

Ecology, sustainable use by local people, and conservation of Morelet's crocodile (*Crocodylus moreletii*) in Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico.

By Gonzalo Merediz-Alonso

A thesis submitted in partial fulfillment
of the requirements for the
Master of Science Degree

State University of New York
College of Environmental Science and Forestry
Environmental and Forest Biology
Syracuse, New York

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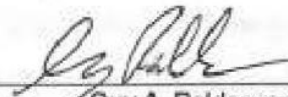
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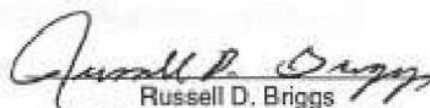
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ABSTRACT.

To evaluate the possibilities of harvesting Morelet's crocodile (*Crocodylus moreletii*) by local people in Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico, I estimated population size with a capture-recapture survey. There were 630 ± 19 individuals. I applied the Bertalanffy growth model to calculate age of crocodiles based on total length. I estimated population age structure and life table, and used the survival and fertility rates of each age class to project a Leslie matrix model of the population. The first age class represents 48% of the population, which has an intrinsic rate of increase of $r = -0.00003$. I used the population model to evaluate nine harvesting and restocking scenarios. Harvesting adult individuals is not feasible. It is possible to implement a ranching program by collecting 50% of wild produced eggs or 75% of yearlings, incubating them until they reach commercial size. About 30% of collected individuals must be restocked after 3 years.

Key Words: *Crocodylus moreletii*, Morelet's crocodile, population ecology, Quintana Roo, Mexico, sustainable use, conservation.

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THESIS SUMMARY.

The central coast of Quintana Roo, Mexico has wetlands that provide important wildlife habitat. To protect these wetlands and other habitats the Mexican government established Sian Ka'an Biosphere Reserve. If local people are not interested and involved, conservation efforts in Sian Ka'an will not be successful. If wetlands can provide some benefits to people, local communities will have more interest in participating in their protection. In wetlands, the crocodile is the most economically important resource. Morelet's crocodile (*Crocodylus moreletii*) can be used for ecotourism, and for selling skins and meat. However, Morelet's crocodile is considered rare by Mexican law, and is cited in Appendix I in CITES. Hence, to initiate a sustainable Morelet's crocodile harvest program, it is necessary to know its population ecology. Then, it would be possible to evaluate the feasibility of a harvest, and facilitate obtaining the certificates from Mexican government and CITES to trade Morelet's crocodile products. To estimate population size of Morelet's crocodile, a capture-recapture survey was implemented between 1993 and 1996 in northern Sian Ka'an. There were 630 ± 19 individuals. I applied the Bertalanffy growth model to calculate age of Morelet's crocodile based on total length. I then estimated the population age structure, constructed a static life table, and used the survival and fertility rates of each age class of the life table to project a Leslie matrix model of the dynamics of the population. The first age class represents 48% of the population, which has an intrinsic rate of increase of $r = -0.00003$. I used the population model to evaluate nine harvesting and restocking scenarios. Harvesting adult Morelet's crocodile is not feasible in Sian Ka'an. The population model suggests the implementation of a ranching system where about 50% of wild produced eggs and 75% of the hatchlings can be collected and incubated until they reach commercial size. About 30% of collected individuals must be restocked after three years. Production would depend on wild population so that producers would be concerned about that population and its habitat. A ranching project does not mean that it will be successful. Local community participation will be an essential factor in developing a positive and useful project.

MEREDIZ ALONSO, GONZALO. Ecología, aprovechamiento sustentable por parte de las comunidades locales y conservación del cocodrilo de pantano (*Crocodylus moreletii*) en la Reserva de la Biosfera Sian Ka'an, Quintana Roo, México.

RESUMEN.

La costa de Quintana Roo, México es un área de humedales, los cuales constituyen un importante hábitat para la fauna y flora silvestres. Para proteger a esos humedales así como a otros ecosistemas, el gobierno federal mexicano decretó el establecimiento de la Reserva de la Biosfera Sian Ka'an. Sin embargo, los esfuerzos de conservación en Sian Ka'an serán estériles sin la participación y el interés de los habitantes de la región. Si los humedales proporcionan beneficios económicos, culturales y estéticos a la gente, las comunidades locales estarán más interesadas en tomar parte en su conservación. En los humedales, el cocodrilo es el recurso económicamente más importante. El cocodrilo de pantano (*Crocodylus moreletii*) puede aprovecharse en programas de ecoturismo y para la venta de pieles y carne. Sin embargo, esta especie está catalogada como rara por la ley mexicana (NOM-ECOL-059-1994) y aparece en el Apéndice I de CITES. Es por ello que, para iniciar su aprovechamiento sustentable, es necesario conocer su ecología poblacional, entre otros aspectos básicos de su biología. Esa información permitiría evaluar la factibilidad y estrategia del aprovechamiento y la obtención de los permisos correspondientes, por parte del gobierno mexicano y CITES, para la comercialización de subproductos del cocodrilo de pantano. Para estimar el tamaño de la población del cocodrilo de pantano, se realizó un estudio de captura-recaptura en la zona norte de Sian Ka'an entre 1993 y 1996. La población promedio estimada fue de 630 ± 19 individuos. Por medio del modelo de crecimiento de Bertalanffy, se calculó la edad de los cocodrilos de pantano con base en su longitud total. Posteriormente, se estimó la estructura de edades de la población así como una tabla de vida estática. Con las tasas de sobrevivencia y fertilidad de cada categoría de edad, se modeló, mediante una Matriz de Leslie, la dinámica de una población con 30 categorías de edad. La primera categoría de edad representa el 48% de la población, la cual presenta una tasa

intrínseca de crecimiento de $r = -0.00003$. Con base en el modelo poblacional se evaluaron nueve escenarios de aprovechamiento y reintroducción de cocodrilos de pantano. El modelo indica que el aprovechamiento de adultos no resulta factible, sin embargo, sugiere la implementación de un programa de ranqueo. En él, el 50% de los huevos y el 75% de las crías silvestres podrían ser colectados e incubados hasta que los cocodrilos alcanzaran la talla comercial, reliberando en los humedales, tres años después, un 30% de los individuos colectados. De esta manera, la producción dependería de la población silvestre y los productores tendrían la motivación de conservar tanto a los cocodrilos como a su hábitat en los humedales de Sian Ka'an. Un programa de ranqueo por sí mismo no garantiza el cumplimiento de sus objetivos de conservación. Por ello, la participación de las comunidades locales en la decisión, planeación e implementación del programa es un factor clave para que éste resulte positivo y útil.

INTRODUCTION.

The central east coast of the Yucatan Peninsula is an area of abundant wetlands that provides important wildlife habitats. These wetlands contain several species such as tapir (*Tapirus bairdii*), jaguar (*Panthera onca*), Morelet's crocodile (*Crocodylus moreletii*), and American crocodile (*C. acutus*), all of which are afforded some protection under Mexican law (NOM-ECOL-059-94). These wetlands are also important as breeding, feeding, and refugee areas for about 50 freshwater species of fish (Gamboa 1992) and some marine fishes (Vásquez and González 1992). Wetlands also provide and regulate the quality of nutrients to the adjacent coral reefs (Molina et al. 1998). The protection of these wetlands is a priority for the Mexican federal government, which in 1986 established the 528,147-ha Sian Ka'an Biosphere Reserve (Sian Ka'an) to preserve wetlands and other habitats (Diario Oficial de la Federación 1986). In 1994, the Federal government added the adjacent lands south of Sian Ka'an to the reserve, under the category of Uaymil Fauna and Flora Protection Area (Diario Oficial de la Federación 1994). Together the protected areas encompass 620,000 ha and represent the second largest protected area on the Yucatán Peninsula.

Establishment of Sian Ka'an does not ensure the conservation of the area. If local people are not interested and involved, conservation efforts will not be successful. Alternatively, people who live in the surrounding area (mostly Mayan people with extensive knowledge about natural resources) face increasing social, economical, and cultural problems. They also have the historical right to use the resources that are on their land, even if the Mexican government declared the area as a reserve. Hence, if wetlands can provide some economical, cultural, and aesthetic benefits to people, they will be more interested in participating in their protection.

In the case of wetlands, the crocodile is probably the most economically important resource present. Crocodiles can be used for ecotourism programs as well as for selling skins and meat (Herrera 1989). Unfortunately, both species of crocodile present in the area are considered rare by Mexican law (NOM-ECOL-059-94), are cited in Appendix I in CITES

(1989), are catalogued as endangered in the IUCN (1990) Red List, and are considered endangered under the U.S. Endangered Species Act (Lee 1996). Hence, to consider initiating a sustainable crocodile harvest program, it is necessary to know their population dynamics and basic natural history. With such information, it would be possible to evaluate the feasibility of a harvest, as well as its type and magnitude. If positive, such information would also facilitate obtaining the certificates from Mexican government and international institutions (i.e., CITES) to trade crocodile products.

Since 1990, the nongovernmental organization, Amigos de Sian Ka'an, initiated a long-term survey of crocodile population dynamics and reproductive biology in Sian Ka'an. Since 1993, samples have been taken twice weekly and almost uninterruptedly to estimate the population size and dynamics of the American and the Morelet's crocodiles. Since the American crocodile seems to be more rare (Platt and Thorbjarnarson 1997, G. Merediz, Pers. obs.), any potential harvesting program would only be focused on Morelet's crocodile.

Very little is known about Morelet's crocodile in general (Platt 1996), and even less about populations in Quintana Roo. The species was first described by Duméril and Duméril (1851) from Guatemalan specimens. There was almost no published information until Schmidt (1924) rediscovered the species in Belize. Very few papers have been published since then (see Abercrombie et al. 1980 for citations). Powell (1965) reported on the status of Morelet's crocodile in Yucatán, and Alvarez del Toro (1974) presented a comparative study of the Mexican crocodillians. However, Alvarez del Toro based his study on general or anecdotal observations made mostly in Chiapas State. Abercrombie et al. (1980) wrote about the status of Morelet's crocodile in Belize based on some nightlighting observations and the capture of 14 individuals. Overall, most work on Morelet's crocodile has been based on occasional field observations or captive animals (e.g., Abercrombie et al. 1980; Pérez et al. 1991; Hunt 1975, 1977; Pérez et al. 1995). Probably one of the most extensive surveys done to date is that by Platt (1996) in Belize. He addressed the nesting ecology, food habit, foraging behavior, size, sex ratios, embryo growth, and the status of the species there.

This species lives in both fresh and brackish waters in southeastern Mexico (states of Chiapas, Tabasco, Campeche, Yucatán, Quintana Roo), and in northern Belize and Guatemala (Lee 1996). Almost every freshwater body in central and northern Quintana Roo, has Morelet's crocodiles (Lee 1996, G. Merediz, Pers. obs.). Morelet's crocodile is a medium-sized species that can grow up to 4,500 mm (Pérez et al. 1991). They breed yearly with females constructing leaf and branch nests at the water's edge when the rainy season starts in June-July. Young crocodiles hatch in September-October.

In Quintana Roo, México, there is no published information about the biology or status of Morelet's crocodile. In 1990, Amigos de Sian Ka'an and Marco Lazcano started to study the crocodile population in northern Sian Ka'an using capture-recapture techniques. The study was redesigned in 1993 to acquire more information, part of which is presented in this work. The sampling efforts continue to date, and the information compiled is probably the most extensive database for a natural Morelet's crocodile population.

In this paper, I use the 1993 - 96 data obtained in Sian Ka'an for Morelet's crocodile to estimate the population size via a geometric capture-recapture model. I also apply a body-growth model for this species and estimate the age of each captured individual. From these estimates, I then determined the population age and sex structure as well as the survival and fertility rates for each age, and the survival rates for each sex class. Finally, I use those data to develop a life table for the population and model its dynamics with a Leslie matrix (Caswell 1989). Using the modeling simulations, I evaluated the feasibility of harvesting crocodiles.

The Mexican federal government will use this work as technical support for their proposal to downlist some Mexican Morelet's crocodile populations from Appendix I to Appendix II of CITES. Such a downlisting would allow the legal international trade for those populations and thus create a new source of income for local people. That could promote their participation in preserving regional wetlands.

STUDY AREA.

This study was conducted in northern Sian Ka'an, Quintana Roo, México (Figures 1, 2, 3, 4). The reserve is located in the east central coast of the Yucatán Peninsula, bordering the Caribbean Sea (between 19°05' and 20°08' N, and 87°23' and 88°02' W).

Sian Ka'an (Figure 3) is divided into three Core Areas where human activities are prohibited with the exception of scientific research: Cayo Culebras in Ascención Bay; Uaimil in the south, at the vicinity of Uaymil Protection Area; and Muyil, in the north. The core areas compose 279,703 ha of Sian Ka'an. The remaining 248,443 ha are buffer areas designed to "protect core areas from external influences" (IUCN Conservation Monitoring Centre 1986). Sustainable and managed use of natural resources by local people is allowed within the buffer zones.

The human population inside Sian Ka'an is relatively low and is concentrated in two coastal villages: (1) Punta Allen, with 362 inhabitants, located on Ascención Bay; and (2) Punta Herrero, on Espíritu Santo Bay, with 36 permanent residents (INEGI 1991). The main productive activity among Sian Ka'an's villagers is commercial fishing, especially lobster (*Panillurus argus*) fishing. In addition, fishing activities also involve 35 bony fish and 14 shark species (Basurto 1996). Ecotourism is a growing activity in Sian Ka'an, especially in the northern part.

Mayan people compose most of the population that uses or might use Sian Ka'an's natural resources. This population lives outside the reserve and totals 10,186 people (INEGI 1995), not including about 17,000 inhabitants of the city of Felipe Carrillo Puerto. The land tenure is based on a few small private lands and large communal properties called "ejidos." The 14 ejidos at the vicinity of Sian Ka'an's boundaries are considered a cooperation zone. Those ejidos have the right to use, under strict regulations, the natural resources within the buffer areas. Currently, most of the exploitation of natural resources occurs outside the reserve. Shifting cultivation, timber and wildlife harvesting, and natural chewing gum extraction are among the most important productive activities.

Sian Ka'an protects different types of ecosystems (Figure 3): medium subperennifolious forest, low flooded forests, emergent wetlands, dwarf red mangroves (*Rhizophora mangle*), fringe mangroves (Olmsted and Durán 1990), and coral reefs. Wetlands constitute about two-thirds of Sian Ka'an's total area.

Following Köppen's classification as modified by García (1964), the climate in the area is warm subhumid with rains during the summer or $Aw^*_2(I')$. Average annual precipitation is 1,153 mm, and average annual temperature is 25.8°C (CEEM 1987). The region experiences two main seasons: "lluvias" (rainy) from May to October, and "secas" (dry) from November to April. Occasional rainfall and temperature drops occur during parts the dry season (from November to February) due to cold fronts or "nortes" coming from the north. Sian Ka'an also experiences hurricanes coming from the Caribbean Sea and the Atlantic Ocean. The hurricane season extends from May to November, with August and September the most frequent months of hurricane occurrence (Morales 1993).

The study site is located within the buffer area just north of Muyil Core Area (Figure 4) between 20°00' and 20°05' N, and 87°29' and 87°38' W. Different wetland types and water bodies dominate the landscape. The fieldwork was concentrated in three main lagoons and a surrounding network of canals: Muyil, Chunyaxché, and Boca Paila. Muyil and Chunyaxché are freshwater lagoons located 9-km from the coast. Muyil is a round lagoon, 2-km in diameter, whereas Chunyaxché is an elongated 8-km lagoon. A narrow, 400-m canal connects both lagoons, which are funnel-type lagoons, with low depth in the perimeter increasing gradually toward the center where they are more than 100-m deep. Water is transparent; the bottom is mostly muddy. The vegetation around Muyil and Chunyaxché is dominated by emergent wetlands with cattail (*Typha dominguensis*), phragmites (*Phragmites australis*), and common rums (*Cladium jamaicensis*) as the most important plant species. These large, flat, emergent wetlands also contain terrain elevations called petenes. Petenes are usually covered by palms (*Acoelorrhaphe wrightii*), red mangroves (*Rhizophora mangle*), or

forest vegetation (*Manilkara zapota*, *Metopium brownei*, *Bursera simaruba*, and others; Olmsted and Durán 1990).

Dwarf red mangroves gradually replace emergent wetlands toward the coast where the third lagoon, Boca Paila, is located. Boca Paila is a shallow, brackishwater lagoon connected to the ocean. Water is less transparent and the bottom is sandy to muddy. The lagoon is surrounded by dwarf red mangroves. Fringe, taller red mangroves dominate the seaside shore. The dwarf red mangrove area contains a canal network that was also part of the study site. These canals are from 1 to 30-m wide, with brackish waters and muddy bottoms. Boca Paila lagoon is connected with Chunyaxché lagoon by the 15-km Chunyaxché canal, where vegetation and salinity gradients become apparent. Chunyaxché canal also was a study site.

The region around the study site is almost undeveloped. A few local people occasionally fish in Muyil and Chunyaxché for self-consumption. Those people live in the Chunyaxché village, which has no more than 11 families. An unknown amount of white-tailed deer (*Odocoileus virginianus*) hunting occurs in the emergent wetlands, which occasionally are burned to facilitate hunting. Chunyaxché and Muyil are accessible by the Federal Road 307 (two lanes) from Tulum and Cancún in the north and from Felipe Carrillo Puerto in the south (Figures 3, 4). A Mayan archaeological site is present at Muyil's shore and is occasionally visited by tourists.

Boca Paila is accessible by a dirt road from Tulum in the north and from Punta Allen in the south (Figures 3, 4). A number of small hotels and cabins are located at the roadside, and tourism activity is increasing. The area received 18,768 tourists in 1998, that is, 1,564 tourists per month (Alfredo Arellano, Pers. com.). Sport fishing as well as scuba diving are the main tourist activities present. Numerous out-board engine boats take tourists to fish bonefish (*Albula vulpes*) and other species in Boca Paila lagoon and canals.

Neither side of the study area has power lines. However, the hotels at the coast have small electric generators. Chunyaxché village has no electricity.

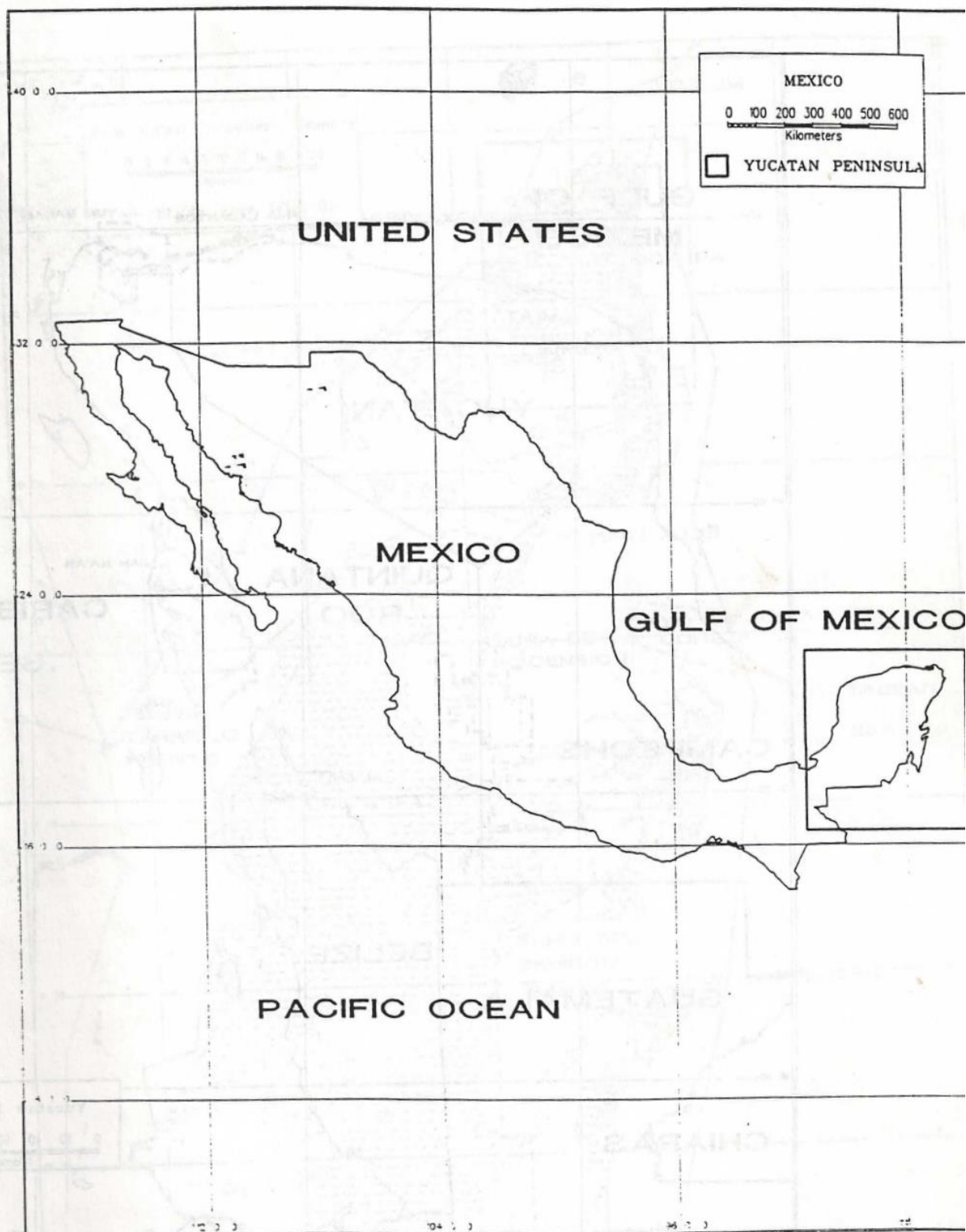


Figure 1. Mexico and the Yucatan Peninsula

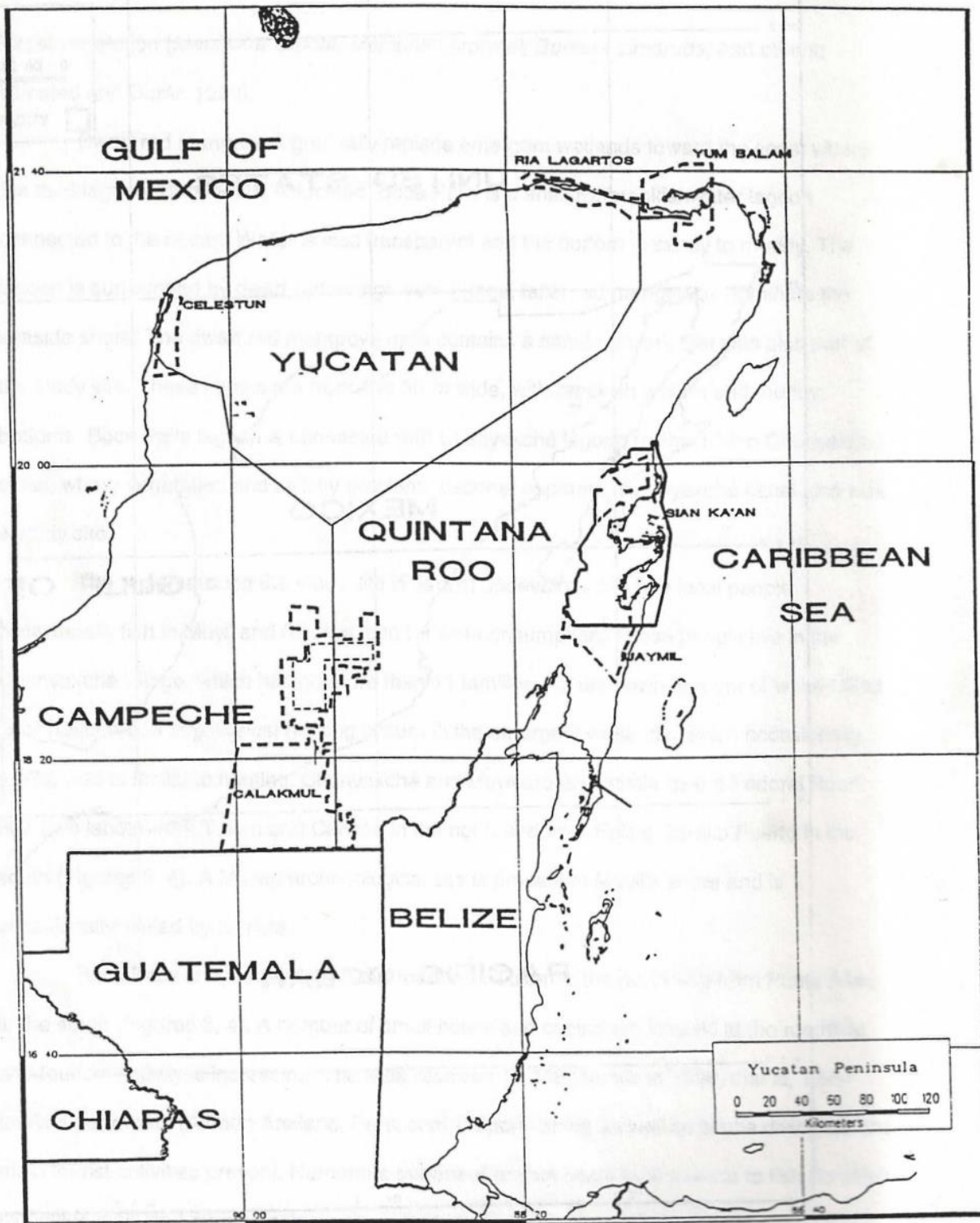


Figure 2. The Yucatan Peninsula

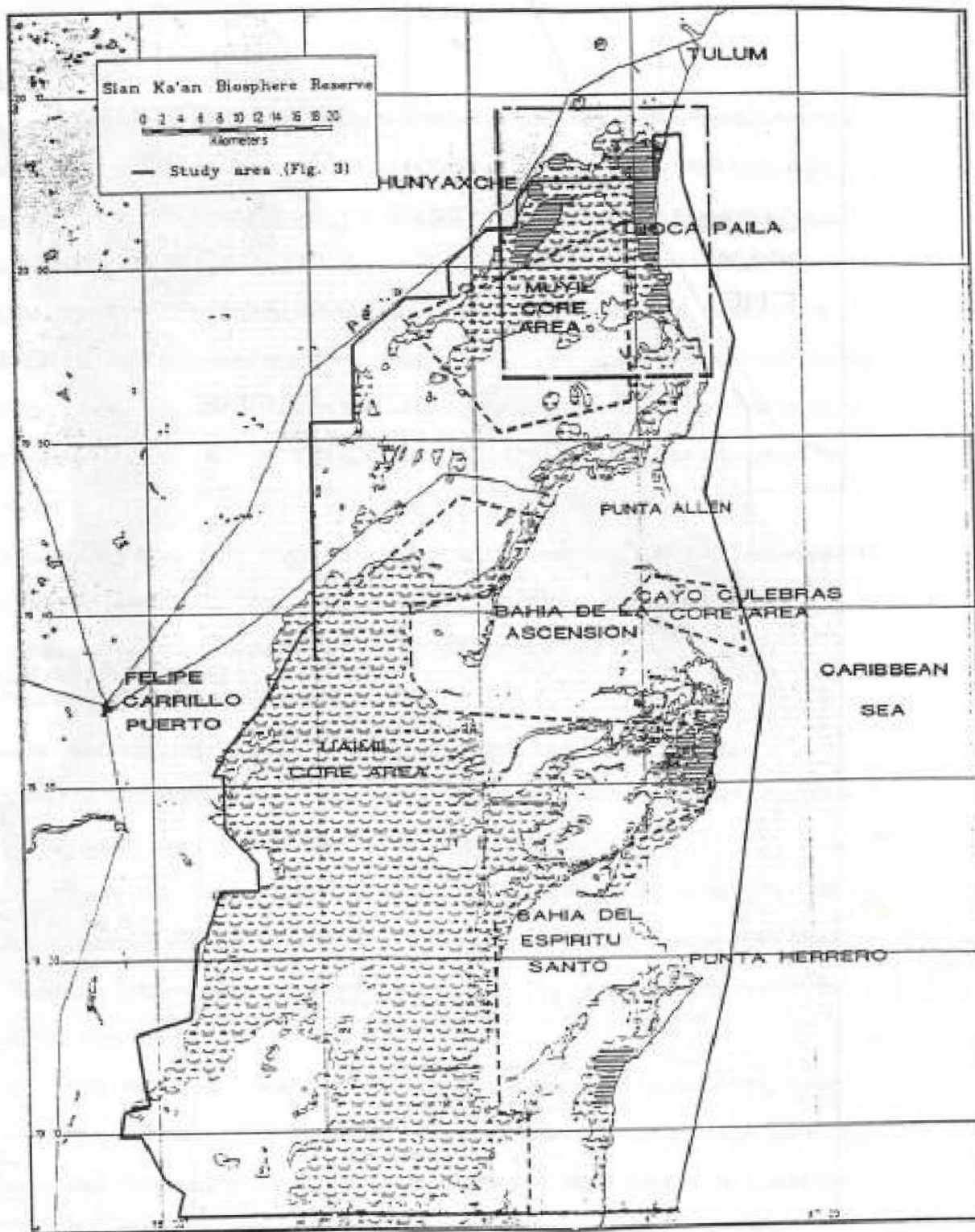


Figure 3. Sian Ka'an Biosphere Reserve

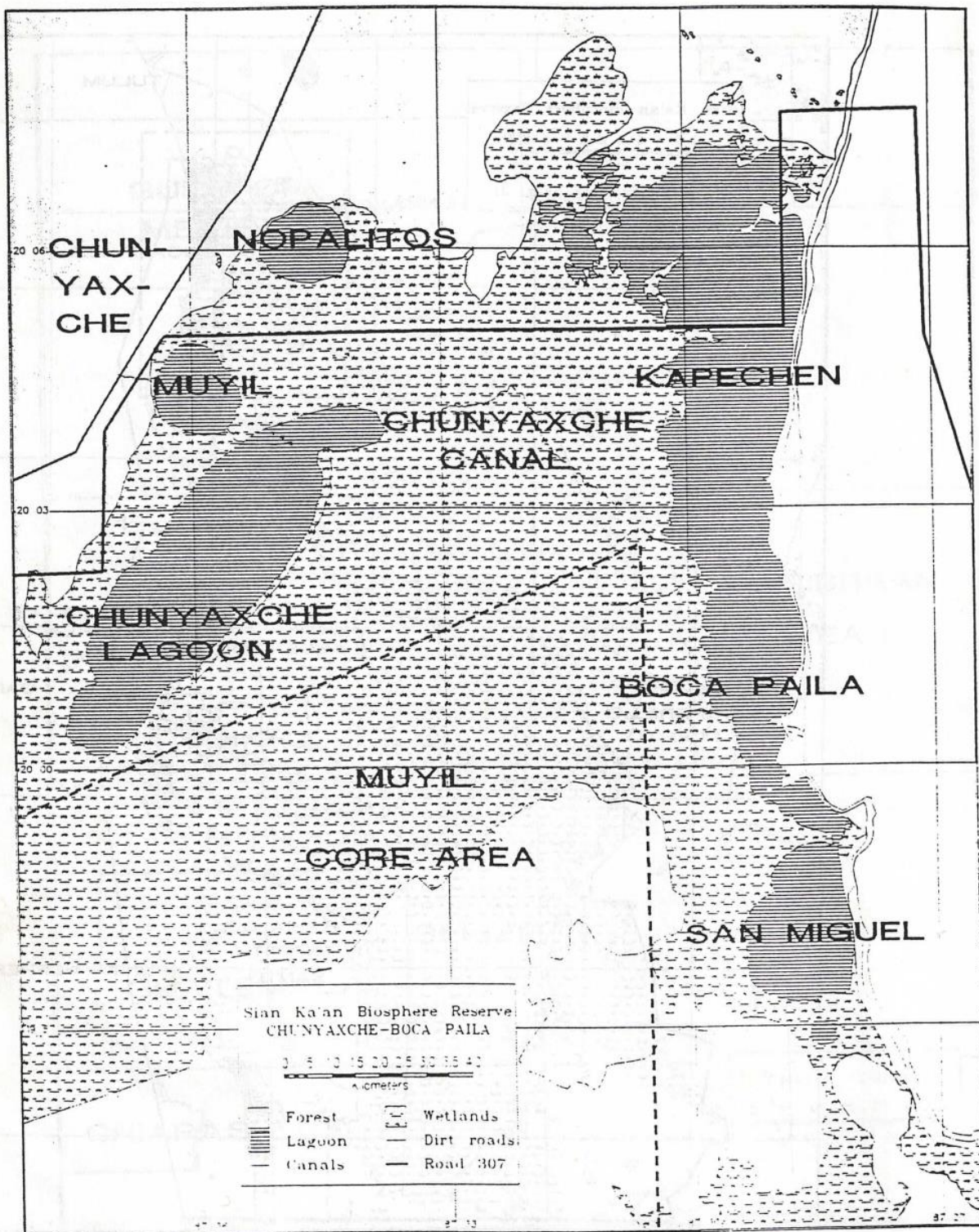


Figure 4. Study site in northern Sian Ka'an Biosphere Reserve

METHODS.

To estimate the population size of Morelet's crocodiles, a capture-recapture survey was implemented in three seasons between October 1993 and October 1996 along eight routes (52.5 km long) established in the lagoons and canals in northern Sian Ka'an (Table 1 and Figure 4). Routes were traveled two nights per week, by boat with an out-board engine. Crocodiles were located with a 400,000-candlepower spotlight (100-Watt), caught with a metallic noose, and taken into the boat. Small crocodiles were caught by hand. The following measurements (with a Bernier ruler and/or tape to the nearest 0.1-cm) were made on every individual (Webb and Messel 1978; parameters marked as "*" are directly relevant for this paper):

Snout-vent length (SVL)*. - From the tip of the snout to the anterior margin of the cloacal vent (Platt 1996).

Tail length (TaL)*. - From the anterior margin of the cloacal vent to the tip of the tail.

Total length (TL)*. - The sum of SVL and TaL.

Total head length (HL)*. - From tip of the snout to median hind length of platform.

Maximum head width (MHW). - Posterior to cranial platform; distance between extremities of the surangular bones, at the level of the articulation of the bones.

Snout length (SL). - From the tip of the snout to the level of the anterior edge of the orbits.

Snout maximum width (SMW). - Snout width at the level of the anterior edge of the orbits.

Body mass (BM in g). - Measured with 0.1, 0.5, 1, 2, 5, 20 kg scales (Pesola) to crocodiles not heavier than 20-kg.

All animals were measured, sexed, marked, and released *in situ*. Three different marking systems were used: numbered cattle ear tags, numbered metallic clips, and cutting tail scutes. Other parameters such as weather, vegetation, water depth, water bottom type, temperature, time, and moon phase were recorded. Every season, nests of Morelet's crocodile were located in the study area. The number of eggs per nest was determined during the first sampling season (1993-94).

Table 1. - Crocodile sampling routes and associated habitat types in northern Sian Ka'an Biosphere Reserve.

| Route name | Code | Location | Type/Vegetation |
|------------------|------|----------------------------------|--------------------------------|
| Muyil | LM | Muyil Lagoon shore | Lagoon/Grass-Petenes |
| Chunyaxché norte | LCN | Northern Chunyaxché Lagoon shore | Lagoon/Grass-Petenes |
| Chunyaxché oeste | LCO | Western Chunyaxché Lagoon shore | Lagoon/Grass-Petenes-Mangroves |
| Chunyaxché este | LCE | Eastern Chunyaxché Lagoon shore | Lagoon/Grass-Petenes-Mangroves |
| Canal Chunyaxché | CCH | Chunyaxché Canal | Canal/Grass-Petenes-Mangroves |
| Boca Paila | LBP | Eastern Boca Paila Lagoon shore | Lagoon/Mangroves |
| Canal Pinos | CP | Canals west of Boca Paila | Canals/Dwarf mangroves |
| Canal Monjas | CM | Canals northwest of Boca Paila | Canals/Dwarf mangroves |

I estimated population size with the capture-recapture geometric estimator of the capture frequency model (Edwards and Eberhardt 1967, Seber 1973, Caughley 1978):

$$N = \frac{(\sum F_i)}{q}, \quad (1)$$

where

$$q = \frac{(\sum F_i(i) - \sum F_i)}{(\sum F_i - 1)}, \quad (2)$$

F_i = capture frequency in the i th category, and

i = number of captures per individual.

In this model, I am assuming that (1) no crocodile is born in a single year after the reproductive season, (2) no immigration occurs, (3) marked and unmarked animals die and leave the study area at the same rate, and (4) no marks are lost. In opposition to other capture-recapture models, the geometric model does not assume equal catchability (Bayliss 1987). The expected frequencies for the model are calculated by

$$E(F_i) = (\sum F_i)(1-q)q^{i-1} \quad (2A)$$

I compared the expected frequencies to the actual frequencies by using a chi-square goodness-of-fit test, so that I was able to test the validity of the geometric frequencies model and its assumptions (Edwards and Eberhardt 1967, Seber 1973, Bayliss 1987).

Determining the dynamics of a population requires knowing its age structure. However, to estimate a crocodiles' age, it is usually necessary to kill the animal (Hutton 1986), which was neither possible nor desirable in this study. Thus, I applied the Bertalanffy growth model to calculate the age based on the total length (TL) (Webb et al. 1978, Andrews 1982, Webb et al. 1983). The Bertalanffy model assumes that (1) growth represents the difference between anabolism and catabolism, (2) anabolism is proportional to metabolic rate, (3) growth is maximal for the youngest crocodiles and growth rate decreases as age (or size) increases (Andrews 1982), and (4) male and female hatchlings grow at the same rate (Webb and Smith 1984; Webb et al. 1983). Based on these assumptions, I did the estimates separately for juveniles, females, and males.

I plotted TL of juveniles, males, and females against growth rates (mm/day) of each recaptured crocodile. The age of crocodiles was estimated, based on growth rate regression equations fitted to these plots, by the Bertalanffy equation:

$$t = \tau \ln \left[\frac{(A_{TL} - TL_0)}{(A_{TL} - TL_t)} \right] \quad (3)$$

where

t = crocodiles age in days,

τ = time constant estimated as the inverse of the growth rate regression slope,

A_{TL} = asymptotic total length (intercept/slope of regression equations 5, 6, 7),

TL_0 = initial total length (in this case, the total length of the smallest hatchling captured), and

TL_t = total length at time t .

I applied Equation 3 to every Morelet's crocodile captured (recaptured or not) to estimate their age in days, and then converted age to years.

Once I estimated the population size and the age of each individual, I could estimate the population age structure. Because the age structure was not based on a single cohort, and age classes had irregular distributions, I fitted two regression lines to the data to smooth the age structure (Lowe, 1969). With a smooth age structure, it was possible to construct a static life table. The parameters estimated in the life table were mortality rate [$q(x) = d(x)/l(x)$; Begon, et al. 1996], survivorship schedule [$l(x) = N_x/N_0$], survival rates [$S(x) = 1 - q(x)$], stable proportion of the population represented by each age class [$C(x) = e^{-\tau}l(x)/\sum e^{-\tau}l(x)$], per capita fertility rate or fertility schedule [$b(x)$], reproductive value [$V(x) = (e^{-\tau}l(x))/\sum e^{-\tau}l(y)b(y)$], net reproductive rate [$R_0 = \sum l(x)b(x)$], generation time [$T_c = \sum l(x)b(x)x/\sum l(x)b(x)$], and intrinsic rate of increase [$r = \ln R_0/T_c$, adjusted with Euler equation; Gotelli 1995].

The per capita fertility rate or fertility schedule [$b(x)$] is here defined as the per capita number of individuals that survived the hatching process. I estimated it by calculating the clutch size (CS) in relation to female TL, using the empirical formula of Thorbjarnarson (1996) who regressed averages of female TL against clutch size for the 22 crocodilian species:

$$CS = 0.12(TL) + 1.092 \quad (r^2 = 0.58) \quad (4)$$

By using the appropriate Bertalanffy model (Equation 3) for females, I correlated the CS estimated for TL with the estimated age of each crocodile. The result was plotted in a CS versus age graph. I fitted a logarithmic curve to the data and used the resultant equation to estimate the CS for discrete integer ages (as are used in the life table). I assumed the minimum reproductive age to be 19 years old, which corresponded to females with 1,500-mm total length. The basis for this assumption was personal communications from local, former crocodile hunters, a conjecture by Schmidt (1924), and observations by Platt (1996).

After estimating clutch size, I determined survival of eggs to hatchlings by dividing the number of hatchlings per nest from 1994 and 1995 data, and the average number of eggs per nest in the 1993-94 sampling season (30 eggs per nest). I multiplied that survival rate by the

clutch sizes per age previously estimated (Equations 3 and 4). The result was the per capita fertility rate $[b(x)]$ column in the life table.

I constructed a second static life table where I calculated the $N(x)$ column by multiplying the $C(x)$ proportions obtained in the previous life table by the total population size. In other words, I used a stable age structure.

I used the survival rates $[S(x)]$ and per capita fertility rates $[b(x)]$ of each age class in the second life table to develop a Leslie matrix model of the dynamics of a population with 30 age classes. The model was projected for 50 and 100 years. The Leslie matrix is an exponential model. Therefore, the model assumes that (1) population is closed, (2) population has no genetic structure and no time lags, (3) survival and fertility rates remain constant, and (4) the population has achieved a stable age structure.

I used the population model to evaluate the feasibility of nine alternative harvesting scenarios. First, three scenarios where survival rates for adults in the Leslie matrix are reduced due to harvesting. Second, three scenarios where, instead of adult removal, yearling survival rates are reduced from harvesting. Third, three scenarios where yearling survival is reduced by 5%, 20%, 30%, and 40% of the removed yearlings are restocked into the wild population when attain 3 years old.

The population analysis previously described has two main assumptions: (1) a 1:1 sex ratio, and (2) equal survival between males and females. To evaluate the first assumption, I estimated the sex structure of the population for each study season and used an analysis of variance (ANOVA; Statistica 1996) to test the null hypothesis of no difference in sex ratio among years ($H_0 : \mu_F = \mu_M$).

To evaluate the equal survival assumption, I calculated, separately, the survival for females and males, for each season, using the same life table procedure as in the case of pooled data. I used the chi square procedure to test the null hypotheses of no difference between female and male survival season by season ($H_0 : \mu_F = \mu_M$), and among seasons for females and for males ($H_0 : \mu_{93-94} = \mu_{94-95} = \mu_{95-96}$; $H_{0M} : \mu_{93-94} = \mu_{94-95} = \mu_{95-96}$).

RESULTS.

Growth Model and Age Estimation.

The average growth rates (dL/dt) \pm standard deviation were 0.54 ± 0.41 mm/day for juveniles, 0.19 ± 0.28 mm/day for females, and 0.28 ± 0.34 mm/day for males. The pooled growth rate was: 0.41 ± 0.40 mm/day.

I plotted the growth rates for juveniles (j), females (f), and males (m) against total length (Figure 5) and fitted regression lines to obtain the following growth rate equations:

$$\frac{dL_j}{dt} = -0.00025 (TL_j) + 0.6575 \quad (5)$$

$$\frac{dL_f}{dt} = -7 \times 10^{-5} (TL_f) + 0.2304 \quad (6)$$

$$\frac{dL_m}{dt} = -8.21 \times 10^{-5} (TL_m) + 0.4090 \quad (7)$$

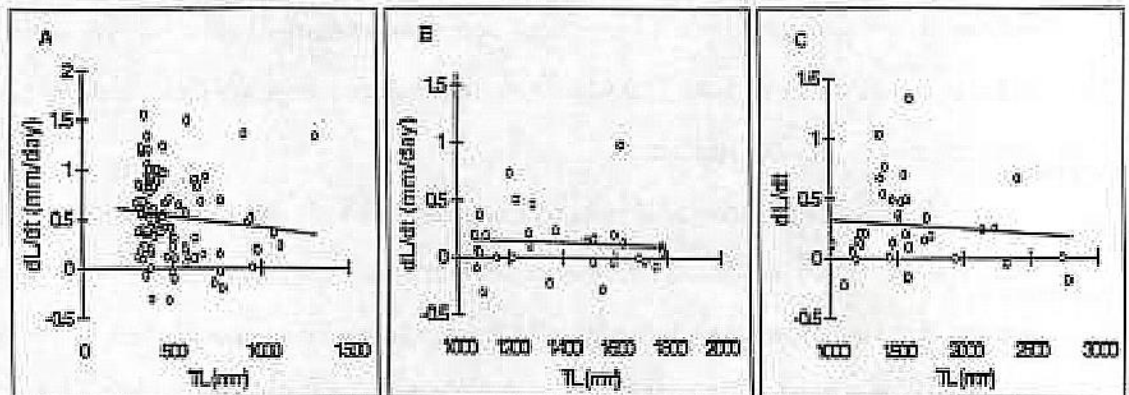


Figure 5. - Growth rates (dL/dt in mm/day) vs. total length (TL in mm) relationship for (A) juveniles, (B) females, and (C) males of Morelet's crocodile in Sian Ka'an.

The correlation and p-values ($\alpha = 0.05$) for each equation were $R^2 = 0.0143$ and $p = 0.2216$ for juveniles ($n = 106$), $R^2 = 0.0042$ and $p = 0.7373$ for females ($n = 29$), and $R^2 = 0.0113$ and $p = 0.5425$ for males ($n = 35$). Although the regression correlations are poor, the regression lines and the data are not significant. Furthermore, I performed a residual analysis

(Statistica 1996) to assess the validity of the linear regression model. The plots of predicted values (from regression equations) for juveniles, females, and males against the residuals (observed minus predicted values) exhibited an even distribution of points in the upper and lower sides of the regression line, indicating a consistent linear trend in the data. Thus, the linear regression model was adequate to describe the relation between total length and growth rate. Large variability is responsible for the low correlation in the regression analyses.

Assuming the validity of the linear model, the general form of Equations 5, 6, and 7 can be described as

$$\frac{dL}{dt} = \alpha (TL) + \beta, \quad (8)$$

where α is a constant for slope and β a constant for the intercept. I used these constants to estimate the parameters needed for the Bertalanffy age model (Table 2): asymptotic total length ($A_{TL} = \beta/\alpha$) and time constant ($\tau = 1/\alpha$). The initial total length (TL_0) was always that of the smallest newly hatched crocodile captured during the survey.

Table 2. - Parameters of the Bertalanffy growth model for estimating the age (days) of Morelet's crocodile. TL_0 = Initial total length; A_{TL} = Asymptotic total length; τ = time constant.

| | JUVENILES | FEMALES | MALES |
|---------------|-----------|----------|----------|
| TL_0 (mm) | 197 | 197 | 197 |
| A_{TL} (mm) | 2630 | 3291.429 | 4881.73 |
| τ (days) | 4000 | 14285.71 | 12180.27 |

I applied the parameters in Table 2 in Equation 3, which represents the Bertalanffy model describing the relation between age of each crocodile and total length (Figure 6). Hence, using total length, I could predict age of each captured crocodile.

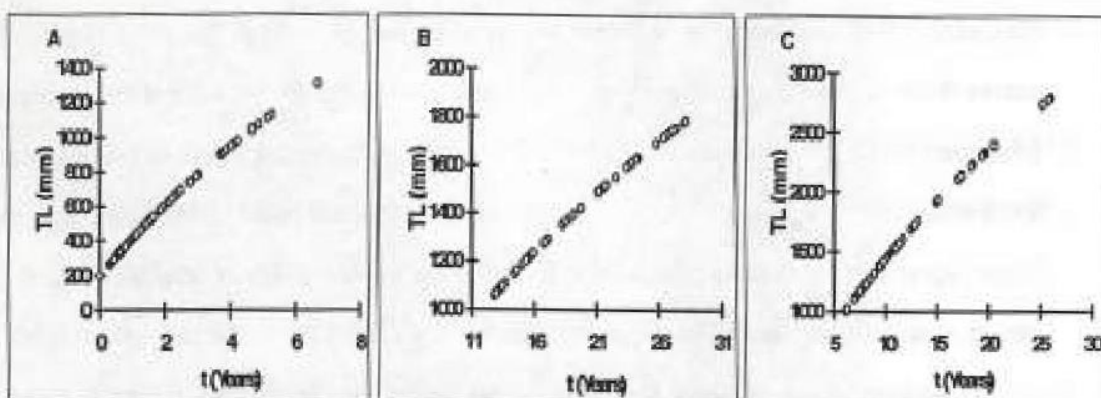


Figure 6. - Age predicted for each observed individual for (A) juveniles, (B) females, and (C) males of Morelet's crocodile in Sian Ka'an, based on the Bertalanffy growth model.

Population Size and Structure.

I estimated the population size of Morelet's crocodile in my study area via the capture-recapture geometric estimator of the capture frequency model. For the 1993-1994 season, there were 556 ± 17 Morelet's crocodiles ($\chi^2_4 = 2.21$; $P < 0.695$). In 1994-1995, 628 ± 17 ($\chi^2_6 = 54.02$; $P < 0.000$), and during the 1995-1996 season, 705 ± 24 ($\chi^2_4 = 3.623$; $P < 0.459$). The chi-square values in parenthesis represent the goodness-of-fit test.

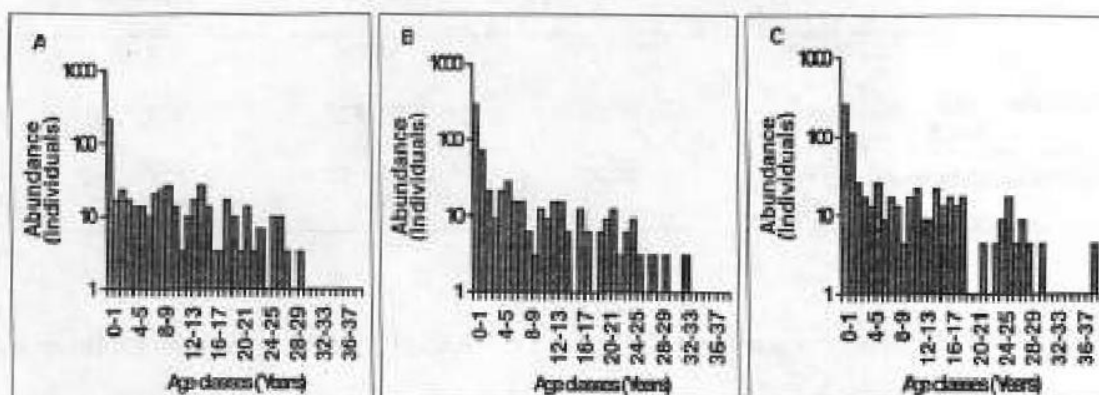


Figure 7. - Age structure of Morelet's crocodile in Sian Ka'an, in (A) 1993-1994, (B) 1994-1995, and (C) 1995-1996. Abundance axis is shown in logarithmic scale.

I calculated the proportion of the population represented by different age classes for every year to estimate the population age structure (Figure 7), and the average age structure for the three years (Figure 8). This crocodile population is characterized by a high reproduction rate but also by a high mortality rate in the first age class. The subsequent age classes have lower and uniform mortality rates. Thus, the population behaves as a type III survivorship curve (Gotelli 1995).

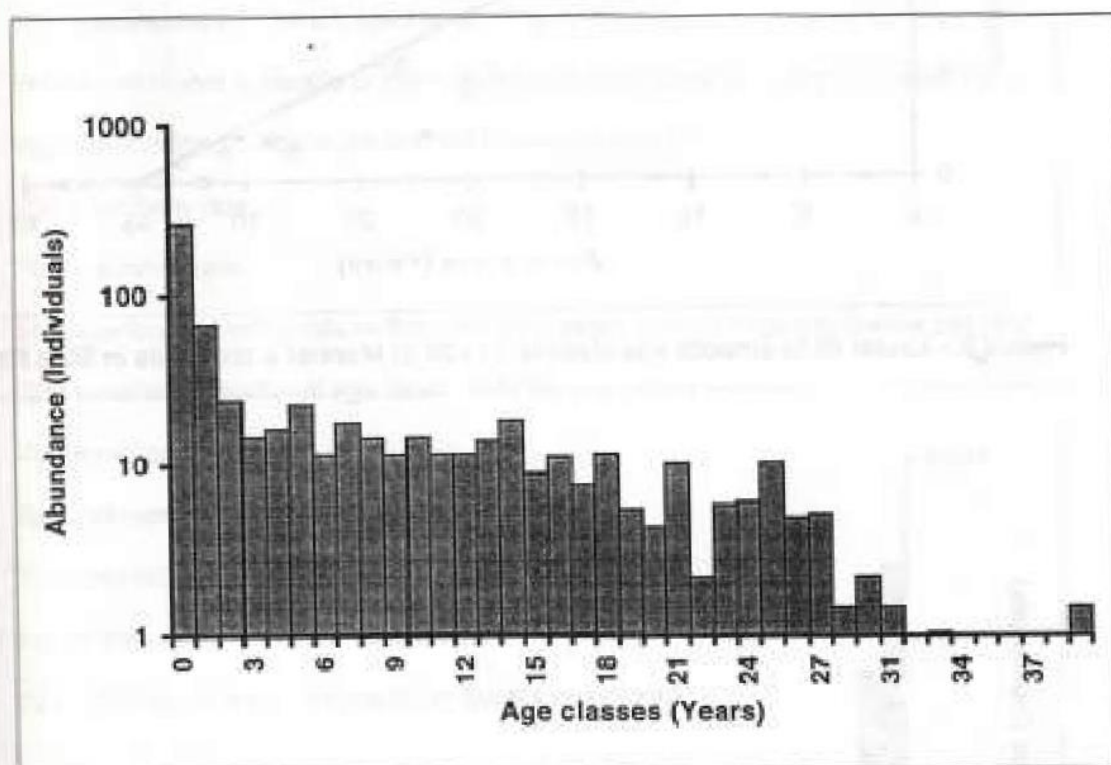


Figure 8. - Average age structure of Morelet's crocodile in Sian Ka'an between 1993 and 1996. Abundance axis is shown in logarithmic scale.

For the average age structure (Figure 8), it was possible to fit a regression line from age class 2 to age class 39 (those with lower mortality rates) (Figure 9). I used the regression equation (Equation 9) to smooth the average age structure (Figure 10). Hence,

$$Y = -0.5507 X + 19.32 \quad (R^2 = 0.823) \quad (9)$$

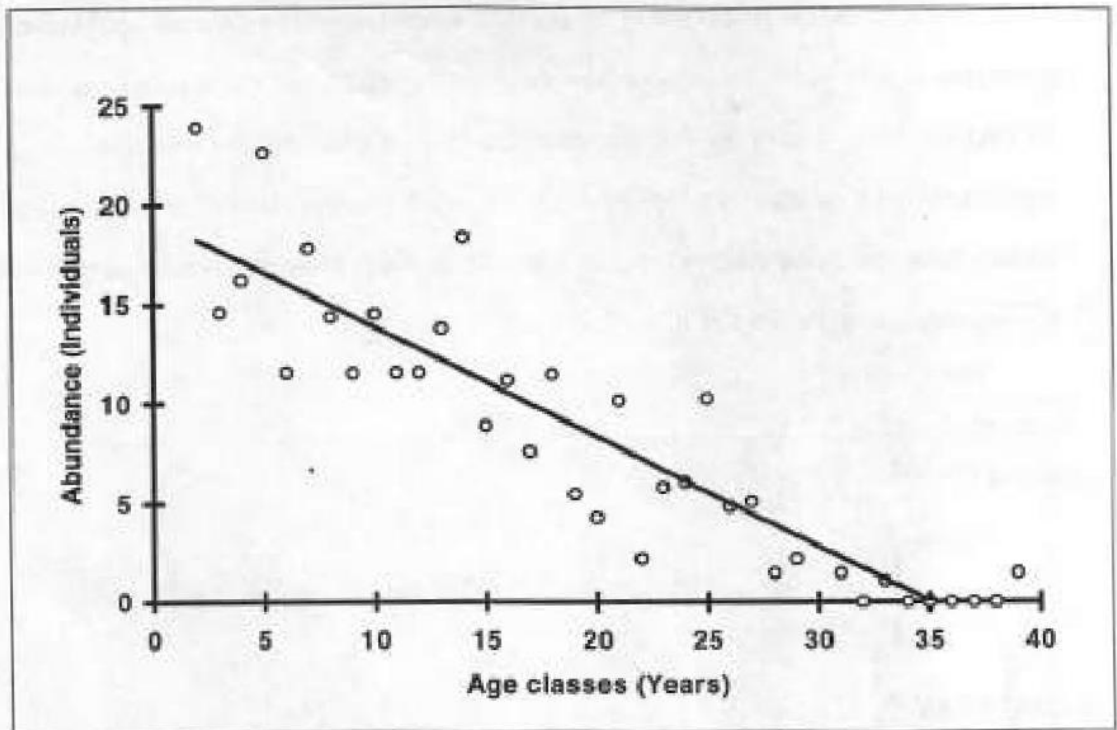


Figure 9. - Linear fit to smooth age classes 2 to 39 of Morelet's crocodile in Sian Ka'an.

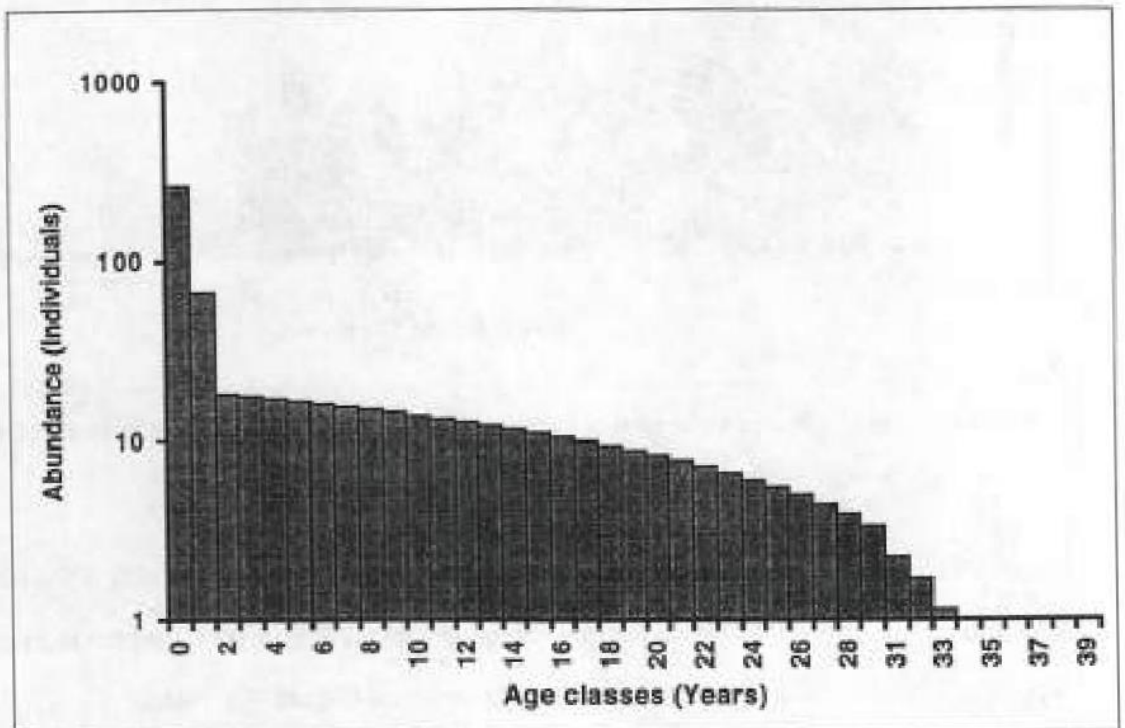


Figure 10. - Smoothed average age structure of Morelet's crocodile in Sian Ka'an.

Abundance axis is shown in logarithmic scale.

The smoothed age structure (Figure 10) simulates a real cohort; therefore, I could construct a preliminary population's static life table from which I obtained the proportion of individuals on each age class at a stable age structure ($C(x)$; Table 3). With the $C(x)$ proportions and total population size in Table 3, I calculated the stable age structure for that population and used it to construct a new life table (Table 4). The definitions of input and output parameters for the life table are

x = age class

$N(x)$ = abundance in the x th age class.

$l(x)$ = survivorship schedule or the proportion of individuals surviving from age 0 to x

$d(x)$ = proportion of individuals that die between x and $x+1$

$q(x)$ = mortality rate

$S(x)$ = survival rate

$b(x)$ = percapita fertility rate or the average number of hatchlings per female per year

$C(x)$ = stable proportional age structure in the population

$V(x)$ = reproductive value

R_0 = net reproductive rate

T_c = generation time

r = intrinsic rate of increase (estimated)

$r(e)$ = intrinsic rate of increase (after Euler's correction)

Table 3.- Static life table to estimate the proportion of individuals on each age class at a stable age structure [C(x)] in Morelet's crocodile population in Sian Ka'an. See text below for keys' definitions.

| X | N(x) | l(x) | $e^{-l(x)}$ | $lx \cdot e^{-l(x)}$ | C(x) |
|--------------|---------------|-------|-------------|----------------------|--------------|
| 0 | 259.85 | 1.000 | 1.000 | 1.0000 | 0.476 |
| 1 | 67.41 | 0.259 | 0.972 | 0.2522 | 0.120 |
| 2 | 18.22 | 0.070 | 0.945 | 0.0662 | 0.032 |
| 3 | 17.67 | 0.068 | 0.919 | 0.0625 | 0.030 |
| 4 | 17.12 | 0.066 | 0.893 | 0.0588 | 0.028 |
| 5 | 16.57 | 0.064 | 0.868 | 0.0553 | 0.026 |
| 6 | 16.02 | 0.062 | 0.844 | 0.0520 | 0.025 |
| 7 | 15.47 | 0.060 | 0.820 | 0.0488 | 0.023 |
| 8 | 14.91 | 0.057 | 0.797 | 0.0458 | 0.022 |
| 9 | 14.36 | 0.055 | 0.775 | 0.0428 | 0.020 |
| 10 | 13.81 | 0.053 | 0.753 | 0.0400 | 0.019 |
| 11 | 13.26 | 0.051 | 0.732 | 0.0374 | 0.018 |
| 12 | 12.71 | 0.049 | 0.712 | 0.0348 | 0.017 |
| 13 | 12.16 | 0.047 | 0.692 | 0.0324 | 0.015 |
| 14 | 11.61 | 0.045 | 0.673 | 0.0301 | 0.014 |
| 15 | 11.06 | 0.043 | 0.654 | 0.0278 | 0.013 |
| 16 | 10.51 | 0.040 | 0.636 | 0.0257 | 0.012 |
| 17 | 9.96 | 0.038 | 0.618 | 0.0237 | 0.011 |
| 18 | 9.41 | 0.036 | 0.601 | 0.0217 | 0.010 |
| 19 | 8.86 | 0.034 | 0.584 | 0.0199 | 0.009 |
| 20 | 8.31 | 0.032 | 0.567 | 0.0181 | 0.009 |
| 21 | 7.76 | 0.030 | 0.552 | 0.0165 | 0.008 |
| 22 | 7.20 | 0.028 | 0.536 | 0.0149 | 0.007 |
| 23 | 6.65 | 0.026 | 0.521 | 0.0133 | 0.006 |
| 24 | 6.10 | 0.023 | 0.507 | 0.0119 | 0.006 |
| 25 | 5.55 | 0.021 | 0.492 | 0.0105 | 0.005 |
| 26 | 5.00 | 0.019 | 0.479 | 0.0092 | 0.004 |
| 27 | 4.45 | 0.017 | 0.465 | 0.0080 | 0.004 |
| 28 | 3.90 | 0.015 | 0.452 | 0.0068 | 0.003 |
| 29 | 3.35 | 0.013 | 0.440 | 0.0057 | 0.003 |
| 30 | 2.25 | 0.009 | 0.427 | 0.0037 | 0.002 |
| 31 | 1.70 | 0.007 | 0.416 | 0.0027 | 0.001 |
| 32 | 1.15 | 0.004 | 0.404 | 0.0018 | 0.001 |
| 33 | 0.60 | 0.002 | 0.393 | 0.0009 | 0.000 |
| 34 | 0.00 | 0.000 | 0.382 | 0.0000 | 0.000 |
| TOTAL | 634.91 | | | | 1.000 |

Table 4.- Static life table of Morelet's crocodile population in Sian Ka'an. See text above for keys' definitions.

| x | N | l(x) | d(x) | q(x) | S(x) | b(x) | l(x)b(x) | lxbx ² | e ^{-l(x)} | lxbx ² e ^{-l(x)} | lx ² e ^{-l(x)} | C(x) | e ^{l(x)} /lx | $\Sigma(e^{l(x)})/yby$ | Vx |
|--------|--------|-------|-------|-------|-------|--------|----------|-------------------|--------------------|--------------------------------------|------------------------------------|----------|-----------------------|------------------------|--------|
| 0 | 302.06 | 1.000 | 0.748 | 0.748 | 0.252 | 0.000 | 0.000 | 0.000 | 1.00000 | 0.0000 | 1.0000 | 0.476 | 1.000 | 1.00 | 1.000 |
| 1 | 76.17 | 0.252 | 0.186 | 0.737 | 0.263 | 0.000 | 0.000 | 0.000 | 1.00003 | 0.0000 | 0.2522 | 0.120 | 3.965 | 1.00 | 3.965 |
| 2 | 20.01 | 0.096 | 0.004 | 0.057 | 0.943 | 0.000 | 0.000 | 0.000 | 1.00006 | 0.0000 | 0.0663 | 0.032 | 15.084 | 1.00 | 15.084 |
| 3 | 18.86 | 0.062 | 0.004 | 0.058 | 0.942 | 0.000 | 0.000 | 0.000 | 1.00009 | 0.0000 | 0.0625 | 0.030 | 16.011 | 1.00 | 16.011 |
| 4 | 17.77 | 0.059 | 0.003 | 0.059 | 0.941 | 0.000 | 0.000 | 0.000 | 1.00011 | 0.0000 | 0.0586 | 0.028 | 17.000 | 1.00 | 17.000 |
| 5 | 16.71 | 0.055 | 0.003 | 0.060 | 0.940 | 0.000 | 0.000 | 0.000 | 1.00014 | 0.0000 | 0.0553 | 0.026 | 18.070 | 1.00 | 18.070 |
| 6 | 15.71 | 0.052 | 0.003 | 0.061 | 0.939 | 0.000 | 0.000 | 0.000 | 1.00017 | 0.0000 | 0.0520 | 0.025 | 19.228 | 1.00 | 19.228 |
| 7 | 14.74 | 0.049 | 0.003 | 0.063 | 0.937 | 0.000 | 0.000 | 0.000 | 1.00020 | 0.0000 | 0.0488 | 0.023 | 20.484 | 1.00 | 20.484 |
| 8 | 13.82 | 0.046 | 0.003 | 0.064 | 0.936 | 0.000 | 0.000 | 0.000 | 1.00023 | 0.0000 | 0.0458 | 0.022 | 21.850 | 1.00 | 21.850 |
| 9 | 12.94 | 0.043 | 0.003 | 0.065 | 0.935 | 0.000 | 0.000 | 0.000 | 1.00026 | 0.0000 | 0.0428 | 0.020 | 23.339 | 1.00 | 23.339 |
| 10 | 12.10 | 0.040 | 0.003 | 0.067 | 0.933 | 0.000 | 0.000 | 0.000 | 1.00028 | 0.0000 | 0.0401 | 0.019 | 24.966 | 1.00 | 24.966 |
| 11 | 11.29 | 0.037 | 0.003 | 0.068 | 0.932 | 0.000 | 0.000 | 0.000 | 1.00031 | 0.0000 | 0.0374 | 0.018 | 26.749 | 1.00 | 26.749 |
| 12 | 10.52 | 0.035 | 0.002 | 0.070 | 0.930 | 0.000 | 0.000 | 0.000 | 1.00034 | 0.0000 | 0.0348 | 0.017 | 28.709 | 1.00 | 28.709 |
| 13 | 9.78 | 0.032 | 0.002 | 0.072 | 0.928 | 0.000 | 0.000 | 0.000 | 1.00037 | 0.0000 | 0.0324 | 0.015 | 30.871 | 1.00 | 30.871 |
| 14 | 9.08 | 0.030 | 0.002 | 0.074 | 0.926 | 0.000 | 0.000 | 0.000 | 1.00040 | 0.0000 | 0.0301 | 0.014 | 33.263 | 1.00 | 33.263 |
| 15 | 8.41 | 0.028 | 0.002 | 0.076 | 0.924 | 0.000 | 0.000 | 0.000 | 1.00043 | 0.0000 | 0.0278 | 0.013 | 35.922 | 1.00 | 35.922 |
| 16 | 7.76 | 0.026 | 0.002 | 0.079 | 0.921 | 0.000 | 0.000 | 0.000 | 1.00045 | 0.0000 | 0.0257 | 0.012 | 38.890 | 1.00 | 38.890 |
| 17 | 7.15 | 0.024 | 0.002 | 0.082 | 0.918 | 0.000 | 0.000 | 0.000 | 1.00048 | 0.0000 | 0.0237 | 0.011 | 42.218 | 1.00 | 42.218 |
| 18 | 6.57 | 0.022 | 0.002 | 0.085 | 0.915 | 0.000 | 0.000 | 0.000 | 1.00051 | 0.0000 | 0.0218 | 0.010 | 45.973 | 1.00 | 45.973 |
| 19 | 6.01 | 0.020 | 0.002 | 0.088 | 0.912 | 6.079 | 0.121 | 2.298 | 1.00054 | 0.1210 | 0.0199 | 0.009 | 50.293 | 1.00 | 50.293 |
| 20 | 5.48 | 0.018 | 0.002 | 0.092 | 0.908 | 6.306 | 0.114 | 2.288 | 1.00057 | 0.1144 | 0.0181 | 0.009 | 55.101 | 0.88 | 48.433 |
| 21 | 4.97 | 0.016 | 0.002 | 0.097 | 0.903 | 6.522 | 0.107 | 2.255 | 1.00060 | 0.1074 | 0.0166 | 0.008 | 60.708 | 0.76 | 46.414 |
| 22 | 4.49 | 0.015 | 0.002 | 0.102 | 0.898 | 6.729 | 0.100 | 2.201 | 1.00062 | 0.1001 | 0.0149 | 0.007 | 67.224 | 0.66 | 44.173 |
| 23 | 4.03 | 0.013 | 0.001 | 0.106 | 0.892 | 6.926 | 0.092 | 2.126 | 1.00065 | 0.0925 | 0.0134 | 0.006 | 74.877 | 0.56 | 41.708 |
| 24 | 3.59 | 0.012 | 0.001 | 0.116 | 0.884 | 7.114 | 0.085 | 2.032 | 1.00068 | 0.0847 | 0.0119 | 0.006 | 83.977 | 0.46 | 39.009 |
| 25 | 3.18 | 0.011 | 0.001 | 0.124 | 0.876 | 7.295 | 0.077 | 1.919 | 1.00071 | 0.0768 | 0.0106 | 0.006 | 94.956 | 0.38 | 36.065 |
| 26 | 2.78 | 0.009 | 0.001 | 0.135 | 0.865 | 7.469 | 0.069 | 1.790 | 1.00074 | 0.0689 | 0.0092 | 0.004 | 108.436 | 0.30 | 32.854 |
| 27 | 2.41 | 0.008 | 0.001 | 0.148 | 0.852 | 7.636 | 0.061 | 1.644 | 1.00077 | 0.0609 | 0.0080 | 0.004 | 125.360 | 0.23 | 29.344 |
| 28 | 2.05 | 0.007 | 0.001 | 0.166 | 0.835 | 7.796 | 0.053 | 1.493 | 1.00079 | 0.0530 | 0.0068 | 0.003 | 147.155 | 0.17 | 25.484 |
| 29 | 1.71 | 0.006 | 0.002 | 0.348 | 0.652 | 7.953 | 0.045 | 1.307 | 1.00082 | 0.0451 | 0.0057 | 0.003 | 176.287 | 0.12 | 21.185 |
| 30 | 1.12 | 0.004 | 0.001 | 0.266 | 0.734 | 8.104 | 0.030 | 0.899 | 1.00085 | 0.0300 | 0.0037 | 0.002 | 270.166 | 0.08 | 20.279 |
| 31 | 0.82 | 0.003 | 0.001 | 0.343 | 0.657 | 8.249 | 0.022 | 0.694 | 1.00088 | 0.0224 | 0.0027 | 0.001 | 368.064 | 0.05 | 16.588 |
| 32 | 0.54 | 0.002 | 0.001 | 0.495 | 0.505 | 8.390 | 0.015 | 0.479 | 1.00091 | 0.0150 | 0.0018 | 0.001 | 560.434 | 0.02 | 12.698 |
| 33 | 0.27 | 0.001 | 0.001 | 1.000 | 0.000 | 8.526 | 0.008 | 0.253 | 1.00094 | 0.0077 | 0.0008 | 0.000 | 1109.047 | 0.01 | 8.526 |
| 34 | 0.00 | 0.000 | 0.000 | 0.000 | 0.000 | 8.658 | 0.000 | 0.000 | 1.00096 | 0.0000 | 0.0000 | 0.000 | 0.000 | 0.00 | 0.000 |
| 634.91 | | | | | | 23.657 | | 1.0000 | | 2.1022 | | | | | |
| | | | | | | Re = | | 0.999 | | | | | | | |
| | | | | | | Tc = | | 23.683 | | | | | | | |
| | | | | | | r = | | -0.00003 | | r(a) = | | -0.00003 | | | |

I calculated the average number of hatchlings per female per year $[b(x)]$ using Equations (4) and (6). Equation (4) relates clutch size (CS) with total length (TL), while Equation (6) translates the result in CS according to female age (t). I plotted the result (Figure 11) and fitted a logarithmic curve (Equation 11; $R^2 = 0.999$) to the data. This equation represents the Bertalanffy growth model adjusted to predict clutch size. Using data from the 1994 and 1995 nesting seasons, I estimated an average egg-to-hatchling survival rate of 0.347 ± 0.083 ($n = 7$). Multiplying this value by the clutch size estimated in Equation 11 results in the $b(x)$ column in the life table (Table 4).

$$CS = 12.767 \ln(t) - 20.085 \quad (11)$$

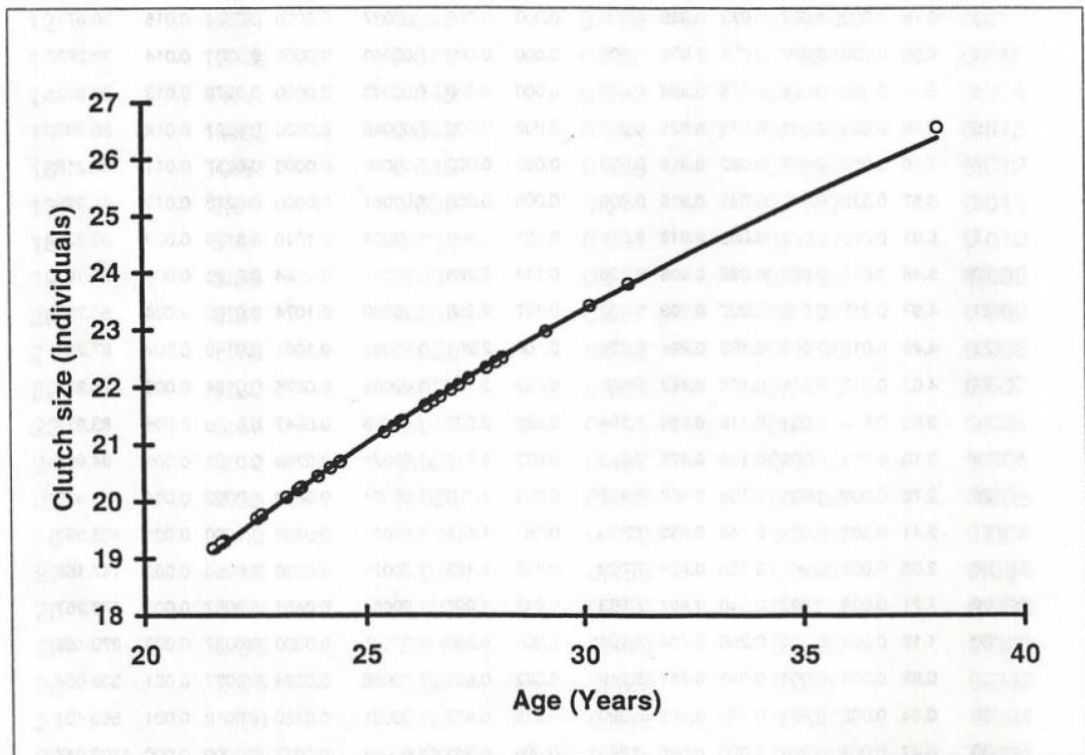


Figure 11.- Clutch size in relation to age of Morelet's crocodile females in Sian Ka'an.

The life table exhibits two major population characteristics. First, hatchlings have a 75% probability of dying during their first year. Second, the population from age class 3 to age

class 21 has a very high and uniform survivorship rate (0.928 ± 0.003). In individuals from age class 22 (two years after reproduction starts) to 28, the survival rate decreases to an average of 0.872 ± 0.005 . Third, hatchlings represent 48% of the entire population, while the remaining age classes have a very even distribution when the population reaches a stable age structure ($C(x)$; Table 3). Fourth, the net reproductive rate (R_0) is 0.999 offspring. Hence, each female will produce during its lifespan an average of 1 female offspring. Fifth, the mean generation time (T_c), the average time between the birth of a female and the birth of its female offspring, is 23.67 years. Sixth, the intrinsic rate of increase (solved with the Euler's correction) is almost stable although slightly negative: $r(e) = -0.00003$ individuals / (individual \bullet year). Seventh, the peak reproductive value ($V_x = 50.23$) occurs in the year of first reproduction.

The population analysis shown previously is assuming a 1:1 sex ratio. I studied the age structure of the population to validate that assumption and to refine the basis for a sustainable harvesting program of Morelet's crocodile. I estimated the sex structure separately for each of the three sampling seasons (Table 5, Figure 12). The average female-male ratio is 0.78 : 1. The non-sexed category refers to those crocodiles for which sex determination was not possible. Most of the individuals that fit into such a category were hatchlings or juveniles whose genitals were not totally developed.

Table 5.- Abundance \pm standard error of non-sexed, females, and males of Morelet's crocodile in Sian Ka'an.

| SEASON | NON-SEXED | FEMALES | MALES | FEMALES : MALES |
|----------------|--------------|-------------|-------------|-----------------|
| 1993-1994 | 217 \pm 6 | 139 \pm 4 | 200 \pm 6 | 0.696 : 1 |
| 1994-1995 | 365 \pm 10 | 107 \pm 3 | 156 \pm 4 | 0.684 : 1 |
| 1995-1996 | 327 \pm 9 | 112 \pm 3 | 116 \pm 3 | 0.962 : 1 |
| Average | 303 \pm 8 | 119 \pm 3 | 157 \pm 4 | 0.781 : 1 |

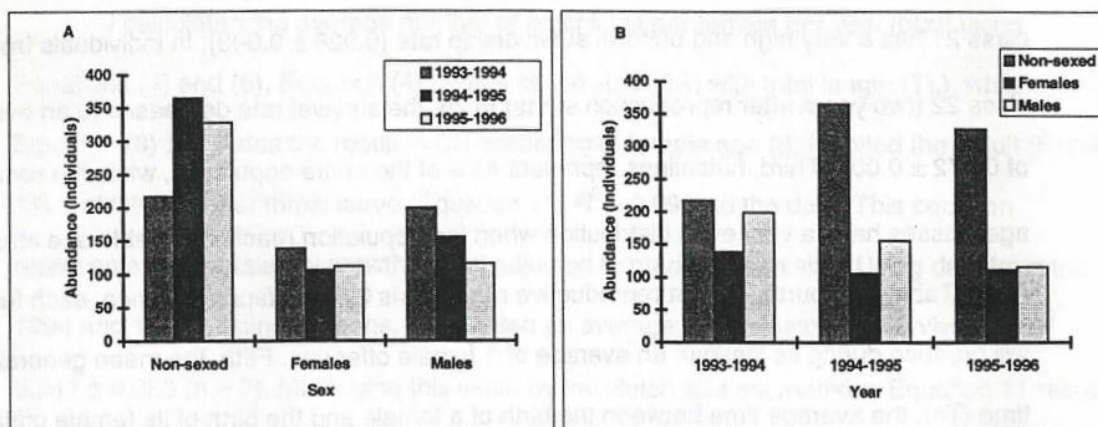


Figure 12.- Sex structure of Morelet's crocodile in Sian Ka'an, grouped by (A) sex category and by (B) year .

I performed an analysis of variance (ANOVA; Table 6) to test the null hypothesis of no difference in abundance between females and males ($H_0 : \mu_F = \mu_M$). The test found no differences ($\alpha = 0.05$; $p = 0.2178$) in the mean abundance of females and males. Thus, the 1:1 sex ratio assumption is statistically valid.

| Table 6.- Analysis of Variance for sex ratios of Morelet's crocodile in Sian Ka'an. | | | | | |
|---|----------------|----|-------------|---------|-----------|
| | SUM OF SQUARES | DF | MEAN SQUARE | F VALUE | Pr > 0.05 |
| SEX RATIO | 2178.279 | 1 | 2178.279 | 2.135 | 0.2178 |
| ERROR | 4080.828 | 4 | 1020.207 | | |

Another assumption implied in the population analysis was equal survival between males and females. I calculated, separately, the survival rates for females and males for each season. I used the chi-square procedure to test the null hypotheses of no difference between female and male survival rates by season ($H_0 : \mu_F = \mu_M$; Table 7, Figure 13B), and among seasons for females and for males ($H_{0F} : \mu_{93-94} = \mu_{94-95} = \mu_{95-96}$; $H_{0M} : \mu_{93-94} = \mu_{94-95} = \mu_{95-96}$; Table 7, Figure 13A). Although male survival is slightly lower than females, that difference is not statistically significant ($\alpha = 0.05$) in any of the three seasons. Similarly, survival differences

among seasons for females or males were not statistically significant. These statistical tests support the equal female and male survival assumption of the population analysis.

Table 7.- Chi Square test for survival rates of Morelet's crocodile males and females in Sian Ka'an.

| SEASON | FEMALES | MALES | AVERAGES | Chi SQR. | df |
|-----------------|-----------------|-----------------|-------------------|----------|----------|
| 93-94 | 0.85181 | 0.827578 | 0.8396938 | 0.001399 | 1 p>0.95 |
| 94-95 | 0.954861 | 0.825149 | 0.89000518 | 0.037809 | 1 p>0.95 |
| 95-96 | 0.935198 | 0.826491 | 0.88084461 | 0.026831 | 1 p>0.95 |
| AVERAGES | 0.913956 | 0.826406 | | | |
| Chi SQR. | 0.00655 | 3.58E-06 | | | |
| df | 2 | 2 | | | |
| | p>0.995 | p>0.995 | | | |

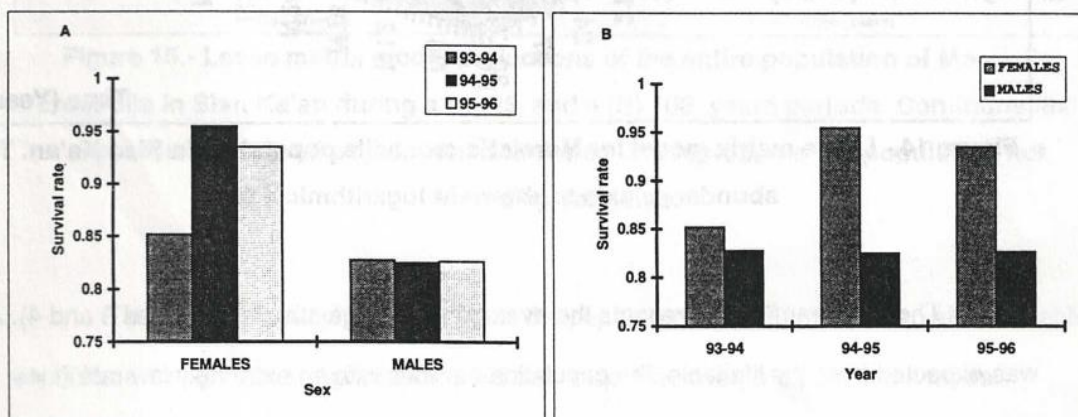


Figure 13.- Survival rate comparison between Morelet's crocodile females and males grouped by (A) sex category and by (B) season.

Leslie Matrix Model and Harvesting Scenarios.

The survival rates $S(x)$ and per capita fertility rates $f(x)$ for each age class were used to construct a model based on a Leslie matrix. The model was run for 50 years and shows the dynamics of the population, which are dominated by the first age class (Figure 14).

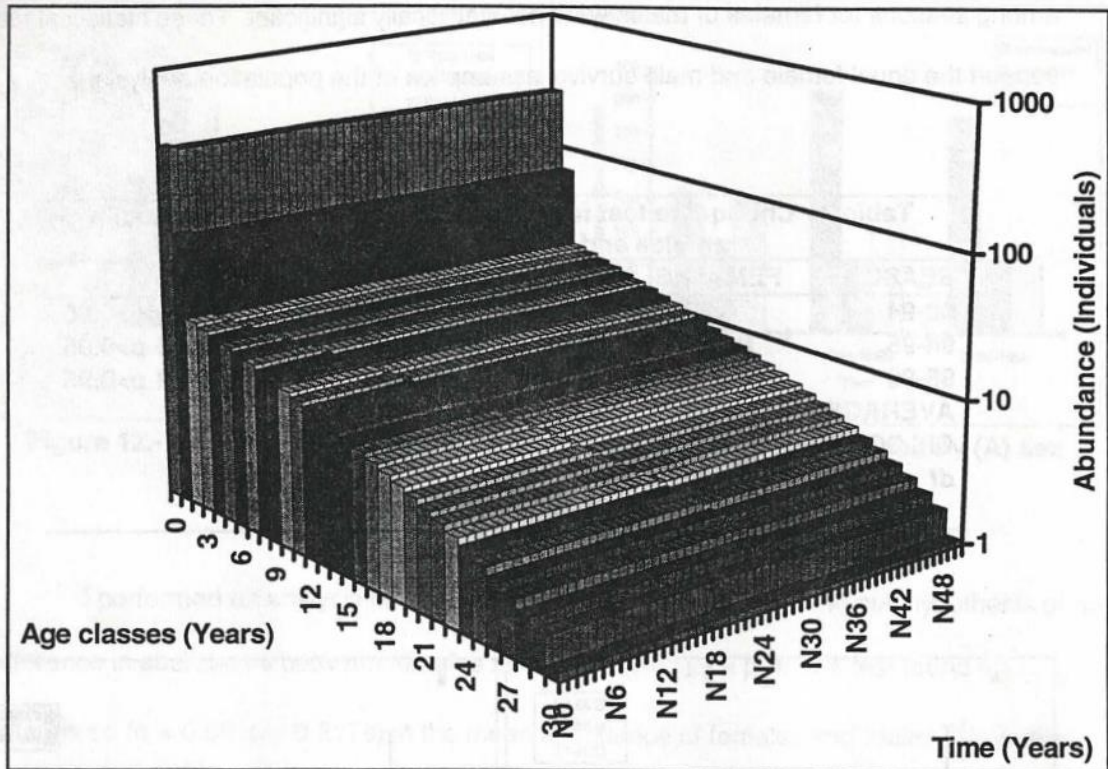


Figure 14.- Leslie matrix model for Morelet's crocodile population in Sian Ka'an. The abundance axis is shown in logarithmic scale.

The first year (N0) represents the average stable age structure (Tables 3 and 4). As was expected from the life table, the population declines with an extremely low rate ($r = -0.00003$). A clearer perspective of the population is achieved if analyzed without considering its age structure. According to the model (Figure 15A), the population will decline exponentially during a 25-year period at a rate of about -0.8 individuals/year. Yearlings predominate in the population as the dotted curve in the graph shows. In the long term, a 100-year period, the population retains its exponential (although approximately linear) decline with a rate of about -0.96 individuals/year (Figure 15B). However, abundance shows a long-term damped oscillation. Each fluctuation represents a period approximately the length of the population generation time (Table 4). Comparing both growth curves (total population in continuous line, and population not including yearlings in dotted line) yearling abundances

account for much of the variation. The average finite rate of increase, or the average proportional change in population size from year-to-year, is $\lambda = 0.998$ (or -0.18%). Consequently, the average intrinsic rate of increase is $r = -0.0018$ (Table 4).

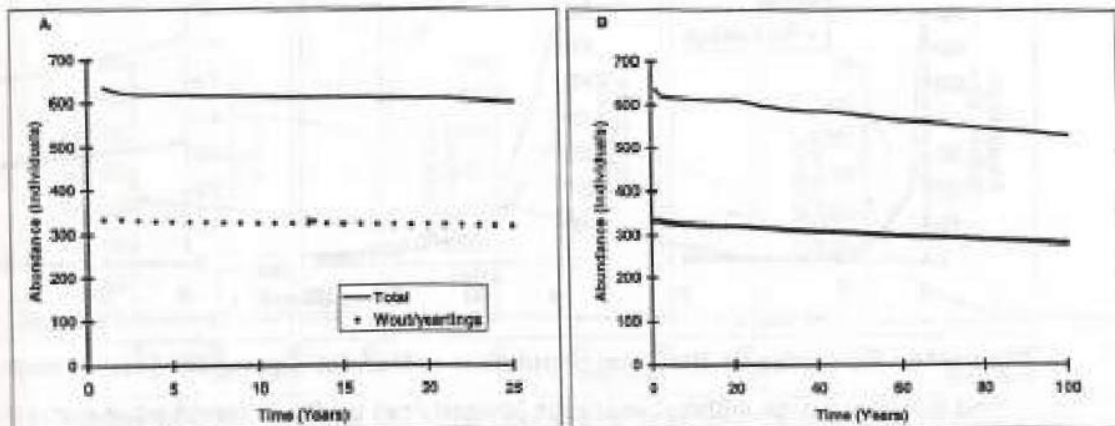


Figure 15.- Leslie matrix model projections of the entire population of Morelet's crocodile in Sian Ka'an during a (A) 25, and a (B) 100 years periods. Continuous line represents the total population, and dotted line represents the population not including yearlings.

The demographic characteristics of the population allow it to stay in an almost stable condition although has a slight exponential decrease. However, the population model responds quite differently under harvesting conditions. Let us consider first the reference case of removing all the largest adults (older than 15 years); that is, setting the survival rate to zero at those ages (>15 years) in the Leslie matrix (Figure 16A). The population would be close to extinction in less than 20 years.

Now let us consider two commercial harvesting scenarios. I reduced the survival of those individuals with a commercial size (more than 7 years old) by 10%. In other words, I assumed a removal of 10% of the commercial population (Figure 16B). Although the population does not go to extinction in a 60-year period, it has a steady exponential decline with an annual average growth rate of $r = -0.07$. Decreasing the survival of the commercial-

sized individuals by only 0.5% produces a stable condition (Figure 16C) in which the population still declines through time. In this case, the average growth rate is $r = -0.03$.

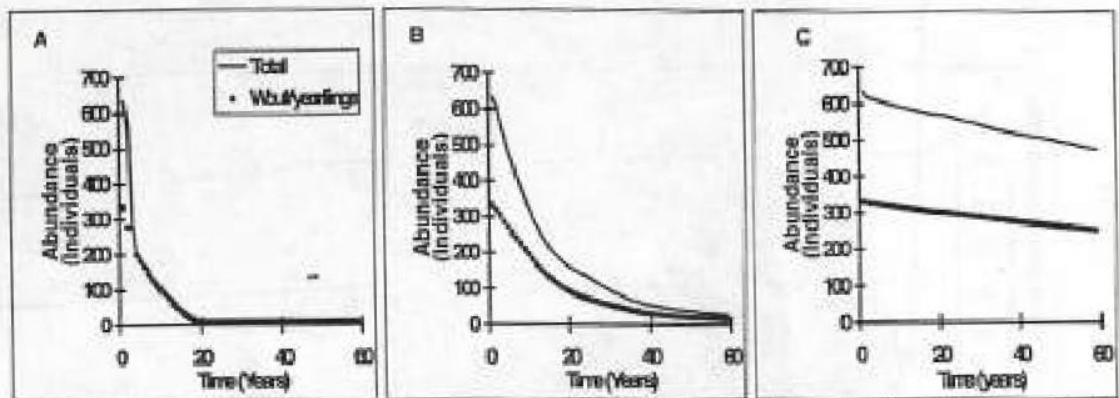


Figure 16.- Dynamics of the total population of Morelet's crocodile (continuous line), and the population without yearlings (dotted line) under different adult harvesting scenarios: (A) removing 100% adults older than 15 years; (B) removing 10% of commercially viable population (older than 7 years); (C) removing 0.5% of commercially viable population (older than 7 years).

Another possible harvesting scenario is removing hatchlings and yearlings but none of the remaining population. If 5% of the yearlings are removed, in addition to those that would naturally died, (i.e., reducing their survival rate from 0.25 to 0.24; Table 4, Figure 17A), the total population tends to decrease exponentially with a rate of about -2 individuals/year, an average intrinsic rate of increase of $r = -0.004$ individuals/(individuals • year), and $\lambda = 0.996$, meaning a decrease of -0.4% per year in the population size.

If 20% of the surviving yearlings are removed, decreasing their survival from 0.25 to 0.20 (Figure 17B), the population declines at a rate of about -4.75 individuals/year. The annual average intrinsic rate of increase is: $r = -0.01$ individuals/(individuals • year), and $\lambda = 0.99$ or 1% decrease of the population size per year.

Finally, if 90% of the surviving yearlings are harvested, reducing their survival rate from 0.25 to 0.025 (Figure 17C), the total population tends to goes rapidly toward extinction

with noticeably population oscillations and a rate of about -11,263 individuals/year. The average rate of increase is $r = -0.066$ individuals/(individuals • year), and $\lambda = 0.94$ or a 6% decrease of the population size per year.

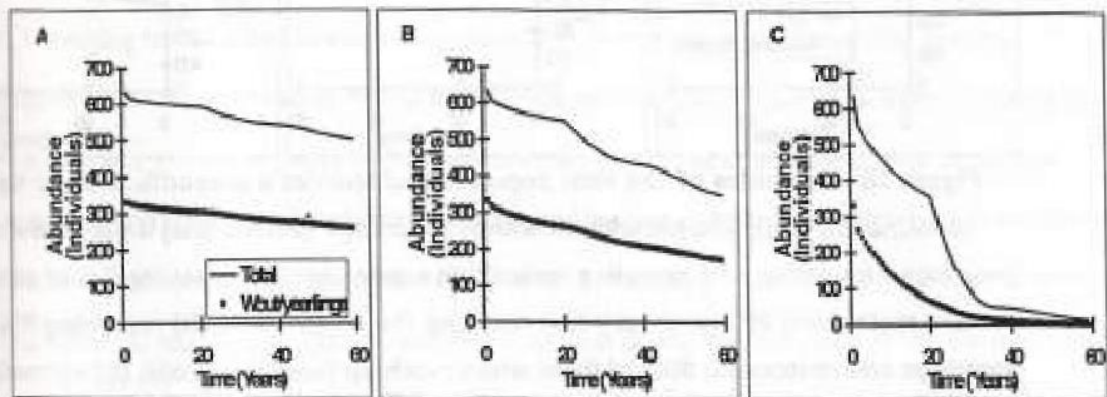


Figure 17.- Dynamics of the total population of Morelet's crocodile in Sian Ka'an (continuous line), and population without yearlings (dotted line) under different yearlings harvesting scenarios: (A) removing 5% of yearlings; (B) removing 20% of yearlings; (C) removing 90% of yearlings.

Finally, three other scenarios to be analyzed are those where survival rate of yearlings is reduced 5% via harvesting as in Figure 17 but now, the proportions of individuals of the third age class (age class 2) were increased by restocking them as could occur in a ranching program (Figure 18; see discussion below). If a proportion of individuals of age class 2 equivalent to 20% of the removed yearlings are restocked, the population increases with an average rate of increase of $r = 0.0015$ individuals/(individuals • year), and a $\lambda = 1.0015$ or a 0.15% increase of the population size per year (Figure 18A). If the restocking is equivalent to 30% of the removed yearlings, the population grows with an $r = 0.004$ and a $\lambda = 1.004$ (Figure 18B). Finally, if the restocking proportion is equivalent to 40% of the removed yearlings, the growing parameters of the population are $r = 0.0064$ and $\lambda = 1.0064$ (Figure 18C).

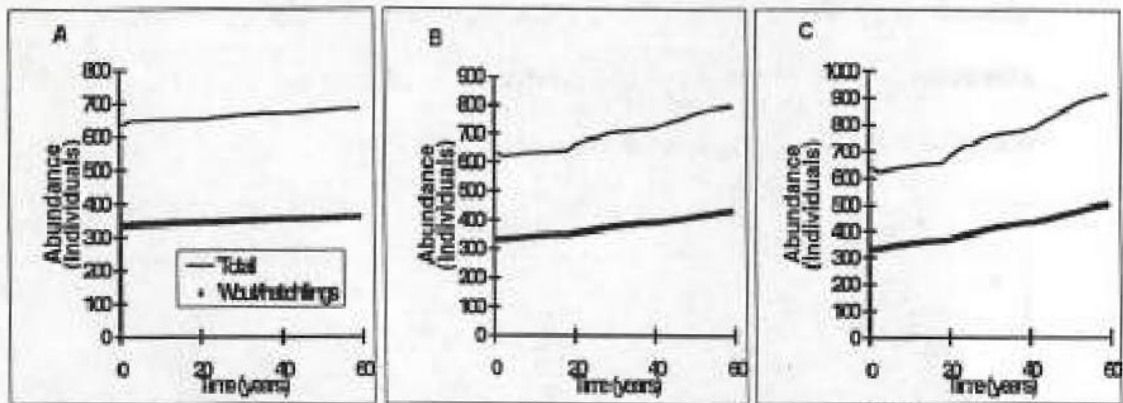


Figure 18.- Dynamics of the total population of Morelet's crocodile in Sian Ka'an (continuous line), and population without yearlings (dotted line) under different yearlings harvesting and juveniles restocking scenarios: (A) removing 5% of yearlings and restocking 20% of them when reaching three years old; (B) removing 5% of yearlings and restocking 30% of them when reaching three years old; (C) removing 5% of yearlings and restocking 40% of them when reaching three years old.

DISCUSSION.

Growth Model and Age Estimation.

The average growth rate for all individuals combined was 0.41 ± 0.40 mm/day, and 0.54 ± 0.41 mm/day for juveniles. Pérez et al. (1995) found an average growth rate of 0.54 ± 0.1 mm/day for juvenile Morelet's crocodiles (0 to 36 months old) hatched and grown in captivity in Veracruz, México; hence the average growth rates for juveniles were the same in both studies. However, because the measurements by Pérez et al. (1995) were on captive animals living under regulated environmental and feeding conditions the high growth variability found in Sian Ka'an's wild population likely occurred because of environmental reasons rather than intrinsic factors (i.e., genetic variability), at least during the first years of life. Some of the external factors affecting metabolism and growth of crocodiles are food and water supply, temperature, habitat type, season, and social environment (Webb et al. 1978, Andrews 1982, Magnusson and Sanaïotti 1995). However, at adult sizes, crocodile growth might be more complex and involve more influence from intrinsic factors such as sex, age, life styles, and genetic variability (Webb et al. 1978, Andrews 1982, Magnusson and Sanaïotti 1995).

For the American crocodile, a larger species living sympatrically with Morelet's crocodile in the coast of Sian Ka'an, the average growth rate reported is 0.77 mm/day (estimated with data from Platt and Thorbjarnarson 1997). In Panamá, the average growth rate of American crocodile individuals 0 to 22 months old is 0.79 mm/day (Thorbjarnarson 1989). Apparently, this species grows faster than Morelet's crocodile but also achieves a larger size (6.25 m; Alvarez del Toro 1974, Pérez et al. 1991, Platt and Thorbjarnarson 1997), which may explain, in part, the difference in growth rates between both species. The saltwater crocodile (*C. porosus*) grows at an average rate of 0.56 mm/day (Webb et al. 1978, Andrews 1982). The Nile crocodile (*C. niloticus*) grows at 0.85 mm/day, and the American alligator (*Alligator mississippiensis*) at 1.5 mm/day (Andrews 1982).

The average growth rates found in this study are ranked as juveniles > males > females, a pattern expected for crocodilians. Hatchling American crocodiles grow faster than individuals older than two years (Thorbjarnarson 1989, Platt and Thorbjarnarson 1997), and males have been reported growing faster than females for American alligators (Rootes et al. 1991), Australian freshwater crocodile (*C. johnstoni*; Webb et al. 1983), and saltwater crocodile (Webb et al. 1978). Magnusson and Sanaiotti (1995) found no differences in growth rates for males and females of spectacled caiman (*Caiman crocodilus crocodilus*). However, they suspected that males must grow faster than females in individuals larger than those captured during their study.

Sex determination in juveniles is extremely difficult. In this study, I analyzed growth rates separately for adult males and females. For juveniles, I analyzed both sexes pooled together, assuming equal growth rates for both. In the case of the Australian freshwater crocodile, "post-hatching male and female survivors grow at the same rate until about five years of age, after which males grow faster than females" (Webb and Smith 1984:322; Webb et al. 1983). Thus, although untested, the equal growth assumption I used for juveniles in this study seems realistic. However, the high variability found in juvenile growth rate may be due, at least partially, to sexually related growth differences.

Some individuals in this study had negative growth rates. I considered those individuals with growth rates lower than -0.5 mm/day as outliers and excluded them from analysis. Eighteen hatchlings (17%) had negative rates; eleven were excluded. Ten females (34.5%) had negative growth, but only one was excluded. Finally, nine males (25.7%) had negative growth rates, and four were excluded from analysis. It is noteworthy that in four hatchlings (3.8%), six females (20.7%), and one male (2.9%), negative growth rates were found for both head and total body lengths. Some size decrease probably occurs in soft tissues during times of food shortage. The high proportion of females with negative growth in total and head lengths might be a consequence of high energetic investment during

reproduction, including eggs production, and nest construction and protection. These hypotheses have to be tested in the future with field or laboratory experiments.

One of the parameters estimated by the growth model was the asymptotic total length (A_{TL}) or the maximum length after which growth is negligible. For females, this length is 3,291 mm, and for males, it is 4,892 mm. The maximum length recorded for a Morelet's crocodile male was 4,160 mm, while for a female it was 3,760 mm (Pérez et al. 1991). These numbers are similar to the A_{TL} reported here. At least two sightings (without direct measurement confirmation) of Morelet's crocodiles larger than 3,500 mm have been reported in Sian Ka'an (E. Pérez, V. Vela, and J. Bezaury, pers. comm.). The largest individual captured in this study was a male 3,040-mm long; the largest female captured for this study was 2,122 mm long. Pérez et al. (1991:35) speculates that the species "... may well reach 4.5 [m]...".

The Bertalanffy growth model is useful to assess the feasibility of the above figures. An individual 4,160 mm long will be 59 ± 0.03 years old, whereas an animal 4,500 mm long will be 76 ± 0.06 years old. However, a crocodile with 4,981 mm in total length would be 293 ± 46 years old, a number that does not seem biologically feasible. Thus, although it seems possible to assign a maximum length of 5,000 mm to the species, the speculation by Pérez et al. (1991) appears more reasonable. As another example, the Australian freshwater crocodile has a maximum size of 3,000 mm and a maximum age of 45 years (Webb et al. 1983).

Andrews (1982) reports an average length for female Morelet's crocodile of 1,512 mm (calculated from snout-vent length converted to total length by the empirical SVL - TL relationship for the species in Sian Ka'an, G. Merediz, unpublished data). The largest female observed at a nest in Belize was 2,130 mm long (Platt 1996), just 8 mm longer than the largest female captured in Sian Ka'an. Thorbjarnarson (1996) reports a mean female total length for this species of 2,030 mm.

Population Size and Structure.

I calculated the population size for each sampling season by using a geometric frequency of capture model. One of the advantages of such a model is that, unlike other capture-recapture models, it does not assume equal catchability (Bayliss 1987). Thus, it is a more realistic model. The goodness-of-fit tests show that the recapture frequencies fit the geometric distribution in two of the sampling seasons: 1993-94, and 1995-96; however, the frequencies in the second season (1994-95) did not. Therefore, 1994-95 is the only season in which there probably was equal catchability (Bayliss 1987). The geometric distribution has been long recognized as an adequate model to estimate abundance in capture-recapture studies (Eberhardt 1969, Seber 1973, Bayliss 1987). The fact that the recapture frequencies in one of the seasons did not fit this distribution might mean that the estimation for that season was biased. However, the estimation is consistent with those on the previous and the following seasons. Even the age structure in the following year (1995-96) reflects the increased hatchling recruitment in the 1994-95 season (Figure 7).

The expected frequencies, the observed frequencies, and the calculated chi-square values may clarify the goodness-of-fit test for the 1994-95 sampling season (Table 8). The actual frequency of seven captures is one (Equation 2; $F_7 = 1.000$), but it cannot be less than one unless no animals would have been captured seven times ($F_7 = 0.000$). However, the expected frequency is extremely low and unrealistic (Equation 2A; $E(F_7) = 0.024$). The large difference between both values brings the overall chi-square estimation to significant levels, while the rest of the frequencies tend to fit the geometric model. Given the low contribution of F_7 to the estimation of the parameters N and q in equations 1 and 2, it becomes clear why the estimation of the 1994-95 season is consistent with the other two seasons. In conclusion, although the overall chi-square test shows a significant deviation of the observed frequencies from the geometric model, most of the frequencies do fit the model, and only the one that contributes the less to the abundance estimation departs from the expected geometric frequencies.

Table 8.- Observed and expected recapture frequencies, and χ^2 goodness of fit test for the 1994-95 sampling season. See equations 1, 2, and 2A.

| i | fi | E(fi) | χ^2 | q | N |
|---|-----|---------|----------|-------|-------|
| 1 | 125 | 115.701 | 0.747 | 0.244 | 627.6 |
| 2 | 16 | 28.206 | 5.282 | | |
| 3 | 8 | 6.877 | 0.184 | | |
| 4 | 2 | 1.677 | 0.063 | | |
| 5 | 0 | 0.409 | 0.409 | | |
| 6 | 1 | 0.099 | 8.138 | | |
| 7 | 1 | 0.024 | 39.202 | | |
| | 153 | 159.992 | 54.024 | | |

In this paper, I present abundances as absolute values, which are similar to abundances reported for the Nile crocodile in Transvaal (Jacobsen, 1984), and higher than values found for spectacled caiman in Surinam (Ouboter and Nanhoe, 1989) and saltwater crocodile in Malaysia (Stuebing et al. 1994). In the 142-ha Gold Button Lagoon, in northern Belize, the estimated abundance of Morelet's crocodile was 172 ± 5 individuals (Platt 1996) or 1.2 ± 0.04 individuals/ha. This abundance is 27% of the average abundance found in Sian Ka'an (630 ± 19 individuals). However, the study site in Sian Ka'an is larger (3,100 ha of lagoons and 18.5 km of canals) and has a greater landscape complexity. Furthermore, sample efforts in this study were concentrated in areas of open water; the emergent and dwarf mangrove swamps in the surroundings were not studied. Thus, I would expect to have a larger population than the estimate presented here, with the Morelet's crocodile population in Sian Ka'an consisting of two parts: one using mostly the lagoon shores and canals, and other one inhabiting the interior of the swamps. However, some migration between both habitats may occur.

Although population size could be considered high in Sian Ka'an, the age structure of the population is mostly comprised by hatchlings (48%; Table 4) with high mortality rates. Even more, nonreproductive individuals compose 94% of the total population. In northern Belize, Platt (1996) found that of 402 Morelet's crocodiles captured, 49.5% were juveniles

(TL < 750 mm), 24.1% were subadults (TL = 750 to 1400 mm), and 26.3% were adults (TL > 1400 mm). Fitting the Sian Ka'an's population to Platt's age classification, I found that, roughly, 63% of the population is composed of juveniles, 31% by subadults, and 6% by adults. The difference between these numbers and Platt's might have various explanations. First, recruitment possibly is higher in Sian Ka'an than in northern Belize; however, considering the age structure separately for different habitat types, Platt (1996) found juvenile proportions up to 76.1% in alluvial lagoons. Second, juvenile mortality could be lower in Sian Ka'an. Third, past harvesting might have been higher in Sian Ka'an than in Belize, reducing today's proportion of adults. Nevertheless, past hunting in Belize seemed to be extremely high and to the point of near extirpation of Morelet's crocodile (Abercrombie et al. 1980, Platt 1996). In Sian Ka'an, although hunting was very common, former hunters describe a situation that seems less dramatic than the Belize accounts (E. Pérez and V. Vela, pers. comm.).

Other crocodilian populations have age structures similar to the Morelet's crocodile population. Examples include Yacaré in the Brazilian Pantanal (Campos et al. 1994) and northern Suriname (Ouboter and Nanhoe 1989), and saltwater crocodile in eastern Malaysia (Stuebing et al. 1994). Populations of American crocodile on the coast of Belize do not conform to the Type III survivorship curve as did Morelet's crocodile and other species (Platt and Thorbjarnarson 1997). The Belizean American crocodile population is composed of 24.2% juveniles (TL = 301 to 900 mm), 39.1% subadults (TL = 901 to 1,800 mm), and 36.5% adults (TL > 1,800 mm).

The Type III survivorship curve of the studied population implies a high mortality rate in the youngest individuals (Gotelli 1995; figures 7, 8, 10). High mortality rates of hatchlings seem common among crocodilians and alligators. Hatchlings of Morelet's crocodiles in northern Belize have a finite survival rate of 11.1% in their first 10 months of life (Platt 1996), although this rate might be due to particularly dry conditions during the year when the study was performed. Nevertheless, survival possibly would not be much higher in a wetter year. Woodward et al. (1987) estimated an average survival of 30% for yearling American alligators

in Florida, U.S.A. Mean survival of American crocodile in north Key Largo, Florida, is 20.4% (Moler 1991, cited by Platt and Thorbjarnarson 1997). The survival of yearlings of the same species was 20.4% in Turneffe Atoll, Belize (Platt and Thorbjarnarson 1997). The estimated survival of hatchlings of Australian freshwater crocodile in northern Australia was between 6.3 and 16.5% (Webb et al. 1983), or 5 to 10% (Webb and Smith 1984). On the other hand, approximate annual survival rate of juvenile spectacled caimans was estimated to be 72% (Ouboter and Nanhoe 1989).

There are three key points in the life of the population of Morelet's crocodile in Sian Ka'an in terms of its survival rates [$S(x)$, Table 4]. First, survival is very low during the first two years of life. However, caution must be used when considering these figures because, with the technique used in this study, it is not possible to distinguish between mortality and migration of hatchlings to inaccessible sites (Platt and Thorbjarnarson 1997). Yet, as discussed before, it is very possible to document such low survival rates, and those could be due to predation by other crocodiles (Webb, et al 1983, Woodward et al. 1987, Platt and Thorbjarnarson 1997), snakes (*Drymarchon corais*, *Boa constrictor*), turtles (*Chelydra serpentina*), felines (*Leopardus pardalis*, *Leopardus wiedii*, *Herpailurus yagouaroundi*), raccoons (*Procyon lotor*), cormorants (*Phalacrocorax olivaceus*), anhinga (*Anhinga anhinga*), herons and egrets (*Ardea herodias*, *Nycticorax nycticorax*, *Casmerodius albus*, *Tigrisoma* sp.), jabiru (*Jabiru mycteria*), hawks (*Buteo magnirostris*), and several fish species (Alvarez del Toro 1974, Ouboter and Nanhoe 1989, Thorbjarnarson 1989). Abiotic factors such as extremely low or high precipitation, and thus water levels, may reduce yearling survival (Webb and Smith 1984).

After the second year of life, Morelet's crocodile survival notably increases up to 0.94 and remains at that level until the second key survival point. This point occurs two years after sexual maturity is reached, when survival drops by an average of 6%. Average survival rate is then 0.95 for females and 0.71 for males. Although the difference is not statistically significant ($\chi^2_1 = 0.0362$; $p < 0.849$, $\alpha = 0.05$), it might have a biological significance. Males are territorial,

and when reproduction starts they "turn more aggressive and do not tolerate the presence of... rivals near them" (Alvarez del Toro 1974:39). Under these circumstances, male mortality rate might rise considerably.

The last key point occurs in the last years of life when survival drops by an average of 32%. Although jaguar (*Panthera onca*) might predate adult crocodiles (Alvarez del Toro 1974, Ouboter and Nanhoé 1989), survival likely diminishes more because of age, diseases, and related causes. Crocodile hunting is not a significant issue in Sian Ka'an at this time.

Overall, survival among females and males did not vary throughout the study period (1993-96). The survival between males and females did not vary significantly either, although, as discussed before, the biological implications of the slight differences found may be important. Conversely, the lack of significance gives statistical validity to the assumption implied in the population analysis of equal survival among sexes.

Among the most intriguing results obtained from the age-TL model and applied to the life table was age of first reproduction. I assumed female size at first reproduction was 1,500-mm (Schmidt 1924, Platt 1996, M. Lazcano, E. Pérez, V. Vela, pers. comm.). However, size at first reproduction in female Morelet's crocodiles remains undetermined (Platt 1996). Captive females in Tabasco, México, became reproductively active when attaining 1,350 mm total length, or 18 years old according to my Sian Ka'an age-TL model (Casas and Barrios 1997). Hall (1991) suggests that, in American alligator and New Guinea crocodile (*Crocodylus novaeguineae*), females are able to nest when attaining 55 to 60% of maximum total length. In Sian Ka'an, that length would be 1,810 mm (29 years old), if I considered the asymptotic total length for females (Table 2), which is probably unrealistic. Therefore, if females start to reproduce when attaining 1,500 mm in TL, they are 19 years old. The generation time, that is, the average age of the parents of all the offspring produced by a single cohort (Gotelli, 1995), is 23.68 years. Hence, first reproductive size seems very high. Australian freshwater crocodile females attain maturity between 9 and 14 years old (Webb et al. 1983). Spectacled caiman females in the Llanos, Venezuela, have been reported to be reproductive at 3 to 4 years old

(Staton and Dixon 1977) and 7 years old (Thorbjarnarson 1994). Saltwater crocodile start reproducing 10 years after hatching (Webb et al. 1978). Females of Nile crocodile in Lake Rudolf reach maturity after 25-30 years (Graham 1968), which is a minimal reproductive age more similar to what is predicted by the age-TL model presented here.

The Morelet's crocodile population at Sian Ka'an seems male biased but the sex ratio is not significantly different from 1:1. That validates the assumption used in the life table analysis. Different studies have found male biased populations for American alligator, spectacled caiman, black caiman (*Melanoschus niger*), dwarf caiman (*Paleosuchus palpebrosus*), smooth-fronted caiman (*P. trigonatus*), and New Guinea crocodile (Thorbjarnarson 1997). In a review by Thorbjarnarson (1997) 45.4% of 33 datasets showed no significant differences from a 1:1 sex ratio in juveniles, subadults, and adult crocodilians; 36.4% of the datasets were male biased, and only 18.2% were female biased. Many of those biases might be due to differential mortality, differences in habitat selection between sexes, or inability to determine sex of juveniles. Therefore, the female-skewed sex ratio hypothesis (Deeming and Ferguson 1989, cited by Thorbjarnarson 1997) might be inaccurate. The results in this paper support Thorbjarnarson's (1997) analysis. Nevertheless, in the study in Sian Ka'an, some sampling biases might be present if we consider that only open water bodies and canals were surveyed. If there is a sexual orientation in habitat selection and females prefer to live in the interior swamps, a male-biased sex ratio would be obtained.

Leslie Matrix Model and Harvesting Scenarios.

The Leslie matrix model (Figures 14-15) projects a population dynamic characterized by stability and slow negative growth rates, assuming that the population is under a stable age structure. These characteristics, in addition to the low proportion of sexually mature individuals (see above), indicate the population might be very sensitive to adverse conditions. Hence, the negative growth rate might be easily increased.

The projections shown here cover very long periods (25 to 100 years), thus, it is unlikely that environmental conditions in the area will remain at their current state, especially with human influences. Thus, unplanned negative effects on the area may result in a significant decline of the Morelet's crocodile population over a short time period. In consequence, the entire ecology of the wetlands in Sian Ka'an may be altered.

In this paper, I presented a detailed analysis of the population dynamics of a single crocodile species. However, the focus of the work is not the population itself. The ultimate goal is to open an economic alternative that may contribute to improving the socioeconomic situation of the people living in the area. The benefits that local communities may receive from that additional income can help create collaboration links to effectively protect the regional wetlands and, therefore, the ecosystems associated with them (i.e., coral reefs and fisheries, which support the economy of Quintana Roo). A contributing factor to achieve such a goal would be to harvest crocodiles (see below). Even though the population size and structure in Sian Ka'an seem adequate for certain harvesting types, the slightly negative growth rates in the population impose restrictions to harvesting.

The low numbers of reproductive individuals in the population make it very sensitive to direct removal of large crocodiles. The hypothetical case of removing all the larger animals (2 m long or more) to reduce, for example, the risk of attacks to humans as occurred on a few occasions in Cancún (Pers. obs.), would lead to population extirpation in less than 20 years. Even the extraction of 10%, or just 0.5% of the commercially viable population (a "rule of thumb" percentage for harvesting male crocodilians; Ross 1997:183) would eventually take the population to extirpation in a relatively short time. Therefore, according to the model presented here, harvesting adult Morelet's crocodile is not an option in Sian Ka'an.

The situation is different for other species of crocodilians. In the Llanos, Venezuela, a commercial management program of the spectacled caiman was initiated in 1983 (Thorbjarnarson and Velasco 1998). The program was based on removal of nonhatchling individuals and, from 1983 to 1995, over one million caimans were legally harvested (Velasco

and De Sola 1997). The institutions in charge of implementing the program considered that the removal of 5% of the nonhatching population, or 20% of the largest size class (≥ 900 mm), was sustainable. However, those figures were based on regional surveys covering more than 9,000,000 hectares inhabited by 1.4 to 1.7 million nonhatchling caimans (Thorbjarnarson and Velasco 1998).

The Leslie matrix model shows a population declining with a very low rate. Harvesting individuals of any age would increase such negative growth rates. However, if the harvesting occurs together with the restocking of some proportion of harvested individuals after they reached a size in which mortality rates are relatively small, the population presents small positive growth rates. Therefore, harvesting could be a good management tool for increasing the population size if it is accompanied by a restocking component.

For the small area studied in Sian Ka'an, the population's age structure and the low survival rates of yearlings clearly indicate that harvesting the first age class under a ranching program is the most feasible strategy. The harvesting of 75% yearlings, simulating natural mortality, would not generate significant changes in the population. Higher numbers of harvested hatchlings would drive the population to a decline. The "rule of thumb" for harvesting eggs is 50% (Ross 1997). The eggs-to-hatchling mortality rate estimated in Sian Ka'an was 65%, 15% higher than harvesting rates suggested. Therefore, egg harvesting might be another commercial possibility, although more information about egg production is required. Nevertheless, we do not know the response of predation and competition to yearling harvesting. A question that arises is, for example, what would happen to predation over yearlings. Will it be more heavily concentrated over the remaining yearlings? Due to a decrease of yearling concentration, will predation occur less frequently over those yearlings? We also have to consider that the model presented here does not account for compensatory effects, which could probably modify the response of the population growth rates to yearling harvesting. Positive compensatory effects have been reported for American alligator in Florida and Louisiana (Chabreck et al. 1997).

Another desirable component of a ranching system is restocking of a certain amount of juveniles, typically between 15 and 20% (Chabreck et al. 1997, Thorbjarnarson and Velasco 1998), after they reach the critical survival age (or size). According to the model presented here, that critical age occurs at year 2 (third year after hatching). This practice would reduce population risks due to lowering recruitment rates by harvesting. In addition, restocking would revert the population growth rates into positive values as the model shows. Restocking around 30% of the harvested yearlings is desirable in northern Sian Ka'an. It is usually assumed that survival of released animals equals that of animals grown in the wild. Nonetheless, recapture rates, and thus survival rates of farm released American alligator in Louisiana, were 65 to 78% lower than those of wild juveniles. In addition, the number of wild alligators cannibalized was 67% lower than the number of cannibalized, farm-released animals. Thus, restocking represented a small contribution to population's growth (Chabreck et al. 1997). To facilitate the positive contribution of juvenile restocking to northern Sian Ka'an Morelet's crocodile population, restocking must occur in densely vegetated areas with low adult populations. Currently, a GIS analysis of Morelet's crocodile distribution in northern Sian Ka'an is taking place (E. Quijano, unpublished data) and will indicate what areas could be appropriate for juveniles restocking.

A caiman ranching program was implemented in the Venezuelan Llanos. The government authorized collection of 388,150 eggs and 10,487 neonates. About 40,000 individuals were released back to the wild after attaining lengths ≥ 600 mm, but "... poor growth of hatchlings and disappointing sales of skins led to export [caimans] as pets in 1992" (Thorbjarnarson and Velasco 1998). By 1996, ranching became unprofitable due to several technical and economical problems (Thorbjarnarson and Velasco 1998:8). Crocodile skin prices have diminished in recent years due to the increased number of ranching projects developing in different countries (J. Thorbjarnarson, Pers. com.). The price of illegal Morelet's crocodile skins in Mexico has been US\$5.00/foot, while in Guatemala it has been US\$1.70/foot (Castañeda 1997).

In summary, the Morelet's crocodile population model developed for Sian Ka'an as well as other studies suggest the implementation of a ranching system where about 50% of wild-produced eggs and 75% of the hatchlings can be collected and incubated until they reach a commercial size, releasing back to the wetlands about 15-20% of the individuals after 3 years (or less if in-captivity growth rates are higher). In this way, the reproductive segment of the population would remain intact. The commercial production would depend on the wild population so that producers would be concerned about those wild populations and their habitat. Thus, they might participate in the conservation programs of the wetlands of Sian Ka'an.

However, the Venezuelan experience (Thorbjarnarson and Velasco 1998) indicates that a Morelet's crocodile ranching program in Sian Ka'an has to be only a complement of other productive activities (i.e. agriculture, fishing, use of different wildlife species, tourism, etc.). The technical, economical, social, and ecological difficulties that the project might entail could be more complicated than the problems intended to be solved via use of crocodiles. Reopening the crocodile's market might bring additional risks in terms of illegal poaching and trade, although direct participation of local people in the project's design and implementation may increase their awareness against illegal traffic (see below).

The discussion above is based on the results of basically two main models describing biological characteristics of Morelet's crocodile. The first is for the total length-age relationship, and the second is for the population dynamics for the species in Sian Ka'an. "Models are metaphorical... descriptions of nature, and there can never be a 'correct' model" (Hilborn and Mangel 1997:xii). More formally defined, a model is "a stylized representation or generalized description used in analyzing or explaining something" (Hilborn and Mangel 1997:24).

The Leslie matrix model developed in this work is a representation, not a description, of the population dynamics of Morelet's crocodile in northern Sian Ka'an. Given the assumptions made and the inputs considered (many of the inputs were merely estimations

based on other models with other assumptions as well), the population will increase or decrease as shown in Figures 14-18. However, those representations are oversimplifications of the real population. They do not consider density dependence, compensatory survival, or stochasticity. Density dependence is probably not affecting the population since it is stable with a slight negative trend. Compensatory effects and stochasticity may have larger effects on the population model. Stochasticity may become critical in those harvesting scenarios where population decreases with a very high rate. The model can be used as a very basic and general guideline to understand how a harvesting program may affect the population. For example, the model allows us to realize that the population might be very sensitive to adult harvesting, but that it would be more tolerant to harvest of hatchlings. The model is a useful first step in designing a harvesting program, but does not mean the population will follow the predicted trends.

Additionally, small variations in the model inputs may generate enormous variations in the output (Abercrombie and Verdade 1995). For example, if the initial population structure in the Leslie matrix model corresponds to the values in the $N(x)$ column in Table 3, the population projection grows exponentially, reaching unrealistic crocodile abundances in very few years. Alternatively, if the initial population size used in the matrix model is that shown in the $N(x)$ column in Table 4, then the population behaves as shown in Figure 14. In both cases, the total population is the same: 635 individuals; the difference is the proportion of individuals in each age class.

Considering the above discussion, it is not appropriate, and it is even dangerous, to base a potential harvesting program on the assumptions and descriptions of the model (Abercrombie and Verdade 1995). The model should be considered just a first step to start a long-term project. Once the project begins, the communities and technicians involved should constantly monitor the different parameters involved in the population dynamics, which is where the real usefulness of the model begins. The model allows us: (1) to understand how the demographic processes in the Morelet's crocodile population occur and to clarify the

theoretical descriptions of those processes; (2) to know what parameters describing the population are poorly known (e.g., egg-to-hatchling survival, causes of growth rate variation, dispersal rates of hatchlings, density-dependent relationships year by year variability of survival and fertility rates, etc.); (3) what parameters are critical in the dynamics of the Morelet's crocodile population (e.g., survival rates, and per capita fertility rates, both of which are necessary in the Leslie matrix), and therefore, where we have to focus our attention in future monitoring surveys (Abercrombie and Verdade 1995, Hilborn and Mangel 1997).

Another crucial issue is the way the researcher communicates the model results to the members of the communities involved in the harvesting program, the government officials, and the public. Presenting a graph of the population trends after harvesting, without the proper framework or out of context, may generate misunderstandings that can lead to incorrect management decisions. Consequently, the confidence of local people in the project and the research upon which the project is based might diminish considerably. Presenting an unrealistic exponential growth model, for example, without stating the real meaning of such a model can erode credibility of biologists and technicians before the community. Confidence and credibility are cornerstones for the adequate functioning of any crocodile harvesting program.

Participation of Local People.

Natural processes are often considered isolated from social processes. This point-of-view rules many conservation efforts throughout the world. Nonetheless, both processes take place together in such a way that "human impacts may enhance or reduce biodiversity" (Pretty and Pimbert 1995:11). Thus, "...conservation efforts must identify and promote those social processes which enable local communities to conserve and enhance biodiversity as part of their livelihood system/security" (Pretty and Pimbert 1995:11).

Participation is here defined as the process by which people interact in joint analysis, forming or strengthening local groups, developing interdisciplinary methodologies, creating a

cooperative learning process, and taking control over the local decision making. Such a process should allow local communities to generate their own initiatives through a self-mobilization process (Pretty 1995).

Participation of local people in the development of conservation programs is crucial. The success of different resource conservation projects, and the reversal of many problems generated by the imposition of external technologies, relies on the participation of local people. Examples can be taken from soil and water conservation efforts (Pretty and Shah 1997), sustainable agriculture (Pretty 1995, 1997), and other issues.

A crocodile ranching project seems biologically and ecologically feasible in the northern Sian Ka'an region. However, that conclusion does not mean that such a program, if developed, will be successful. Local community participation in a ranching program will be an essential factor in developing a positive and useful project.

Local participation may occur in different levels. First, based on their own interests and knowledge, and in the information available from this study and other sources, local communities would decide if producing crocodiles and preserving wetlands is part of the local priorities. Second, if a certain community is interested in developing the project, then it would have to organize itself to plan the research and the production mechanisms required. Third, they would have to find the mechanisms to control and monitor the production and trade of crocodiles. The participation of every social sector in all the project's processes would help to develop the sense of responsibility that is required to make the project sustainable and useful.

Different mechanisms have been designed to generate and promote people participation in the conservation of their natural resources. These include integrated conservation-development projects (ICDP; Wells and Brandon 1993), "campesino a campesino" (farmer to farmer) educational and development programs (Holt 1990), participatory research (including methodologies involving group and team dynamics, sampling methods, interviewing and dialogue, and visualization and diagramming; Pretty 1995), and many others. All these methodologies imply the existence and development of community

self-organization, and a large educational component. In this case, education should be a process of mutual teaching and learning between teachers and students, or community and technicians. Education is a process by which every body learns from culture and nature, and creates a conscious vision of the social, economical, political, and environmental reality (J. Moure, pers. comm.).

In addition to local participation, a crocodile ranching program in Sian Ka'an requires the creation of appropriate relationships between local communities, technicians and researchers, and governmental authorities. The parrot-harvesting program in Tres Reyes, a community neighbor of Sian Ka'an, is an example of the creation of those links. The community is currently harvesting white-fronted parrots (*Amazona albifrons*) based on the studies developed together by Amigos de Sian Ka'an's researchers and the community, and with the authorization and support of the federal government through SEMARNAP, the Secretariat of Environment, Natural Resources, and Fisheries (C. Gracida, pers. comm.; Gracida 1998). A similar participative approach has been proposed for the management of crocodilians in La Encrucijada Biosphere Reserve, Chiapas, Mexico (Arellano et al. 1997).

In northern Sian Ka'an Biosphere Reserve harvesting crocodiles under a ranching program may contribute to create a collaboration between local communities, conservation organizations, and the government to preserve wetlands and related ecosystems. Harvesting crocodiles may also contribute to improve the quality of life of local communities if the project understands and integrates the social and cultural dynamics of those communities. In other words, a crocodile ranching program must be integrated in the social context of the region. It can not be an isolated "biological" project.

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