a nest cavity on 15 March, and the following night began excavating another hole from 0015h to 0400h. Once the digging was completed, the female remained motionless atop the nest until egg laying began at 0525h. Oviposition was accomplished with the female positioned with her hind legs over the edge of the hole, head slightly elevated, pectoral region pressed against the ground, and abdomen arched upwards. The first abdominal contractions lasted 5 minutes. During the next 21 minutes, 15 eggs were laid, the time interval between eggs diminishing from 5 min. 20 sec., to 5 seconds. Eighteen minutes after the last egg was deposited, the female began covering the eggs with soil and leaf litter, gradually shaping a mound 80 cm in diameter, and 10 cm high. This was apparently the females' (2.36 m TL) first nesting attempt and this may partially account for the small clutch size (Medem 1981).

Female C. acutus will remain in the vicinity of the nest during incubation (Alvarez del Toro 1974, Ogden 1978, Thorbjarnarson 1984, 1988). In some areas females are reported to actively protect nests, excluding other crocodiles or potential nest predators from the nest locale: Mexico (Alvarez del Toro 1974), Cuba (Varona 1980), Panama (Dugan et al. 1981); although this behavior is individually variable. In other areas females provide little or no nest protection: Florida (Ogden 1978) and Haiti (pers. obs.). There is no evidence that males play any role in nest defense in the wild.

Dugan et al. (1981) observed an adult female C. acutus protecting her nest by chasing away ovipositing iguanas. Iguanas would dig up crocodile eggs during the construction of nest burrows, and on 12 occasions the crocodile seized iguanas near her nest. The authors concluded that this behavior was a mixture of nest defense and predation.

Towards the end of the incubation period, female crocodiles will begin to make nocturnal visits to their nests, laying their heads atop the nest to listen for the release calls of the hatchlings (Ogden and Singletary 1973). Triggered by the grunts of the young, the female opens the nest using her front feet. Photographs of a wild crocodile opening a nest in Florida suggest that the female will help the hatchlings emerge from their eggs by gently squeezing the eggs between the tongue and palate (Ogden and Singletary 1973). Following hatching, the young are gathered in small groups into the female's mouth, where they are carried in the depressed gular pouch, and ferried to the water's edge. The female photographed in Florida (using an automatic device) carried a total of 34 hatchlings in 12 trips between the nest and the water (Ogden and Singletary 1973). Similar nest opening behavior has been observed or inferred for *C. acutus* throughout the species range (Alvarez del Toro 1974, Inchaustegui et al. 1980, Medem 1981, Thorbjarnarson 1984, 1988).

In some instances hatching is not simultaneous for all eggs and females may leave underdeveloped eggs buried in the nest, returning at a later date to open them (Ottenwalder, pers. comm.; pers. obs.). Mazzotti (1983) also noted that in Florida females may leave fully developed, vocalizing eggs in the nest. In one case a female hatched a nest during three visits over a four day period. In Lago Enriquillo, female crocodiles may remain on land in shaded areas with their hatchlings, or leave them under vegetation during the day (Inchaustegui et al. 1980). This behavior may have been related to the hypersaline lake water and resultant osmotic problems for hatchlings (pers. obs.; see Temperature and Salinity Relations).

The degree of maternal care for recently hatched *C. acutus* appears to vary considerably throughout the species range. The results of most studies suggest that the formation of distinct pods of young and maternal care of neonates is minimal in this species (Mazzotti 1983, Thorbjarnarson 1984, 1988; Rodda 1984). However, under certain conditions the formation of pods may be influenced by the habitat into which the young are born. In areas exposed to wave action or in hypersaline water the dispersal of hatchlings is almost immediate (see Habitat Selection, Activity and Movements) and there is virtually no group cohesion among the hatchlings. Nevertheless, in some areas adult crocodiles have been seen in the vicinity of loosely grouped hatchling assemblages (Mazzotti 1983, Thorbjarnarson 1984). Alvarez del Toro (1974) reported that in Mexico, hatchlings would remain grouped together near the female for several weeks following hatching. However, even in suitable juvenile habitats in south Florida and Haiti, pod formation is also ephemeral (Gaby et al. 1985, Thorbjarnarson 1984, 1988; P. Moler, pers. comm.). Campbell (1973) noted that young *C. acutus* are relatively non-vocal, and this observation has been supported in the wild by observations made by Mazzotti (1983). In as much as hatchling vocalizations serve to maintain group integrity, and/or communication with an adult, the non-vocal nature of hatchling *C. acutus* is another indication of lack of social cohesion in the young.

The seemingly unremarkable amount of maternal protection for hatchlings *C. acutus* may be a consistent character of the species, or it may reflect a recent change in behavior associated with human-related disturbance. Rand and Troyer (1980) have suggested that in Gatun Lake, Panama, past hunting has selectively eliminated adults that protected their young. Furthermore, as crocodilians are long lived animals with recognized learning ability (Bustard 1968, Webb and Messel 1979), a diminution in parental care may also be a learned response based on past experience with humans. Indeed, some historical accounts suggest that a higher degree of parental care may have existed in the past (e.g. Esquemeling 1678).

Timing of Nesting

The American crocodile, following the typical pattern for hole-nesting species, nests during the dry season, with hatching occurring near the beginning of the rainy season. According to the generally accepted hypothesis first presented by Cott (1961) for *C. niloticus*, oviposition during the dry season reduces the probability of nest flooding, and results in the young emerging during a time of increasing habitat and food availability. However, in *C. acutus* there exists a considerable amount of variation in the timing of egg-laying in relation to rainfall pattern. Nests in some regions hatch prior to the beginning of the rainy season, and in others during the early to mid-rainy season. A summary of *C. acutus* nest timing by geographic area is presented in Table 2. A more detailed analysis awaits further information on local nesting patterns and rainfall/water level schedules.

In Mexico, and along the Caribbean coast south to Costa Rica, *C. acutus* oviposits from March to May, the eggs hatching during the first half of the rainy season (June-August; Schmidt 1924, Carr 1953, Casas and Guzman 1970, Alvarez del Toro 1974, A. Carr, L. Ogren, pers. comm.). In Panama, and the Pacific coast of Costa Rica and Colombia, crocodiles tend to hatch somewhat earlier, even though the rainfall patterns are similar (Breder 1946, Dugan et al. 1980, Rodda 1984, W. Timmerman, pers. comm.). In these areas crocodiles hatch prior to the initiation of the rains. In the extremely wet Choco region of Pacific Colombia where little seasonal variation in rainfall exists, crocodiles apparently follow the same timing of nesting (Medem 1981).

Table 2: Timing of *C. acutus* nesting in relation to geographic area and rainfall pattern. See text for references.

Region	Timing of Nesting		
	Oviposition	Hatching	Rainy Season
Mexico:			
Pacific coast	March-May	June-Aug	June-Oct
Atlantic coast			
south to Costa Rica	March-May	June-Aug	May-Dec
Pacific coast			
Costa Rica-Colombia	Jan-Feb	April-May	May-Nov
Ecuador, Peru	Oct-Dec	Jan-March	Jan-April
Caribbean:			
Colombia	March	June	May-Nov
Venezuela	April-May	July-Aug	May-Nov
Caribbean Islands:			
Jamaica	March-April	June-July	May-Oct
Cuba	March	June	May-Oct
Hispaniola	Jan-April	April-July	April-Oct
Florida	April-May	July-Aug	May-Oct

South of Colombia rainfall patterns change drastically, becoming much dryer with a rainy season extending from January to April. The crocodiles in this region adapt accordingly and oviposit from October to December, suggesting that the eggs would hatch during the first half of the wet season (Medem 1981, Fiallos et al. ms).

Data are scanty for crocodile nesting along the Caribbean coast of Colombia and Venezuela, which has a typical Caribbean weather pattern (rains May-Oct/Nov). In Colombia, Medem (1981) reports that C. *acutus* nests hatch in April-May, but it is not clear to which part of the country he is referring. The only site specific datum is from Isla Salamanca where a captive female laid on 16 March (Medem 1981). Information from Venezuela suggests that in most coastal areas C. *acutus* hatch in April (Rio Yaracuy) or May (Lago Maracaibo region) (A.E. Seijas, pers. comm.), but in the arid region of Falcon state, the nests of one crocodile population near Chichiriviche are known to hatch in late August or early September. One nest at the Jatira Reservoir was found in the process of hatching on 28 August 1987 (A.E. Seijas, pers. comm.). However, in this arid region the peak rainfall is in November-December. These data would suggest that nesting in Venezuela follows the general Caribbean pattern, with the exception of the Falcon region where nesting is delayed, perhaps due to arid conditions and a delayed peak in rainfall.

The islands of Cuba, Jamaica, and Hispaniola share the typical Caribbean climatic pattern, and here C. *acutus* have a nesting schedule comparable to other Caribbean areas. Oviposition takes place primarily during March and April, and nests hatch during June-July (Inchaustegui et al. 1980, Varona 1980, L. Garrick, pers. comm.), i.e.during the first half of the rainy season. The notable exception to this is in Etang Saumatre, Haiti, where nests are constructed in late January and early February, and hatch late April-early May at the very beginning of the rainy season (Thorbjarnarson 1984, 1988).

In southern Florida, a similar seasonal rainfall pattern exists, but crocodiles are delayed by low winter and spring temperatures and do not nest until April-May, with the young hatching July-August (Ogden 1978, Kushlan and Mazzotti 1986). Captive crocodiles in southern Florida that originated from Jamaica follow the typical Florida nesting schedule (ovipositing April-May; Garrick and Lang 1977), indicating that at least with respect to temperature limitations timing of nesting is environmentally malleable.

Incubation and Nest Environment

Reported incubation periods for C. *acutus* nests range from 80 to 90 days (Table 3), although in one artificially incubated nest it was 107 days (Duval 1977). The length of incubation is temperature dependent, but under natural conditions nest temperatures appear not to fluctuate greatly. Over a 24 day period, Lutz and Dunbar-Cooper (1984) found a mean daily temperature variation of $1.4°$ C in a nest in southern Florida. During a 30 hour interval, the maximum temperature fluctuation among 6 nests in Haiti was $0.9°$ C (top of egg clutch), and $0.6°$ C (bottom; Thorbjarnarson 1984, 1988). Due to the thermal buffering effects of the soil, in both studies maximum nest temperatures were reached at night.

Among seven nests in Florida, Lutz and Dunbar-Cooper (1984) noted a trend of increasing nest temperature with time. Mean nest temperature increased from $30.9°$ C in late May-early June, to $34.3°$ C in early August. The rise in mean nest temperature was correlated with an increasing trend in mean air temperature.

The study of Lutz and Dunbar-Cooper (1984) also examined gas exchange in *C. acutus* nests. In southern Florida crocodiles nest in two distinct soil types, and the physical properties of the soil play an important role in determining gas exchange characteristics of the nest. Marl nests have a much finer soil particle size (primarily less than 246 microns), a higher mean water content (29.2% by weight), and a lower oxygen diffusion (1.96 x 10 cm/sec at 15% water content). Sand/shell nests have a larger particle size (0.5-3.3 mm), a lower mean water content (10.3%), and a higher oxygen diffusion (1.51 x 10 cm/sec at 16% water). Although the results were more clear-cut in the sand/shell soil, nests in both soil types demonstrated an increase in PCO_2, and a decrease in PO_2 during incubation. The lower potential for gas diffusion resulted in lower PO_2 and higher PCO_2 levels in the marl nests.

Lutz and Dunbar-Cooper (1984) also noted a 15% decrease in egg mass (water loss) during incubation. Somewhat similar results were reported by Moore (1953) who suggested that under normal conditions a clutch of crocodile eggs loses 8.6% of its mass by day 70 of incubation.

Table 3. Reported egg incubation periods in *C. acutus*. Data from Alvarez del Toro (1974); Varona (1980); Inc and Kushlan and Mazzotti (1986).

Location	Incubation Period (days)
Cuba	80-90
Florida	85
Mexico	80
Dominican Republic	84

Table 4: Reported values of clutch size for *C. acutus* N is the number of nests examined. Data from Kushlan and (1986); Lutz and Dunbar-Cooper (1984); Ogden (1978); Medem (1981); Breder (1946); Schmidt (1924); Inchausteg (1980); Thorbjarnarson (1988); and Alvarez del Toro (1971).

Location	Clutch Size	N
Florida	38.0	46
	39.1	8
	44	20
Colombia	40-60	-
Panama	46	1
Honduras	22	1
Dominican Republic	23.8	80
Haiti	22.5	14
Mexico	30-60	-

Clutch Size, Fertility and Egg Mortality

Reported values for clutch size in *C. acutus* (Table 4) range from lows of 22 (Schmidt 1924) and 22.5 (Thorbjarnarson 1984, 1988), to high figures of 81 (Ogden 1978) and 105 (Medem 1981). Extremely large clutches of eggs may be the result of more than one female ovipositing at the same nest site (Kushlan and Mazzotti 1986). This interpretation is supported by evidence from Florida and Haiti where two clutches known to have been laid by different females were laid in the same nest hole (Kushlan and Mazzotti 1986, Thorbjarnarson 1984, 1988).

Clutch mass from one nest in Florida was 5.2 kg (Lutz and Dunbar-Cooper 1984). Mean clutch mass from 14 nests in Haiti was 2.18 kg, and averaged 4.4% of adult female body mass (Thorbjarnarson 1984, 1988). Reported values of individual egg masses (early in incubation) are 91.3 g (Lutz and Dunbar-Cooper 1984), 97.0 g (Thorbjarnarson 1984, 1988) and 103.4 g (Duval 1977).

Mean egg dimensions are more often reported in the literature than egg mass and can be used to better show the variation in egg size. However, there is not enough evidence to determine if egg size varies with female size, or between populations. The largest reported mean egg dimensions are from Panama (52.0 x 79.0 mm, N = 46; Breder 1946), and Chiapas, Mexico (54 x 80 mm; Alvarez del Toro 1974). Smaller eggs have been reported from Haiti: 45.4 x 76.5 mm (Thorbjarnarson 1984, 1988), Cuba: 42-47 x 73-81 mm (Barbour and Ramsden 1919), and Honduras: 42-42.5 x 70-76 mm (Schmidt 1924), 46.6 x 75.4 mm (Thorbjarnarson and Vliet, unpubl. data). Large eggs containing two embryos have been reported from Cuba (Barbour and Ramsden 1919), where one nest contained two twin eggs (100 x 50 mm). The embryos were apparently well formed and healthy. A similar twin egg has been reported by Blohm (1948) for *C. intermedius* in Venezuela.

Egg fertility levels (determined by egg banding) have been reported from nests in south Florida and Haiti. Unbanded eggs could be the result of infertility, or early embryonic failure. In Florida, Kushlan and Mazzotti (1986) reported 90% of 314 eggs examined were banded. The range of values for individual nests was 46-100%, with only one nest having fewer than 84% banded eggs. In Haiti a similar value of 9.9% unbanded eggs was determined from seven clutches (range 70.6-100% banded) (Thorbjarnarson 1984, 1988).

Other than egg fertility rates, nest hatching success is influenced by three environmental factors: flooding, desiccation, and predation. An increase in soil moisture reduces soil oxygen diffusion capacity (Lutz and Dunbar-Cooper 1984), as well as that of the eggshell (Ferguson 1985). Although *C. acutus* nests during the dry season, in areas where nests are located in low-lying areas, flooding may be an important factor in egg mortality. In the Florida Bay region, flooding drowned two of 17 (11.8%) of the nests studied by Kushlan and Mazzotti (1986), and partially destroyed two other nests. Flooding was subterranean and hence was not recognizable unless the nests were excavated. It is perhaps significant that four of nine "hole" nests experienced flooding mortality, whereas none of the eight "mound" nests flooded.

In areas where female *C. acutus* have access to higher, well drained nesting sites, flooding mortality is usually minimal. On Key Largo and at Turkey Point in Florida, females nest in raised spoil banks and the nests experience little or no flooding mortality (P. Moler, pers. comm.). In Etang Saumatre, Haiti, only one of 15 (16.7%) nests examined was lost to flooding and this was due to excessive surface runoff from a nearby arroyo.

Egg desiccation has been reported to cause egg mortality in Florida. Mazzotti (1983), found 27 eggs from four different nests to have air sacs, which according to Ferguson and Joanen (1983) are indicative of excessive egg water loss.

Although predation is usually considered to be the most important factor governing nest success in *C. acutus*, few quantitative estimates of predation rates are available. Kushlan and Mazzotti (1986) reported that during 1971-1982, 14% of 99 clutches in Florida were predated. Raccoons (*Procyon lotor*) were the only nest predators observed. Although Dugan et. al. (1981) reported that nesting iguanas would dig up crocodile eggs, all other reported nest predators are mammals: *Procyon lotor*, *P. cancrivora*, *Nasua narica*, *Dusicyon thous*, *Conepatus* sp., *Canis latrans*, *Mephitis macroura*, and *Spilogale augustifrons* (Alvarez del Toro 1974, Medem 1981, Camacho 1983, Kushlan and Mazzotti 1986). On Hispaniola, an island with a depauperate mammalian fauna (both natural and man induced), few natural nest predators are found and nests are rarely depredated other than by man. A 0% natural predation rate was found among nests in Etang Saumatre (Thorbjarnarson 1984, 1988).

DIET

The diet of *C. acutus* follows the typical ontogenetic shift described for other species of crocodilians (Cott 1961, Chabreck 1971, Taylor 1979, Webb et al. 1982). Hatchlings and juvenile crocodiles feed primarily on aquatic and terrestrial invertebrates (Alvarez del Toro 1974, Medem 1981, Thorbjarnarson 1984, 1988) or small fish (Schmidt 1924, Alvarez del Toro 1974). With increasing size, crocodiles feed increasingly on larger vertebrate prey with fish being the dominant food item (Alvarez del Toro 1974, Medem 1981, Thorbjarnarson 1984, 1988).

Among hatchling and juvenile *C. acutus* the most commonly reported prey are aquatic insects (Dyctisidae, Hydrophilidae, Belastomatidae) and their larvae (Libellulidae), and snails (Alvarez del Toro 1974, Medem 1981). In Etang Saumatre, Haiti (Thorbjarnarson 1984, 1988), the dominant prey items flushed from the stomachs of hatchling crocodiles (less than 0.5 m TL; N = 8) in terms of biomass were fiddler crabs (*Uca bergersii*, 33.5% of prey mass), Hymenoptera (25.0%), and amphipods (25.0%). Among juveniles (0.5-0.9 m TL; N = 28), the principal prey were *Uca* (62.3% by mass), odonate larvae (10.3%), and Coleoptera (8.9%). Other frequently encountered prey were: Arachnida, Lepidoptera, Scolopendera, Hymenoptera, and Gerridae. Only 9.3% of the crocodiles under 0.9 m TL contained fish (N = 64), principally small poeciliids (*Limia* sp., *Gambusia hispaniole*). Other than fish the only vertebrate remains found in juveniles' stomachs were one turtle (*Pseudemys decorata*), and unidentified bird remains.

Alvarez del Toro (1974) reported that in Mexico, subadult crocodiles feed on insects (*Belastoma*, *Disticus*, *Hydrophilus*), fish, frogs, small turtles, birds, and small mammals. Two specific crocodiles mentioned (1.1 m, 1.2 m TL) had catfish (*Mollinesia*), a dove (*Zenaidura macroura*) and a marsupial (*Philander laniger*) in their stomachs. Subadult crocodiles in Etang Saumatre (0.9-1.8 m TL; N = 5) fed principally on aquatic invertebrates including odonate larvae (35.3% by mass), *Uca* (32.6%), and spiders (14.5%), but also took an increasing number of birds (17.7%; Thorbjarnarson 1984, 1988).

Adult crocodiles, while primarily piscivorous, feed on a variety of prey. Schmidt (1924) reported that one 3 m crocodile in Honduras contained a turtle shell, remains of a 1.2- 1.5 m crocodile, and peccary hoofs. Besides two marine catfish, Medem (1981) found fragments of *Pomacea* snails in the stomach of a 3.17 m crocodile in Colombia. Medem (1981) also mentions observing a crocodile eat a turtle (*Podocnemis lewyani*). Alvarez del Toro (1974) comments on the

formerly widespread problem of crocodiles eating domestic livestock in Mexico. Based on a small sample of crocodiles in Etang Saumatre, fish (primarily Cichlidae) and birds were the most common prey items. Adults were also seen to eat turtles and domestic animals (dogs, goats; Thorbjarnarson 1984, 1988).

Observations on feeding behavior in Etang Saumatre indicate that crocodiles use both active and passive modes of foraging. Juvenile crocodiles were frequently seen at night along shallow water shorelines making rapid sideswipes at surface disturbances. This method of foraging probably accounted for the high percentage of non-aquatic invertebrates in their diet. The presence of odonate larvae in crocodile stomachs suggests young crocodiles may also actively forage amongst submerged vegetation and/or bottom sediments (Thorbjarnarson 1984, 1988).

Adult crocodiles in Etang Saumatre were also frequently observed in shallow water areas where concentrations of cichlids (*Cichlasoma hatiensis*, *Tilapia mossambica*) were found. Crocodiles were observed to remain stationary on the bottom, occasionally making sideswipes at passing fish. Crocodiles also concentrated under a heron rookery during the birds nesting period, ostensibly to catch young that fall out of the nest (Thorbjarnarson 1984, 1988). Medem (1981) mentions an unconfirmed fishing technique used by crocodiles in Colombia. Floating at the surface with the mouth partially open, the crocodile regurgitates small quantities of partially digested food. The food attracts fish to the vicinity of the crocodile's mouth were they are caught using rapid sideswipes.

POPULATION ECOLOGY

Population Density, Biomass, and Size-Class Structure - Published values for crocodilian population density rarely reflect true steady-state population levels, but tend rather to indicate the intensity of past or present human exploitation of crocodiles. Furthermore, differences in census methodology, and habitat type frequently make interpopulation comparisons difficult. Nevertheless, density values can be informative, and published figures are tabulated for crocodile populations in southern Florida, Honduras, Venezuela, and Haiti (Table 5).

Density values from Florida are expressed in units of time and so are not directly comparable to the other figures which are calculated on the basis of crocodiles per kilometer of shoreline. Nevertheless, the data for Florida indicate a very low density crocodile population.

The density values for Honduras (0.51/km) and Venezuela (1.57/km) are principally from coastal lagoons and mixed coastal habitats respectively, and represent populations severely depleted by hunting.

The highest reported densities of *C. acutus* come from lacustrine habitats. Schmidt (1924) reported an extremely high crocodile density in Lago Ticamaya, Honduras. Etang Saumatre, in Haiti, had an overall crocodile density of 6.3/km (including all crocodile size-classes), even though the population has been somewhat depleted by hunting and other human-related mortality. Excluding the exposed, rocky shorelines avoided by crocodiles, the ecological density in Etang Saumatre was 9.6/km. The crude and ecological densities for crocodiles over 1.8 m total length were 1.0/km and 1.5/km respectively. Within the lake crocodile density varied between habitats. Among the major habitat subdivisions (with more than 1 km shoreline) mean densities ranged from a high of 14.5/km (*Conocarpus* fringe) to 0.2/km for the rocky, steep shore gradient areas (Thorbjarnarson 1984, 1988).

Table 5: Reported densities of wild populations of *C. acutus*. Sources: Mazzotti (1983); Klein (1977); Seijas (1986 Thorbjarnarson (1988).

Location	Survey Method	Mean (Range)	Habitat Type
Florida, Everglades N.P.	boat,night	0.21/hr (0.13-0.40)	coastal mangrove
	helicopter (day)	0.61/hr (0.30-1.15)	
	fixed wing (day)	0.63/hr (0.0-0.97)	
Eastern Honduras	boat,night	0.51/km (0.0-2.4)	river
Venezuela	boat,night (day)	1.57/km (0.08-3.67)	river, coastal mangrove
Haiti, Etang Saumatre	boat,night	6.3/km (0.16-21.25)	lake

A population estimate was made for Lago Enriquillo, Dominican Republic, based on nesting levels reported by Inchaustegui and Ottenwalder (pers. comm.), and nesting effort information and population demographic data from adjacent Etang Saumatre (Thorbjarnarson 1984, 1988). The total adult crocodile population was calculated to be 385-525 (based on 100-150 nests annually), or 3.0-4.0 adults/km of shore (crude density). Assuming a similar population structure as in Etang Saumatre, overall density (including all size-classes) is estimated to be 18.9-25.7/km (Thorbjarnarson 1984, 1988). Even using the conservative lower figure, Lago Enriquillo would have the highest density for any *C. acutus* population known, and among the highest reported for any species of crocodile.

The most complete data set for *C. acutus* density in a variety of coastal habitats is that of Seijas (1986b) from Venezuela. Among 6 coastal rivers, the highest mean density of crocodiles was 2.2/km (Rio Yaracuy, maximum subsection density 3.5/km, section B). Of those areas that had crocodiles, the lowest riverine density was 1.07/km (Rio Neveri). In mangrove swamp habitats, crocodile densities ranged from 3.67/km (Turiamo) to 0.08/km (Cuare). The only density value for a freshwater reservoir was 1.02/km.

Crocodile biomass values have been calculated only for lake habitats in Hispaniola (Thorbjarnarson 1984, 1988). In Etang Saumatre, crude biomass was estimated to be 66.6 kg/km shoreline. Excluding habitats avoided by crocodiles the ecological biomass figure was 101.7

kg/km. Based on the above mentioned population estimate for Lago Enriquillo, Dominican Republic, crude biomass in this lake was calculated to be 188.4-256.1 kg/km.

The size-class distribution of three *C. acutus* populations have been reported: Florida (Gaby et al. 1985, Mazzotti 1983), eastern Honduras (Klein 1977), and Etang Saumatre, Haiti (Thorbjarnarson 1984, 1988; Table 6). Whereas the values for Florida and Haiti represent data obtained during nocturnal boat surveys, the Honduras figures are from commercially harvested animals and hence may be somewhat biased towards larger individuals, and do not include crocodiles less than one meter total length.

A large percentage of the crocodiles sighted in Everglades National Park (46.9%) were subadults (1.5-2.0 m TL).

Although the size-class limits vary somewhat, a smaller percentage of the population at Turkey Point, Florida (18.7%, 1.21-1.83 m TL, Gaby et al. 1981) and Etang Saumatre (10.7%, 0.9-1.8 m TL, Thorbjarnarson 1984, 1988) were in the subadult size range. In both these two populations, a larger percentage of small crocodiles was found: 56.3% Turkey Point, 74.3% Etang Saumatre (less than 1.21 m and 0.9 m TL respectively).

Among these three crocodile populations the percent composition of adults was similar: Everglades 24.5%, Turkey Point 25.0%, Etang Saumatre 15.7%. As the Etang Saumatre figures include hatchling crocodiles, a comparable figure to the Florida values for percentage of adults would be somewhat higher. Seijas (1986b) estimated that only 35 of 293 (11.9%) of the crocodiles (including hatchlings) seen in Venezuela were adults. An even smaller percentage of adults (3.7%) was noted by Garrick (pers. comm.) from a sample of 268 crocodiles captured in Jamaica.

Sex Ratio - Figures for *C. acutus* population sex ratios are available for Florida, Etang Saumatre, Haiti, and eastern Honduras. Among adult and subadult crocodiles captured in the Everglades National Park, Mazzotti (1983) found a female biased sex ratio of 2.4:1 (N = 17). At the nearby Turkey Point site, a slightly male biased ratio (0.75:1, N = 7) was noted (Gaby et al. 1985). Together these data suggest an overall 2:1 female biased sex ratio (Kushlan and Mazzotti 1986).

In Etang Saumatre, the sex ratio of 28 adult and subadult crocodiles captured was 0.75:1. Including juveniles, the overall sex ratio was still male biased 0.69:1 (N = 54; Thorbjarnarson 1984, 1988) although the difference was not found to be significant (binomial test Z = 1.22).

Based on a sample of 32 *C. acutus* commercially harvested in Honduras, Klein (1977) reported 14 females and 18 males (0.78:1). A larger sample of 92 wild captured crocodiles over 1.83 m TL was sexed at the Hacienda El Tumbador crocodile farm in Honduras (King, Thorbjarnarson and Vliet, unpubl. data). The majority of crocodiles in this sample came from the Rio Aguan and were composed of 40.2% males, 59.7% females. Although strongly female biased, this difference was not significantly different.

Growth Rates - Published values of growth rates in *C. acutus* are mostly from the first year or two of life (Table 7) and indicate that during this period animals can grow extremely rapidly. Over the first several months following hatching, growth rates are very high, and in some instances (e.g. Florida) may exceed 0.3 cm TL/day, although the more normal value for this time are in the 0.1-0.2 cm TL/day range (P. Moler, pers. comm.).

In most populations the initial rapid burst of growth slows considerably in older hatchlings and juveniles (Haiti and Panama 0.05-0.10 cm TL/day), but in Florida crocodiles up to 621 days old have been reported with mean growth rates of up to 0.134 cm TL/day (Gaby et al. 1981).

Table 6: Size-class distributions of four *C. acutus* populations. SC=Size class, PP=Percent of population. References in text.

				LOCATION			
	Florida			Honduras		Haiti	
Everglades NP		Turkey Pt					
SC	PP	SC	PP	SC	PP	SC	PP
0.50	6.1					0.3-0.9	74.3
0.75	12.2	0.60-					
1.00	8.2	1.20	56.3	1.0-			
1.25	2.0			1.5	20.3	0.9-	
1.50	20.4	1.21-				1.8	10.0
1.75	14.3	1.83	18.7	1.5-			
2.00	12.2			2.0	31.3		
2.25	18.4					1.8-	
2.50	2.0	>1.83	25.0	2.0-		2.7	10.7
2.75	4.1			2.5	26.6		
				2.5-		>2.7	5.0
				3.0	14.1		
				3.0-			
				3.5	6.2		
				>3.5	1.6		
Sample size	49		16		64		447

Table 7: Reported growth rates of free-living juvenile *C. acutus*. Sources: Thorbjarnarson (1988); P.Moler (pers. comm.); Gaby et al. (1981), Mazzotti (1983), Rodda (1984).

Location	Size or Age Class	Mean Growth Rate (cm TL/day)	N
Haiti	0-3 months	0.111-0.135	13
	0.3-0.9 m	0.058	10
	0.9-1.8 m	0.090	2
Florida	0-81 days	0.117-0.214	85
	0-124 days	0.158	9
	0-621 days	0.134	5
	0-17 months	0.112	-
Panama	0-10 months	0.088-0.105	-
	0-22 months	0.052-0.070	-

These latter data, from Turkey Point, may be considered somewhat anomalous in that the crocodiles are inhabiting cooling canals with elevated temperatures. However, comparable growth rates in *C. acutus* have been noted in other parts of Florida (Lang 1975b, P. Moler, pers. comm.). The rapid growth of Florida crocodiles is all the more remarkable as due to low winter temperatures, crocodiles do not grow during 4 months of the year (December-March, P. Moler, pers. comm.).

Growth data from crocodiles more than two years old are scanty. Two crocodiles in the 0.9-1.8 m size class in Etang Saumatre grew at an average rate of 0.09 cm TL/day (Thorbjarnarson 1984, 1988). Garrick (pers. comm.) recaptured a 6 year old crocodile (tagged when 58.7 cm long) that grew at an average rate of 0.05 cm TL/day over the interval. A six year 11 month old crocodile from Key Largo was 2.03 m TL (P. Moler, pers. comm.). This indicates an average growth rate of approximately 0.08 cm TL/day.

Mortality - Mortality in post-hatching *C. acutus* is highest during the first few years of life when the crocodiles are small and vulnerable to a host of predators, or environmental problems (e.g salt balance, low temperature). Quantitative estimates of survivorship of hatchling crocodiles in southern Florida indicate that mortality rates vary considerably from place to place. Gaby et al (1985) noted that at Turkey Point, approximately 11% of captured hatchlings survived at least one year. Ogden (1978) and Lang (1975b) radio tracked a group of 17 hatchlings for periods of up to 6 weeks. Ogden (1978) reported that at least one half of this sample died during the course of the study. On Key Largo, based on recaptures and resightings of marked individuals, hatchling survivorship can be much higher and in some years > 50% of the hatchlings may survive their first year (P. Moler, pers. comm.). Based on recaptures from one cohort, an estimate of minimal survivorship to 4 years is 25%. However, hatchling and juvenile mortality vary considerably from year to year, and these values may represent near maximum survivorship values (P. Moler, pers.comm.).

Potential predators of young crocodiles are numerous and include large wading birds (*Ardea herodias*, *Nycticorax nycticorax*, *Casmerodius albus*), raptors (*Buteo magnirostris*, *Herpetotheres cachinnans*, *Heterocnus mexicanus*) and mammals (*Procyon lotor*, *Felis pardalis*, *F. weidii*, *F. jagouarundi*, *Canis latrans*; Alvarez del Toro 1974, Inchaustegui et al. 1980, Medem 1981, Camacho 1983, Thorbjarnarson 1984, 1988). Crabs (*Callinectes* sp., *Cardisoma guanhumi*) have also been observed depredating, or implicated in predation on hatchling crocodiles in Florida (Lang 1975b, Ogden 1978). Several species of predatory fishes have been reported to eat small crocodiles (*Pseudoplatystoma fasciatus* (Medem 1981), *Lepisosteus tropicus* (Camacho 1983)). Mazzotti (1983) mentions lemon sharks (*Negaprion brevirostris*), snook (*Centropomis undecimalis*) and tarpon (*Megalops atlantica*) as potential natural predators of *C. acutus* in Florida coastal waters.

With increasing crocodile size the predators of *C. acutus* diminish rapidly in number. Other than man, large crocodiles have few potential predators. Alvarez del Toro (1974) reports that jaguar (*Panthera onca*) will kill subadult crocodiles and mentions one instance of an adult jaguar killing a 2.5 m *C. acutus*. Medem (1981) states that near Isla Fuerte, Colombia, fatal attacks by white sharks (*Carcharodon carcharias*) on adult crocodiles were not uncommon in the past.

Mortality due to cannibalism in *C. acutus* is not well understood, but apparently occurs under certain circumstances, particularly in high density situations. In the formerly dense *C. acutus* population in Lago Ticamaya, Schmidt (1924) reported finding the remains of a 1.2-1.5 m crocodile in the stomach of a 3 m individual. He also reports a colleague seeing a large crocodile eating a smaller one. Varona (1980) cites Gundlach reporting that large *C. acutus* will eat small ones.

Under certain circumstances mortality of hatchling or small juvenile crocodiles may be directly related to environmental factors. The cool winters in Florida are known to limit growth in small crocodiles, and it is possible that short-term cold spells could cause mortality. Osmoregulatory failure is also important in some areas. In at least one population, Lago Enriquillo, it is the primary source of hatchling mortality (Inchaustegui et al. 1980, pers. obs.). Ogden (1978) and Mazzotti (1983) also mention hurricanes as potential factors in crocodile mortality in southern Florida.

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PRESENT KNOWLEDGE ON
THE WEST AFRICAN SLENDER-SNOUTED CROCODILE,
Crocodylus cataphractus CUVIER 1824
AND THE WEST AFRICAN DWARF CROCODILE
Osteolaemus tetraspis, COPE 1861

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INTRODUCTION

Very little has been published on the three crocodile species occurring in west Africa. This is particularly true for the two species endemic to west Africa, the west African long-snouted or slender-snouted crocodile (*Crocodylus cataphractus*, Cuvier 1824) and the west African stumpy, broad-fronted or dwarf crocodile (*Osteolaemus tetraspis*, Cope 1861). By contrast, for the Nile crocodile (*C. niloticus*, Laurenti, 1766), which ranges over the whole of tropical Africa, there is much information available from east and southern Africa. This lack of information on the west African crocodile populations results from a number of factors:

- the very secluded habitat of the forest dwellers *C. cataphractus* and *O. tetraspis*, which severely restricts field investigations;
- the evolution of national parks and the development of wildlife management has been comparatively slow in west African countries. This has been particularly the case in the forest zones;
- The belly skin of the west African forest crocodiles is less valuable for commercial exploitation, this reduces the interest of the skin industry;
- The size of west African crocodiles is less spectacular and their population density is lower, so reducing their show effect in reserves and on farms.

In essence this chapter tries to give a short overview on our present understanding of the biology and ecology of *C. cataphractus* and *O. tetraspis*, gathered by researchers both on field investigations in west Africa and in captive-breeding in zoos on several continents.

SPECIES PRESENTATION

The 3 species of crocodiles occurring in west Africa belong to 2 genera: The genus *Crocodylus* represented by two species and the genus *Osteolaemus* represented only by one.

Based on exact description of these species, given by Villiers (1958), the basic distingishing characteristics of these crocodiles are shown in Table 2.

Table 1. Species of west African crocodiles.

Scientific name	*Crocodylus niloticus* Laurenti 1766	*Crocodylus cataphractus* Cuvier 1824	*Osteolaemus tetraspis* Cope 1861
English name	Nile crocodile	Slender-snouted crocodile	Dwarf crocodile
French name	Crocodile du Nil cuirassé	Crocodile à nûque large	Crocodile à front
German name	Nil-krokodil	Panzer-krokodil	Stumpf-krokodil
Dioula name	Bamba gbèman	Bamba da Jan	Bamba fiman

Table 2.

Species	*Crocodylus niloticus*	*Crocodylus cataphractus*	*Osteolaemus tetraspis*
snout length	1-2/3 - 2X > basal width	2-2/3 - 3-1/3 X > basal width	about = basal width
dental format	18-19 / 15	17-18 / 15	16-17 / 14-15
nuchal scales	2 transverse series 1st 4 scales 2nd 2 scales	2 transverse series 1st 2 scales 2nd 2 scales	3 transverse series 1st 2 big scales 2nd 2 big scales 3rd 2 very small scales
coloration	back: bright olive/ bronze or dark green; belly: pale yellowish	back: dark olive; belly: bright yellowish with dark patches	back: black with yellowish patches on tail & jaw; belly: pale yellowish with many blackish patches
Maximum length	4-5 m*	3-4 m	1.8 m

* in west Africa

SYSTEMATICS AND EVOLUTION

The crocodiles were first classified in a the order Crocodilia by Gmelin in 1788. In 1766 Laurenti established the species *C. niloticus*. In 1824 Cuvier became the first to distinguish a second species in Africa, *C. cataphractus*. It was only in 1861 that the species *O. tetraspis* was established by Cope. Another crocodile from Zaire was described by Schmidt (1919) as *Osteoblepharon osborni*. Inger (1948) later annulled this new genus and described this crocodile as *Osteolaemus osborni*, but since Wermuth and Mertens (1961) it has been regarded as a subspecies of *O. tetraspis*, called *O. tetraspis osborni*.

The systematic classification of the three west African crocodile species is shown in Table 3.

Table 3.

Phylum	Chordata
Sub-Phylum	Vertebrata
Class	Reptilia
Order	Crocodilia
Suborder	Eusuchia
Family	Crocodylidae
Subfamily	Crocodylinae
1st Genus	*Crocodylus*
1st Species	- *niloticus*
2nd Species	- *cataphractus*
2nd Genus	*Osteolaemus*
2nd Species	- *tetraspis*

According to a theory of Greer (1970), all Recent crocodilians derive from a hypothetical ancestor which built its nest by digging a hole in the ground. From this ancestor some crocodilians evolved in such a way that they started to construct mound nests on the surface of the ground by heaping up dead leaves and rotting vegetation. In terms of their pattern of nest construction the two forest species of west African crocodiles belong to this branch of evolution, whereas the Nile crocodile remained in the principal line, continuing to construct their nests under the earth.

GEOGRAPHICAL DISTRIBUTION

In contrast to *C. niloticus*, which is found all over tropical Africa and Madagascar, the range of the two other species is limited to the equatorial forest zones, centered in the tropical rain forest around the Gulf of Guinea and the River Congo. Passing through the deciduous forest coming to the gallery forests in the Guinean and Sudanese savanna, they are found more and more rarely. Table 4 shows the countries and river systems from west to east where their presence has been documented.

Table 4.

Country	*Crocodylus cataphractus*	*Osteolaemus tetraspis*
Senegal and Gambia	Saloum delta, River Gambia and its tributaries Senegal-, Falémé- and Casamance rivers and their tributaries (Pooley 1982)	Saloum delta, River Gambia and its tributaries (Villiers 1956a, b, 1958, 1959, Pooley 1982)
Guinea Bissau	no information available	no information available
Guinea	tributaries to River Niger Kourai, Sankarani and Boa rivers (Waitkuwait 1986)	Kourai, Sankarani, Boa Bafing, Mafou rivers (Waitkuwait 1986)
Sierra Leone	Moa and Morro rivers (Waitkuwait 1986)	River Jong at Magburaka (IUCN 1979)
Liberia	Mano, Loffa, St. Paul, Mani, Cess, Sangwin and Douabé rivers (Waitkuwait 1986)	Mani, Loffa, St.Paul, Mani Cess, Sangwin and Douabé rivers (Waitkuwait 1986)
Mali	Baoulé, Bagoé, Kankélaba rivers (Waitkuwait 1986)	Baoulé, Bagoé, Kankélaba rivers (Waitkuwait 1986)
Ivory Coast	Baoulé, Bagoé, Sassandra, Bafing, Nzo, Lobo, Cavalla, Hana, Meno, Néka, Tabou, Dodo, Néro, San Pedro, Bandama, Maraoué, Badénou Solomougou, Nzi, Boubo, Go Comoé, Iringou, Kongo, Kolonkoko, Agnéby, Bia and Tanoé rivers; Grand Lahou, Ehrié, Aby, Tendo and Ehy lagoons (Waitkuwait, 1986)	Baoulé, Bagoé, Sassandra Bafing, Nzo, Lobo, Cavalla, Hana, Meno, Néka, Tabou, Dodo, Néro, San Pedro, Bandama, Maraoué, Badénou, Solomougou, Nzi, Boubo, Go, Comoé, Iringou, Kongo, Kolonkoko, Agnéby, Bia and Tanoé rivers, Grand Lahou, Ebrié, Aby, Tendo and Ehy lagoons (Waitkuwait 1986)
Burkina Faso	Comoé, Black-Volta, Bougouriba rivers (Waitkuwait 1986)	Comoé, Black-Volta, Bougouriba rivers (Waitkuwait 1986)
Ghana	Black-Volta, Tanoé, Bia rivers (Waitkuwait 1986); Densu, Pra, Mole, White Volta rivers, Obosum and tributaries, Dwija and tributaries, Sene and tributaries, Lake Volta and Lake Kainji (Pooley 1982)	Black-Volta, Tanoé, Bia rivers Offin and (Waitkuwait 1986) Bia rivers, other small forest rivers, Volta Lake (Pooley 1982)

Table 4. (cont.).

Togo	Mono and Oti rivers (Tornier 1901, Waitkuwait 1986)	Mono and Oti rivers (Waitkuwait 1986); Mare at Kini Kopé (Tornier 1901, IUCN 1984)
Benin	River Ouémé (Pooley 1982, Waitkuwait 1986	Ouémé, Mékrou and Alibori rivers (Pooley 1982, Waitkuwait 1986)
Niger	no information available	no information available
Nigeria	Gaji, Yankari, Barkono, Benue rivers (Pooley 1982)	River Sombreiro near Abua (King 1955); more common in forest rivers in central east, less common in west (Pooley 1982)
Cameroon	tributaries of the River Cross (Torniet 1902, Abercrombie 1978)	near Douala, small rivers of Mount Cameroun (Tornier 1902, Pooley 1980)
Chad	Chari, Aouk, Aoukalé, Bangoran rivers, Lake Chad (Pooley 1982)	no information available
Central African Republic	River Oubangui and tributaries (Gournay pers. comm.)	Birao region (Pooley 1982)
Gabon	River Ogooué, small coastal and inland rivers (IUCN 1979, Pooley 1980)	mangroves near Libreville, swamp areas of Woleu N'tem and Ogooue Ivindo (Pooley 1982)
Congo	Oubangui, Sanga and other rivers near to the Central African border (Pooley 1982, Waitkuwait 1986)	Oubangui, Sanga and other rivers near to the Central African border (Pooley 1982, Waitkuwait 1986)
Zaire	Dungu, Népoko, Uele, Oubangui, Zaire rivers (Pooley 1982, Waitkuwait 1986)	Subspecies *O. t. osborni* in the northeast, lower parts of River Zaire. Subspecies *O. t. tetraspis* in the upper parts of River Zaire (Pooley 1982)
Tanzania	only in Lake Tanganyika in Luichi, Malagarasi rivers (Pooley 1982)	not present
Angola	only in rivers at the border to Zaire and Cabinda (Pooley 1982)	only in the Cabinda enclave (Pooley 1982)
Zambia	Luapula, Kalungwishi rivers, Lakes Mweru, Mweru Wantipa and Tanganyika (Pooley 1982)	not present

BIOLOGY AND ECOLOGY

A comparative analysis of the biology and ecology of two related species living in the same environment should show particular adaptations in terms of different habitat preferences, nesting areas, reproductive timing and behavior, feeding resources, according to the different ecological niches inhabited. In this way the two species coexist rather than compete within the ecosystem. For this reason one can find a situation of only partial competition reflecting the degree of the relationship between the two species.

Habitat - Table 5 shows the habitat preferences of the two crocodile species indicated by hunters and fishermen in 60 villages in the Ivory Coast in questionnaires conducted by Waitkuwait (1986).

Table 5.

Species	Crocodylus cataphractus	Osteolaemus tetraspis
uncovered, bright water	23 (38.3%)	4 (6.7%)
covered shady water	23 (38.3%)	13 (21.7%)
swamps and swamp forests	14 (23.3%)	43 (71.7%)
total number of answers	60 (100%)	60 (100%)

This table shows that *C. cataphractus* prefers to stay mainly in the open waters of rivers, lakes or lagoons. *O. tetraspis* enters these only occasionally, preferring swamps beside the open water systems and water pools remaining in periodically flooded swamp forests. It remains in the vicinity of slow flowing waters and calm bays, and stays in burrows beside the waterline.

These results are confirmed by night-counts in different biotopes of the Ivory Coast (Waitkuwait 1986). In the Comoé National Park situated in Sudanese savanna only 1 *O. tetraspis* for every 15 *C. cataphractus* could be found. In the Tai National Park in rain forest the crocodile population of the Hana River was found to be composed of 95.5% *C. cataphractus* and 4.5% *O. tetraspis*. In the Azagny National Park, a swamp area separating two lagoons, all crocodiles found on the actual floating vegetation mat which constitutes the Rhaphia Swamp were *O. tetraspis*; whereas all *C. cataphractus* observed in this area were found in the water of the channels dug out for the tourist management of the park.

Also, elsewhere *O. tetraspis* has been found in small water pools, often far away from the nearest open water. In the interior of Comoé National Park it has been observed several times in the so called "mares," where they remain during the dry season in self-made burrows (Waitkuwait 1986, Gilbert pers. comm.). Similar observations have been made by Villiers (1956a) in the Niokolokoba National Park in Senegal. This was again confirmed for the Marahoué National Park in the contact zone forest savanna in the Ivory Coast (Waitkuwait 1986). Even in the tropical rain forest in the interior of Tai National Park it shows this habitat preference. Up to 10 individuals of different age classes (juveniles, subadults, adults) have been observed throughout the year in the same small water pools. They stayed there permanently, some individuals going on short journeys

and returning afterwards (Waitkuwait 1986). It was found that *O. tetraspis* walks around often in the forest, especially during the night or after a heavy rainfall. Several times it has been observed crossing tracks in the forest some km away from the nearest flowing water (Waitkuwait 1986, Hoppe, Merz, Martin pers. comm.).

It has also been observed in water collecting basins at the head of rain forest creeks (Boesch, pers. comm.) and in banana plantations situated on low lying grounds (Gournay, pers, comm.). One *O. tetraspis* stayed for several years in a well, the only water point, isolated in the center of a large oil palm plantation in the Ivory Coast (Maroncelli, pers. comm.).

In contrast to this in all these biotopes *C. cataphractus* has never been observed far from water. It stays in all kinds of rivers mainly covered by dense, shady vegetation, and it avoids uncovered bright sunny areas. The conditions in which its typical habitat is found becomes more scarce as one moves away from rain forest to savanna, as well as where the water courses become wider (Villiers 1956a, 1958, Waitkuwait, 1986).

Nest construction - As *C. cataphractus* and *O. tetraspis* live in habitats covered by dense vegetation, insolation - the normal source of heat for other reptiles - is reduced. One would suppose that it is for this reason both species construct mound nests of dead leaves and rotting vegetation collected from within a diameter of several meters. The mounds are flat on two sides and steeply sloped on the other two sides and have a furrow across the top made by the female lying on the nest or creeping over it. The nests are built in several stages. The female uses fore and hind limbs for the construction. It is thought that the decomposition of the vegetative materials of the mound guarantees the heating of the egg chamber, necessary for embryo development. This nest building behavior has been described in the wild by Villiers (1956, 1958) and Waitkuwait (1982, 1986), and in captive breeding by King (1955), Beck (1978), Sims and Sing (1978), and Tryon (1980).

Table 6 shows the nest dimensions for the two west African mound nest builders as found by Waitkuwait (1986) in the wild.

Table 6 Dimensions of the mound nests.

Species	Crocodylus cataphractus	Osteolaemus tetraspis
height (cm)	58.6 ± 11.6	47.5 ± 17.1
length (cm)	134.7 ± 36.7	131.3 ± 19.3
width (cm)	152.4 ± 29.6	123.8 ± 50.2
sample	n = 31	n = 4

The sizes of the nests seem to vary according to environmental temperature which depends on the season and on the density of the vegetation surrounding the nesting place. For this reason the size doesn't allow species classification of the nests. Tryon (1980) used damp hay as nesting material in captive breeding of *Osteolaemus* and found that the nest size varied directly to the amount of added material. The nests at Fort Worth Zoo were tightly packed and urination and defecation took place on the clutch and throughout the nest mound. Teichner (1976) gave one

nest dimension for *Osteolaemus* of 91 x 61 x 41 cm, and Sims and Singh (1978) described a nest 70 x 50 cm for this species.

Nest site - In contrast Waitkuwait (1986) found that a species classification of the nests is possible according to the species specific nest site chosen by the female crocodile, as can be seen in Table 7.

Table 7. Nest sites of mound nests.

Species	*Crocodylus cataphractus*	*Osteolaemus tetraspis*
Distance from water (m)	3.8 ± 2.2	16.9 ± 22.2
Height over water level (m)	1.8 ± 0.7	1.4 ± 0.6
Sample	n = 73	n = 4

Corresponding to their habitat preferences, the two species also avoid any competition in the choice of their nesting areas. The distribution of *C. cataphractus* mound nests was found to be linear, following the river banks, whereas the distribution of *Osteolaemus* nests was found to be bi-dimensional.

In 3 successive years from 1981 to 1983, 12 nests of *C. cataphractus* were observed by Waitkuwait (1986) alongside the Gabo River in the interior of the Tai National Park. Table 8 shows the average distance between the nests.

Table 8. Average distance between *C. cataphractus* nests.

Year:	1981	1982	1983
distance (km)	1.13	0.7	1.66
standard variation (km)	±0.67	±0.49	±1.72
sample (nests)	n = 12	n = 12	n = 12

From the observed variations of the distances between two nests, it can be derived that either the females choose a new nest site every year within their territory, or they change their territory, or even that some females do not reproduce every year.

In 1982 and 1983, only two nests were found to be constructed on a nest of the previous year.

Knoepfler (1974) speculated that *Osteolaemus* may use the same mound in successive years.

Nesting period - Table 9 shows the period of nesting activities of *C. cataphractus* and *O. tetraspis* in the tropical rain forest of the Ivory Coast found by Waitkuwait (1981, 1982, 1985, 1986).

Table 9. Dates of nesting activities.

Species	*Crocodylus cataphractus*	*Osteolaemus tetraspis*
date of nest construction	April 8 ± 18 days	April 30 ± 60 days
date of hatching	July 17 ± 18 days	September 15 ± 76 days
main nesting period in the year	March 21 to Aug. 4 over 136 days/year	March 1 to November 30 over 274 days/year

Nest construction for both species starts at the end of the dry season in the Tai forest when the most of fallen leaves are available for the nest mounding, so the subsequent nesting period covers principally the season of high rainfall. One can see that the main nesting period stretches over a longer period of time for the *O. tetraspis* than for the *C. cataphractus*.

High water levels in the small forest rivers during egg incubation and hatching seem to be very important for *C. cataphractus* so that the female can remain in water close by to guard the eggs and hatchlings. Whereas in rivers these conditions are found for only part of the year, the swampy habitat chosen by *O. tetraspis* offers almost all year round the necessary hydrological conditions for its nesting almost all the year. The main nesting period for both species has been defined as the period during which 2/3 of all nests constructed per year can be observed (data based on the standard variation calculation), 1/3 of nests being constructed outside this period according to climatic fluctuations or to differences in the individual behavior of the females.

Chronological order of reproductive activities - Available data are very scarce. Tryon (1980) states that both sexes of *Osteolaemus* mature at age five years and that courtship and mating of captive *Osteolaemus* starts every year in late November in Fort Worth Zoo. Copulation peaks during March and April. Drumming, neck rubbing, and male combat are described as courtship behaviour by Beck (1978), Teichner (1976, 1978) and Tryon (1980). The last author found that *Osteolaemus* females are unreceptive in late April and early May. Nest building began in June (Teichner 1976, 1978, Tryon 1980), actual laying occurred 5 to 47 days after mounding. Waitkuwait (1982) mentions that courtship and mating of *C. cataphractus* in Abidjan Zoo takes place in February and March. Actual oviposition occurred between a few days and one week after nest mounding.

Eggs and incubation - Just as the *Osteolaemus* female is small in size (about 1.50-1.60 m) in comparison with the *C. cataphractus* female (about 2.2 m), the same difference in clutch and egg size has been found by Waitkuwait (1986), as shown in Table 10.

Table 10. Clutch and egg size.

Species	*C. cataphractus*	*Osteolaemus tetraspis*
egg number per nest	16.0 ± 7.0	10.0 ± 4.0
egg length (mm)	85.5 ± 3.2	68.9 ± 2.4
egg diameter (mm)	52.9 ± 1.5	37.1 ± 1.2

The mean clutch size shown above for *Osteolaemus* is consistent with data published by Greer (1975), Knoepfler (1974), Beck (1978), Wilson (1977), Hara and Kikuchi (1978), Sims and Singh (1978), Teichner (1976, 1978), and Helfenberger (1981), gathered during captive breeding of this species. Tryon (1980)found that the mean egg number for 25 *Osteolaemus* clutches was 13.28. Data on egg length and diameter published by him are consistent with the data in Table 10.

In contrast the data on egg incubation show no species-specific differences. The length of the incubation period is determined to be 100 ± 10 days for *C. cataphractus* as well as for *O. tetraspis* (Waitkuwait 1981, 1982, 1986). Other data on length of incubation period are available from the captive breeding of *O. tetraspis*: 84 days (Wilson 1977), 118 days (Hara and Kikuchi, 1978), 109 days (Tryon 1980), and 84 days (Helfenberger, 1981). Incubation temperatures range between 26°C and 34°C in mound nests of both species (Waitkuwait 1981, 1982, 1986), being constant in each nest (with daily fluctuations of less than 0.5°C) and about 5°C greater than the environmental temperature.

Figures 1 and 2 show temperature data gathered on a *C. cataphractus* mound nest in the Tai National Park. The endogenous heat in conjunction with the insulation given by the nest walls creates a largely autonomous microenvironment. However, as shown in Figure 1, the outside influences are not completely cut off. A longterm drop in the outside temperature, as recorded in June and July, resulted also in a lowering of the temperature in the nest.

O. tetraspis was bred successfully in captivity at incubation temperatures fluctuating between 25°C and 34°C (Tryon 1980) and 27°C and 33°0 (Helfenberger 1981). The humidity in mound nests of both species was also found to remain constant over the whole incubation period (Waitkuwait 1981, 1982, 1986). Table 11 shows the percentage of dry matter in the nesting material.

In the air space of the egg chamber the relative humidity was therefore almost always at saturation point.

Table 11. Dry matter of mound nests.

Nest of	% Dry matter
C. cataphractus from forests	45.3
C. cataphractus from savanna	47.8
O. tetraspis from swamps	37.2

Hatching of the young and behavior of the mother - As for most of the crocodile species, it has also become apparent for *C. cataphractus* and *O. tetraspis* that the mother crocodile guards and visits the nest during the whole of the incubation period (King 1953, Tryon 1980, Waitkuwait 1982, 1986). On captive *Osteolaemus* it could be observed that the female spent up to 50% of her time on guarding the nest, that vocalization and aggressiveness, even against man, increased (Tryon 1980, Helfenberger 1981). Wild breeding *C. cataphractus* females were found to be very shy (Waitkuwait 1981, 1982). Cracks developed on the eggs and the young became vocal in answering movements in the nest surroundings by croaking heavily for about 1-2 days before actual hatching.

The mother crocodile is alerted by the calling of the young and is stimulated to excavate the nest and to help in hatching the young. For this she picks up the neonates partly emerged from the eggs, rolls them between her jaws until the eggshells have been removed, and transports the neonates in her mouth into water. This hatching process has been described by Tryon (1980) on captive *Osteolaemus* in the Fort Worth Zoo and has been observed on wild *C. cataphractus* and *O. tetraspis* (Waitkuwait 1981, 1982, 1986).

After hatching, the mother crocodile stays in the vicinity of the young to protect them. Communication is guaranteed by the vocalization of the young; Tryon (1980) found the calling of the young was not species-specific.

Waitkuwait (1982) observed that of the 17 eggs in a wild *C. cataphractus* nest 2 eggs were predated, 10 hatched successfully, embryonic death occurred in two, and 3 eggs were probably infertile.

Of 85 *Osteolaemus* eggs incubated at Fort Worth Zoo, Tryon (1980) found that 37 hatched, 39 were infertile, 2 contained fully formed but dead embryos, 2 contained living anomalies, and 1 contained twin crocodiles. Table 12 shows the total length of neonate *C. cataphractus* and *O. tetraspis* (Waitkuwait 1986).

Table 12.

Species	Crocodylus cataphractus	Osteolaemus tetraspis
total length (mm) at hatching	315.1 ± 23.3	279.3 ± 4.0
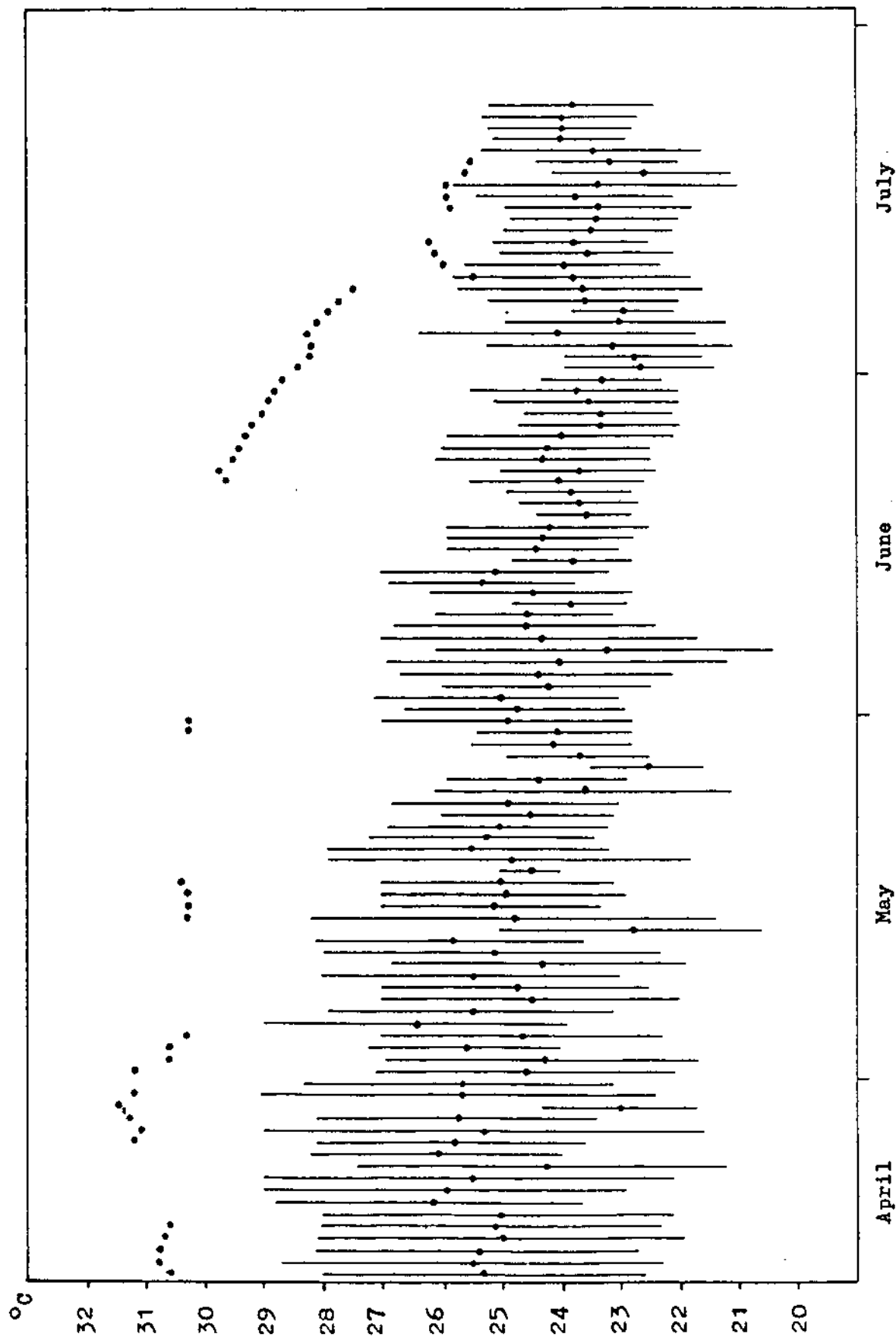
Figure 1. The nest temperature (above) in relation to the amplitudes outside the nest (below) from 14 April to 24 July 1980.
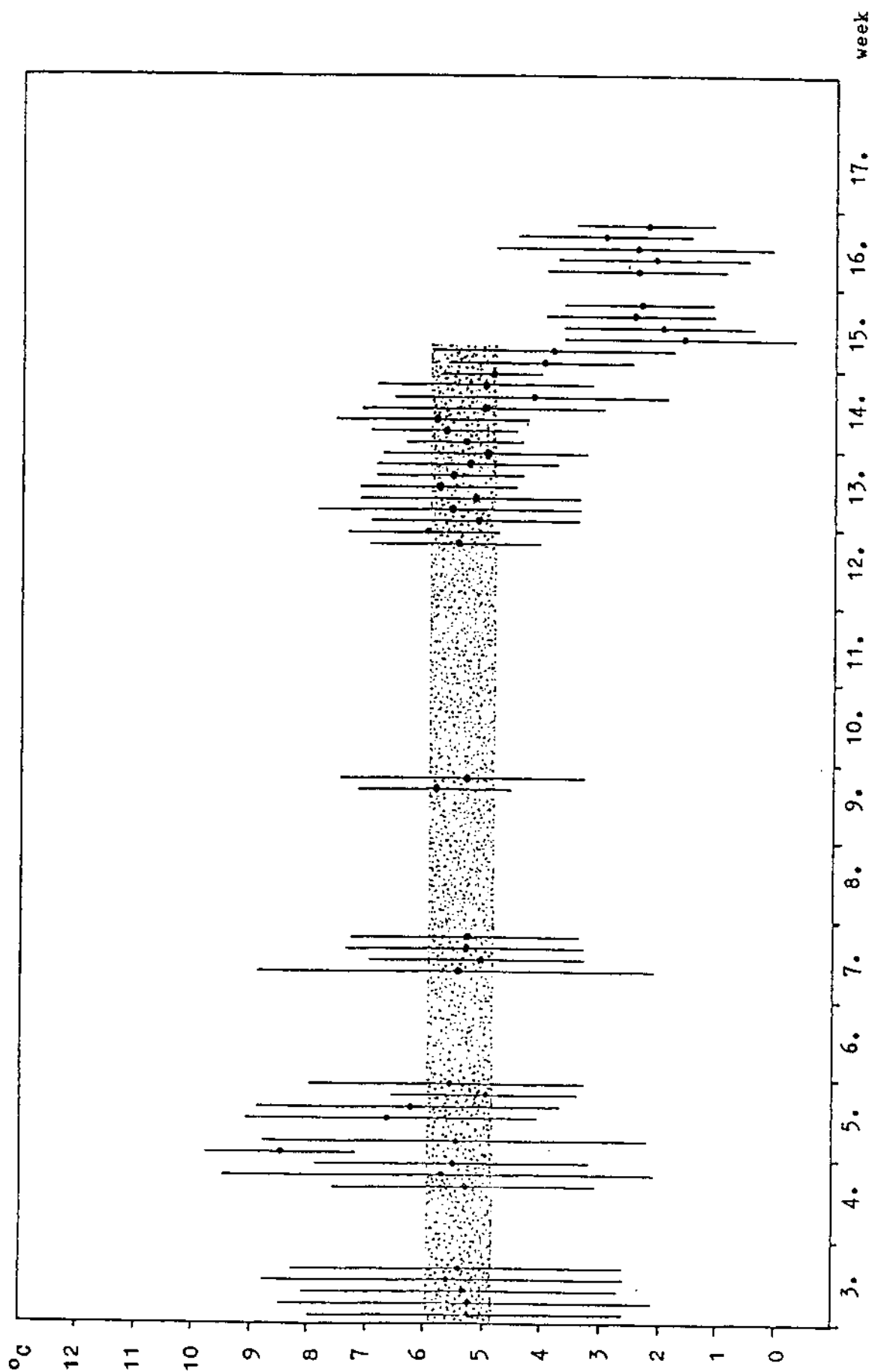
Figure 2. The constant difference between the incubation temperature and the mean day temperature outside the nest from the third week of incubation to the opening of the nest in the fifteenth week.

Tryon found the mean total length per clutch of *Osteolaemus* hatchlings at Fort Worth Zoo to be between 216.7 and 242.5 mm . Captive bred *Osteolaemus* neonates measured by Helfenberger (1981) showed a total length of 19 cm.

Feeding - Progressive differentiation of the body proportions of the two species occurs during growth. This finally results in adult *C. cataphractus* having a total length and a relative head and tail length greater than that of *O. tetraspis*. One would suppose that this phenomenon of allometry reflects different specializations concerning species-specific modes of hunting and ranges of prey.

C. cataphractus develops a slender snout and a long tail, both of which are necessary for a rapid hunting in water. The slender-snouted crocodile preys principally on fish and aquatic birds. Its large size also allows it to attack small- or medium-sized mammals, such as duikers (Cephalophinae), rodents (Rodentia), genettes (Viverrinae), monkeys (*Colobus* sp., Cercopithecidae), etc., which come to drink in the rivers (Waitkuwait 1986). In contrast, *O. tetraspis* has a stumpy, large snout and a short tail which favor land-based hunting in its swampy habitat. Some rare observations indicate that it feeds on amphibians, reptiles, annelides, crabs, and fish, (Villiers 1958, Waitkuwait 1986). Hatchlings of both species seem to have the same feeding regime as *C. niloticus* hatchlings, which was described in detail by Cott (1961): larvae of aquatic insects, tadpoles, etc.

Enemies - In general, predation on crocodiles occurs principally at the egg and hatchling level. According to Waitkuwait (1982, 1986) the following animals in the tropical rain forest of the Ivory Coast are potential predators against crocodile eggs and juveniles: Nile monitor (*Varanus niloticus*), otters (*Lutra maculicollis*, *Aonyx capensis*), water mongoose (*Atilax paludinosus*), tree civet (*Nandinia binotata*), genets (Viverrinae), leopard (*Panthera pardus*), golden cat (*Felis aurata*), herons (*Egretta alba*, *Ardea purpurea*), birds of prey (Accipitridae), and soft-shelled turtles (*Trionyx triungius*). Although predation has been observed several times, it is apparent that the density of predators in tropical forests is too low to severely reduce the crocodile population. The only predator threatening crocodile populations in west Africa is, like elsewhere, man, both through commercial hunting and increasingly through habitat destruction. As a consequence of human influences the west African crocodile populations are presently collapsing. This was confirmed by Ivorian hunters and fishermen (Table 13; Waitkuwait 1986).

Table 13. Frequency of Crocodiles in the Ivory Coast according to hunters and fishermen.

Frequency	*Crocodylus niloticus*	*Crocodylus cataphractus*	*Osteolaemus tetraspis*	Total
no answer	0 (0%)	7 (8.6%)	3 (3.7%)	10 (4.1%)
not or no more occurring	10 (12.3%)	14 (17.3%)	6 (7.4%)	30 (12.3%)
rare	62 (76.5%)	55 (67.9%)	60 (74.1%)	177 (72.8%)
less rare to locally frequent	9 (11.1%)	5 (6.2%)	12 (14.8%)	26 (10.7%)
frequent	0 (0%)	0 (0%)	0 (0%)	
Total number of answers	81 (100%)	81 (100%)	81 (100%)	243 (100%)

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ECOLOGY OF THE MUGGER CROCODILE

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Distribution and Status.-- The mugger crocodile (*Crocodylus palustris*) has a roughly triangular range. In the west they are found in southeastern Iran in the Sarbaz River where there are probably fewer than 50 left. Eastwards, in Pakistan, their position is also precarious where perhaps less than 100 survive in two or three localities including a manmade lake and the Nara Canal. The once famous captive groups at the sacred Muslim shrine, Mango Pir near Karachi now consists of just a few individuals.

In Nepal there are small populations of mugger in several of the tributaries of the Ganges that cross the "terai", the plains at the base of the Himalayan foothills. These include the Karnali in the west and the Rapti/Narayani which flows through Chitawan National Park.

In Bhutan there may have been a few mugger in the cold Manas River, but like the gharial it is extinct there now. In Bangladesh are 5 individuals living in a sacred tank at Bagerhat near Khulna.

Sri Lanka has more mugger than the rest of the subcontinent put together, mostly concentrated in the two large National parks, Yala and Wilpattu. There were an estimated three thousand mugger in Sri Lanka in 1977 but there has been no follow-up survey since then. Rapid agricultural and industrial development are putting mugger under the same pressure that led to their extirpation in India.

In India mugger were once widespread and common, living in a wide range of habitats. India has few freshwater swamps and the species name *palustris* is not really appropriate. The mugger is now rare throughout its Indian range but is still found in rivers, reservoirs, tanks (man made lakes), jungle ponds, irrigation channels and streams. The highest elevation recorded for a mugger is at 420 m in Corbett National Park. Table 1 gives a state by state breakdown of mugger status in India.

Historical Record.-- The mugger figures in Hindu mythology and the local myths of many groups and tribes of people in India. Makara is the Sanskrit name for the mugger and is the vehicle of the rain god Varuna. The mugger is the unlikely totem of the Mogri people in a part of Gujarat where a live mugger hasn't been seen for at least two generations. The mugger is often depicted as being the vehicle of the river goddess Gangadevi, a benign aspect which is a welcome relief from the usual deadly approach.

Table 1. Mugger in India

	Mugger in the past	Wild mugger now excluding hatchings)*	Rearing projects	Captive mugger	Release
Jammu & Kashmir	?	NIL	--	--	--
Himachal Pradash	NIL	NIL	--	--	--
Rajasthan	YES	100+	YES	300+	10
Punjab	YES	NIL	--	--	--
Harayana	YES	NIL	--	--	--
Uttar Pradesh	YES	100+	YES	100+	50
Bihar	YES	100+	YES	100+	50
West Bengal	YES	20+	YES	--	--
Sikkim	NIL	NIL	--	--	--
Assam	YES	FEW	--	--	--
Tripura	?	NIL	--	--	--
Mizoram	?	NIL	--	--	--
Nagaland	?	NIL	--	--	--
Manipur	?	NIL	--	--	--
Orissa	YES	200+	YES	200+	75
Andhra Pradesh	YES	300+	YES	400+	250
Tamil Nadu	YES	200+	YES	3000+	210
Kerala	YES	100+	YES	100+	--
Karnataka	YES	100+	YES	50+	--
Goa	YES	NIL	YES	FEW	--
Maharashtra	YES	100+	YES	100+	15
Gujerat	YES	300+	YES	500+	--
Madhya Pradesh	YES	100+	YES	--	25
TOTALS		1720		4850	685

*Estimates only

Makara often appears on Indian temples as gargoyles and may be fused with the body and feet of another animal, typically a lion. A stone crocodile devours a fish in one prominent carving at the Sun Temple in Konarak, Orissa (Fig. 1).

Till recent decades crocodiles used to inhabit temple tanks in Kerale where they remained unmolested never bothering human bathers. Similarly, mugger were common in most of the North Indian rivers and Kipling in his story "Mugger Ghat" makes ironic reference to their cleansing presence in rivers into which hundreds of human corpses are still consigned each week.

Today the traditionally amicable relationship between man and mugger can rarely be illustrated in India; mugger are too scarce. In Sri Lanka, however, there are many places where people bathe in "crocodile infested waters" without fear. The occasional attacks that occur have invariably been attributed to saltwater crocodiles. Mugger attacks may sometimes happen but these are likely to be cases of mistaken identity or mispredation.

There were enough hide hunters and sportsmen with few reverent feelings for crocodiles to reduce them to shreds in the first half of this century. By the 1960s mugger were only holding out in a few reserves or very remote areas and in 1974 the total population of wild adult mugger in India was probably under 1000.

Feeding Habits and Role in the Environment.-- As we have already indicated, mugger are a more "socially acceptable" species of crocodile, some of which will routinely attack man.

Their food in the wild has been little studied and what is known is summarized in Table 2. Dunbar Brander (1927) lists animal remains which he found in mugger shot by him; men, leopards, wild dogs, hyaenas, spotted deer, sambar, nilgai, four-horned antelope, barking deer, monkeys, dogs, goats, calves, pigs, ducks, storks, and other birds. The remains of mammals and hard-bodied insects are frequently recorded partly because of the hair, hooves and chitin which are relatively easy to detect. Remains of fish, frogs and reptiles are harder to see yet may form the larger part of the mugger's diet in some areas and in some seasons.

One sample of 60 mugger scats collected at the rice-growing area of Vakkaramani, Tamil Nadu indicated selective hunting for rats during the period (May) rats must live close to water (Table 3). Crocodiles can therefore be unlikely, but effective agents of pest control.

In general, the mugger's role in nature is as master predator of its aquatic environment. The implications of this role to man was described by Cott (1961) in a classic study on the Nile river system in Africa. There, wherever crocodiles were exterminated the Tilapia fishery declined; precisely the opposite of what was intended by ridding the rivers of this predator. What was not realized, however, is that crocodiles control the numbers of the voracious catfish which feed predominantly on the eggs and young of the commercially more desirable Tilapia.

Here in India such studies have been made. However, there is a made to order study area in the form of Amaravathi Reservoir in Tamil Nadu. Stocked with the exotic Tilapia mossambica in the 1950s it had the highest fish yield per acre in the state and possibly the entire country by the 1970s. Amaravathi has plenty of cormorants, turtles, otters and other fish predators including crocodiles. It has south India's largest wild breeding population of crocodiles which is no coincidence and certainly indicates the positive effects of crocodiles on commercial fisheries.

As master aquatic predator, the mugger helps raise genetic quality by feeding on weak, sick and injured fish, birds and mammals. As a scavanger the mugger probably once played a role in keeping the rivers clean, feeding on human bodies and animals carcasses.

Figure 1.   Stone crocodile at the Sun Temple, Konarak, Orissa, India.

Table 2. Food Item Found in Stomachs of or Observed Being Eaten by Mugger.

Food Item	Reference
Water beetles, water bugs	D'Abreu, 1915
Winged termites, moths, beetles	Authors, pers. obs.
Snails, bivalves	D'Abreu, 1915
Frogs: *Rana*	D'Abreu, 1915
Fish: *Tilapia, Chela, Mystus, Bagarius*, eel	Various authors & pers. obs.
Snakes: *Ptyas, Xenochropis, Vipera*	Whitaker & Whitaker, 1984
Birds: Egrets, herons, kites, waterhens, peacocks, dadchicks, pigeons	Various authors
Mammals: monkey, otter, dog, rats (and see text)	Authors, pers. obs.

Table 3. Contents of Scats Collected at Vakkaramari, Tamil Nadu.

Prey remains	% occurence
Fish scales	10%
Lesser bandicoot hair	100%
Gerbil hair	20%
Watersnakes scales	10%
Bird feathers	10%

Small mugger have been regularly observed feeding on insects attracted to lights put over the hatchling pens. They are agile and often catch moths and flying termites on the wing. Large mugger have been observed catching monkeys, dogs and brahminy kites. When pools are drying out mugger are seen to "herd" fish by moving slowly sideways and locking them off in small inlets. The mugger will gradually shrink the area until the fish start darting and leaping in panic. Many of the fish try to escape via the only opening available-the open mouth of the mugger-and are caught.

Like other crocodiles a healthy mugger may go for months without food. Because of common droughts in the range of the mugger, it may have no access to food for long periods. But this cycle of periodic drought is a dynamic one for crocodiles, the most dramatic examples of which can still be observed in parts of Sri Lanka. In and around Yala National Park in the south, most of the tanks (man made lakes) dry up each year. Huge concentrations of fish are confined to smaller and smaller areas which crocodiles sometimes walk overland considerable distances to visit and gorge themselves. This short, sudden surfeit of fish can tide over the mugger for months to come if necessary. Walking overland is also a strategy to find water and the authors have found mugger in dry, thorny scrub jungle, apparently headed for permanent water many kilometers away. Tunnelling is another favorite mugger strategy to beat the heat. Nineteen mugger tunnels were found at Hiran Lake in Gujarat one drought year (1975). They had flattened entrance holes averaging 75 cm across and most were 2 meters to 4 meters deep. Stream dwelling mugger use tunnels as year round residences, preferring embankments with heavy root systems.

REPRODUCTIVE BIOLOGY AND RESEARCH

Sexual Maturity.-- Female mugger of 1.8 meters lengths and others of 6 years 8 months of age (2.2 m) have laid fertile eggs. However, smaller and younger females (1.6 m, 41/2 years) have laid infertile eggs and are likely to be able to breed at the age and size under some circumstances.

Timing of Breeding Season.-- The period between and including courtship, mating, nesting and hatchling of young extends from November to June in South India. Courtship and mating commence in November coinciding with the north-east monsoon, nesting in February with the beginning of the dry season, hatchling with the height of the dry season and the beginning of the south-west monsoon (April-June) (see Fig. 2). In northern India the breeding cycle tends to be one month later. At Jaipur Zoo, Rajasthan from 1967-71, occurred between 26 June and 6 July. In Sri Lanka, June-July are reported as the laying months and August-September the hatchling months for mugger.

Territoriality and Dominance.-- Although fighting sometimes occurs on the introduction of a new individual in an established captive group, mugger are fairly tolerant of conspecifics, particularly during the seasonal concentrations which occur in the dry season. During the breeding season both sexes become increasingly territorial. The dominant male asserts his dominance by swimming displays in the 'tail up' position, head-slapping and chasing and biting subordinate males, sometimes onto the shore. This behavior has been recorded for males of other species as well, such as Crocodylus novaeguineae and C. niloticus. D'Arbreu (1915) noted that large wild mugger "usually" have shortened tails, some missing the terminal 9-10 segments. This is not the case with most wild mugger observed today and could be a indication of much less frequent interaction (i.e. chasing and fighting) among the adults of once large and concentrated populations.

Roaring or bellowing has rarely been heard in mugger but it is reported in the literature; this vocalization is likely to be a territorial signal as it is in the American alligator.
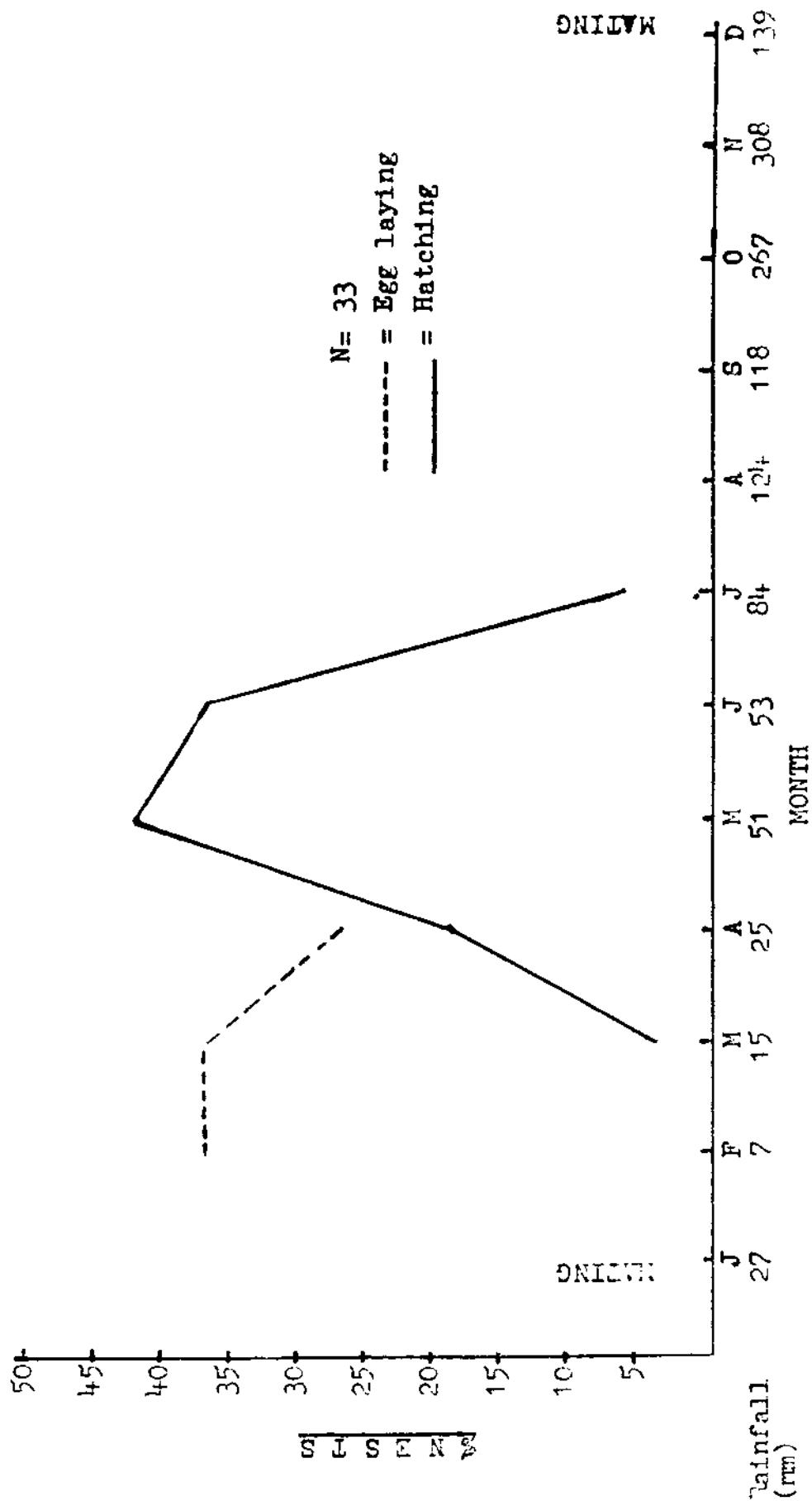
Figure 2. Timing of mugger breeding season.

A raised, threatening posture, called 'slimming' by Garrick et al. (1978) is frequently observed in captive juveniles and subadult males. The animal raises its body by fully extending its legs, sometimes slightly compressing its body laterally and breathing deeply. This is occasionally initiated by the approach of another mugger to a favored basking spot but also by apparent individual rivalry and seems to be an early manifestation of the establishment of social hierarchy. This posture is rarely used when confronted by an animals (or human), the most common threat then used being a raised forebody with open mouth, hissing and leaping forward if cornered or further threatened. A challenged, subdominant mugger of either sex may run or raise the head in submission, often accompanying the signal with a low, openmouthed gurgling sound. Other behaviors observed in mugger which are possible social signals include 'yawning' and 'ear flapping'.

Courtship and Mating.– Often a headslap by a male (which starts from the head up position) signals approach and courtship. Male approach to a female prior to courtship is usually in the tail-up position, with pointed, single caudal scales arched well out or slightly out of the water. Following a head slap, geysering may be observed as described by Garrick et al (1978): "a stream (spout) of water about 10 to 20 cm in height resulting from a release of air from the external nares while the snout is just under the surface of water".

During courtship, circling, bubble blowing, raising and touching jaws is usually observed. Figure 3 provides a summary of these behaviors.

Females were observed bubbling at times other than during mating and it is perhaps a courtship signal. Female mugger occasionally head-slap in answer to males as do *Alligator mississippiensis*, and were twice observed to roll over in the water, exposing the belly as reported by Cott (1961) for *C. niloticus*.

During one courtship sequence a female mugger was observed repeatedly mock biting the male's head. When the male mounts the female the pair submerges, often surfacing and submerging alternatively. Mating progresses while they are fully or partially submerged. Copulation lasts from five to fifteen minutes. During courtship and mating a high degree of tolerance is shown toward other animals. Adult females and a sub-adult male were seen circling, nudging and in intermittent physical contact with a pair during courtship on several occasions. Courtship and mating were always observed in water through copulation on dry land was recorded at the Jaipur Zoological Gardens. At Madras Crocodile Bank a male mounted and made repeated copulation attempts on a female in the act of nesting.

On several occasions during courtship the throat glands of females in the head-raised posture were briefly everted and withdrawn. It is likely that the scent glands function in some attraction and stimulatory capacity during pre-mating courtship. Prater reported that the scent glands in the throat and vent secretes a brownish liquid with a musty odor. He feels that the secretion is most active during the mating season and postulates that is release in the water enables individuals to find each other. This secretion has been observed as a waxy brown substance but seems to have very little detectable odor.

Dharmakumarsinhji (1947) made the first observations on breeding of wild mugger. He described the tail up and head emergent posture of the female prior to copulation. His observations agree with those of the authors, including the submerging, re-emerging cycle seen during copulation.

Nest Construction and Egg Laying.-- The female digs a body pit with alternate scraping of all four limbs and the nest hole with alternate scooping motions of the hind limbs. Nest hole digging
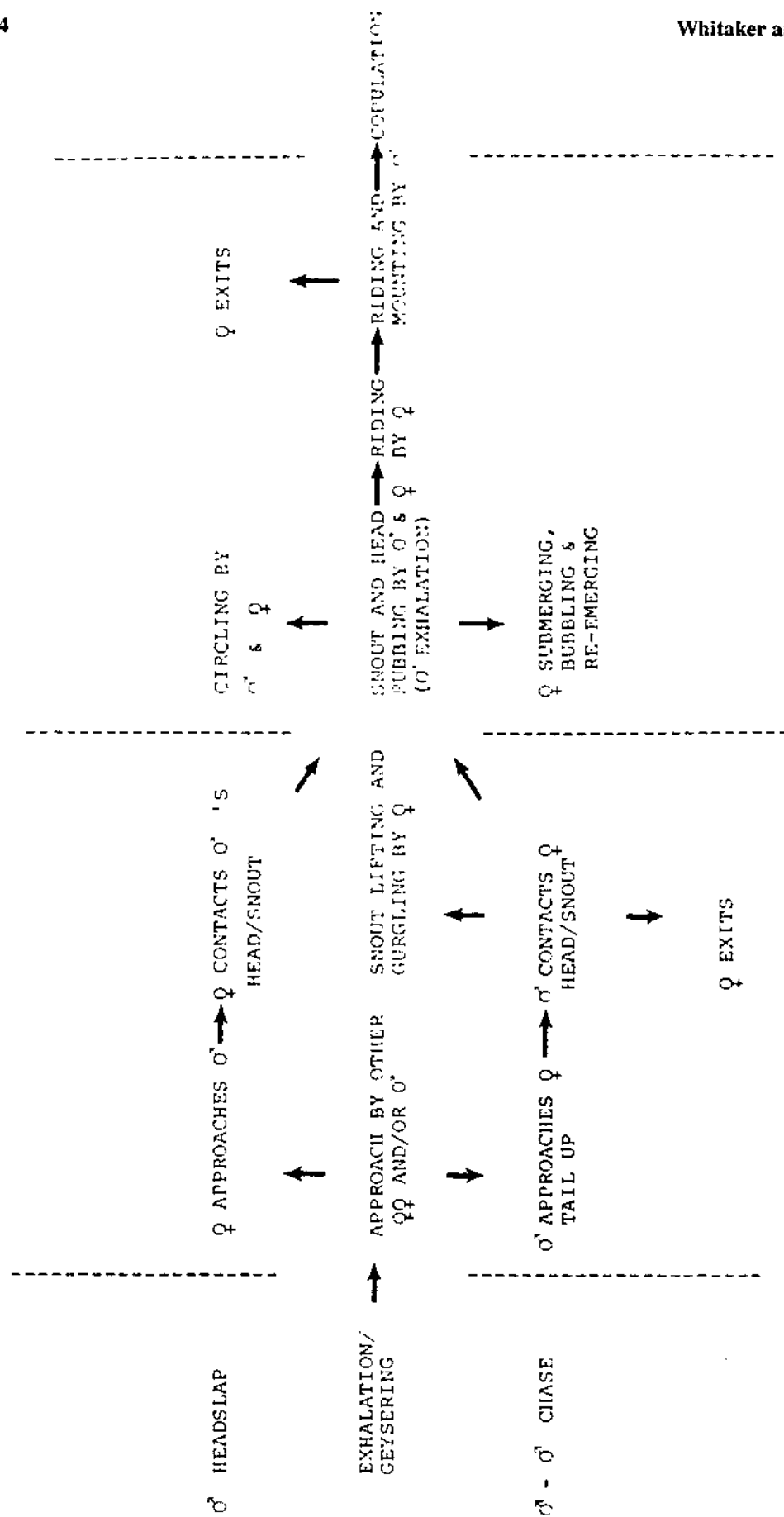
Figure 3. Summary of mugger courtship behavior (after Garrick and Lang 1977).

may take 30 to 60 minutes after which the female straddles the hole and lays her 26 to 30 eggs in about 20 minutes.

After laying, the female may insert both feet into the egg chamber and gently push the entire clutch to the back of the cavity of the L-shaped hole (Fig. 4). For this manoeuvre and while nest-packing the tail and chest are used for support. She then begins a slow scratching with alternate movements of her hind legs, gently pushing sand into the nest hole. Sand is scraped over the nest and periodically packed by treading with the hind feet, then she may start turning on her nest, making a number of full circles, completely flattening the nest area.

During wild egg collection programs, in field study and surveys over 50 wild nests were observed. Tables 4 and 5 give some of the physical characteristics of the nests. Hole length apparently corresponded to the length of the female mugger's hind leg. In most nests the soil at the egg cavity level was damp.

Locations included artificial reservoirs without shade, small densely vegetated streams, and tidal lagoons. At Amaravathi Reservoir the tracks of a mugger were followed into a hilly scrub forest over 1 km from the reservoir to where a 2.4 m female was found. She later nested here but unsuccessfully, as the soil was too shallow. This unusual nesting behavior was postulated to be due to the excessive human disturbance in the area (before protection, 90% of the eggs were taken each season by herdsmen and firewood collectors). At Amaravathi, nine out of eleven nests were situated on slopes facing east.

At Amaravathi, Kilikudi and Sathanur, trial nest holes were a common feature near nests. Mugger usually dig one or more trial nest holes before making the final egg chamber. At Vakkarameri a female was seen making a trial nest in daylight and 2-3 trail nest holes were found for each nest.

Clutch and Egg Size.-- Mugger lay 25-30 eggs; details of clutch sizes in different localities are given in Table 6. Clutch sizes were similar in north and south Indian nests. The average size of 340 eggs from wild nests in south India was 7.7 x 4.7 cm and weighed an average of 128 gm, closely corresponding to captive bred eggs measured at Madras Crocodile Bank (MCB).

Incubation Period and Nest Temperature.-- In captivity mating begins about two months before the first egg laying, suggesting a developmental period of 40-60 days. Incubation of mugger eggs averages about 2 months. Nest temperatures in wild nests in south India ranged from 18°C at 6 AM to 33°C in early afternoon. In 1980 the overall nest temperature average at MCB was 31.3°C for the four months of February - May.

Multiple Clutches Per Season.-- When double clutching was first observed at MCB in 1976 in a 19 year old female (Nova) it was thought to be exceptional or aberrant behavior. Since then however, the laying of two clutches per season has become the norm for 6 females. Table 7 illustrates the details of the multiple nesting which occurred in 1979-1985. Clutch size and hatching success were slightly lower in 'B' nests. The mean distance between A and B nests was 22.5 m, while nests of different females averaged only 5 m apart.

Double clutching at MCB may be a result of the combination of high temperatures and high feeding rates. There seem to be three possibilities which might explain the phenomenon:

a)   single mating with arrested development of second clutch
b)   single mating and storage of sperm
c)   double mating

Crocodylus palustris
EGG PLACEMENT WITHIN NEST

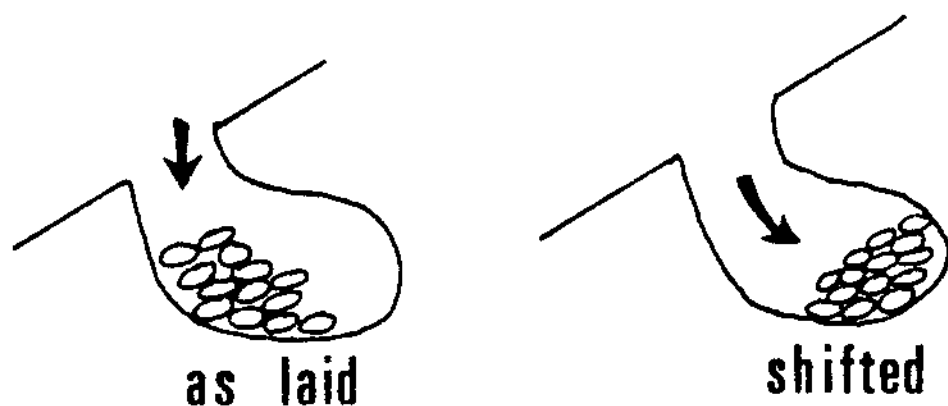**as laid**   **shifted**

Figure 4. The female uses her feet to shift the egg clutch to the back of the nest cavity.

Table 4. Data on 50 Wild Mugger Nests in Tamil Nadu.

Hole length (cms)	Hole width (cms)	Distance from water	Height above water line (m)	Layer of sand/ earth covering eggs (cms)
35 - 56	22:14-31	10m:1m-2km	6.2:1.5-10	19.5:13-26

Table 5. Soil Type and Shade at 59 Wild Mugger Nest Sites (% Nests).

Gravel/sand	Sand	Black clay	Loamy soil	Humus
37	34	17	10	1.7

Unshaded	Partly shaded	Fully shaded
86	7	7

Table 6. Clutch Sizes of Mugger Nests.

Place	N	Clutch Size x : range
Sathanur reservoir, Tamil Nadu	5	27:17-35
Amravathi reservoir, Tamil Nadu	11	31:26-35
Vakkaramari, Tamil Nadu	3	32:18-46
Kilikudi, Tamil Nadu	3	19:16-21
MCB (9 females)	49	24: 8-39
Hiran Lake, Gujerat	2	25
Powai Lake, Maharashtra	1	17
Jaipur Zoo, Rajasthan	5	32:22-41
TOTAL	79	26: 8-46

Table 7. Number of Females Double Nested 1979 - 1985 (MCBT).

Year	Number of females nested	Total number of nests	Number of females double nested
1979	7	13	6
1980	11	15	6
1981	9	16	7
1982	12	15	4
1983	9	12	3
1984	12	20	6
1985	18	27	9

Sporadic mating of mugger is observed late in the season (March/April) and more recently a second peak similar to the December activity has been noted. While the period of egg development in first and single clutches appears to be about 60 days there was an average of only 41 days between first and second nests. There is no evidence of double clutching in wild mugger and indeed has not been observed as a normal strategy in any other crocodilian. The implications of double clutching for commercial farming are obvious, whether it could be of some survival value for wild mugger is a matter for conjecture. There may be a complex relationship between double nesting and temperature determined sex (see Research); a strategy that could enhance survivorship of hatchlings during a drought year.

Protection of Nest.-- Nest defense has been observed both in the wild and in captivity. At MCB nesting females defended nest sites and adjacent water areas and engaged in threat displays. They often thrashed their tails from side to side and made repeated serious charges at intruders, both crocodilian and human. If undisturbed the female will spend most of the incubation time at her nest and in the water near by. One female fasted throughout incubation, while other, younger females were less attentive to nests and did not fast. An MCB employee, checking early morning nest temperatures was attacked and badly bitten by a nest guarding female. Now temperatures are recorded electronically.

The role of the male mugger in nest attendance was recently observed at MCB. The male *C. niloticus* takes part in nest excavation and hatchling transport as does the New Guinea crocodile. In 1985 the adult male of pit 8 (Makara), was observed excavating a nest, transporting hatchlings to the water and excluding all of the adult females from the vicinity (Fig. 5).

Hatchling, Release and Transport of Young.-- The following observations were made on a captive female at Madras Snake Park and typify activity at a mugger nest upon hatching.

A female was observed at 0100 excavating her nest with her front feet and head, leading 6 hatchlings to the pond 6 m away, and communicating with them by grunting. She later excavated 5 more young and they were heard calling sporadically all night. At 0900 the female chased the keeper from the enclosure. She pushed hatchlings out onto the palm leaves outside the pool with her snout.

At 0950 the male was with the hatchlings in the main pond and the female in the adjacent pond. The female picked up a hatchling in her mouth and carried it to the main pond, shaking it out of her mouth where the other hatchlings, were grouped.

At 1010 she went again to her nest (in response to the muted grunt of another hatchling) and dug with her front and (less often) hind feet. She moved clockwise over her nest, sometimes putting her nose in and biting clods of earth.

An egg was removed with the jaws, jerked back, and gently punctured by the front teeth. The hatchling slipped into the buccal pouch, squirming. She brought it, tail visible between her teeth, to the pond. It was observed that the hatchlings spent the first day almost entirely on dry land.

At 1100 another hatchling was picked up at the nest by the female and brought to the same spot next to the pond.

Creche Formation and Defense of Young.-- In one captive group 13 hatchlings remained in the group or creche initially formed by the female for two months. They stayed with the male and female for 12 months through the next breeding season and no aggression toward the young on the
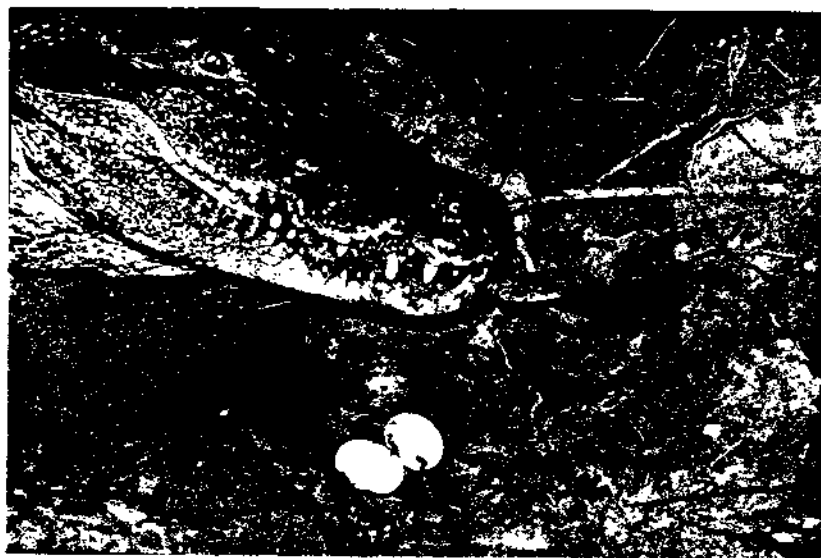
Figure 5. Male mugger transporting young from nest (photo: Jeff Lang).

part of either was observed. Groups of hatchlings were reported several times by fishermen and others and wild creche groups of mugger hatchlings were found by the authors at Kedarhalla in Tamil Nadu, and at several places in Sri Lanka.

At MCB during capture of hatchlings from undetected nests, mature males, females and sub-adult males will make repeated lunges and charges out of the water and almost over the 1.5 m wall. Wild mugger, apparently of both sexes, responded to distress cries mimicked by us by approaching, leaving the water and charging.

Conservation and a Future for the Mugger.-- Realization that the mugger was on its way to oblivion on the Indian subcontinent came just in time. Surveys carried out be the Zoological Survey of India, Bombay Natural History Society and Madras Snake Park startled the environmental community when results showed how few mugger were actually left. South India's largest wild breeding population, at Amaravathi reservoir in Tamil Nadu, had a mere 14 breeding females. The largest population in the north, at Hiran lake in Gir National Park, had perhaps 20 breeding females.

Tamil Nadu has taken the lead in producing large number of captive hatched mugger from eggs collected at the wild nesting sites with perhaps 6000 eggs collected since 1977. Survival rates of eggs and hatchlings have been variable but are somewhere in the region of 30 to 60% from available data.

Mugger from Tamil Nadu have been sent to a number of states for restocking, an activity that was questioned from the standpoint of mixing different geographic forms of mugger. However, to establish and re-establish wild breeding populations was the first urgent priority and in most cases there were not even remnant populations remaining at the restocking sites.

Because of the lack of input on the field research and public relations side of mugger conservation it is getting more and more difficult to find release sites. In Tamil Nadu, objections from the State Fisheries Department, Public Works Department (dams) and local fishermen have effectively blocked several restocking proposals. Arguments that mugger are good for commercial fisheries by eating predators and won't hurt dam maintenance crews are simply not supported by scientific studies and the right public education.

Research.-- The Government rearing centers and the Madras Crocodile Bank have been carrying out research on the mugger since the early 1970s. Some of the basic findings have already been described but there are a number of other avenues of work not yet given much airing.

For example, mugger are now known to use the gaits described as the high walk and gallop as do better known species like the Nile crocodile. Recent work at the Madras Crocodile Bank has demonstrated that the sex of the mugger is determined in the egg. Temperature is the key factor, as has been found for other crocodilians and many turtles species. In the case of the mugger, higher temperature produce males which is reflected in the overall sex ratio averages for three years breeding at the Bank. Eggs laid in the cooler month of February had 7% males, in March 32% males and those laid in April, the hottest month, 45% males. Continuing research will eventually determine the exact temperatures that produce males and females and the critical period of embryonic development in which sex is determined. Other studies include behavior analysis and its relation to environmental parameters and the phenomenon of double clutching.

Crocodile Management.-- But the entire FAO/UNDP and Government input into crocodile conservation in India was not only to halt the extinction of the species. Conservation demands a dynamic full circle approach to caring for wildlife, that's when it becomes management.

Table 8. Captive Breeding of Mugger in India.

I. Zoological Parks	Breeding since	Total stock reared
Ahmedabad	1960	250+
Baroda	1964	?
Bannerghatta	1984	?
Delhi	1976	100
Goa	1983	?
Indira Gandhi Park	1978	150
Jaipur	1960	300+
Kanpur	1985	?
Madras Snake Park	1975	150
Nandankanan Park	1982	100+
Nehru Park	1980	150+
II. Crocodile Rearing Centers		
Madras Crocodile Bank	1976	1800+
Tikerpada, Orissa	1982	100+
Silipal, Orissa	1983	50+
Hyderabad, Andhra Pradesh	1984	50+
Sathanur, Tamil Nadu	1983	50+
Amaravathi, Tamil Nadu	1983	50+
Guindy, Tamil Nadu	1985	?
Kukkrail, Uttar Pradesh	1985	?
	TOTAL	3300+

Table 9. Egg Collection and Rearing Centers for Mugger in India.

India	Year commenced	Number of eggs collected	Number of muggers reared
Hoganakal, Tamil Nadu	1976	800+	500+
Amaravathi, Tamil Nadu	1977	2000+	1200+
Sathanur, Tamil Nadu	1976	2000+	1500+
Guindy, Tamil Nadu	1977	500+	100+
Gir, Gujerat	1977	1500+	600+
Hyderabad, Andhra Pradesh	1977	900+	500+
Neyyar and Parambikulam, Kerala	1977	300+(?)	150+(?)
Taroba, Maharashtra	1979	200+	75+
Others	--	200+	50+
TOTALS		8700+	4775+

Figure 6. The mugger.

Mugger are resources to be managed. There is a thoughtful but slightly unrealistic attitude by a vocal segment of people living in the range of the mugger that crocodiles should not be farmed or culled. What is becoming more and more easy to demonstrate is that this attitude can be certain death to wildlife species that compete with or even seem to compete with man in any way.

Mugger have had little positive publicity. The only mystique surrounding them is that from the horror stories. They elicit fear and loathing from most people and are probably second only to snakes in lowness on the animal popularity poll. Without some very strong economic (and perhaps secondly, ecological) motives to save and propagate mugger, there is little likelihood of drumming up sustained support for the cause, particularly here in India. The harshness of living conditions for several hundred million people seems to leave little scope for worrying about the future of the mugger. In fact it is remarkable, a considerable credit to the late Prime Minister, Indira Gandhi, that crocodile conservation has received the attention it has in India.

The merits of a closed cycle mugger breeding operation or a ranching scheme is beyond the scope of this chapter and is discussed elsewhere. It is true that mugger are ideal candidates for propagating for skins and by-products. A single female can produce an average of 20 surviving offspring per year, each of which would be worth Rs. 1500/- in the third year. Thus a female mugger's annual "production" is worth about Rs. 30,000/- (US $2500).

The Government of Tamil Nadu was given the first go ahead signal for commercial farming by the Indian Board for Wildlife in 1982 but the project is not yet underway. While divergent opinions will continue to exist, no one can dispute the fact that the mugger has a better chance surviving in large numbers as a managed resource than as a generally unwelcome predator (Tables 8 and 9).

ACKNOWLEDGMENTS

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STATUS AND CONSERVATION OF THE ASIAN CROCODILIANS

Rom and Zai Whitaker

Madras Crocodile Bank
Madras India

INTRODUCTION

The eight species of Asian crocodilians have declined drastically in numbers, especially in the past 25 years. The story of their extermination is now into what could be the final chapter. Of the eight only the New Guinea crocodile is still fairly common in the wild. Intensive hide hunting managed to shift the focus from Africa to Asia and then South America as each area dried up (Fig. 1). Often there has been a second or third round of mopping up where a second, "inferior grade" species was available or when remote areas were opened up. Areas such as the island of Borneo, now split between Malaysia, Indonesia and tiny Brunei, which still contain large tracts of unsettled land, have only fragments of once substantial *Crocodylus porosus* and inland *Tomistoma* populations.

There is little accurate documentation of skin harvests of Asian crocodilians but what recent statistics are available are given in Table 1 to put into perspective what a profitable industry crocodiles could be for many indigenous peoples if used as a properly managed resource. Ross (1982b) asks a key question: "How do we integrate a policy dealing with an animal which is potentially dangerous, disliked and lives in areas suitable for fish ponds and rice paddy without completely eradicating it"?

For the purpose of this chapter, "Asia" is defined as ranging from the mugger habitat of Iran eastward to the Indonesian border with Papua New Guinea.

THE ASIAN CROCODILIANS

Crocodylus palustris -- **Mugger, marsh crocodile**

The mugger has the widest range of any of Asian freshwater species. It is highly adaptable and occupies a variety of habitats including hill streams and saltwater lagoons. In Iran, Pakistan, Nepal and Bangladesh there are very few left and with the exception of those in the few protected areas there is little future for the mugger in these countries. If considerable effort was made to rehabilitate the mugger, combined with stringent habitat protection and perhaps a commercial motive in these four countries, the mugger would have the chance of making a limited comeback.

In India the mugger has been fully protected under the Wildlife Protection Act to 1972 and is the subject of a conservation program that began in 1975. Nearly every state had at least a few
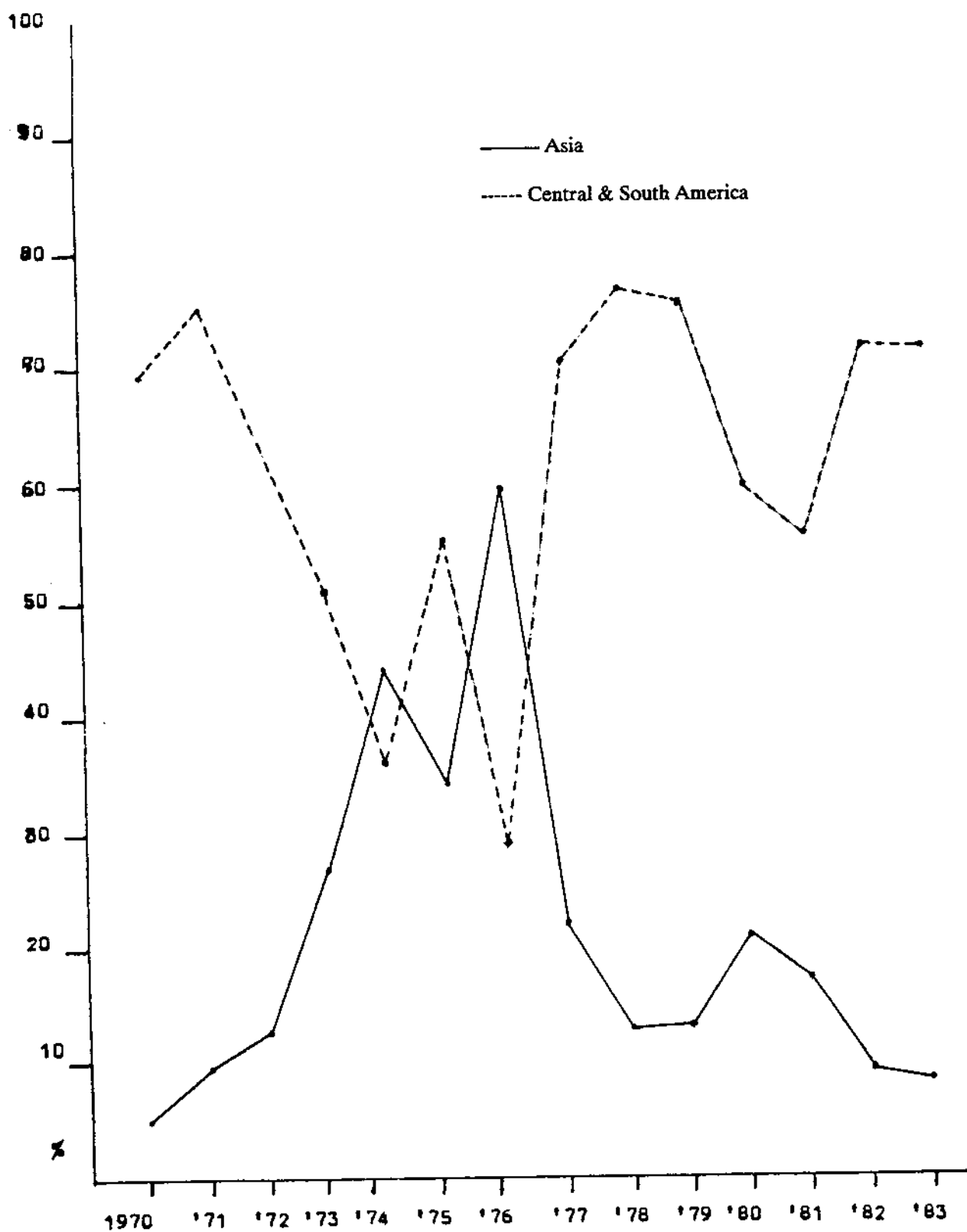
Figure 1. Rise and fall of the Asian crocodile skin trade since 1970 (courtesy of Tom Milliken, TRAFFIC/Japan).

Table 1. The Asian Crocodile Skin Trade (in Kilograms).

Country	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	TOTAL
Singapore	3064	2457	7930	17213	7285	10503	7619	6782	2475	4244	6552	3434	1424	91	80073
Malaysia	3292	5497	2582	1046	289	–	–	260	–	–	–	1357	1000	–	15341
Philippines	688	2568	891	809	617	104	664	353	264	1479	215	110	55	193	7950
Indonesia	770	275	1962	3162	1889	5037	5439	9373	5731	9543	7476	9554	15222	19348	94781
Thailand	–	–	20	–	–	–	2500	–	4576	6035	4008	2885	1299	–	21323
Pakistan	–	–	–	–	–	–	–	–	–	–	64	–	–	–	64
Sabah	–	28	–	–	–	–	–	–	–	–	382	621	100	–	1131
TOTAL	7814	10825	13385	22320	10080	15644	16222	16768	3046	21301	18697	17979	18100	19632	220663

Courtesy of Tom Milliken, TRAFFIC (Japan).

mugger left by the early 1970's but past hunting for skin and meat, collection of eggs for food and loss of habitat made the prognosis for mugger survival look grim.

Now, a decade later, government efforts (in some cases with FAO/UNDP assistance and private input), have secured a future for the mugger in India. At least 17 different zoos and rearing centers in the country have bred mugger in captivity and thousands of eggs have been collected from the wild for captive hatching and rearing for restocking programs. Several sanctuaries have been set up specifically for mugger and one state, Tamil Nadu, has been given Central Government approval to set up an experimental commercial crocodile farm.

In Sri Lanka mugger were common as recently as the late 1970's but were taking a battering from itinerant fishermen who netted them for the meat, discarding the skin. Large reservoir populations of mugger outside of the two large National Parks, Yala in the south-east and Wilpattu in the north-west have been decimated, particularly during drought years. Even now there are tanks (man made lakes) on the periphery of the Parks in which 100 or more mugger can be seen. Meanwhile massive development projects like the Mahaweli Ganga scheme in North Central Province take little note of the importance of the mugger as an economic resource nor of its role in the aquatic ecosystem. Mugger will survive in Sri Lanka's National Parks but it will be unfortunate if nothing is done to ensure that they remain an integral part of the island's remarkable wildlife. The Sri Lankan mugger population offers us the only chance to study an Asian freshwater crocodile in what must be close to original population densities.

Crocodylus siamensis -- Siamese crocodile

Once reportedly common in parts of Thailand, the Siamese crocodile's range extended to the Indochinese region and parts of Indonesia (Kalimantan, Sumatra, Java). Today the only known wild individuals survive at Bung Boraphet Reservoir in Nakhon Sawan province, Thailand where there may be 50 left.

The Siamese crocodile breeds readily in captivity and the Samut Prakan Crocodile Farm near Bangkok has over 20,00. Here they have been encouraged to hybridize with *C. porosus* though the owner assures us that pure stock is being separately maintained. It has also been bred in at least two zoos in the United States and at this time captivity seems to be where the species will remain.

Crocodylus porosus -- Saltwater crocodile, estuarine crocodile

The saltwater crocodile has the widest present day range of any crocodilian. Its ability to swim long distances in the open sea allowed it to colonize almost the whole of tropical coastal Asia besides many inland areas. The female produces large clutches of eggs and can be a formidable defender of her nest. But the large size and occasional man-killing tendency of big saltwater crocodiles have worked against the species. In addition, the skin industry prefers the smaller scales and larger surface area of saltwater crocodile skins to any other. More accessible to hunters than the inland freshwater species, saltwater crocodile populations were quickly reduced to remnants by the mid 1960's.

In the extreme east of its range the saltwater crocodile exists in safer numbers than most of the Asian crocodiles. Australia and Papua New Guinea have both spent considerable money and effort on managing their crocodiles and it is paying off, particularly in Papua New Guinea where the million dollar skin industry brings money to the poorest districts with few or no other exportable resources.

Just over the border from Papua New Guinea is the Irian Jaya Province of Indonesia where adult saltwater crocodiles are being rapidly wiped out for skins. In a few locations, important populations such as at the large, peninsular island of Pulau Kimaam near Merauke in the southeast are receiving some protection. From here westwards to India, the situation gets progressively worse. Probably the only significant populations in the entire remaining area of Asia are in some of the more remote inland areas of northern Sumatra (for example Sungai Kuba, Rian Province), the well managed breeding populations at Bhitarkanika Sanctuary in Orissa (India) and in parts of the Andamans and Nicobars (India).

Areas like Sabah and Sarawak on the island of Borneo would seem to be likely repositories of some of the old saltwater crocodile population densities but unfortunately it is not so. World Wildlife Fund sponsored surveys carried out in 1983 by Rom Whitaker and in 1985 by Jack Cox have turned up low density figures of about 0.05 crocodiles per kilometer of river surveyed by night. Much of the area surveyed was uninhabited and still forested and contained habitat capable of supporting much higher densities of crocodiles. Hunting for skins is obviously the most important recent factor for the continued decline of crocodiles here, but as early as 1881 the British Government had been paying rewards for killing crocodiles "to encourage destruction of a pest".

Recommendations for the rehabilitation and management of the saltwater crocodile have been officially made to the governments of Sabah and Sarawak (East Malaysia) and Indonesia. Project proposals based on crocodile ranching and farming have been made in the hopes that aid agencies such as FAO/UNDP and USAID will provide funding and expertise. Major elements in the proposals include detailed surveys, establishment of reserves, crocodile farming, research, and population monitoring programmes. In specific cases, such as Sarawak, any hope of bringing crocodiles back to areas in which they have long been extinct is linked to public relations and the forming of an effective crocodile control team to deal with the occasional nuisance crocodile.

Crocodylus mindorensis -- Philippine crocodile

Recent surveys and studies by C.A. Ross and A.O. Alcala demonstrate the extremely depleted status of the Philippine crocodile. Hide hiding and now loss of habitat to agricultural development are the main reasons for the decline. It is still found scattered in small numbers in remaining suitable inland habitats, mainly on Mindanao and the Sulu Archipelago. It is estimated, perhaps optimistically, that there are 500 to 1000 left in the world.

As Ross (1982a) noted, "conservation of non-essential wildlife resources is not given high priority in the Philippines; any conservation program which offers some possibility of ultimate utilization is more likely to win support from the government." At present the Philippine program for *C. mindorensis* consists of a World Wildlife Fund aided project of the Silliman University where a small captive group at Dumaguete City are being bred to provide young for release in protected areas.

Crocodylus novaeguineae -- New Guinea crocodile

A four month survey of the New Guinea crocodile was carried out (October 1984 to February 1985) and over 1500 kilometers covered by boat in the interior of Irian Jaya by Rom Whitaker and his assistants, Paul Sukran of Indonesian Environmental Forum (WALHI) and Chadiz Hartono of Directorate of Forest Protection (PHPA).

During the day villages were visited to interview the people about crocodile natural history, status and the skin industry. At night spotlight surveys were carried out to assess relative numbers of crocodiles and capture of a sample for measuring, marking and release. Visits were made to mission stations and discussions were held with people responsible for rural development in Irian Jaya. Visits were made to the main crocodile rearing farms and skins exporters. A survey of the trash fish resources was also carried out to determine feed availability for crocodile farms. The main crocodile habitats that were visited and surveyed were:

a)   Bian Lakes, Merauke District
b)   Asmat Area, Merauke District
c)   Rouffaer River (Upper Mamberamo), Paniai District
d)   Bintuni Bay, Manokwari District

In addition, the main towns and other areas visited were:

a) Jayapura   d) Kaimana   g) Sorong
b) Merakue   e) Manokwari
c) Fak Fak   f) Nabire

It was found that crocodile populations have been heavily reduced in the accessible river areas due to overhunting for skins. However, deep inland crocodile populations are more stable.

Some illegal killing of crocodiles and export of their skins continues. In general it was found that the local hunters will respect laws but are induced by the skin traders to organize periodic crocodile hunts. Most of the crocodile farms seen were of a mediocre standard and only one (Skyline in Jayapura) had significant numbers (1500-2000). So far very few skins of farmed animals are being exported.

Village hunters and rural developers all expressed a keen interest in participating in a proposed crocodile project. It was found that there is no other viable long-term alternative to help swamp-dwelling people (about 100,000 of them) to earn a living with cash income. For example, the small-scale timber industry in the Asmat area provides only a small renumeration (Rp. 5000 (US $5) per cubic meter or about Rp. 10,000 for a large tree) for the hard work of felling and hauling logs along the river. The necessity of extracting timber near the river (in the absence of hauling machines) is causing rapid degradation to the riverbanks. A managed crocodile industry could provide the Asmat villagers with Rp. 10.000 for one baby crocodile, a wiser use of the forest than removal of its timber!

It was found that there are sufficient trash fish resources (the by-catch of the shrimp trawlers) to feed 20,000 crocodiles or more in the towns of Sorong, Jayapura and Merauke.

It was recommended that a project proposal be drafted to initiate a crocodile project in Irian Jaya consisting of three basic components:

a)   large commercial farms at Sorong, Jayapura and Merauke
b)   a network of village collection farms and appropriate rural extension work and
c)   a crocodile population monitoring and research program to assure the sustainability of the industry and conservation of the species.

It was recommended that aid agencies be approached for technical and financial assistance in implementing this project. It was also recommended that the protection of wild adult crocodiles in

Irian Jaya be given priority. The New Guinea crocodile will have a safe future in Irian Jaya if it can become a managed resource upon which a large number of economically depressed people are dependent.

Tomistoma schlegelii -- Malayan (or false) gharial

One of the least known of all the crocodilians, *Tomistoma* is rarely seen in the wild anymore and has only bred in captivity at the Samut Prakan Crocodile Farm, Thailand. *Tomistoma* ranges from southern Thailand across to Borneo and down into Sumatra.

Today *Tomistoma* is apparently absent from southern Thailand and only a few live on peninsular Malaysia. On Borneo the situation may be little better. On a recent crocodile survey in Sarawak for WWF-Malaysia, consultant Jack Cox saw three *Tomistoma* at only one location, the Ensengai swamp system near Kuching. Rom Whitaker found no evidence that *Tomistoma* ever existed in Sabah; *Tomistoma* habitats in Kalimantan and Sarawak are cut off from Sabah by fairly high hill and mountain ranges. It is probable that there are viable populations of *Tomistoma* in Kalimantan (Indonesia) but no surveys have yet been made.

Small numbers of juvenile live *Tomistoma* still appear at Singapore crocodile "farms" and it is likely that their origin is nearby Sumatra which has never been surveyed.

Gavialis gangeticus -- Gharial

The gharial is one crocodilian that people acknowledge as harmless to humans. But being a fisheater it is treated as a competitor. In 1974 the world gharial population, captive and wild, was estimated to be under 250. Now, in 1986 it is over 2500 due mainly to the efforts of several State Forest Departments (see Table 2). The Government crocodilian rehabilitation program, initially aided by FAO/UNDP, initially concentrated its efforts on saving the gharial which looked like it was on its way out. Even today there are apparently fewer than twenty adult male gharial both captive and wild.

The only large area of protected habitat for the gharial in India is the National Chambal Sanctuary, covering 600 river kilometers and running through three states, Uttar Pradesh, Madhya Pradesh and Rajasthan. The other gharial areas in India such as Katerniaghat in Uttar Pradesh, Sathkoshia Gorge in Orissa and bits of the Son, Ken (Madhya Pradesh) and other rivers are very small and in the long run, very vulnerable. There is a small population in Corbett National Park (Uttar Pradesh). Besides the Chambal in India, the other major gharial population that is reasonably secure is that of about 20 adults in Chitwan National Park (Rapti-Narayani River) in Nepal.

Although it has been so far bred at only one center, (in 1985 six nests were laid at Nandankanan Biological Park, Orissa) the gharial responds well to captive rearing and growth rates make it acceptable for commercial farming or ranching. Considering the large quantities of fish gharial consume, it is critical that the ecological/economic advantages of having gharial back in the river ecosystems outweigh the disadvantages.

Table 2. Juvenile Gharial Released for Restocking Protected Habitat (1977-1984).

Place	State/Country	Number released
National Chambal Sanctuary	Madhya Pradesh, Uttar Pradesh, Rajasthan	912
Sathkoshia Gorge Sanctuary	Orissa	150
Katerniaghat Sanctuary	Uttar Pradesh	83
Chitawan National Park	Nepal	50
Ken Sanctuary	Madhya Pradesh	3
Son Sanctuary	Madhya Pradesh	2

Alligator sinensis -- **Chinese alligator**

This small (under 2 m) alligator was once widespread throughout the eastern portion of the Yangzi River basin. There is now little or no wild habitat left for the Chinese alligator and it survives precariously in the midst of human agriculture. Concentrated in the Xuancheng region, the center of the alligator's current range, smaller populations are found in Zhejiang and Jiangau Province. Watanabe and Chu-chien (1984) estimate that there are about 300-500 wild alligators in the Xuancheng region and a total of 1500-2000 (both on farms and in the wild) in the country.

Chinese alligators depend on being able to dig extensive dens to hide in and to hibernate in over winter months. Being docile and fairly small they are frequently disturbed and nests destroyed by children and farmers.

The Chinese alligator is the subject of several ongoing studies and captive breeding has been achieved at the Chinese Alligator Breeding Center, Anhui Province (where 300 hatchlings were produced in 1983), Shanghao Zoo and Rockfeller Wildlife Refuge in the U.S. Emphasis on captive breeding is important to ensure the survival of adequate genetic stocks of the species. The establishment and maintenance of wild reserves for the Chinese alligator has very limited scope, but unless these efforts are made this interesting reptile will no longer be able to survive in the wild.

SUMMARY

The outlook for the Asian crocodilians is bleak indeed. Table 3, which is made up in many cases of very approximate data, dramatizes their plight. The Chinese alligator, gharial and Siamese crocodile are all more numerous in captivity than in the wild. The New Guinea crocodile is the only species that still exists in anything resembling "safe" numbers and only because of its original swamp habitat remains difficult of access and unaltered.

Conservation and management approaches range all the way from India's preservation/rehabilitation program to Papua New Guinea's managed ranching scheme. Ranching, (that is, the collection of eggs and/or young for captive rearing and culling) can be a most effective method of guaranteeing attention to habitat protection. As long as it is profitable to take crocodiles from a swamp, that swamp will be protected with everything in it.

In general, two activities are needed in each of the Asian countries where crocodiles are found: (a) public education and reassurance (which includes an effective, mobile nuisance crocodile catching squad); and (b) the setting up of management programs, if necessary with outside help. Indonesia has a special responsibility since three of the eight Asian species--Malayan gharial, saltwater crocodile, and New Guinea crocodile--are found mainly in the Indonesian archipelago and Kalimantan. India is particularly responsible for the continued survival of the gharial, China the Chinese alligator, and Thailand the Siamese crocodile.

Demonstrating that (a) crocodile farming is a logical form of land use, (b) crocodiles are needed in aquatic ecosystem, (c) crocodiles are rarely dangerous to man, and (d) crocodiles are edible and produce the most valuable and durable leather in the world will help people accept that we cannot dismiss crocodiles. These reptiles have been denizens of the earth for 100 million years. Each country and indeed each set of circumstances may demand a novel approach to the problems of accepting and living with crocodiles. But it is worth the effort. The various Asian crocodile

Table 3. Status of Asian Crocodilians.

Species	Distribution	Wild population	Captive population	Conservation management efforts	Legal Status	CITES	IUCN Red Data Book
Crocodylus palustris	Iran	50-100	Few	?		I	Vulnerable
	Pakistan	30-50	Few	Moderate			
	India	2-3000	3000+	Active			
	Nepal	30-50	Few	Moderate			
	Bangladesh	5		Nil			
	Sri Lanka	2-3000	Few				
Crocodylus siamensis	Thailand	50-100	20,000	Private farm		I	Endangered
	Vietnam	?	Few	?			
	Kampuchea	?	Few	?			
Crocodylus porosus	India to Irian Jaya	25-50,000	10,000**	Nil to active in various countries		I	Endangered
Crocodylus mindorensis	Philippines	500-1000	500-1000	Moderate		I	Endangered
Crocodylus novaguineae	Irian Jaya	100-200,000	3000	Surveys		II	Vulnerable
Tomistoma schlegelii	Malaysia (Sarawak)	500-1000	100+	Surveys		I	Endangered
	Indonesia (Kalimantan, Sumatra)	1000-3000	200+	Nil		I	Endangered
Gavialis gangeticus	Pakistan	30	Few	Little		I	Endangered
	Nepal	30-120	100+	Active			
	India	1000+	2000+	Active			
	Bangledesh	25-35	Few	Little			
Alligator sinensis	China	500+	800+	Active		I	Endangered

Legal Status: PROTECTED BY LAW IN ALL ASIAN COUNTRIES EXCEPT VIETNAM AND KAMPUCHEA

* excluding first year hatchlings

**excluding *C. porosus* in Papua New Guinea and Australia

Table 4. Breeding results--Madras Crocodile Bank.

Year	Mugger hatchlings	Saltwater crocodile hatchlings	Caiman hatchlings
1976	30	--	--
1977	50	--	--
1978	399	--	--
1979	164	--	--
1980	236	--	--
1981	289	--	--
1982	228	--	37
1983	240	74	34
1984	252	30	60
1985	235	45	36
TOTAL	1813	92	167

programs are forerunners to what will hopefully become an accepted profitable form of land use. Man's first domestic reptile is the crocodile.

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