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
	Myeeli 1 Nest
1360	0.073
1362	0.071
1367	0.074
1370	0.084
1389	0.083
1394	0.080
1403	0.094
Mean	0.080 ± 0.008
All wet season growth	

RECORD B	0-(37-39) days
	Myeeli 2 nest
1316	0.085
1344	0.095
1348	0.122
Mean	0.100 ± 0.019
All wet season growth	

RECORD C	0-53 days
	Liverpool km 47.5 Nest
	Released on Tomkinson
1404	0.126
1405	0.125
1406	0.132
1407	0.109
1410	0.138
1414	0.081
1415	0.158
1416	0.132
1418	0.134
Mean	0.126 ± 0.021
Almost all wet season growth	

RECORD D	13-52 days
	Liverpool B22 Nest
1486	0.029
1492	0.047
1506	0.026
1514	0.028
1510	0.053
1517	0.053
Mean	0.039 ± 0.013
All dry season growth	

RECORD E	53-82 days
	Liverpool km 47.5 Nest
	Released on Tomkinson
1404	0.083
1406	0.072
1407	0.041
1413	0.038
Mean	0.058 ± 0.022
All dry season growth	

RECORD F	0-96 days
	Myeeli 1 Nest
1360	0.075
1364	0.074
1370	0.081
1391	0.083
1394	0.067
Mean	0.076 ± 0.006
40 days are dry season	

RECORD G	0-65 days
	Myeeli 1 Nest
1358	0.080
1360	0.0815
1370	0.098
1394	0.083
1396	0.102
1403	0.098
Mean	0.090 ± 0.010
Almost all wet season growth	

RECORD H	0-82 days
	Liverpool km 47.5 Nest
	Released on Tomkinson
1404	0.111
1406	0.111
1407	0.085
Mean	0.102 ± 0.015
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 $\Delta SVL = a\ \Delta T_W + b\ \Delta T_D$. 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 ± 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 obtaln 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.

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