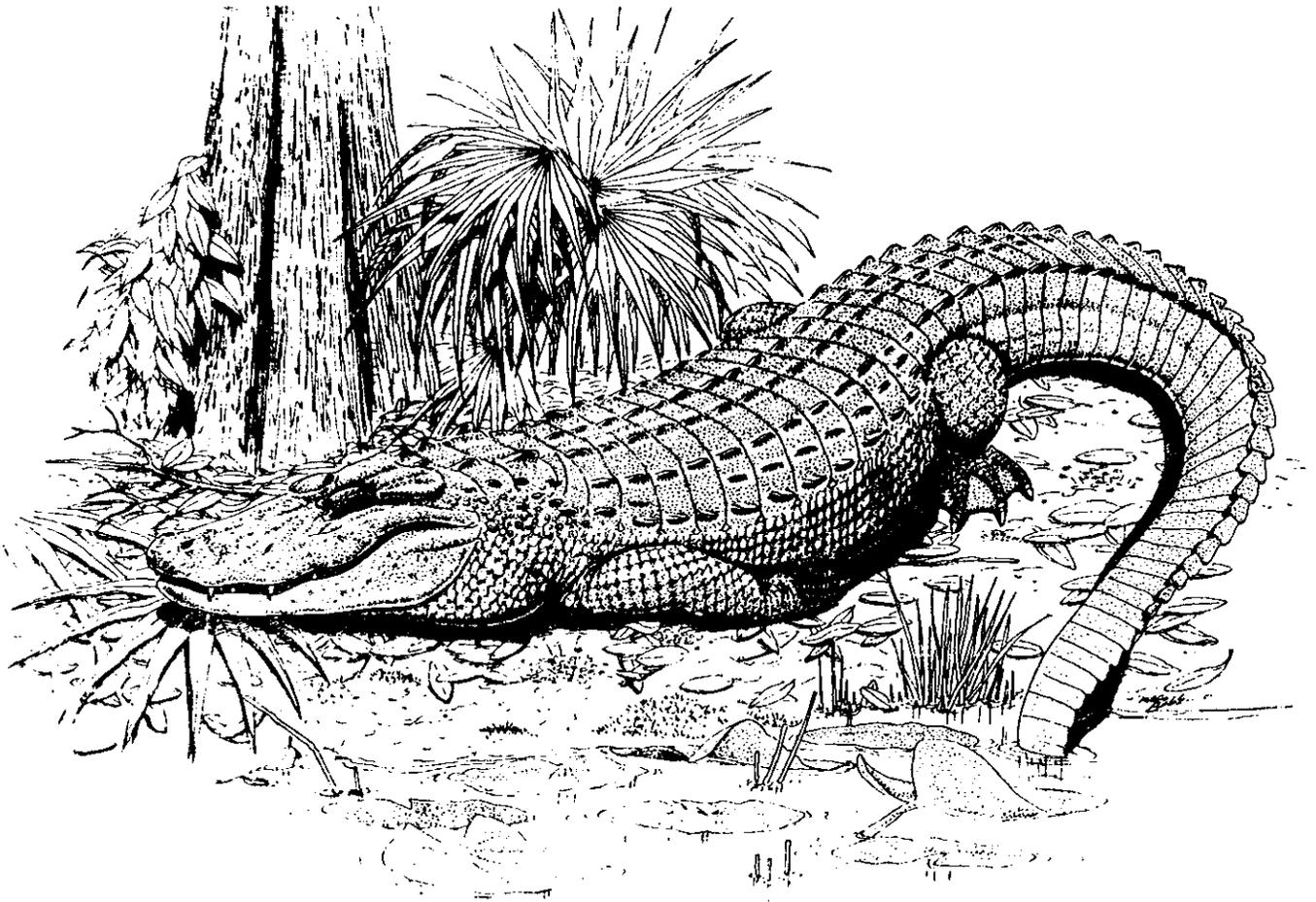


EXPERIMENTAL ALLIGATOR HARVEST

by

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Final Report
Study Number: 7567
Study Period: 1 July 1981 - 30 June 1991

Bureau of Wildlife Research
Florida Game and Fresh Water Fish Commission
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Abstract--An experimental harvest of commercial-size (≥ 122 -cm) American alligators (*Alligator mississippiensis*) was conducted on treatment areas, Lochloosa, Orange, and Newnans lakes in northcentral Florida during 1981-90 and response to harvest was compared with control areas Paynes Prairie and Lake Woodruff. An overall mean of 13% of the estimated population was harvested annually but this varied slightly by area. The median total length (TL) of harvested alligators varied by area and smaller alligators constituted an increasingly greater proportion of the harvest over years. The harvest was predominantly (69.9%) male. Increased hunter effort was necessary over years to maintain success rates because of an apparent increase in wariness of larger alligators.

No changes were detected in the physical condition of harvested alligators. Night-light counts of harvestable alligators remained stable on all harvest and control areas, but some evidence of declining counts of adult (≥ 183 cm) alligators was detected on lakes Orange (-45%), Lochloosa (-63%), and Woodruff (-18%). Declines were attributed primarily to wariness from hunting and live-capture. Counts of juvenile alligators increased on Orange and Lochloosa lakes. Nest production was mostly influenced by May and September water levels and remained stable on all areas except Orange Lake and Lake Woodruff where nesting increased. Nest survival increased during the study, primarily due to decreasing incidence of flooding. Nest predation was attributed to raccoons and was greatest on Orange Lake (51%). Predation occurred throughout incubation. Nest flooding rates were variable among years but similar among areas (4.8%).

Clutch size distributions varied among areas sampled (Orange Lake, Paynes Prairie, and Lake Woodruff) and mean clutch size on Lake Woodruff (42.9) was greater than those on Orange Lake (32.8) and Paynes Prairie (33.8). Clutch size did not change over years on either treatment or control areas. Clutch banding and viability rates (97% and 87.5%) were similar among areas and higher than rates reported for other Florida alligator populations. Minimum size at maturity was 180.5 cm for an Orange Lake female but only 64% of ≥ 183 cm females were mature. Proportions of mature females at a given size class varied by area with Newnans Lake females maturing at a greater size. Proportion of mature females ovulating did not change over years but was less on Newnans (15.8%) than either Lochloosa (38.5%) or Orange Lake (39.8%).

The largest alligator recorded on study lakes from 1981-90, an Orange Lake male, was 423 cm TL and 473 kg. The largest female, taken on Orange Lake, was 297 cm and 115.5 kg. Subadult (122-182 cm) alligators grew faster on Lochloosa and Newnans than they did on Orange and Woodruff lakes. Estimated years for females to reach minimum reproductive size (180 cm for Lochloosa and Orange, and 211 cm for Newnans) ranged from 8.9 on Lochloosa to 12.4 on Orange. Mark-recapture data and femur annuli analyses indicated that growth rates of females did not change during the harvest but that growth rates of the subadult males did.

Sex ratios varied among areas, were balanced on Newnans and Paynes Prairie, and weighted toward males on Lochloosa, Orange, and Woodruff. Cannibalism was the largest source of non-hunting alligator mortality found during our study and was estimated to account for 6.3-8.1% of the <91 cm population annually. Movements of alligators between areas was greatest for Orange and Lochloosa, but some movement was detected among other pairs of study areas. Diets changed with size of alligator. A growth slowdown of alligators between 61-122 cm corresponded to a transition in diet.

We found no evidence that alligator harvests affected fish populations or nutrient levels in lakes. Daylight visibility of alligators dropped immediately after hunts but recovered fully by the following year suggesting that harvests had only a temporary effect on daylight viewing of alligators.

Average annual wholesale value of hides and meat produced by the harvest was \$107,476 with hides comprising 62% of the value. The average value of a harvested alligator was \$332 and gross hunter income, adjusted for license fees, was \$4183 for a mean annual take of 15.8 alligators. Hunter composition changed from 40.9% commercial fishermen during 1981-87 to 3.6% in 1989 following opening of alligator hunts to the general public in 1988.

A sustained 13% proportional harvest of commercial size alligators had no measurable negative affects on alligator populations. Differences among study areas in response of demographic parameters to harvest indicate that wetlands with dissimilar demographics may not respond in a like manner to harvests.

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INTRODUCTION

American alligators have been commercially exploited for their skins since the early 1800's yet harvests based on sound biological data are a relatively recent event. Intense hunting for the skin trade began in the early 1800's in Louisiana (Audubon 1931, McIlhenny 1935) and the latter half of the 1800's in Florida (Smith 1891, Stevenson 1904, Kellogg 1929, Kersey 1975) and continued through the 1960's (Allen and Neill 1949, Hines 1979, Joanen and McNease 1987a). Unregulated and illegal hunting for the leather trade was a major factor contributing to alligator population declines during 1950-71 (Chabreck 1967, Hines 1979, Joanen and McNease 1987a). Depressed alligator populations and a concern for the future of the species led to the closure of hunting seasons in Florida in 1981 and in Louisiana in 1962 (Chabreck 1967, Joanen and McNease 1987a). Legal hunting and international trade of most crocodylians, including the American alligator, were severely restricted during the 1970's, and opportunities for development of a harvest program were limited.

Alligator populations in Louisiana and Florida increased rapidly in response to protection in the early 1970's (Palmisano et al. 1973, Schemnitz 1974, Hines 1979, Hines and Woodward 1980, Wood et al. 1985, Woodward and Moore 1990). The ability of alligators to survive intense, unregulated hunting suggested that populations might tolerate sustained harvest at a lower level. Because of the high commercial value of alligator skins and the tradition of alligator hunting, Louisiana resumed hunting in 1972. Their objective was a sustained-yield harvest with a regulatory framework that controlled harvest levels and trade (Palmisano et al. 1973, Joanen and McNease 1981).

In Florida, conflicts between alligators and the public led to development of a nuisance alligator control program that entailed an unconventional concept; harvesting problem alligators and selling the skins to offset program costs (Hines and Woodward 1980). The early success of the nuisance alligator control program in Florida and a strong tradition of alligator hunting stirred interest in developing a comprehensive sustained-yield harvest program similar to Louisiana's. However, because of past over-exploitation, the Florida Game and Fresh Water Fish Commission (GFC) resolved to establish a sustained-yield harvest program based on biologically sound harvest rates and field-tested harvests conducted over a long period of time (1981 Alligator Manage. Plan, GFC, Gainesville).

In developing an alligator hunting program, 4 primary factors were considered: (1) biological capacity of populations to sustain harvest, (2) ecological and aesthetic effects of alligator hunting, (3) sociological aspects of alligator hunting, such as tradition, user groups, and economic impact, and (4) wildlife conservation implications.

Although life history information was available for Louisiana alligators, little was known about absolute abundance, long-term growth rates, survival, age-specific fecundity, and sex ratios for Florida alligators. Furthermore, relatively little has been reported about alligator population and harvest dynamics (Nichols 1987, Abercrombie 1989). Harvest quotas in Louisiana have been determined by using nest counts to estimate population size (Chabreck 1966, McNease and Joanen 1978) and harvesting 7-8% of the estimated population of ≥ 4 ft. (122 cm) total length (TL) alligators (Taylor and Neal 1984, T. Joanen, pers. commun.). Specific methods of determining harvest rate have not been described but apparently are based on recommendations by Nichols et al. (1976) and trial and error harvesting. Taylor and Neal (1984) reported that harvest rates in Louisiana were not sustainable. However, they concluded that the harvestable population, particularly subadults (122-183 cm TL), had been underestimated and over-harvest had been avoided. This underscores a major problem with attempting to manage alligator populations through quota harvests: Sustainable *a priori* harvest rates and associated quotas can only be developed from population models with realistic values for demographic parameters (Nichols 1987, Abercrombie 1989).

The ecological role of alligators is somewhat vague. McIlhenny (1935), Craighead (1968), Hines et al. (1968), and Kushlan (1974) discussed the use of "gator holes" by fish and wildlife in shallow marshes, but little is known of the influence of alligators on lake and river ecosystems. Goodwin and Marion (1977) and Deitz and Jackson (1979) reported the use of alligator nests as nest sites by turtles and discussed its ecological implications. Little is known about the effects of alligators on prey populations and nutrient cycling.

Alligators are an important component of Florida's natural history (van Doren 1928), and southern folklore is generously laced with alligator mythology (Kellogg 1929, Audubon 1931, Neill 1971). Alligators hold the precarious position of being both esteemed and feared by humans. This was apparent from a survey that found that 90% of Floridians valued alligators for ecological, aesthetic, or commercial reasons, but 48% felt that they were dangerous (Hines and Scheaffer 1977). Concern for declining alligator populations during the 1960's and widespread support for restoration of populations attest to the public's strong positive feelings toward alligators. Delany et al. (1986) found that a majority of people with close contact with alligators enjoyed seeing them.

Prior to 1981, managed hunting of large crocodilians worldwide was limited to the Louisiana alligator harvest program (Palmisano et al. 1973, Joanen and McNease 1981, 1984, 1987a). However, Louisiana's hunts were primarily designed for large, privately owned marshes and impoundments with extensive canal systems. The constraints imposed by management objectives in Florida suggested that Louisiana's population estimation techniques, harvest rates, hunter selection procedures, harvest methods, and allocation of the resource would not be suitable for large, public-owned lakes and rivers. Therefore, development of a harvest program in Florida required several major deviations from the Louisiana program.

In 1981, the GFC resolved that a Florida alligator management program should have incentives for conservation of alligators and their wetland habitats (GFC 1981 Alligator Manage. Plan). This concept was termed "Value-Added Conservation" and proposed that the economic value of the resource would encourage constituents to support the conservation of alligators (Hines et al. 1986, Hines and Percival 1987, Hines 1990). The 1981 alligator management plan concluded that commercial hunting for skins and meat could help accomplish this while providing consumptive use of a valuable, renewable natural resource. We were then charged with the responsibility of developing an ecologically benign commercial alligator hunting program that would provide for sustained harvest with significant income to participants, attract a broad base of participants, provide recreational qualities, and be manageable from biological and law enforcement perspectives.

The objectives of this study were to: (1) determine the effects of a sustained commercial harvest on alligator populations; (2) improve the accuracy of estimates for basic alligator population demographic parameters, and (3) develop guidelines for administering hunts.

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STUDY AREAS

Investigations were conducted on 5 wetlands in the St. Johns River watershed in Florida (Fig. 1). Lochloosa Lake, Newnans Lake, Orange Lake, and Paynes Prairie near Gainesville, Alachua County, in northcentral Florida (Fig. 1), are part of the Orange Creek drainage which flows into the Oklawaha River, which eventually empties into the St. John's River near Lake George. Lochloosa, Newnans, and Orange lakes have high nutrient levels (Table 1) and all are considered eutrophic (Canfield 1981:128). Average annual rainfall in this area is 132 cm (52 in.), mean maximum and minimum temperatures are 27.8 and 14.5 C, and the area receives 100 hours per year of freezing temperatures (Winsberg 1990). Wetlands in the Lake Woodruff National Wildlife Refuge, near DeLeon Springs, Volusia County, flow into Lake Dexter and then into the St. Johns River (Fig. 1). Trophic condition was not available for Lake Woodruff, but Lake Dexter, adjoining Lake Woodruff (Table 1), was considered eutrophic (Canfield 1981:152). Annual rainfall is 124 cm (49 in.) per year, mean maximum and minimum temperatures are 26.7 and 16.1 C, and the area receives approximately 67 hours of freezing temperatures per year (Winsberg 1990). Rainfall and associated water levels in both areas followed the typical north Florida pattern with an Oct-Dec dry period and a Jun-Aug wet period (Fig. 2). Water levels for Lochloosa, Newnans, Orange, and Woodruff were obtained from U. S. Geological Survey gauge stations located at or near the study areas (Woodward and Moore 1990). Hydrilla coverage was obtained from surveys conducted 1-4 times per year by the Bureau of Aquatic Plant Manage., Fla. Dept. of Nat. Resourc. Hydrilla coverage on Woodruff was not measurable, and could not be used as a covariable in analyses for this area.

Lochloosa Lake

Lochloosa Lake (Fig. 3) is comprised of a large, shallow lake, an extensive adjacent emergent marsh dominated by sawgrass (*Cladium jamaicense*), and a patchwork of bald cypress (*Taxodium distichum*) swamp (Table 2). Little Lochloosa, a bay on the western side of the lake, is characterized by floating mats (Reid 1952) and stands of spatterdock (*Nuphar luteum*). Right and Left Arm Marshes are shallow, sand-bottomed, sawgrass marshes interspersed with wax myrtle (*Myrica cerifera*) - buttonbush (*Cephalanthus occidentalis*) islands. Hydrilla (*Hydrilla verticillata*) coverage fluctuates but is extensive during some years (Fig. 4). Water levels are largely dependent on drainage from surrounding flatwoods, and water discharges through 1-km Cross Creek into Orange Lake. Water levels on Lochloosa Lake fluctuated similar to Orange Lake. For this study, Cross Creek was considered part of Lochloosa Lake.

Newnans Lake

Newnans Lake (Fig. 5) is primarily composed of a relatively shallow open water area and a large cypress swamp. Scant (13 ha) emergent vegetation occurs on the perimeter of open water and in several unwooded depressions in the swamp. During the early 1980's, emergent vegetation on the open lake was minimal, but during the late 1980's, fragrant water lily (*Nymphaea odorata*) and American lotus (*Nelumbo lutea*) increased in abundance, as did hydrilla (Fig. 4). Water levels were stabilized in 1967 by a water control structure constructed at the Prairie Creek outlet. A drawdown, initiated by the GFC in 1989 (Fig. 4) may have contributed to increased densities of emergent plants. Water inflow is primarily from runoff from surrounding flatwoods to the north of the lake through Hatchet Creek and Gum Root Swamp.

Orange Lake

Orange Lake (Fig. 6) is a diverse wetland with a large open lake and an extensive emergent marsh (Table 2) characterized by floating islands (Reid 1952). These islands begin as floating peat masses and are colonized by arrowhead (*Sagittaria lancifolia*), pickerelweed (*Pontederia cordata*), water pennywort (*Hydrocotyle umbellata*), maidencane (*Panicum hemitomon*), smartweed (*Polygonum spp.*),

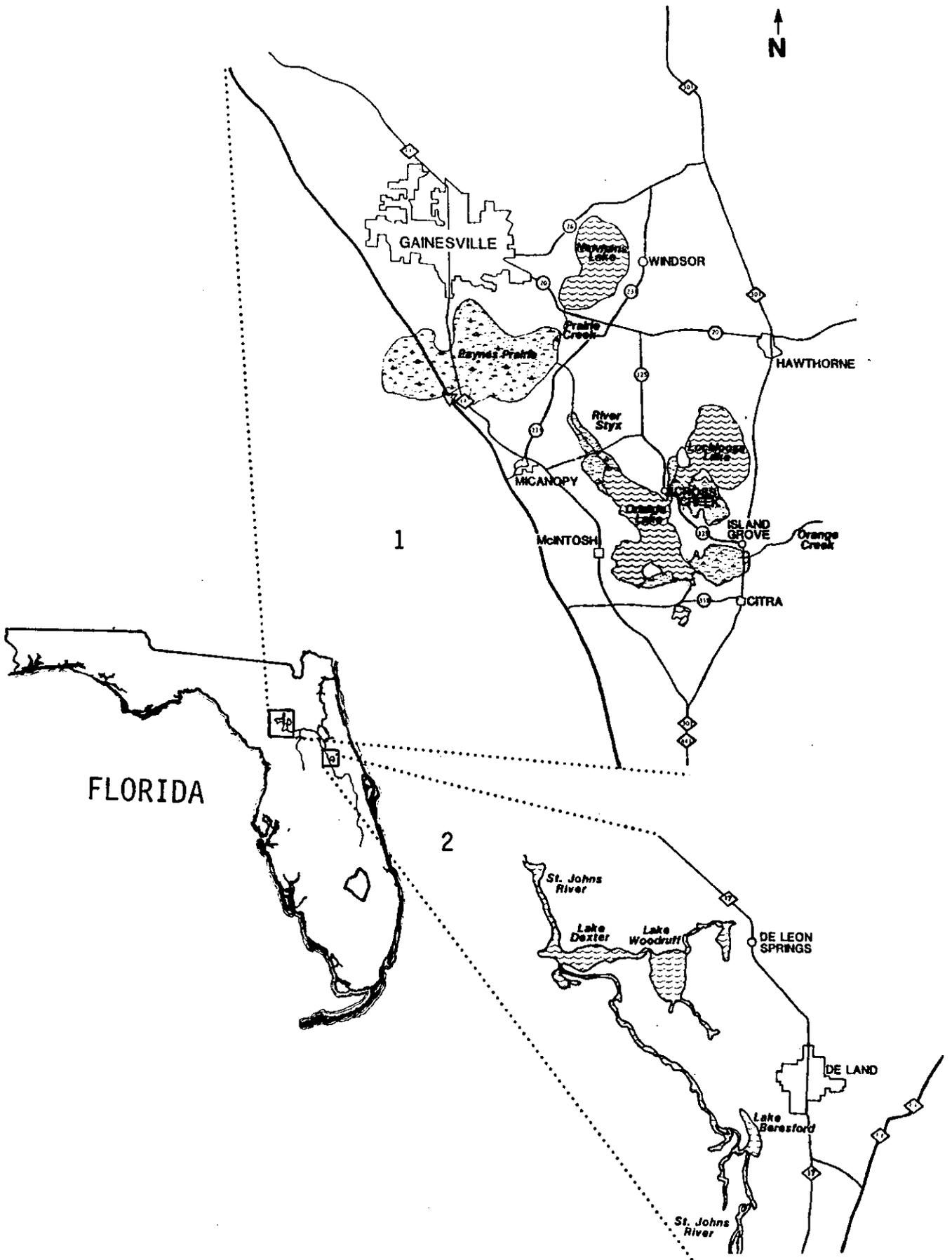


Fig. 1. Study areas, (1) Paynes Prairie, and Lochloosa, Newnans, and Orange lakes (Orange Creek drainage, Alachua Co., Florida) and (2) Lake Woodruff National Wildlife Refuge (St. Johns River drainage, Volusia Co., Florida).

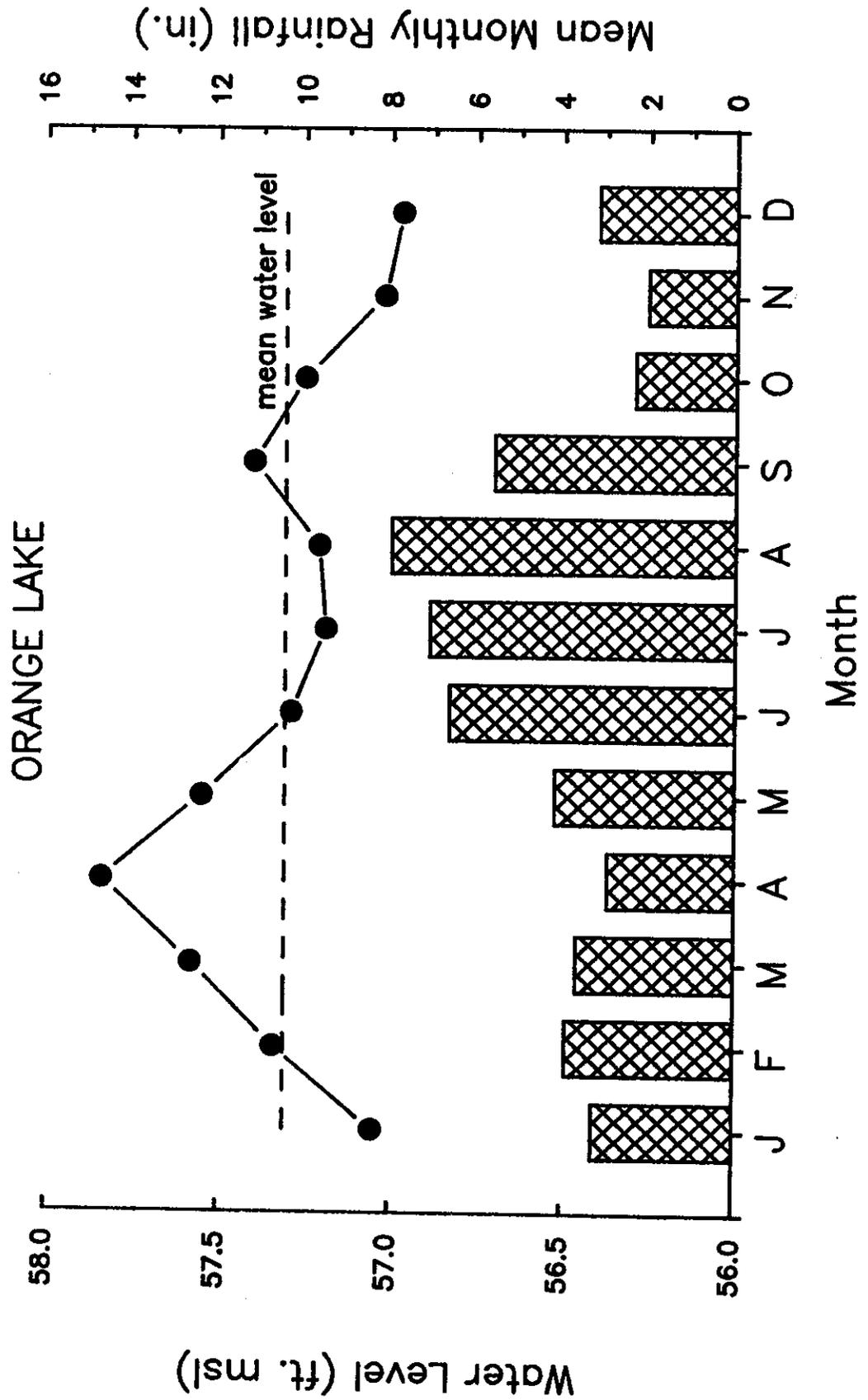


Fig. 2. Mean monthly surface water levels (solid line) and rainfall amounts (cross-hatched bar) during 1976-90 on Orange Lake.

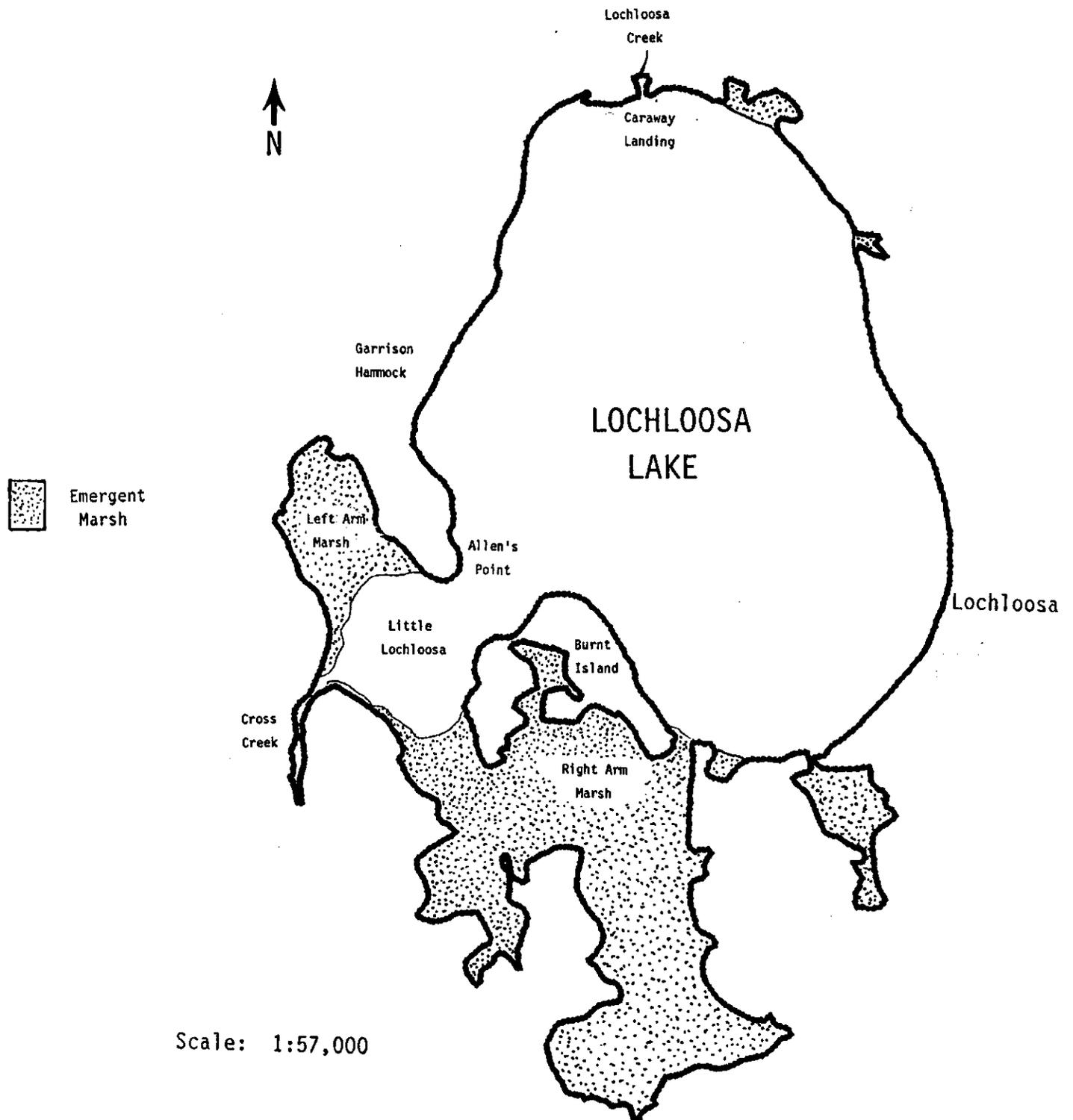


Fig. 3. Landmarks and major aquatic habitat types for Lochloosa Lake.

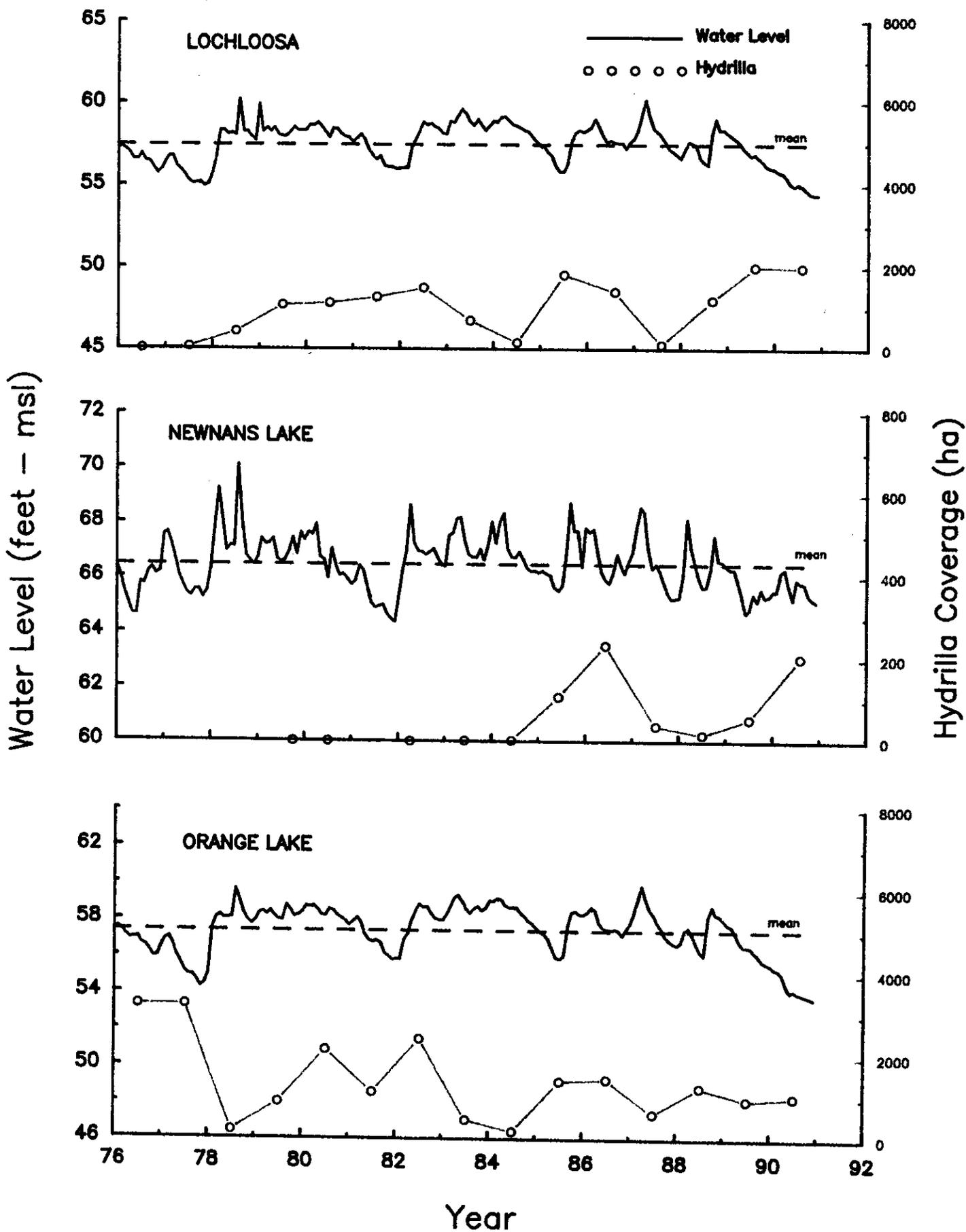


Fig. 4. U.S. Geol. Surv. surface water guage station readings for Lochloosa (#2242400), Newnans (#2240900), and Orange (#2242450) lakes, and mean Jul-Aug hydrilla coverage during 1976-90.

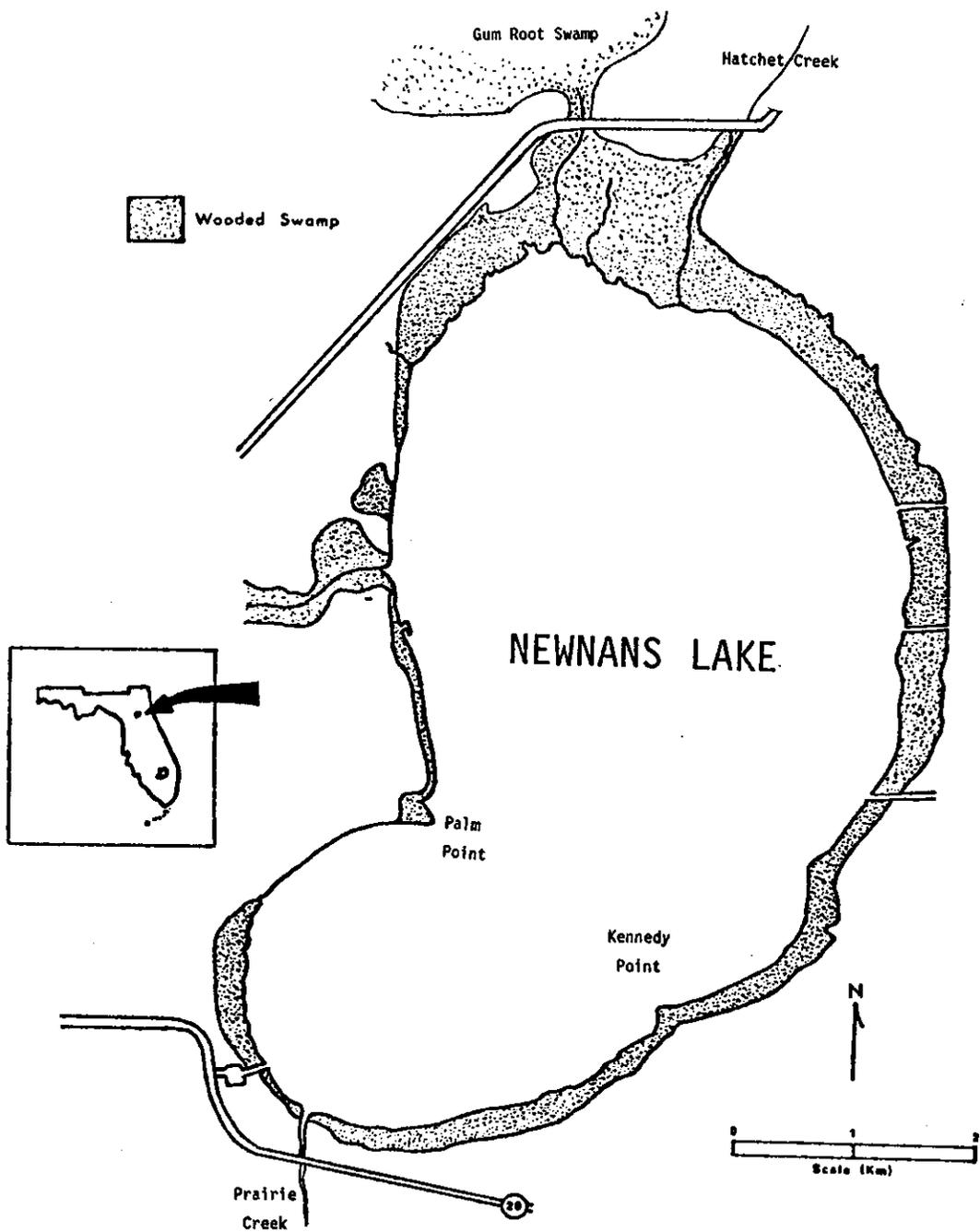


Fig. 5. Landmarks and major aquatic habitat type for Newnans Lake.

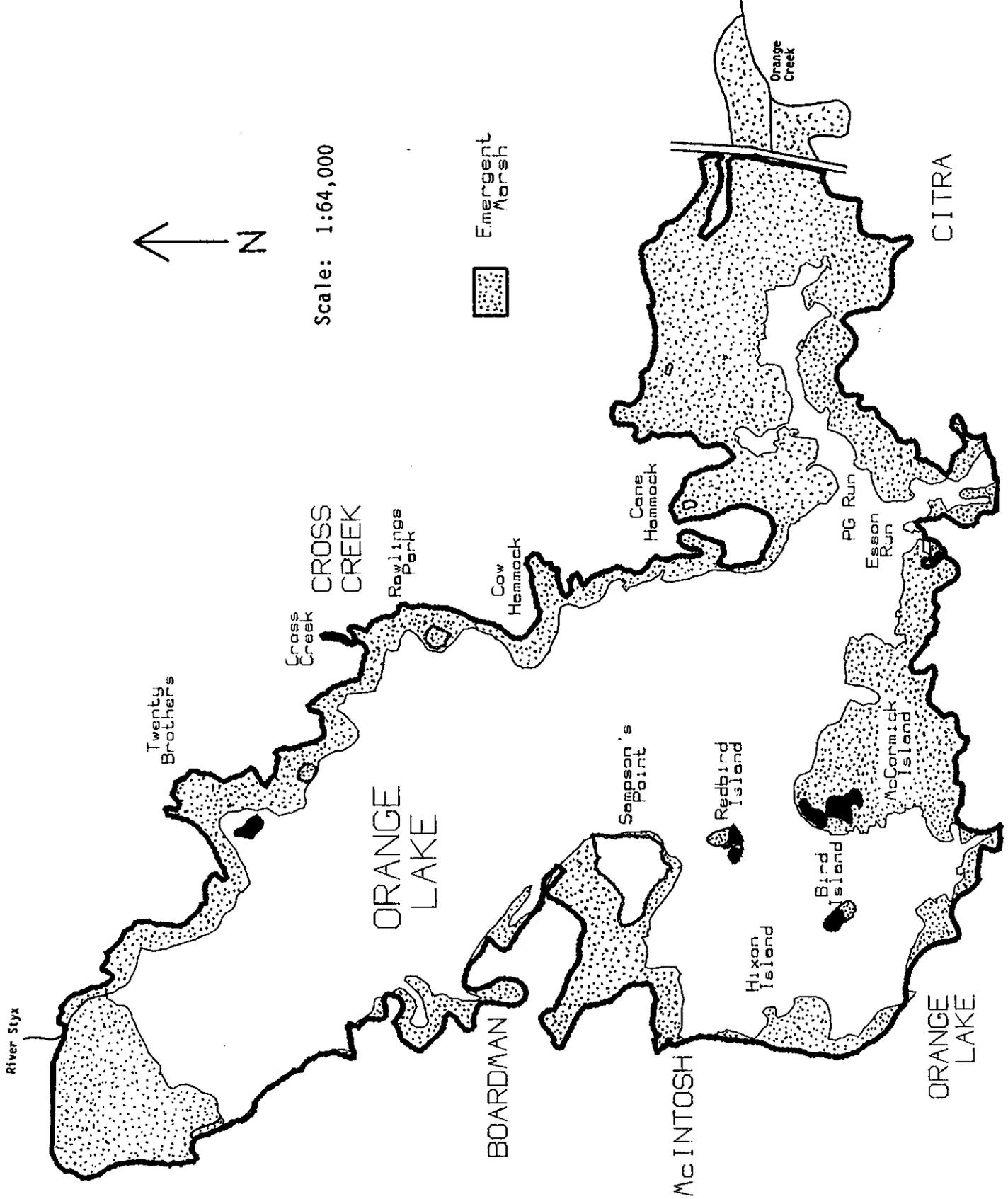


Fig. 6. Landmarks and major aquatic vegetational types for Orange Lake.

Table 1. Mean pH, nitrogen (N), phosphorous (P), and chlorophyll-a (Chl-a) levels (mg/m³) for 4 Florida lakes, 1979-80 (Canfield 1981).

Lake	pH	N	P	Chl-a
Lochloosa	7.4	1200	36.4	32.0
Newnans	6.8	1300	52.3	38.0
Orange	7.2	1100	31.0	35.4
Woodruff ¹	7.2	994	115.0	17.6

¹Values derived from samples on Lake Dexter, which adjoins Lake Woodruff.

and cattail (*Typha spp.*) during early development. They eventually develop successionaly into floating tree islands dominated by sweet gum (*Liquidambar styraciflua*), willow (*Salix spp.*), wax myrtle, and buttonbush. Other emergent marsh was dominated by sawgrass, cattail and maidencane. Open water was generally fringed with spatterdock and, to a lesser extent, American lotus. In some years, much of the limnetic zone was covered with hydrilla (Fig. 4) and water hyacinths (*Eichhornia crassipes*), which were sprayed regularly with herbicides to control their abundance. Water levels fluctuated substantially during the study, with droughts in 1981 and 1990 and flooding conditions in 1982 and 1988 (Fig. 4). A water control structure at the Orange Creek outlet at U.S. highway 301 tends to stabilize water levels.

Paynes Prairie

Paynes Prairie (Fig. 7) is a shallow wet marsh or "prairie" (Table 2) within Paynes Prairie State Preserve. Wetlands were dominated by maidencane, pickerelweed, cattail and willows (White 1974), and water hyacinths frequently covered canals. Wetland area varied from < 190 ha during extreme drought conditions to 4850 ha during flooding conditions (Fla. Dept. of Nat. Resourc., unpubl. data). Mean wet area during our study was 876 ha at a mean water level of 17.0 m (55.8 ft.) mean sea level (msl). Open water (190 ha) was limited to Alachua Lake, Alachua Sink, and canals. Water flow was significantly affected by a dike and canal system excavated during the 1920's and 1930's and by highways, U.S. 441 and I-75, which transect the mid-section of the wetland (White 1974). Historically, water levels have fluctuated substantially (White 1974), as was observed during our study (Fig. 8).

Lake Woodruff National Wildlife Refuge

The Lake Woodruff National Wildlife Refuge study area consisted of Lake Woodruff (935 ha), Spring Garden Lake (211 ha), Tick Island Mud Lake (123 ha), extensive cordgrass (*Spartina bakeri*) marsh, wooded swamp, Spring Garden Creek, Norris Dead River, Scoggins Creek, Harry's Creek, and Tick Island Creek (Table 2, Fig. 9). Water sources for these wetlands are DeLeon Springs and runoff from surrounding uplands. Water levels on Lake Woodruff (Fig. 8) fluctuated considerably in response to elevation changes in the St. John's River which flows along the west side of the refuge. Major vegetation included cordgrass, cattails, and sawgrass in the emergent marsh; spatterdock, banana lily

Table 2. Water depths (m) (Brezonik and Shannon 1971, Gottgens and Montague 1987) and surface area (ha) of major habitat types for 5 Florida wetlands in 1987.

Study area	Water depth		Habitat type				Total
	\bar{x}	max.	Open water	Emergent vegetation	Wooded swamp	Spatterdock	
Lochloosa Lake	2.1	3.4	2111	915	273	202	3501
Newnans Lake	1.2	3.7	2398	13	555	0	2966
Orange Lake	1.8	3.0	2788	2150	30	286	5254
Paynes Prairie			190	4660	0	0	4850
Lake Woodruff			1269	3968	1198	118	6554

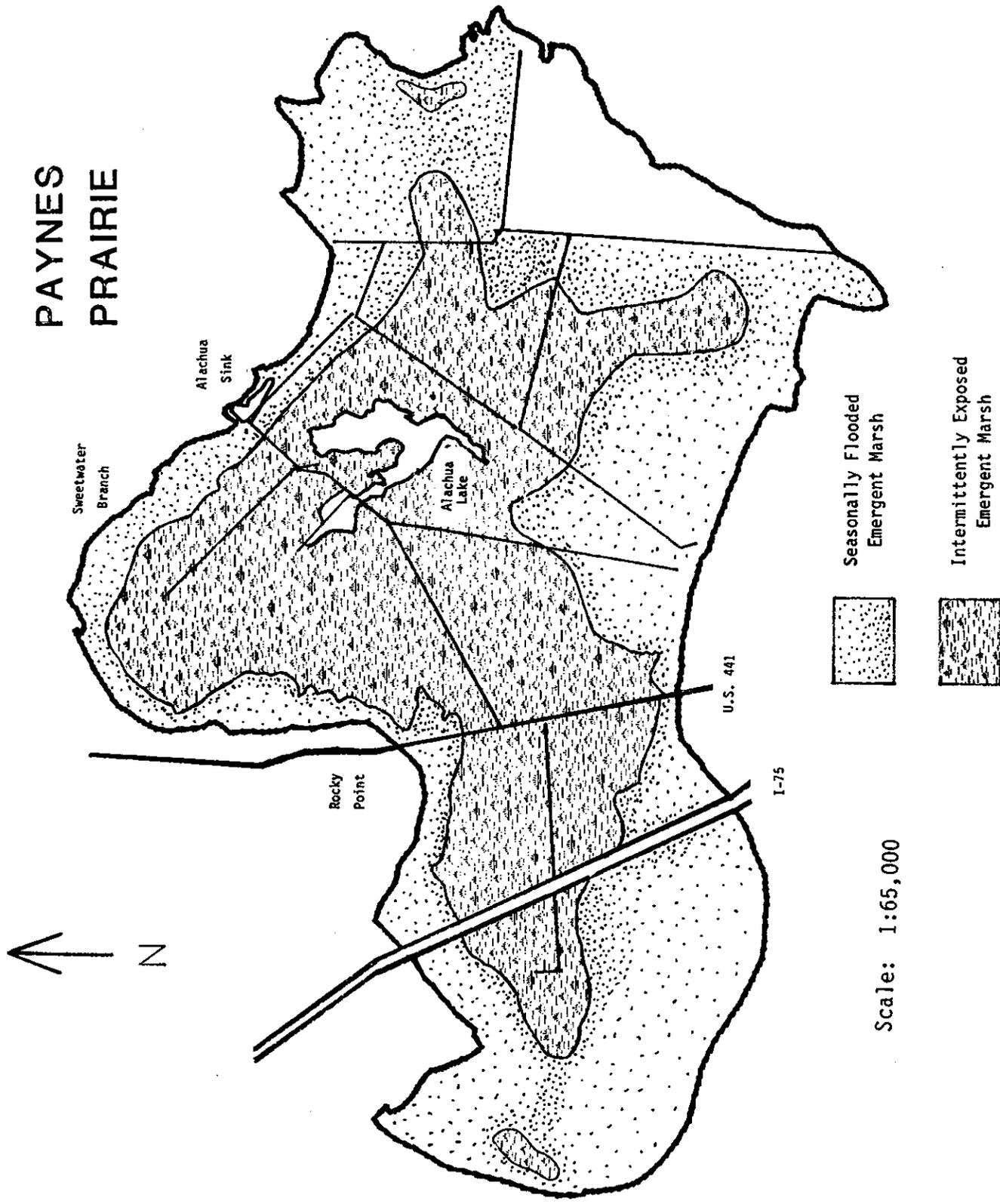


Fig. 7. Landmarks and major aquatic vegetational zones for Paynes Prairie.

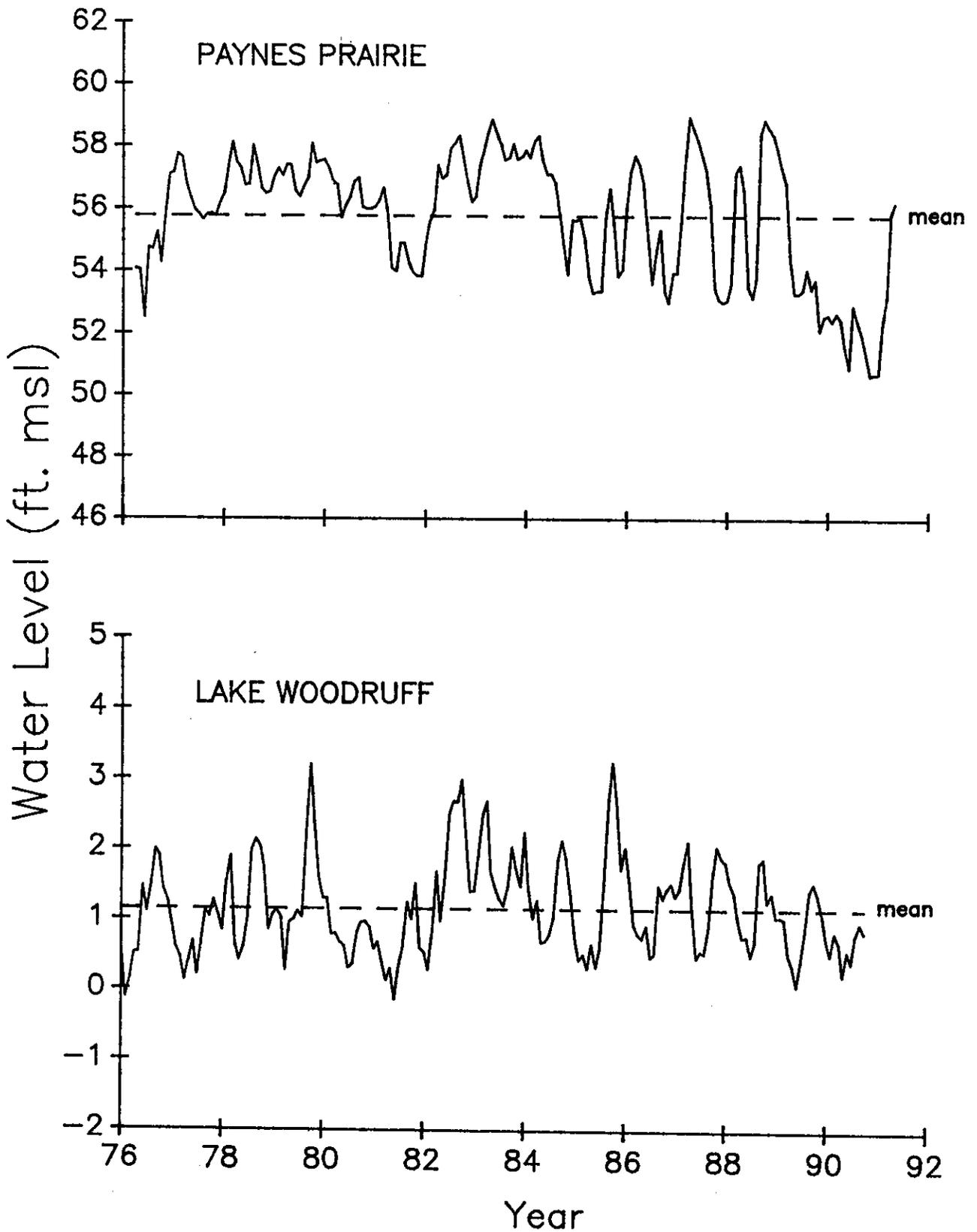


Fig. 8. Surface water levels for Paynes Prairie (Fla. Dept. Natur. Resourc., unpubl. data) and Lake Woodruff (U.S. Geol. Surv. gauge station no. 223600 at the St. Johns River near Deland)

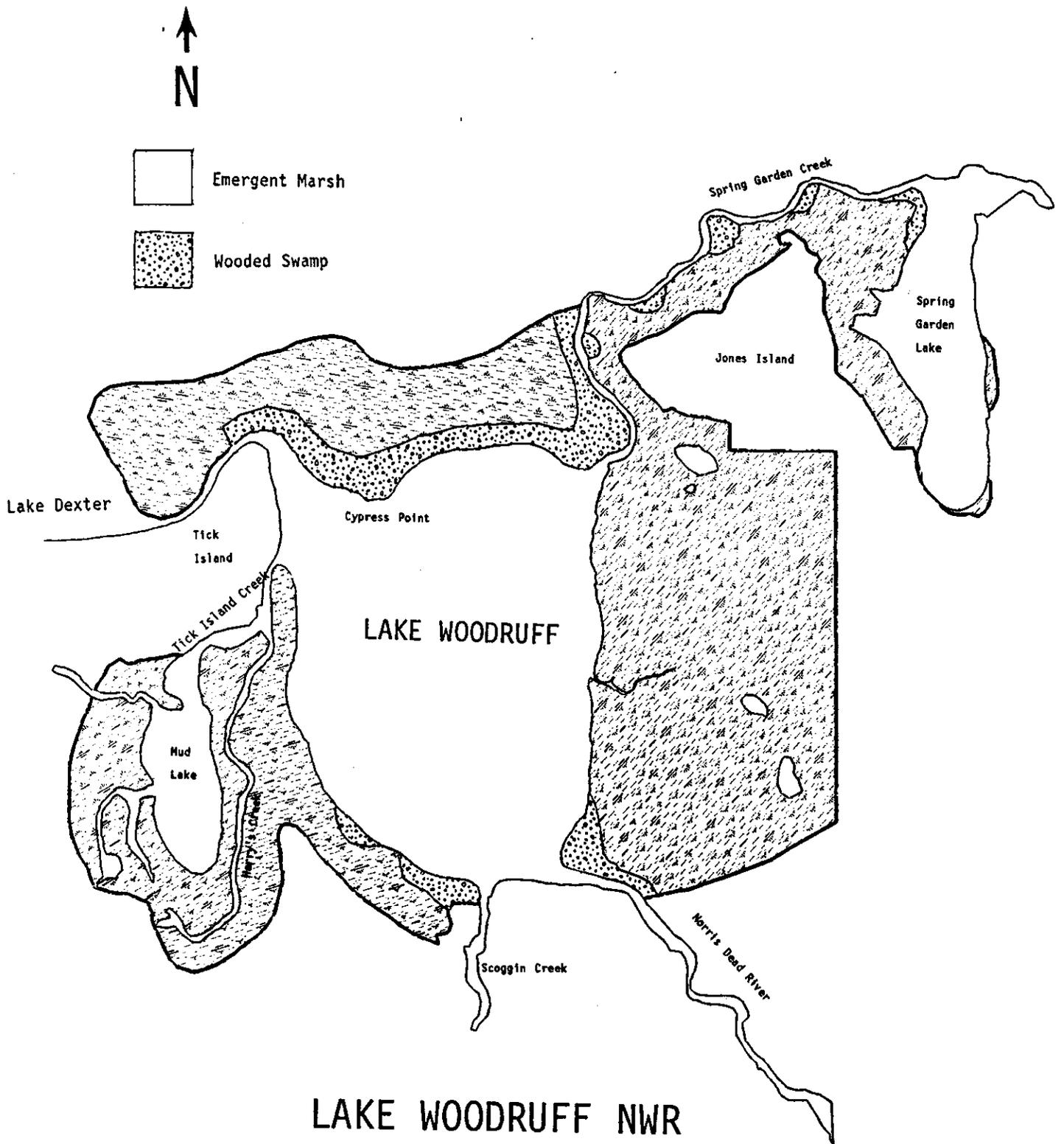


Fig. 9. Landmarks and major aquatic habitat types for Lake Woodruff National Wildlife Refuge.

(*Nymphoides aquatica*), and water hyacinths on the open water; and red maple (*Acer rubrum*), willow, sweet gum, and wax myrtle in the surrounding wooded swamps. Ninety-nine ha of marsh were impounded and primarily managed for waterfowl and wading birds.

METHODS

Terminology

Throughout our design, analysis, and reporting we found it convenient and functional to group alligators by life history attributes represented in general TL size classes. They are *hatchling* (< 30 cm), *juvenile* (< 122 cm), *subadult* (122-182 cm), *harvestable* (≥ 122 cm), *breeder* (183-273 cm), *adult* (≥ 183 cm), and *bull* (≥ 274 cm) alligators.

Quotas

An alligator population harvest model was developed in 1981 using the best available demographic data for Florida alligators (C. L. Abercrombie, pers. commun.). A critical component of the model was density dependent control of physical growth rates. Harvest areas were considered to be at equilibrium or carrying capacity (k) based on low estimated growth rates of Orange Lake alligators (C. L. Abercrombie, pers. commun.) relative to growth rates reported by Chabreck and Joanen (1979) for Louisiana. For the model, growth rate was considered greatest (rates reported for Louisiana) when population densities were $\leq k/2$ and smallest (pre-1981 growth rates for Orange Lake) at k . Different harvest strategies (varying combinations of harvest rates, size class compositions, and sex ratios) were simulated to find a regimen that would sustain maximum hide and meat production. Simulations indicated that *proportional* harvests, i.e., harvest of all size classes at equal rates (Nichols et al. 1976) of either 15% all-male or 7% both-sexes harvest could be sustained.

In determining an experimental harvest rate, we considered several conditions: (1) to detect the response of various population parameters to harvest, harvest rates had to be sufficient to significantly affect population densities, (2) except for bull alligators, hunters would not be able to distinguish males from females, and (3) hunting equipment (primarily harpoons) would probably preclude returning alligators after they were caught. For these reasons, we attempted a 15% proportional, either-sex harvest of ≥ 122 cm TL alligators. Hereafter, length will refer to TL, unless otherwise specified. Because we desired a proportional harvest of all size classes, an aggregate length (AL) quota was imposed (assuming an average TL of 195 cm) to discourage overharvest of larger alligators. Harvest levels were managed by setting maximum allowable take (quotas) of individuals and/or AL for each harvest area during 1981-87. After 1987, no AL quota was imposed. In 1981, we attempted to limit the take of adult female alligators by restricting the take of 183-259 cm alligators. After 1 restricted alligator had been taken, a hunter's quota was reduced by 1 alligator and 213 cm for each additional restricted alligator killed. After 1981, no special size restrictions were imposed. Nightly AL limits of 914 cm were imposed during 1981-87 to prevent hunters from taking more alligators than could be processed in 24 hours.

The harvest was implemented on Orange and Lochloosa from 1981-1990 and on Newnans from 1982-1990. Woodruff and Paynes Prairie were maintained as controls. Harvestable population (N_h) estimates were determined by the following equation:

$$N_h = \frac{V}{(M)(A)(C)}$$

where: V = Mean number of harvestable alligators observed during night-light surveys.
 M = Proportion of harvestable alligators observed (0.35) on survey route during average August water temperatures (31 C) (Murphy 1977).

A = Proportion of harvestable alligator population surveyed by night-light survey, based on judgements by the authors.

C = Survey conditions (as affected by wave action and visibility) expressed as a proportion (perfect conditions = 1.0), based on judgements by the authors.

For comparison, harvestable population estimates (N_c) were derived from nest counts using a modified estimator developed by Chabreck (1966):

$$N_c = \frac{C}{F P}$$

where: C = Estimated number of nests,

F = Proportion of adult female alligators in the harvested population,

P = Proportion of adult females nesting annually.

C was derived from initial nest counts adjusted for unobserved nests (K. Rice, Fla. Coop. Fish and Wildl. Res. Unit, pers. commun.). F was estimated for the mean day of the season from harvest data, and for the final day of the season from hunter success data. P was estimated from reproductive tract evaluation of harvested adult females.

Hunt Procedures

In 1981, 7 nuisance alligator agent-trappers (Hines and Woodward 1980) living within 100 km of the town of Cross Creek were invited to participate in the hunt. Seven additional hunters were selected from other applicants. From 1982-1987, 20 hunters were randomly selected from a group of 45-65 applicants who met the following minimum standards: (1) resided within a 25-km radius of a point located mid-way between the harvest lakes and Gainesville, (2) possessed the proper equipment and boats for hunting alligators, (3) owned or had access to an approved meat processing facility, (4) had not been convicted of a crocodylian-related wildlife violation within the past 7 years, (5) were ≥ 18 years of age, and (6) no other member from the same household applied. Quotas for individual hunters were determined by dividing number and AL quotas for all treatment lakes by the total number of hunters. To satisfy area quotas, individual quotas of successful hunters were sometimes increased near the end of the hunt to compensate for lower success of other hunters. After 1987, hunters were selected from a drawing of applicants for statewide alligator hunts, and quotas were limited to 15 alligators per licensee. The number of licensees was determined by dividing harvest quotas for each lake by 15. Licensees and their agents could use 1-2 boats hunting per night during 1988-89, but only 1 boat per night in 1990. Hunting was conducted from sunset to 0100 hrs during 1981-87 and from 1/2 hour before sunset to 0100 during 1988-90. Hunters registered at a GFC check station prior to and immediately after each hunting session. In 1981, the hunt on Orange and Lochloosa was scheduled for 10 consecutive days. After 1981, hunts on Newnans were interspersed with the Orange-Lochloosa hunt, and hunting was limited to Monday-Thursday to reduce wariness in alligators.

Methods of take were restricted to harpoons, snatch hooks, and archery equipment with retrievable lines. No baited set hooks or firearms were permitted. Hunters were required to kill retrieved alligators immediately with hatchets, hammers, or powerheads designed to deliver a fatal blow to the brain or sever the spinal cord. County health departments required meat intended for human consumption to meet guidelines established by the Fla. Dep. of Health and Rehabilitative Serv. (1981-87) and the Fla. Dep. of Agric. (1988-90).

Harvest Data

At check stations, alligators were positioned with their ventral side facing up and were measured along the ventral line from tip of snout to tip of tail for TL and to the posterior margin of the cloaca for

snout-vent length (SVL). Alligators were weighed (WT) with 10 kg (\pm 250 g) or 227 kg (\pm 1 kg) spring scales, sexed by cloacal probe (Chabreck 1963), inspected for previous marking tags, tagged with CITES export hide tags provided by the U.S. Fish and Wildlife Service, and tagged in the right rear foot webbing for future carcass identification. Losses of portions of the tail (bobtailed), missing limbs, and other gross injuries or deformities were noted. Tail girth (TG) at the third whorl of scales posterior to the cloaca was measured during 1985-87. On the day after alligators were killed, we visited processing facilities to remove female reproductive tracts, stomachs, and femurs from carcasses. Meat yield (MY) was reported by hunters during 1983-88. Hide length (HL) was obtained from grading reports during 1987-88.

Reproductive Tracts. -- Complete reproductive tracts, including ovaries, tube, and uterus (Palmer and Guillette 1992), were removed from a sample of \geq 67.5 cm SVL female alligators taken on harvest areas. Tracts collected during 1983-84 were frozen, and those collected during 1987-90 were fixed and stored in 10% neutral-buffered formalin (NBF). We measured several reproductive tract structures identified by Lance (1989) and Palmer and Guillette (1992) including: (1) diameter, to the nearest 0.5 mm, of the compressed uterus 2-4 cm posterior to its junction with the fiber region of the tube, (2) diameter, to nearest 1.0 mm, and number of the largest follicles, (3) diameter and number of the largest atretic follicles, and (4) number and length of corpora lutea. We subjectively evaluated the degree of muscle striation in the uterus and of general vascularity of the ovaries and uterus. Tracts with a narrow ($<$ 13 cm), non-striated uterus and granular ($<$ 3 mm diameter) follicles were considered *immature*. *Pubescent* tracts had an enlarged (13-17 cm diameter), moderately striated uterus and some larger follicles ($>$ 3 mm), but no corpora lutea (Guillette et al. 1992). We considered ovaries with old corpora lutea, indicating past ovulation, as sexually mature. *Mature* tracts generally comprised enlarged ($>$ 16 mm), striated uteri and $>$ 3 mm diameter atretic or vitellogenic follicles. Tracts with $>$ 4.5 mm corpora lutea were considered postpartum.

Femurs. -- Right rear femurs were removed from fresh alligator carcasses, cleaned, labelled, and frozen (1981-88) or preserved in 10% NBF (1989-90). A 7 mm thick transverse slab was cut from the mid-diaphysis of each femur and placed in a histological microcassette for fixing in 10% NBF. Matson's Lab (Milltown, Mont.) provided histological processing. Slabs were decalcified, dehydrated in ethanol, cleared in xylene, embedded in paraffin, and sectioned to a thickness of 6-10 μ . Sections were mounted on a glass slide, stained with Giemsa blue, and examined with bright field microscopy for bone growth zones. Fast periosteal bone apposition during the warm or growing season followed by a period of slow growth during the cool season characterizes the pattern of long bone growth in alligators (Ferguson 1982; A. Watson, unpubl. rep., 1984). When stained, slow growth appears as a dark ring and contrasts with lighter-stained fast growth zones. Variability and irregularities in crocodylian growth rings may represent environmental growth conditions within the growth period caused by temperature changes, stress, reproduction, and normal resorption and remodeling activity (Elsey and Wink 1986, Wink and Elsey 1986, Wink et al. 1987, A. Woodward, unpubl. data). We considered two rings closer together than 0.25 of the average radius between 2 rings, or 2 rings merged into 1, as 1 winter ring. In cases where we observed a wider-than-average growth zone with no discernible ring, we looked for a differentiation in the cellular pattern of cortical bone located near where a winter ring would be expected. If a transition in bone cells was observed, we assumed a winter period had occurred.

Night-Light Surveys

Night-light surveys were conducted with airboats in late August or early September on Orange, Newnans, and Lochloosa, and in early-mid June on Woodruff. Paynes Prairie was mostly inaccessible by boat and, therefore, not surveyed. At least 1 survey/yr was conducted on each area. Two surveys/yr were conducted during 1983-90 on Lochloosa, Newnans, and Woodruff, and during 1986-90 on Orange. Routes generally followed the open water-shoreline interface (Murphy 1977, Woodward and Marion 1978). Over years, expanding spatterdock stands on Orange, Lochloosa, and Woodruff increased cover

for alligators, and additional transects were established through vegetated stands to help compensate for decreased visibility. Dense marsh, wooded swamp, and other inaccessible alligator habitat was not surveyed. Searches for alligator eye reflections were conducted with an airboat at a planing speed of 20-25 km/hr, depending on water conditions. When dense groups of alligators were encountered, the airboat was slowed sufficiently to allow a thorough count. We used a 200,000 c.p. spotlight and attempted to judge size of detected alligators by approaching at normal survey speed. Otherwise, surveys were conducted as described by Woodward and Marion (1978).

To estimate alligator size, we used both the snout length:TL index described by Chabreck (1966) and a general impression of size, periodically calibrated by catching and measuring size-judged alligators. Alligators were classified in 30.48-cm (1-ft.) size classes when possible or placed into broader TL categories (0-60 cm, 61-121 cm, 122-182 cm, ≥ 122 cm, and ≥ 183 cm) when size class could not be determined but other indications of size were evident, such as bubble trails and size of splash or wake. Alligator size was classified as unknown when alligators were observed in habitat occupied by all sizes and no other indication of size was apparent.

Nest Production and Survival

To monitor nest production and success, we conducted aerial nest surveys annually during 1983-90 on Woodruff and during 1981-90 on other areas from 2-passenger, piston-engine helicopters. Nests were easily observed on all areas except Newnans where dense canopy cover hampered visibility. A 40-m altitude and 50-km/hr air speed were maintained during searches and nest checks. Except for Paynes Prairie, we searched suitable nesting habitat on all study areas along the same routes every year. The Paynes Prairie survey area was expanded in 1983 from approximately 70% to 90% of the basin. Only nests observed along the original Paynes Prairie route were used for trend analysis, whereas those counted in expanded surveys were used for nest production and population estimation. Each year during 1981-90, flights were made during 15-25 July, and nest locations were plotted on 1:800 aerial photographs. Supplemental earlier flights were made on Orange in 1980, 1981, and 1989. An early August flight was made during most years to monitor nests and provide interim seasonal survival information. A final flight was made during 2-27 September to determine nest fates. During the middle and final nest checks, we flew directly to previously sighted nests and looked for new nests only along the flight path. Nests were classified as intact (well-domed with no evidence of predation or flooding), depredated (evidence of digging, a flattened appearance, or exposed alligator eggs), partially flooded (water covering the bottom 1/2 of the nest), flooded (water covering $> 1/2$ of the nest), or false (noticeably smaller or unfinished nest observed in association with a larger, well-domed nest). Nests under dense canopy cover or recently destroyed nests covered with new vegetation frequently could not be relocated on subsequent checks; fates of these nests could not be determined. Nest status surveys for each area were completed during a 2-day period for most years. However, early in the study, smaller portions of Orange were surveyed on different days over a longer period of time, and data from the smaller surveys were considered an unbiased sample of the overall nest population.

During 1983-90, ground crews were directed by helicopter to a sample of nests to determine nest status and collect nest and clutch information. The latter included total number of eggs, number of eggs with an opaque band (Ferguson 1985, Webb et al. 1987), and viability of banded eggs (Woodward et al. 1989). In some years, we collected clutch weight and dimensions of every third or fourth egg, depending on clutch size. One representative viable egg from each clutch was retained for age determination. After clutch information was collected, eggs were returned to the nest in their original orientation and covered with nest material. Nest material was compacted to resemble pre-excavation appearance and integrity. During 1985, 1987, and 1989, 3-13 clutches were collected and artificially incubated. We noted the presence of turtle eggs during clutch surveys. In 1989, nests with collected clutches were razed during turtle egg searches.

Retained eggs were opened on the collection day or shortly thereafter, and embryo age was estimated using ontogenetic developmental stages (P. Cardeilhac, unpubl. chart, Univ. of Fla., 1985). Estimated oviposition date was calculated by backdating from embryo age. Hatch date was derived by

adding a 65-day mean estimated incubation period at 33 C (Joanen et al. 1987, G. Masson, Univ. of Fla., pers. commun.) to the estimated oviposition date.

Live Capture

Live capture efforts were begun in 1975 on Orange, Lochloosa, and Paynes Prairie; in 1976 on Newnans; and in 1981 on Woodruff. Thereafter, live recapture efforts were conducted at irregular intervals through May, 1991. Many alligators were fatally recaptured during experimental hunts on Lochloosa, Newnans, and Orange, 1981-90. Capture methods included hand, tongs (Woodward et al. 1987b), snare, or harpoon, depending on alligator size. We sampled all portions of Lochloosa, Newnans, and Woodruff, but we were not able to sample inaccessible marshes on Orange and Paynes Prairie. TL, SVL, and WT were recorded, and alligators were tagged with numbered monel web tags (Woodward et al. 1987b). An additional monel tail tag was attached to the second or third single crest whorl on some larger alligators. We used the clitorio-penis protrusion or cloacal probe method (Chabreck 1963, Joanen and McNease 1978) to determine sex of all ≥ 35 -cm alligators and of some < 35 -cm alligators.

Daylight Visibility Surveys

We conducted daylight (sunrise - 01:00 hrs) alligator visibility surveys by a 4.3 m flat-bottomed boat with an outboard motor on Newnans in pre-hunt (27 Aug - 9 Sep) and post-hunt (20 Sep - 4 Oct) periods in 1982, and in pre-hunt periods only during 1983-85. We recorded the number of alligators at 11 points along 2, 7-km transects approximately 50 m from and parallel to the shoreline. Transects were located in areas where alligators were usually seen. Observation stations were selected to minimize count overlap. Counts were made at 0 and 10 minutes following arrival at each station and during travel between stations. Water and air temperatures, wave height, and wind speed were recorded at each station.

Hide and Meat Processing

Skins (or hides) were removed from dead alligators as belly hides (Van Jaarsveldt 1987, King and Wilson 1989). Hides were scraped and cleaned (King and Wilson 1989), salted, rolled, and stored under refrigeration or in brine. Hunters inspected and re-salted hides after 1 or 2 weeks in storage. Most hides were soaked in a brine solution (David 1987, King and Wilson 1989) to extend storage life and increase pliability prior to grading. Hides were stretched by 2 men pulling at opposite ends, measured, graded for quality and size (Van Jaarsveldt 1987, King and Wilson 1989), and validated by GFC personnel for sale and export.

Hunters reported yield of boneless, defatted meat from all portions of the carcass including tail, legs, jowls, belly, ribs, and back. Sales of other products such as heads, skulls, and teeth occurred occasionally, especially during the latter years of the hunt, but were excluded from our analysis. Hides were sold by the GFC from 1981-87, and exact prices were known. Representative prices for privately sold hides from 1988-90 were estimated from hunter and trader reports. Meat prices for all years were obtained through interviews with hunters. Most hunters processed alligators and sold hides and meat at the wholesale level. However, during 1988-90, some carcasses were sold intact to intermediate buyers for processing. A small percentage of meat was consumed by the hunters and their agents. Harvest value and hunter income levels represent potential earnings at average wholesale prices rather than actual earnings. From 1981-87 the GFC retained 30% of hide sales to partially offset costs. After the experimental harvest was incorporated into the statewide harvest regulations, the GFC charged \$250 for each licensee and \$30 per hide validated.

Hunter background and satisfaction with the hunt were derived from questions posed on application forms, informal personal interviews during 1981-87, and questionnaires during 1988-89.

Analysis

General Approach. -- Our objective in almost all the analyses described below was to assess variability in diverse population measures with respect to area (AREA) and time (YEAR) factors. Depending on the measure, other factors (alligator sex or length, water level, etc.) were also considered. We often lacked data in every AREA \times YEAR sample, so although time was measured in discrete years, we usually treated YEAR as a continuous (regression) covariate. Therefore, with exceptions as noted, we analyzed population measures (or their transformations) in statistical models that investigated differences among areas, trend over time, and area differences in trend.

With few exceptions, all analyses fell into 1 of 3 types of statistical model: (1) linear factorial models with replication (replicated ANOVA), (2) linear factorial models of weighted cell means (unreplicated ANOVA), and (3) logit models. Replicated ANOVA models referred to those analyses in which the data were available as replications within each AREA \times YEAR combination. The specific form of an ANOVA model was either classical factorial ANOVA, (multiple) regression, or analysis of covariance, depending upon the mix of discrete factors ("class" variables), continuous covariates ("regression" variables), and interactions present in the model.

An unreplicated ANOVA model treated a statistic (e.g., median or regression slope) derived for a sample as the dependent variable, and its influence in the analysis was determined by a weight inversely proportional to its variance. We generally relied on unreplicated ANOVA when we could reason that sample summary statistics followed a normal distribution though replicate data within each sample did not, or when a set of unbalanced (no replicates in some samples) data would be too cumbersome to analyze in a replicated ANOVA model. We also used this type of model when only 1 data replicate was available in each sample; in this case, each observation was assigned the same weight.

Logit models (Agresti 1990) may best be thought of as ANOVA models for discrete outcome data. Chi-square analysis of an $r \times k$ contingency table is a special example of a logit model for a dependent variable with r outcomes over k levels of a factor. Some advantages of a logit model over chi-square analysis are the flexibility of considering several factors at once, the ability to include continuous covariates in the model, and the ease of testing effects and interpreting results. Like prediction of Y for values of X in regression analysis, the logit model provides predicted probabilities of membership in each outcome category at desired settings of the independent effects.

Interactions among effects were considered in each analysis. Although interactions are often unwieldy to analyze and report, they are instructive, and their presence suggests that inferences drawn from data in 1 biological system may not be applied to other systems. However, including unimportant interactions in a model detracts statistical power from testing other effects. We began each analysis by fitting a general model containing all interactions induced by the main effects or as many interactions as were biologically reasonable or interpretable. We removed interactions, from most to least complex, in successive steps of model fitting. For a set of interactions of equal complexity (e.g., all 2-way interactions), we fit all models consisting of all combinations of these interactions. We continued model reduction until the model could withstand no more simplification. This determination was made when F (replicated and unreplicated ANOVA) or G^2 (logit) for the remaining effects was large ($P < 0.05$).

Upon selection of a model in the stepwise procedure, we tested differences in means (or regression slopes, where pertinent) among levels of discrete factors in the model. For factors with no ordinal relationship among levels (e.g., AREA), we investigated all pairwise differences among levels. To protect against the increase in type I error associated with such comparisons, we declared a difference significant when P did not exceed the Bonferroni criterion of $0.05/k$, where k was the number of comparisons to be made. For factors with inherently ordered levels (e.g., size class), we tested for a significant slope among the level means. Either type of comparison could be validly performed regardless of the test outcome for the factor.

Harvest Results. -- In a sample of alligators, size and sex distributions based on TL may not reflect distributions based on SVL. Because the relative abundance of bobtailed alligators in our sample (4.2%) was not negligible, we developed an equation for prediction of TL from SVL (see *Allometric*

Relationships, below) to allow the use of bob-tailed alligators in analyses of TL, size distribution, and sex comparisons. TL distributions of harvested alligators were skewed (long-tail) toward larger alligators for most area-year combinations, thus median TL (TL_{md}) was a better central measure of size than was mean TL. We analyzed TL_{md} weighted by area-year sample size in an unreplicated ANOVA that included AREA, YEAR, and interaction effects. In another analysis, we investigated AREA, YEAR, SEX, and interaction effects in TL skewness. To facilitate trend analysis and to compensate for the design imbalance caused by absence of the 1981 Newnans data, YEAR was modelled as a continuous covariate.

To evaluate the cumulative effects of hunting on the size and sex composition of the harvest, we partitioned alligators into 3 size classes, subadults, breeders, and bulls. Because relatively few females occurred in the bull size class, we omitted this size class from the sex composition analysis. Using logit analysis, we evaluated area and year-related variation in size class and area, year, and size class effects on sex composition. We also investigated area and time differences on the proportion of adult females in the total harvest. In all analyses, we incorporated YEAR as a continuous covariate and tested all interactions induced by the main effects.

Hunter Success. -- Hunter success was evaluated for the Orange-Lochloosa hunts only. Boat-hours of hunting per licensed hunter were recorded for each night. When 2 hunters worked on the same boat, we used half the total time for each to more accurately reflect effort. We did not include time spent on non-hunting activities such as equipment repair. We estimated hunter success (mean annual nightly yield) of number (N), $TL_{\bar{z}}$, proportion of female (F), and proportion of adult female (F_{ad}) alligators taken. These quantities were further evaluated for variation due to annual trend (YEAR) or September mean water level (MWL). Number of hunters and season length varied from year to year, and we found that hunter success was influenced by hours of hunter effort (E) and day of hunt into the season (D). Within each year, we regressed each yield variable on E and D, and we predicted values of yield at mean (over years) values of E and D. Because the predicted values corresponded to fixed values of E and D, differences in yield among years were not differentiated by annual variability in E and D. Therefore, we analyzed predicted yield values in an unreplicated ANOVA with continuous YEAR and MWL covariates, and we assigned equal weight to the observations. In each analysis, we tested the size of (1) the overall mean, (2) the partial regression on YEAR, and (3) partial regression on MWL. The partial regression coefficients for E and D in the yearly analyses represented measures of hourly efficiency (yield/hr) and seasonal efficiency (yield/day) for the yield variables. We analyzed both sets of efficiency measures for each yield variable in unweighted ANOVA's similar to those performed for predicted yield.

Allometric Relationships. -- We conducted a multivariate regression analysis of associations among the morphological characteristics, TL, SVL, WT, TG, MY, and hide length (HL) (dependent variables) on independent variables AREA, YEAR, and SEX to assess variability in allometric relationships. Morphological variables of animals are frequently scaled geometrically relative to one another in the form:

$$(1) \quad Y = a X^b$$

(Peters 1983). In equation (1), Y and X are measurements of morphological characteristics, and a and b are unknown parameters that describe the shape of the relationship. Taking logarithms of both sides of equation (1) allows analysis by means of simple linear regression:

$$(2) \quad \log Y = \log a + b \log X$$

Initial plots confirmed this relationship among log-transformed morphological variables for alligators with complete tails and limbs. When 2 morphological variables were used to predict a third, we incorporated the additional variable, Z , in equation (1) by multiplying by Z^c , and in equation (2), by adding $c \log Z$. For each AREA x YEAR x SEX combination, we used linear regression (replicated ANOVA) to estimate the parameters a and b for allometric relationships between TL (Y) and SVL (X), WT and TL, WT and SVL, HL and TL, and MY and WT. We estimated parameter c in the relationship

between WT(Y), TL(X), and TG(Z). We analyzed each sample of estimated b (and c) in an unreplicated ANOVA model with main effects AREA and SEX, the continuous covariate YEAR, and all interactions among effects and the covariate. We weighted b and c by corresponding elements from the diagonal of the "cross products" matrix. These quantities, provided by the linear regression procedure, were related to the number of data parameters (X , Y) in the regression and to the width of the range of X . The analysis provided tests of area and sex differences in means and trends of the allometric parameters.

Population trends. -- For trend analysis, we assumed the size distribution of unknown-size alligators was consistent with the distribution of known-size alligators and apportioned them accordingly in 4 TL classes (≥ 30 cm, 30-121 cm, harvestable, and adult) for analyses (see Woodward and Moore 1990). Neonatal (< 30 cm) alligators on Lochloosa, Newnans, and Orange were excluded from analyses because of their aggregated distribution and lack of independent observability (Woodward and Marion 1978). We considered hatchlings (approx. 9 months old) from June surveys on Woodruff to be sufficiently dispersed and included them in analyses.

We conducted a replicated ANOVA on log-transformed counts of harvestable and adult alligators with main effect AREA, covariates YEAR and deviation from MWL (DMWL), and the AREA \times YEAR, YEAR \times DMWL, AREA \times DMWL, and AREA \times DMWL \times YEAR interactions. Within areas, we tested for trend in count densities by regressing log-transformed counts of alligators in each general size class on YEAR, and adjustment covariates, MWL and proportion coverage by hydrilla. For comparing the 1-covariate model for Woodruff with the 2-covariate model for other areas, we reported adjusted R^2 (Rawlings 1988) which allows valid goodness-of-fit comparisons among regression models having different numbers of parameters.

To test for evidence of wariness in adult alligators, we used the "signed" Durbin-Watson statistic for detecting negative correlation (Draper and Smith 1981) in water level adjusted count densities. We tested the mean Durbin-Watson value from harvested area vs that of the control area.

Nest Production and Survival. -- Nest densities were estimated for all areas except Newnans by adjusting initial aerial nest counts for the proportion of unobserved nests during helicopter surveys (K. Rice, pers. commun.). For Newnans, nest production estimates were calculated by combining nests observed from aerial and ground searches with hatchling pods found that were not associated with observed nests. We assumed a 50% predation rate on unobserved nests on Newnans. For nest density estimation, we considered all emergent marsh and wooded swamp associated with study areas as potential nesting habitat.

We did not include Paynes Prairie in survival analyses because not all nests were checked during all years. We excluded from survival analyses nests with uncertain fates. However, our inability to relocate nests was assumed to be due to visual obstruction rather than nest fate, and we assumed the success rate of uncertain nests were equal to known-fate nests. Nests from which clutches were removed for artificial incubation were also excluded from subsequent analyses.

We evaluated nest production trends in an unreplicated ANOVA on square root of annual nest count (unweighted) with respect to an AREA factor, YEAR, fall MWL, spring MWL covariates and 2-way interactions with AREA as independent variables. Specific months chosen to represent fall and spring MWL were selected through regressing transformed count on YEAR and each of all possible combinations of 2 mean fall monthly water levels (Sep and Oct) with 4 mean spring monthly water levels (Mar, Apr, May, and Jun) for each area (8 combinations/area). We selected the best fall-spring single month combination as the combination resulting in the greatest average R^2 rank over all years. We tested the hypothesis that nest production may respond to spring water level in a curvilinear fashion (production levels increased to a maximum at flood stage, then declined at higher water levels) by including the squared value of spring MWL as a third water level covariate in the ANOVA.

For all nests with known fates, we analyzed relative probabilities of nest success (predation and flooding) using logit analysis. Our model included an AREA effect, YEAR and Jun-Aug MWL covariates, and interactions with AREA.

Survival of nests was evaluated for Orange on the basis of proportion of nests surviving at varying time intervals (DAY) after 1 June, the assumed earliest possible oviposition date. Flooded or uncertain fate nests, or nests from which clutches were removed, were omitted from the analysis. Most years had 3 survival observations (range = 2-8). Data from 1986 (obs. = 2) were deleted. We had only 1 year (1989) with a June observation during the study years 1981-90, so we added the 1980 nesting year to provided a supplementary June observation. The proportion of surviving nests during each aerial nest survey was regressed on DAY and DAY². We had no reason to believe that rate of nest loss would be constant among years, but we recognized that, because of the small within-year sample size, detecting a YEAR × DAY interaction would be unlikely. Therefore, we analyzed data on a yearly basis. We hypothesized that a negative coefficient estimate for DAY² would model nest predation occurring in late incubation, and a positive estimate would indicate predation occurring mostly early in incubation. We used the sign test (Steel and Torrie 1980) to determine positive or negative tendency of annual DAY² effects.

Fecundity. -- Shapes of clutch size distributions for undisturbed nests varied among areas sampled for clutch characteristics (Orange, Paynes Prairie, Woodruff), and no single transformation could eliminate skewness sufficiently for a common parametric analysis. We elected to analyze medians and skewness coefficients for each area-year combination, weighted by sample size, in an unreplicated ANOVA with an AREA main effect, a YEAR covariate, and their interaction.

Because opaque banding and viability rate data exhibit both extreme skew (between 0 and 100%) and truncation (at 0 and 100%) (Woodward et al. 1992), we conducted 2 analyses on different portions of the data to investigate variability due to an AREA main effect, a YEAR covariate, and their interaction. First, we used all data for undisturbed nests and examined the probability of complete (100%) relative to incomplete (<100%) banding success in a logit analysis. Second, we ranked the incomplete banding success data from smallest to largest. We converted the ranks to proportions by dividing each rank by the total sample size, then we analyzed the proportions in a replicated ANOVA. Analysis of viability rate data from high and dry undisturbed nests proceeded similarly to the analysis of banding rate ranks. However, we analyzed all values of viability rate in this manner because data at 0 and 100% viability rate comprised a small part (12%) of the sample.

Oviposition dates were derived from clutch inspections after 15 July except for 11 July 1984 (Woodruff), 9 July 1985 (Orange), and 11 July 1985 (Paynes Prairie). Oviposition dates for area-year combinations showed no evidence of skewness, so we concluded they were normally distributed. We analyzed mean oviposition dates in an ANOVA with main effect AREA, covariate YEAR, and their interaction.

For sampled female reproductive tracts, we evaluated the relationship of size (SVL) to maturity status (immature, pubescent, or mature) by logit analysis in a model with main effects, AREA and general time period (1983-84, 1987-88, 1989-90), the covariate SVL, and interactions among these effects. We used the same model and analysis to evaluate reproductive status (non-productive or postpartum) of mature alligators. For Orange, on which sample data existed for each year, we further investigated the effects of September MWL and E on the postpartum/mature female relationship.

Growth Rates. -- Measurements of SVL during tagging, recapture, and harvest operations were assigned to 2 databases depending on the alligator's capture history. If an alligator's hatch year could be confidently determined, SVL and date recorded at its last capture event were placed in a known-age last-capture (KALC) database. Using 1 capture event of each alligator for growth modelling purposes eliminated the possibility of autocorrelation between successive observations (White and Brisbin 1980), and selection of the last event provided the most information on size at advanced age for rarely-captured old animals. We assumed that all alligators hatched 23 Aug, the earliest capture date of any hatchling. We determined age (*t*, yr) and Julian date (*J*), the number of days since the most recent 23 Aug birthday.

Date and SVL measurement at both capture events of an animal caught and later recaptured or harvested were recorded in a multiple-capture (MC) database. Because size increments obtained between several successive captures of the same individual were less likely to be autocorrelated than sizes

themselves (White and Brisbin 1980), additional data from animals captured >2 times were included. As before, we calculated J at both captures.

Each alligator was assigned the sex value recorded at its last capture, and we assumed the alligator was hatched and remained in the study area where it was last captured. We classified alligator gender as indeterminate when we either could not distinguish the animal's sex or did not attempt to determine sex of a hatchling.

Growth curves were first adjusted for seasonal variability by calculating from J a growing age (t_g) in the KALC database and a growing interval (i_g) in the MC database (Appendix A.1).

Adaptations of the power and Richards growth models of $\log(\text{SVL})$ were fit to t_g values in the KALC database (Appendix A.2) by area and sex. For values in the MC database, we calculated an empirical growth rate from SVL at successive captures and i_g . The empirical growth rate was related to mean SVL between captures in reparameterized versions of the power and Richards models (Appendix A.3). We then adapted Kirkwood's (1983) methodology for simultaneous estimation of growth parameters shared by the KALC and MC forms of each growth model (Appendix A.4). We chose either the power or Richards model as the best model for these data based on weighted R^2 values (Appendix A.5). For the chosen growth model, we then tested for AREA, SEX, and AREA \times SEX differences in each of the estimated parameters via an unreplicated ANOVA (Appendix A.6).

Growth Rate Trends. -- To test for trends in growth rates we used 2 approaches; analysis of SVL growth between successive captures and evaluation of femur growth rings. For mark-recapture data, we used the power growth model:

$$\log(Y/D) = a + b \log(X)$$

where $Y = \log(\text{SVL}_R/\text{SVL}_C) = \log(\text{recapture size} / \text{capture size})$, $D = \text{time interval between captures}$, $X = (\text{SVL}_R + \text{SVL}_C)/2 = \text{mean capture size}$, and a and b are the power model parameters. Because of the paucity of recapture data on Lochloosa and Newnans, we used only Orange data. To further simplify analyses, we used only recapture records for animals caught during Sep-Nov in intervals of ≥ 1 year. Recapture data occurring outside the harvest period 1981-90 were excluded. We approximated D by calculating the whole number of years between successive captures (INT). For each sex, we built a replicated ANOVA model for $\log(Y)$ with the main effect INT, covariates $\log(X)$ and recapture year, and interactions involving INT. This model fit $\log(Y)$ to a multiple regression on $\log(X)$ and YEAR for each level of INT. We then tested the size of each trend coefficient and the mean of the trend. Because data were sparse for intervals ≥ 2 years, we also combined those years and tested for mean trend.

For growth rate analysis from growth ring in femurs, we compared the relationship of mean SVL at given ages (as indexed by number of bone growth rings) over years. To ensure that changes in growth rate did not affect medullary bone erosion rates (and, therefore, the number of rings counted), we first regressed rings on SVL and age for known-age alligators. If we found no SVL effect, we assumed no variation in medullary erosion rates resulting from growth rate variation.

The relationship between age and rings changes as alligators sexually mature (A. Woodward, unpubl. data). We, therefore, limited our data set to alligators <100 cm SVL (194 cm TL). For known-age alligators with 5-12 rings, the relationship between age and rings was proportional but the number of rings counted declined relative to age. Because of this proportionality, SVL could be homogenous within each level of ring count unless harvest year affected the outcome. We used an ANOVA model for SVL containing a ring COUNT effect, a harvest YEAR covariate, and the COUNT \times YEAR interaction. The interaction allowed the time trend to vary by age. We tested for harvest year trends for each ring count class, and the mean of all ring classes (5-13) and for ring classes 6-10 for females and 6-9 for males. Transformations of the data were not necessary.

Sex Ratios. -- We examined the extent and probability of incorrect sex classifications during capture activities by reviewing all instances of sex classification changes on individual alligators. From a plot of these data, we observed that, for ≥ 60 cm-SVL alligators, classification changes were negligible. We

then assumed that all alligators ≥ 60 cm-SVL were correctly sexed and analyzed sex change information in a logit analysis with the model:

$$P_{\log} = \text{SEX SIZE TIME SEX} \times \text{SIZE SEX} \times \text{TIME SEX} \times \text{SIZE} \times \text{TIME},$$

where:
$$P_{\log} = \frac{P(\text{wrong})}{1 - P(\text{wrong})}$$

and TIME = 2 time classification periods; 1982 and thereafter, and prior to 1982.

We used a logit analysis of the dependent variable, SEX RATIO (male:female) with the following independent variables, AREA (Lochloosa, Newnans, Orange, Paynes Prairie, and Woodruff), and SIZE (0-60, 61-121, 122-182, and 183-273 cm TL) to evaluate variability in sex ratio.

POPULATION ESTIMATES AND HARVEST QUOTAS

Mean estimated population size of harvestable alligators was 422 (0.120/ha) for Lochloosa, 436 (0.147/ha) for Newnans, 1794 (0.341/ha) for Orange, and 669 (0.102/ha) for Woodruff during 1981-90 (Appendix B). Except for Newnans, estimates derived from our night-light survey population estimation model (N_n) were substantially less than nest count-based estimates (N_c) when proportion of adult females in the populations was derived from the mean day of the hunting season (Table 3). N_c more closely approximated N_n when the proportion of adult females in the population was estimated from the last day of the hunting season, but N_c still substantially exceeded N_n for Orange (Table 3). Harvestable alligators comprised 44% of the of observed alligators on Lochloosa, Newnans, Orange, and Woodruff and ranged from 34% (Orange) to 60% (Newnans) (Appendix B). The mean number of harvestable alligators per nest for areas with complete nest surveys and night counts ranged from 11.0 on Woodruff to 27.6 on Lochloosa (Table 3).

Crocodylian population size has been estimated from mark-recapture (or resight) methods (Murphy 1977, Taylor 1984, Bayliss et al. 1986, Brandt 1989, Hutton and Woodhouse 1989) and nest counts (Chabreck 1966, Taylor and Neal 1984). Mark-recapture estimates are usually related to night-light or aerial counts so that surveys can be converted to population estimates (Murphy 1977, Taylor 1984, Bayliss et al. 1986, Brandt 1989, Hutton and Woodhouse 1989). Night counts are either not feasible or yield underrepresentative counts in dense marshes or wooded swamp because vegetation obstructs visibility and accessibility (Woodward and Marion 1978, Taylor 1984). Alligator wariness may also influence the proportion of alligators sighted, especially on areas where alligators are hunted with boats and spotlights. Wariness in crocodylians is difficult to quantify, but Woodward and Marion (1978) found evidence of increased wariness over time on intensively-surveyed Newnans Lake. Wariness of *Crocodylus porosus* in Australia was attributed to harassment with boats and lights (Webb and Messel 1979, Bayliss et al. 1986).

Similarly, extrapolation of population size from nest counts (use of nest counts as a basis for population estimation) has several drawbacks, foremost of which is the uncertainty of the relationship between nest numbers and population size (Chabreck 1966, Taylor and Neal 1984). Furthermore, under constant adult female density, nest counts may vary with environmental conditions, especially water level (Joanen and McNease 1989, Taylor and Neal 1984) or extent of tree canopy in nesting areas (Chabreck 1966, Jennings et al. 1988). Unlike nest counts, night counts are a direct count of the population and rely less upon inferences about population structure.

We based population estimates on night-light counts because of the uncertain relationship between nests and harvestable alligators. We attempted to reduce annual variation in our population estimates by conducting night-light counts under conditions of low wave action during August when annual water temperatures were relatively stable (Woodward and Marion 1978). However, water availability in the marshes on Lochloosa, Orange, and Woodruff probably affected counts most greatly and was the most

difficult factor to accurately measure (see Night-Light Counts below). We also found that hydrilla coverage significantly affected alligator observability on Orange and Newnans (see POPULATION TRENDS below). We were not able to quantitatively account for variation due to water level and hydrilla coverage until the end of the study but had to assess their effects on counts when establishing quotas. Population estimates derived from night-light counts were direct counts, adjusted for proportion of submerged alligators (Murphy 1977), proportion of population sampled (A), and survey conditions (C), as judged by staff biologists. The combined adjustments for A and C resulted in expanded estimates of 34% on Lochloosa, 19% on Newnans, 57% on Orange, and 29% on Woodruff. In mark-resight studies (A. Woodward, unpubl. data), the estimated size of the harvestable alligator population on Orange in 1991 was 1749, close to the averages estimated from night-light counts ($N_n = 1794$) but substantially less than from nest counts ($N_c = 2588-2917$; Table 3). However, on Woodruff, the population estimate of harvestable alligators ($N_n = 669$) was substantially less than the 1991 mark-resight (1062) and nest estimate ($N_c = 2099$), suggesting that we underestimated the population.

Quota management relies upon accurate population estimates. Our estimates from night-light counts were variable on Orange, but over the long-term, and despite subjective adjustments for survey conditions and proportion of population surveyed, they concurred with mark-resight estimates. Greater estimates from nest counts on Orange may represent inaccurate estimates of adult and postpartum females in the population or underestimation of the population by our night-light count estimator. Greater nest count estimates for Woodruff probably resulted from underestimation of the proportion of alligators in inaccessible canals and impoundments. Greater than average alligators/nest on Lochloosa may reflect a combination of limited, stable nesting habitat but good subadult habitat.

HARVEST RESULTS

Attainment of Quotas

Mean annual quotas ranged from 64 on Newnans to 283 on Orange (Appendix C). Mean take of alligators per year ranged from 46 on Newnans to 236 on Orange (Appendix C). Mean proportions of estimated harvestable population taken/year ranged from 11.3% on Newnans to 13.5% on Orange and averaged 13.0% for all harvest areas (Appendix C). The proportion of the harvestable population aggregate length (AL) taken/year ranged from 12.8% on Lochloosa to 13.8% on Newnans with a mean of 13.4% for all harvest areas (Appendix C). The percentage of males in the harvest ranged from 64.6% on Orange to 74.0% on Newnans and averaged 69.9% for all harvest lakes (Appendix C). Harvest rates fell somewhat short of targets. We credit this to the relatively short season length, elevated wariness of alligators from intensive hunting, and a tendency for hunters to select for, but fail to take, larger, more elusive alligators.

Size Distribution

In all analyses of size distribution except TL skewness, we detected AREA \times YEAR interactions, an indication that a size distribution trend on an area could not be generalized to other areas. Alternatively, comparison of size distribution of harvested alligators among areas depended on whether the comparison was to be made in early, middle, or late phase of the hunt. In general, we observed that size characteristics of harvested alligators became more homogeneous among areas through time.

TL_{md} declined ($P = 0.001$) 7.00 cm/yr for all areas, but the rate of decline was greater ($P = 0.016$) on Newnans (12.26 cm/yr) than on Orange (2.27 cm/yr). TL_{md} for the mean year of the study (1985.5) was greater ($P < 0.001$) on Newnans than on either Orange or Lochloosa (Table 4).

TL distribution of harvested alligators was skewed (0.59) toward larger alligators on all areas (Fig. 10). Evidence for AREA \times YEAR interaction was not strong ($P = 0.055$), so skewness means were comparable among areas in any time period. Mean skewness was greater on both Orange and Lochloosa than on Newnans ($P \leq 0.007$), was greater among males than females ($P = 0.030$), and

Table 3. Mean estimated alligator nest production, population size estimates from night-light surveys (N_n), and estimated alligator per nest for 5 Florida wetlands, 1981-90. Population estimates from nest counts (N_c) were based on the Chabreck (1966) estimator (see Methods) using \bar{x} nests in the numerator divided by the product of % adult females (% ad F) and % adult females nesting. Estimates were calculated for mean estimated % adult females at the mean day ($D_{\bar{x}}=9$) and the last day (D_{last}) of hunt seasons.

Study area	\bar{x} est nests ^a	D_n	N_n / nest	% ad F		F nesting	N_c	
				mid	last		$D_{\bar{x}}$	D_{last}
Lochloosa Lake	15.3	422	27.6	12.3	15.9	23.9	519	401
Newnans Lake	2.8 ^b	436	155.7	16.0		10.5	166 ^b	
Orange Lake	111.4	1794	16.1	15.3	17.3	25.0	2917	2588
Paynes Prairie	130.0			14.5 ^c		19.9 ^c	4512	
Lake Woodruff	60.5	669	11.0	14.5 ^c		19.9 ^c	2099	

^aInitial number of nests counted adjusted for observability of 0.7667 (K. Rice, Fla. Coop. Fish and Wildl. Res. Unit pers. commun.).

^bBiased low because of incomplete nest surveys.

^cDerived from mean of Lochloosa, Newnans, and Orange means.

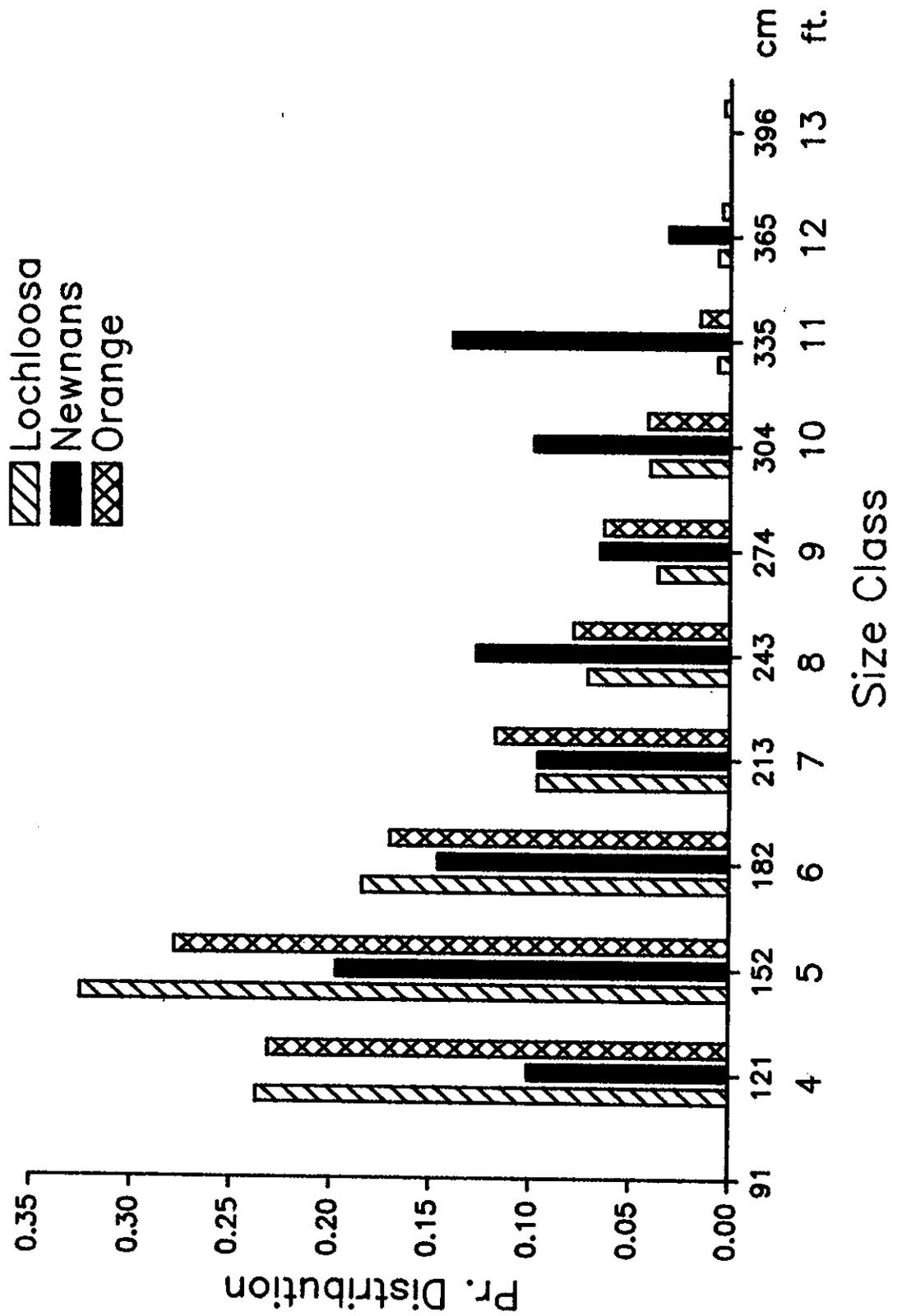


Fig. 10. Size distributions of harvested alligators in 30.5-cm (1.0-ft.) TL classes for Lochloosa, Newnans, and Orange lakes during 1981-90.

increased during 1981-1990 ($P = 0.001$). Therefore, smaller alligators constituted an increasingly greater proportion of the harvest on all areas during the study, but a greater proportion of larger alligators persisted in Newnans harvests relative to Orange and Lochloosa harvests.

We found differences ($P < 0.001$) in size distribution among harvest areas and over years. Over years, the proportion of subadults increased relative to adults on all areas, but the estimated rate of change varied among areas ($P \leq 0.001$, Fig. 11). The rate was greatest on Newnans, where the estimated proportion of subadults increased from 0.086 in 1982 to 0.595 in 1990 (Fig. 11). At year value 1985.5, subadults comprised a smaller proportion of the harvest on Newnans than on either Orange or Lochloosa ($P \leq 0.001$ Table 4). By 1990, the proportion of subadults harvested was similar on all 3 areas ($P \geq 0.067$ Fig. 11). The proportion of bull alligators harvested decreased with time relative to smaller (≤ 274 cm) alligators, but the estimated rate of decrease varied by area ($P \leq 0.001$, Fig. 11). The decrease was more rapid on both Newnans and Lochloosa than on Orange ($P \leq 0.004$, Fig. 11). The estimated ratios of bull to smaller alligators varied by area at year value 1985.5 ($P \leq 0.005$, Table 4) but were indistinguishable on Lochloosa and Orange in 1981 ($P = 0.309$) and on Newnans and Orange in 1990 ($P = 0.345$) (Fig. 11).

Table 4. Median total length (TL_{md}) and size distribution of harvested alligators on 3 lakes in Florida, 1981-1990. Because annual rates of change in TL_{md} and size distribution varied among areas, estimates are based on \bar{x} year 1985.5.

Study area	TL_{md}	% size distribution (cm)			% females	% adult females
		122-183	183-274	≥ 274		
Lochloosa Lake	181.2 ^a	54.6 ^a	37.1	8.3 ^a	32.0 ^a	12.3 ^a
Newnan's Lake	237.5	24.0	41.8	34.2 ^b	37.9 ^{ab}	16.0 ^a
Orange Lake	184.2 ^a	50.8 ^a	36.2	13.0 ^c	40.5 ^b	15.3 ^a

^{a,b,c} Values among lakes with same letters are not different at Bonferroni-adjusted P -values of 0.0056 for model with AREA x YEAR interaction (TL_{md} , % size distribution, and % female composition) and 0.0167 for models lacking AREA x YEAR interaction (% adult female composition).

Size distributions of harvests on Lochloosa and Orange conformed relatively well to night-light survey distributions, especially when general size classes were compared (Table 5). The harvest:night-light survey size distribution ratio on Newnans (3.1:1) suggested a disproportionately greater harvest of bull alligators relative to subadults (Table 5).

Harvest models by Nichols et al. (1976), Taylor and Neal (1984), Taylor et al. (1991), and C. L. Abercrombie (pers. commun.) indicated that harvest yields for either-sex hunts could be economically maximized by proportional harvests. Disproportionately greater harvest of adult alligators (*differential*) reduced yields at all harvest rates, primarily because of a reduced overall reproductive effort resulting from "overharvest" of adult animals (Nichols et al. 1976). The models lacked direct density-dependent control on fecundity, although the density-dependent growth rate function in Abercrombie's model would have decreased generation time for females at lower densities and thereby increased fecundity. Lower harvest yields for differential harvests also reflected the slower growth of adult alligators relative to subadults. It is important to note that Nichols et al. (1976) considered only hide values but based his model on area of hides rather than length. Taylor and Neal (1984) and C. L. Abercrombie (pers.

Table 5. Size distributions of ≥ 122 cm alligators from night-light surveys (s^a) and harvests (h^b) on 3 Florida lakes. Ratios (h/s) provide a measure of the departure from equality (Ratio = 1) of size proportions.

Size class		Study area								
		Lochloosa		Newnans		Orange				
cm	ft	s	h	Ratio	s	h	Ratio	s	h	Ratio
122-151	4	0.291	0.237	0.81	0.305	0.101	0.33	0.284	0.230	0.81
152-182	5	0.235	0.325	1.38	0.223	0.197	0.88	0.171	0.278	1.62
183-212	6	0.177	0.184	1.04	0.234	0.146	0.63	0.202	0.170	0.84
213-243	7	0.098	0.096	.98	0.172	0.096	1.34	0.140	0.117	0.84
244-273	8	0.066	0.071	1.08	0.060	0.127	2.12	0.086	0.078	0.91
274-304	9	0.066	0.036	.54	0.021	0.065	3.02	0.053	0.064	1.19
305-334	10	0.051	0.040	.77	0.054	0.098	1.82	0.038	0.041	1.09
335-365	11	0.008	0.006	.72	0.021	0.139	6.56	0.022	0.015	0.67
≥ 365	≥ 12	0.008	0.006	.72	0.010	0.031	3.21	0.003	0.007	2.07
122-182	4-5	0.526	0.562	1.07	0.528	0.297	0.56	0.456	0.508	1.12
183-273	6-8	0.341	0.351	1.03	0.366	0.369	1.01	0.428	0.365	0.85
≥ 274	≥ 9	0.133	0.086	0.65	0.106	0.333	3.13	0.117	0.127	1.09

^aBased on surveys conducted in 1990 during drought conditions.

^bBased on total 1981-90 size distribution.

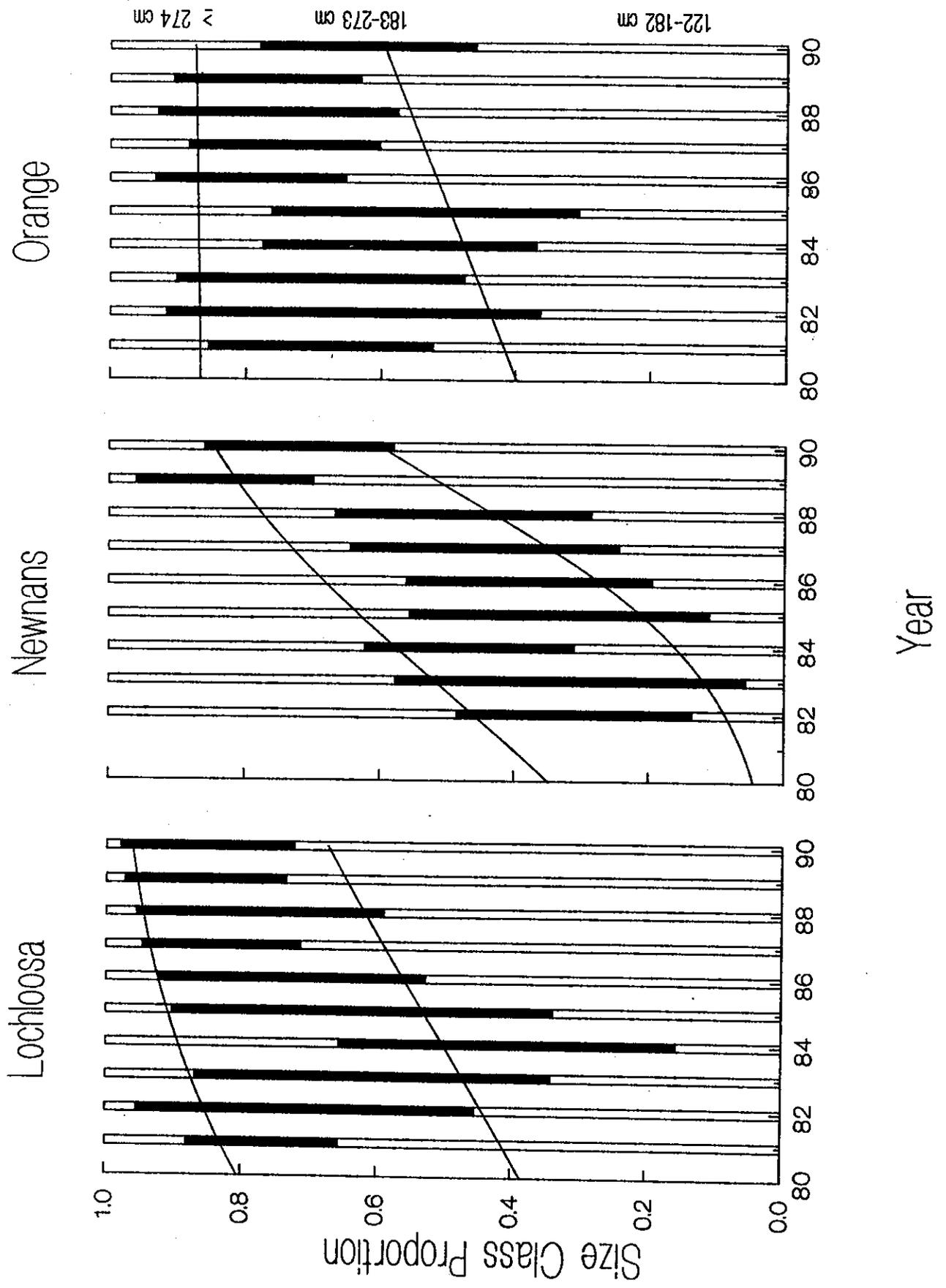


Fig. 11. Harvest proportions and estimated trends of 3 major size classes (122-182, 183-273, and ≥ 274 cm) of alligators on harvest lakes during 1981-90.

commun.) assumed equal values/linear increment for hides of different size, and only the Abercrombie model incorporated meat values. Meat constituted 38% of the value of alligators and, during the latter part of our experiment, hide values for larger alligators brought greater per-foot prices, reflecting the geometrically increasing yield in leather surface area with increasing length. Therefore, all 3 models failed to completely reflect the proportionally greater economic value of larger alligators that developed during the 1980's. However, the evaluation by Nichols et al. (1976) probably provided the best indication of response to various harvest regimes.

In the Abercrombie model, response of harvest yields to differing harvest distributions was similar. These models implied that if adult alligators are harvested in disproportionately greater numbers, harvest rates must be reduced accordingly to sustain yields. We were able to control harvest proportions through enforcing the AL limit during 1981-87 and maintaining a short season length during 1988-1990.

Sex Distribution

Over all areas, there was no trend in female:male sex ratio in the harvest (proportionate annual change = 0.023/yr, not different from 0.0, $P = 0.239$), but we found weak evidence ($P = 0.064$) that trends varied by area. Specifically, the proportion of females increased on Orange (0.076/yr proportionate change, $P < 0.001$) but remained relatively stable on Newnans ($P = 0.509$) and Lochloosa ($P = 0.438$) (Fig. 12). Estimated proportions of females were comparable among areas in 1981, but over years, the proportion on Orange departed from the proportion on Lochloosa at the mid-point ($P = 0.001$) and at the end of the hunt ($P = 0.003$, Fig. 12). The proportion of females on Newnans (0.379) did not differ from Orange (0.405, $P = 0.411$) or Lochloosa (0.320, $P = 0.133$) for the mean year, 1985.5 (Table 4).

Because the size class effect did not interact with any other effect, sex ratio differences among areas and sex ratio trends over time were equivalent for both subadult and adult females (Fig. 12). In any area at any time, we estimated a greater proportion of females in the breeder size class than in the subadult size class ($P = 0.046$). Slower post-adult growth of females relative to males can result in an accumulation of females in the breeder size class.

The proportion of adult females taken in the total harvest did not differ among areas ($P = 0.104$; Table 4) or change linearly with time ($P = 0.963$). However, we detected unexplained non-linear yearly fluctuations (Fig. 13).

Joanen and McNease (1987a) reported that average size and sex composition of 1972-83 Louisiana alligator harvests remained relatively constant over years. Our data indicate a shift of the harvest composition over years towards smaller alligators and subadult females, although the rate of this shift was not consistent among areas. We suspect that our findings have resulted more from increased boat accessibility to females due to declining water levels than from increases in female abundance.

HUNTER SUCCESS

The number of hunt nights per season varied between 7 (1984 and 1985) and 12 (1989) nights ($\bar{x} = 9.1$ nights). Season length was variable because of the experimental nature of the study and spanned 13 (1981) to 23 (1989) days ($\bar{x} = 18.5$ days). The average season half-way point was 9.3 days. The number of participating hunters ranged from 14-35 depending on quotas. Therefore, hunter effort varied yearly. Annual mean nightly hunter effort varied between 48.5 (1981) and 113.2 (1989) hr ($\bar{x} = 80.4$ hr). We calculated predicted annual yield values for N , $TL_{\bar{x}}$, F , and F_{ad} at standard values of 80 hr hunting effort and 9 days from the season start.

Number Taken

The mean 1981-90 harvest success in number of alligators taken/night, adjusted for effort and night, was 33.4 alligators and decreased during the study ($P = 0.033$, Table 6). Water level did not

Table 6. Multiple regression results of rates (mean, hourly, and daily) of alligator harvest (numbers, TL, % female of total harvest, and % female of adult harvest) on year and mean water level (quantity/m) for hunters on Orange and Lochloosa lakes, 1981-90.

Harvest quantity	<i>n</i>	Multiple regression				
		Parameter	Estimate	SE	<i>P</i>	<i>r</i>
Mean Number	10	Mean	33.4	2.99	<0.001	
		Year	-3.16	1.20	0.033	-0.707
		Water Level	-10.5	7.82	0.233	-0.451
Number/hr	9 ^a	Mean	0.553	0.0773	<0.001	
		Year	-0.0597	0.0298	0.092	-0.633
		Water Level	-0.0205	0.195	0.919	-0.043
Number/day	10	Mean	-0.454	0.181	0.040	
		Year	0.202	0.0723	0.027	0.726
		Water Level	0.381	0.472	0.446	0.292
TL \bar{x} (cm)	10	Mean	199	4.88	<0.001	
		Year	-0.716	1.95	0.724	-0.137
		Water Level	3.82	12.7	0.773	0.113
TL (cm)/hr	10	Mean	0.175	0.120	0.190	
		Year	-0.0406	0.0481	0.427	-0.303
		Water Level	0.0248	0.315	0.939	0.030
TL (cm)/day	10	Mean	-1.44	0.156	<0.001	
		Year	0.292	0.0624	0.002	0.870
		Water Level	1.54	0.408	0.007	0.819
Mean % <i>F</i> (All)	10	Mean	32.9	3.36	<0.001	
		Year	3.91	1.34	0.023	0.740
		Water Level	11.9	8.78	0.216	0.457
% <i>F</i> (All)/hr	10	Mean	0.0002	0.199	0.999	
		Year	0.0701	0.0794	0.407	0.317
		Water Level	0.0586	0.519	0.913	0.043
% <i>F</i> (All)/day	10	Mean	0.713	0.224	0.016	
		Year	-0.277	0.0898	0.018	-0.760
		Water Level	-1.47	0.587	0.040	-0.688
Mean % <i>F</i> _{ad}	10	Mean	30.1	4.01	<0.001	
		Year	5.83	1.60	0.008	0.809
		Water Level	30.2	10.5	0.024	0.737
% <i>F</i> _{ad} /hr	10	Mean	-0.0714	0.186	0.712	
		Year	0.0974	0.0742	0.231	0.444
		Water Level	0.0739	0.485	0.883	0.057
% <i>F</i> _{ad} /day	10	Mean	0.450	0.280	0.152	
		Year	-0.256	0.112	0.056	-0.654
		Water Level	-0.679	0.733	0.385	-0.331

^a1983 sample excluded.

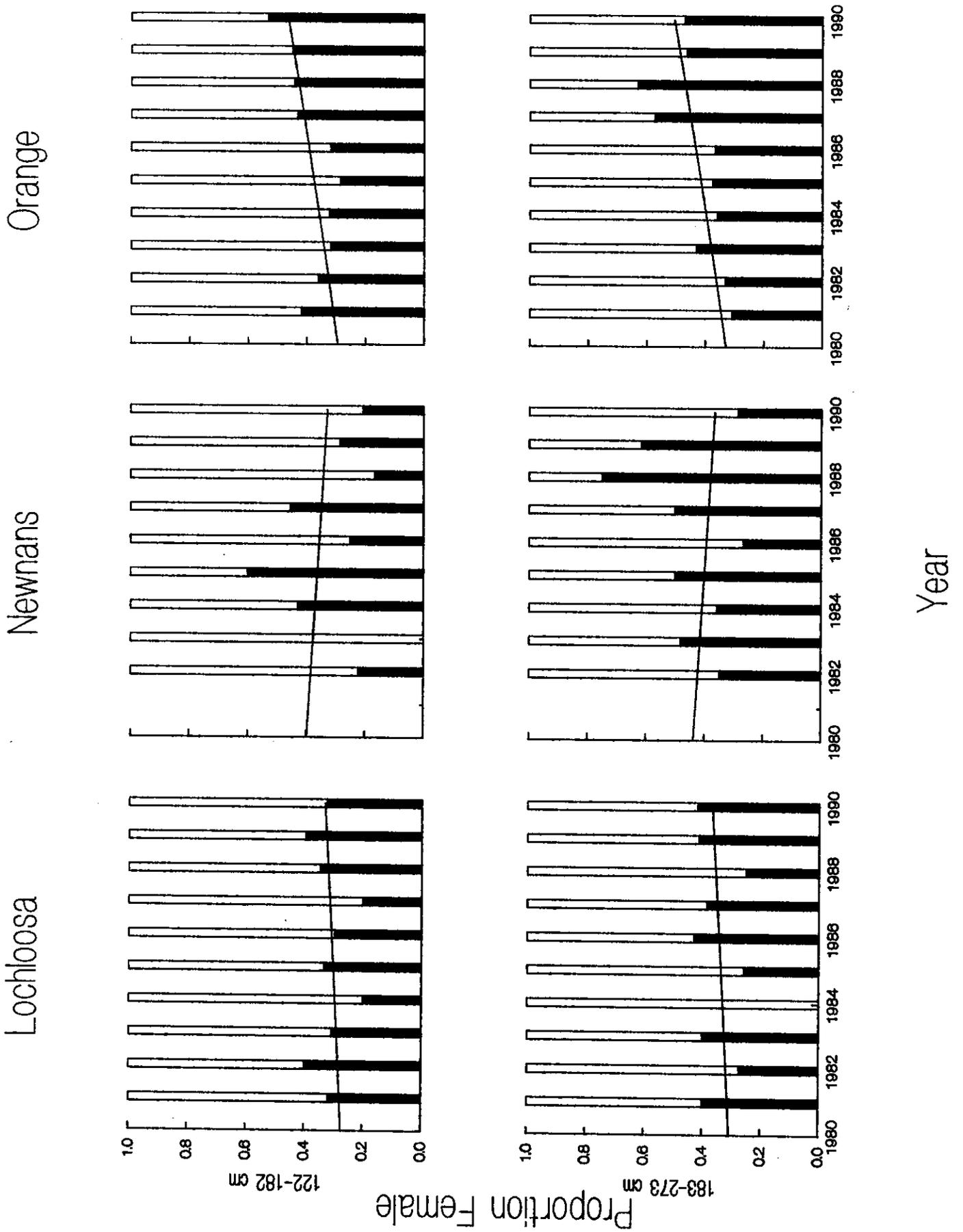


Fig. 12. Proportions and estimated trends of subadult female (122-182 cm) and reproductive (183-273 cm) female alligators harvested during 1981-90 on Lochloosa, Newnans, and Orange lakes.

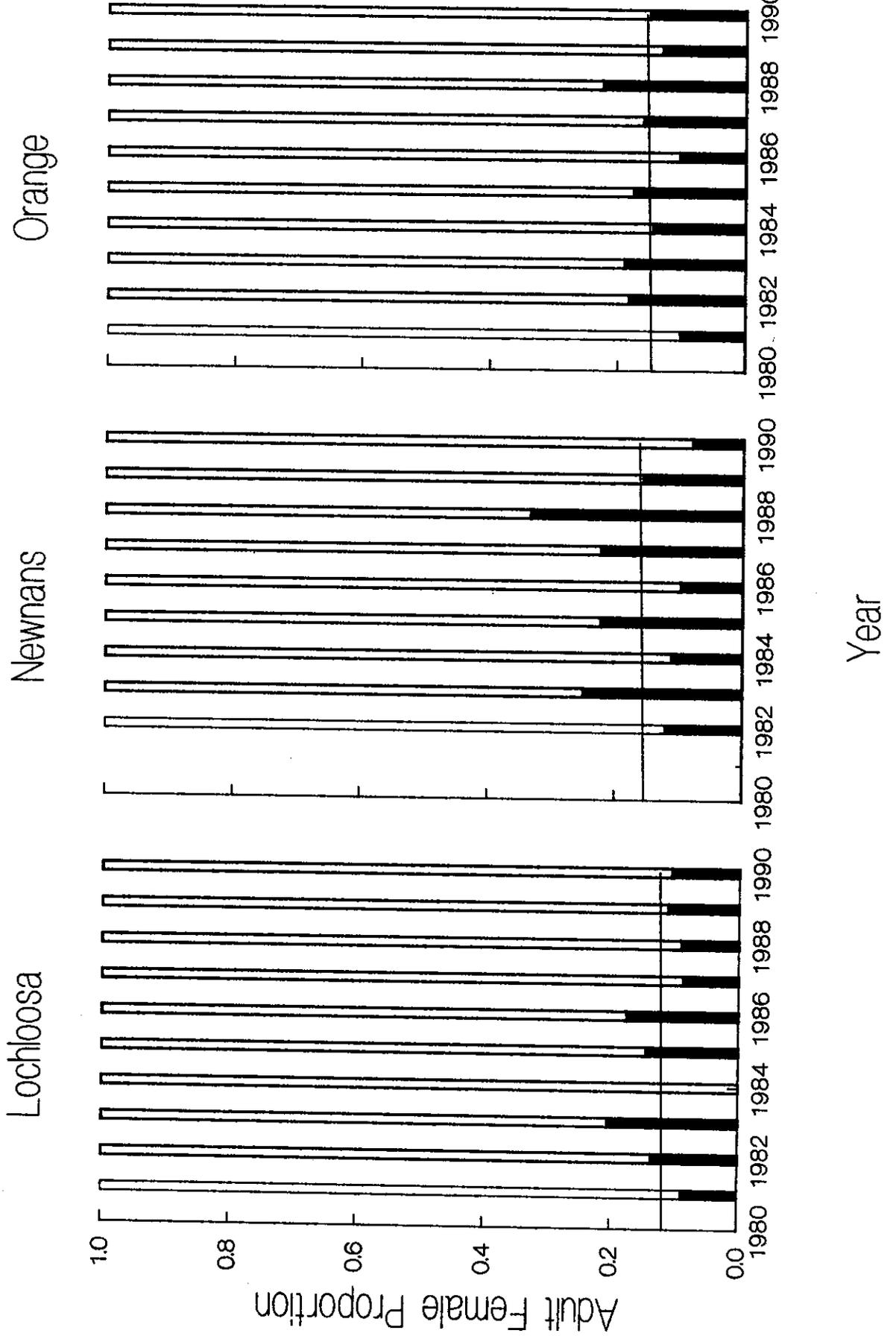


Fig. 13. Proportions and estimated trends of adult females relative to the overall harvested alligator population on Lochloosa, Newnans, and Orange lakes during 1981-90.

affect harvest success ($P = 0.223$). Mean 1981-90 hunter efficiency was 0.45 alligators/hr and remained relatively stable during the study. However, when aberrant year 1983 was excluded from the analysis, we detected a near significant ($P = 0.092$) decline in number taken/hr. Number of alligators taken declined with day of season ($P = 0.040$), but the decline changed from severe at the beginning of the study period (1981) to non-existent in 1990 ($P = 0.027$, Table 6).

Mean Total Length

The mean harvest success in $TL_{\bar{x}}$ adjusted for hunter effort and days into season did not vary with year or MWL (Table 6). Our data suggested that the adjustment of $TL_{\bar{x}}$ for E was superfluous, as the mean hunter efficiency for $TL_{\bar{x}}$ was not different from 0.0 cm/hr ($P = 0.190$), and no annual or MWL trends in efficiency were detected ($P > 0.427$, Table 6). However, smaller alligators tended to be taken more frequently in later parts of each season than in earlier parts ($P < 0.001$), but this phenomenon diminished with time ($P = 0.002$) and with higher water levels ($P = 0.007$).

We note the inconsistency between the estimated yields of $TL_{\bar{x}}$ (199 cm, Table 6) and of TL_{md} (184 cm, Table 4) for Orange. Apart from the obvious differences in the analysis procedures, this outcome resulted from the mean lying to the right of (has greater value of TL than) the median for right-skewed data. We also note that TL_{md} was slightly more precise (SE = 4.12) than was $TL_{\bar{x}}$ (SE = 4.88). This may indicate that $TL_{\bar{x}}$ was more sensitive to variations in the sample distribution than was TL_{md} .

Proportion of Females

Success at taking female rather than male alligators increased over years ($P = 0.023$), but water levels did not affect success ($P = 0.216$, Table 6). We detected no overall relationships between hourly effort and female proportion ($P = 0.999$), nor did we detect linear trends between annual values of hunter efficiency and time ($P = 0.407$) or MWL ($P = 0.913$, Table 6). However, hunter efficiency estimates followed a cyclic pattern over time. Success at taking females increased as the season progressed ($P = 0.016$), but the rate of increase declined over years ($P = 0.018$) and with increasing MWL ($P = 0.040$, Table 6). Lack of a water level effect may have resulted from similar responses of hunting success under extreme low or high water conditions; females are forced out of the marsh during low water and hunters have greater access to marshes during high water periods.

Proportion of Adult Females

Hunter success at taking adult females increased over years ($P = 0.008$) and with increasing water levels ($P = 0.024$) (Table 6). Mean nightly success at taking adult females did not depend on hours expended, nor were annual estimates of hunter efficiency related either to year or to MWL. Overall, success at taking adult females did not depend on time of the season, but annual seasonal efficiency may have decreased from higher values in early phases of the season to lower values in later phases. MWL did not influence annual seasonal efficiency (Table 6).

As seasons progressed in early years of the study period, hunter success per night at taking female rather than male alligators increased, but mean TL decreased. The alligator meat market was in the early stages of development in 1981, so demand for meat was sluggish. Consequently, most hunters were not as selective of alligator size as during later years, although they avoided penalty (183-259 cm) alligators early in the season in 1981. Success of meat sales in 1981 permanently shifted emphasis toward taking larger alligators. In general, hunters sought larger alligators early in the season and frequently passed opportunities for smaller alligators. As alligator wariness increased near the end of a season, hunters took all legal sizes to fill their quotas, and increasingly hunted in less accessible marshes preferred by females.

Overall hunter success in TL declined as the season progressed, but this relationship diminished with time and with increasing water level. Success at taking adult females increased with higher water levels. High water encouraged use of protective marsh and swamp by larger alligators but also allowed

hunters access to marsh and female habitat (Joanen and McNease 1970, McNease and Joanen 1974, Goodwin and Marion 1979, Wilkinson 1983), thereby increasing the opportunity for taking females. Joanen and McNease (1987a) attributed a similar increase in proportion of mature females harvested in Louisiana in 1973 to increased hunting in female habitat due to high water levels.

Changes in hunt regulations, hunter composition, and season scheduling may have affected the above analysis and probably contributed experimental error to the overall variability. Therefore, we may have failed to precisely detect all responses in hunter success over the duration of the study. Nevertheless, we believe the above findings provide a good indication of major hunter success relationships.

ALLOMETRIC RELATIONSHIPS OF HARVESTED ALLIGATORS

Total Length - Snout-Vent Length

Bob-tailed alligators comprised 4.2% of the population on harvest lakes. Because the probability of an alligator being bob-tailed increased with size, omitting bob-tailed alligators would have introduced bias in analyses of changes in TL or size composition, or would have required analysis by SVL. Because TL is commonly used in management of alligators, we found it preferable to estimate TL of bob-tailed alligators from the TL-SVL relationship.

The TL-SVL relationship was strong ($R^2 = 0.9956$, pooled over AREA \times YEAR \times SEX samples), and the overall power coefficient ($b = 0.9664$), a measurement of the rate of change in one variable (in this case TL) relative to the change in another variable (SVL), was different from 1.0 ($P < 0.001$), the proportional growth coefficient. The TL:SVL ratio decreased with increasing alligator size (Fig. 14). For all areas and sexes, TL for an average-sized alligator (100 cm SVL) was 1.95 times SVL, and the relationship was described by the equations:

$$TL_{cm} = 2.276 (SVL_{cm})^{0.9664}$$

$$TL_m = 2.205 (SVL_m)^{0.9664}$$

where the constant a necessarily differs for metric and English measurements. No interactions among AREA, SEX, OR YEAR effects were detected, and we found no YEAR trend in TL-SVL relationships. The mean power coefficient was greater for Newnans than for Orange ($P = 0.009$), indicating that for comparative increases in SVL, Newnans alligators grew proportionally more in tail length than did Orange alligators (Table 7). The mean power coefficient for Lochloosa was not different from those of other areas. For all areas, females grew proportionally longer tails ($P = 0.028$) relative to males (Table 7) for comparable increases in SVL.

Chabreck and Joanen (1979) found TL to be slightly greater than twice SVL for Louisiana alligators, but they found no sex-related difference. Their data set included juvenile alligators, and they used a linear model to describe the relationship, imposing a constant TL:SVL ratio over size which may have influenced the outcome. Because of the influence of juvenile alligators in their sample, the TL-SVL relationship reported by Chabreck and Joanen (1979) would not be directly comparable to our data. Hall (1991) concluded that female Louisiana alligators had longer TL than did Florida alligators of equivalent SVL. However, his limited sample size and use of linear regression for evaluating the TL-SVL relationship may have been deceiving. The TL-SVL relationship changes with size and extrapolation of TL-SVL relationships to body weights can lead to erroneous conclusions if size structures of compared samples are not similar, as was the case in Hall's analysis.

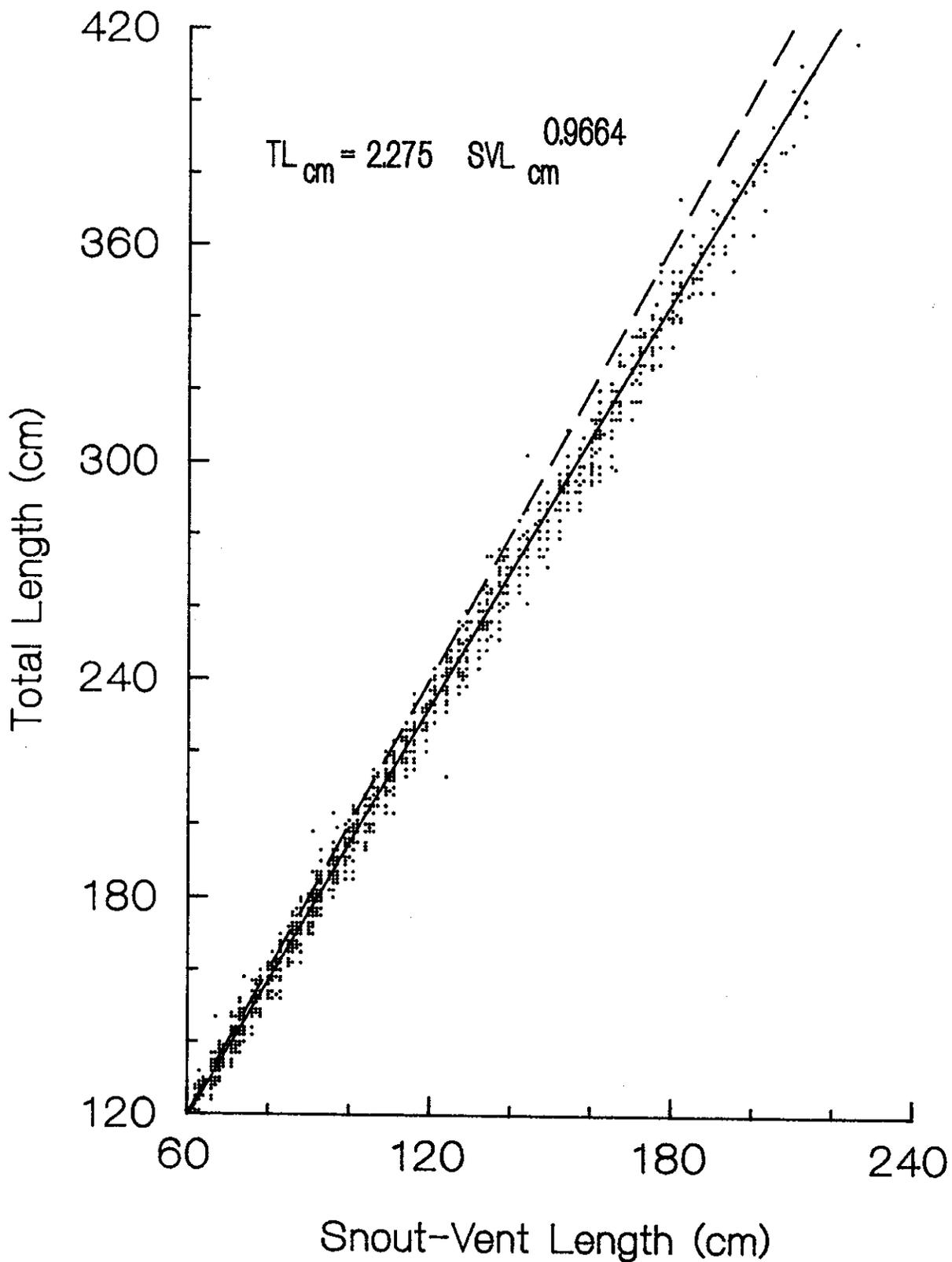


Fig. 14. Estimated relationship of total length to snout-vent length of harvested alligators (solid line) for all harvest areas. Dashed line represents a 2:1 relationship.

Table 7. Intercept (*a*) and power coefficient (*b*) estimates for total length (cm) - snout-vent length (cm) (TL-SVL), weight (kg) - total length (WT-TL), and weight - snout-vent length (WT-SVL) allometric relationships for alligators harvested on 3 Florida lakes 1981-90. Power coefficients with the same letters were different at $P = 0.017$ (area comparisons) or at $P = 0.05$ (sex comparisons).

Relationship	Sex	<i>a</i>	<i>b</i>
TL-SVL			
All areas	Both	2.2755	0.9664
Lochloosa	Both	2.2428	0.9696
Newnans	Both	2.2405	0.9703 ^a
Orange	Both	2.3440	0.9594 ^a
All areas	Fem.	2.2390	0.9707 ^b
All areas	Male	2.3121	0.9622 ^b
WT-TL			
All areas	Both	2.67×10^{-7}	3.469
Lochloosa	Both	2.11×10^{-7}	3.515 ^a
Newnans	Both	2.55×10^{-7}	3.484 ^b
Orange	Both	3.56×10^{-7}	3.407 ^{ab}
WT-SVL			
All Areas	Both	4.642×10^{-6}	3.351
Lochloosa	Both	3.618×10^{-6}	3.408 ^a
Newnans	Both	4.288×10^{-6}	3.377 ^b
Orange	Both	6.459×10^{-6}	3.267 ^{ab}

Weight-Length

The relationship between WT and length can provide an index of relative health or condition of animals and has been used extensively in fisheries management (Hile 1936, Le Cren 1951). A positive relationship between growth and condition has been demonstrated for largemouth bass (*Micropterus salmoides*) (Wege and Anderson 1978) and the toad *Bufo bufo* (Jorgensen and Wind-Larsen 1987).

TL accounted for slightly more of the variation in WT (pooled $R^2 = 0.9885$) than did SVL (pooled $R^2 = 0.9873$). The overall mean power coefficient was > 3.0 for either relationship, indicating that WT change was greater than that predicted by isometric growth. We found no evidence of trend in power coefficients for either relationship (TL: $P = 0.556$, SVL: $P = 0.236$), but in considering pooled residual variability from individual linear regressions, power coefficients did vary with respect to year for both the TL ($P = 0.0006$) and SVL ($P = 0.0004$) relationships. No interactions among effects were detected in either relationship. Newnans and Lochloosa alligators were more robust than Orange alligators (Fig. 15) but were not different from each other (Table 7). Sex did not influence the WT-TL and WT-SVL relationships ($P = 0.918$, $P = 0.236$). WT was predicted from TL by the following equations:

$$WT_{kg} = 2.675 \times 10^{-7} (TL_{cm})^{3.469}$$

$$WT_{lb} = 1.496 \times 10^{-5} (TL_{in})^{3.469}$$

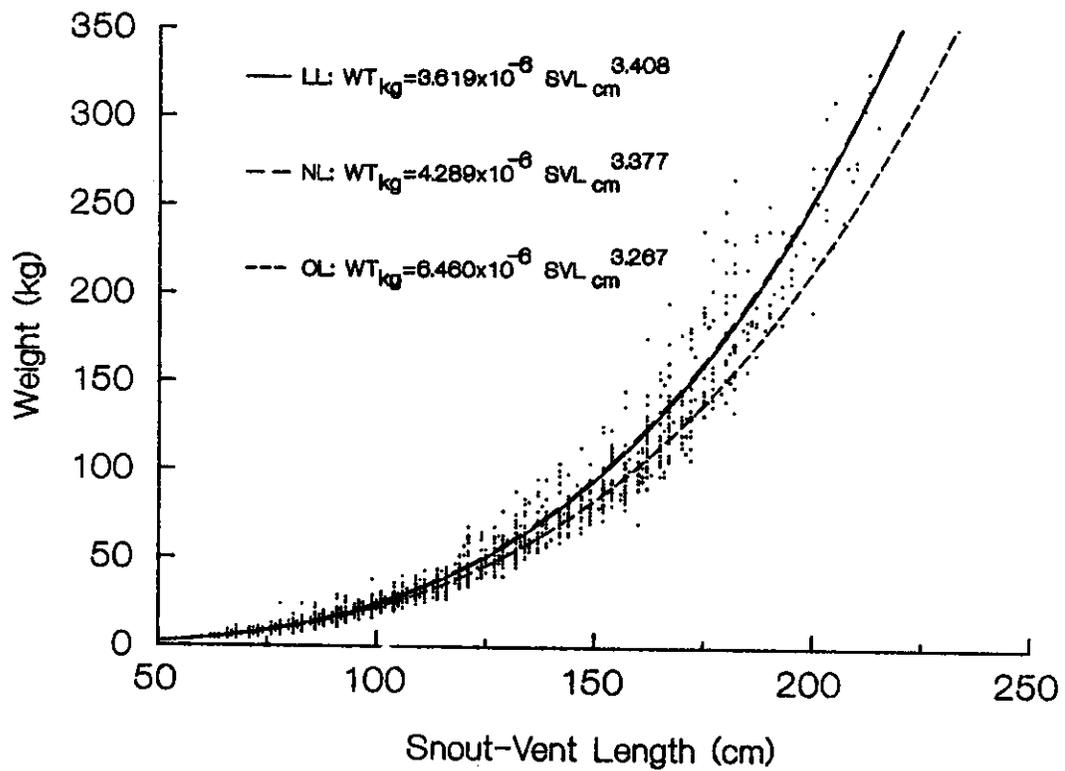
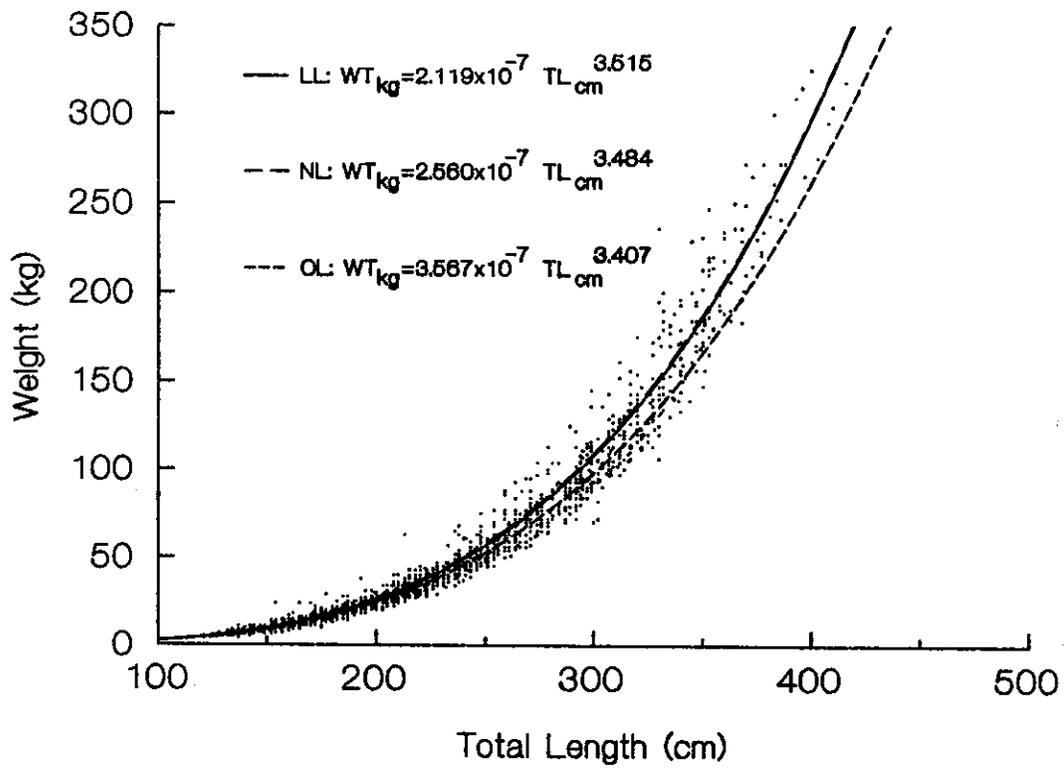


Fig. 15. Estimated relationships between weight and total length (upper) and snout-vent length (lower) for harvested alligators on Lcholoosa, Newnans, and Orange lakes during 1981-90.

and from *SVL* by the following equations:

$$WT_{kg} = 4.642 \times 10^{-6} (SVL_{cm})^{3.351}$$

$$WT_{lb} = 2.326 \times 10^{-4} (SVL_{in})^{3.351}$$

Taylor (1979) used physical condition as an index of habitat quality for *C. porosus* but did not provide evidence to support the association of condition with health and growth. Although Joanen and McNease (1987b) provided some evidence of a link between condition and growth for captive alligators, the concept lacks scientific confirmation for wild alligators.

Overlooking the limited evidence for the association between condition and growth in crocodylians, we assumed a positive relationship. Further, we hypothesized that reduced alligator densities throughout much of the year would reduce competition for food and, thereby, lead to improved physical condition of alligators over years. Although during the first 5 years we detected an increase in condition (A. R. Woodward and M. F. Delany, Ann. Alligator Rep., GFC, Tallahassee, 1987) we saw no evidence of such a phenomenon over the 10-year study. This response suggests that condition may be affected more by cyclic environmental factors than by density. Differences in condition among areas may be caused by dissimilar overall nutrient levels or genetic variation. Joanen and McNease (1987b) reported that early nutrition affected weight gain and early survival of farm-raised alligators. We suspect that food availability during the early years of life may be a critical factor affecting long-term condition.

Comparisons of estimated *WT* of alligators at 122 and 183 cm indicate a Louisiana (Chabreck and Joanen 1979) and a North Carolina (Fuller 1981) population were more robust than Florida alligators (Table 8). Condition of South Carolina alligators was comparable to that of Florida alligators. Thus, if condition is related to growth rate, we would expect growth rates of those populations of Louisiana and North Carolina alligators to exceed growth rates of alligators from our areas. The above comparisons provide only a crude measure of relative condition among populations because of varying size distributions of alligators sampled and different data modelling strategies chosen by the authors.

Meat Yield - Weight

Meat yield proportions can be used to estimate meat production for economic assessment of hunts or for law enforcement purposes to determine whether meat yields reported by hunters are commensurate with biological limitations.

MY was very closely associated with *WT* (pooled $R^2 = 0.9534$). The equation describing the *MY-WT* relationship was:

$$MY_{kg} = 0.2995 (WT_{kg})^{1.027}$$

$$MY_{lb} = 0.2932 (WT_{lb})^{1.027}$$

The overall *MY-WT* power coefficient (1.027, SE = 0.0066) indicated that *MY* increased disproportionately with increasing *WT*. Power coefficients in the *MY-WT* relationship did not vary with area or sex but declined with year ($P = 0.004$, Fig. 16). *MY* composed 31-35% of body weight for 122 cm (4.62 kg) to 400 cm (284 kg) alligators.

We attribute the decline in *MY/unit* body *WT* over years to changes in meat processing tendencies rather than changes in meat composition of alligators. During 1981-87, hunters primarily comprised commercial fishermen and frog hunters (see ECONOMICS below) and were inclined toward maximum utilization of harvested alligators. After 1987, the composition of hunters shifted toward recreational hunters who processed meat less thoroughly.

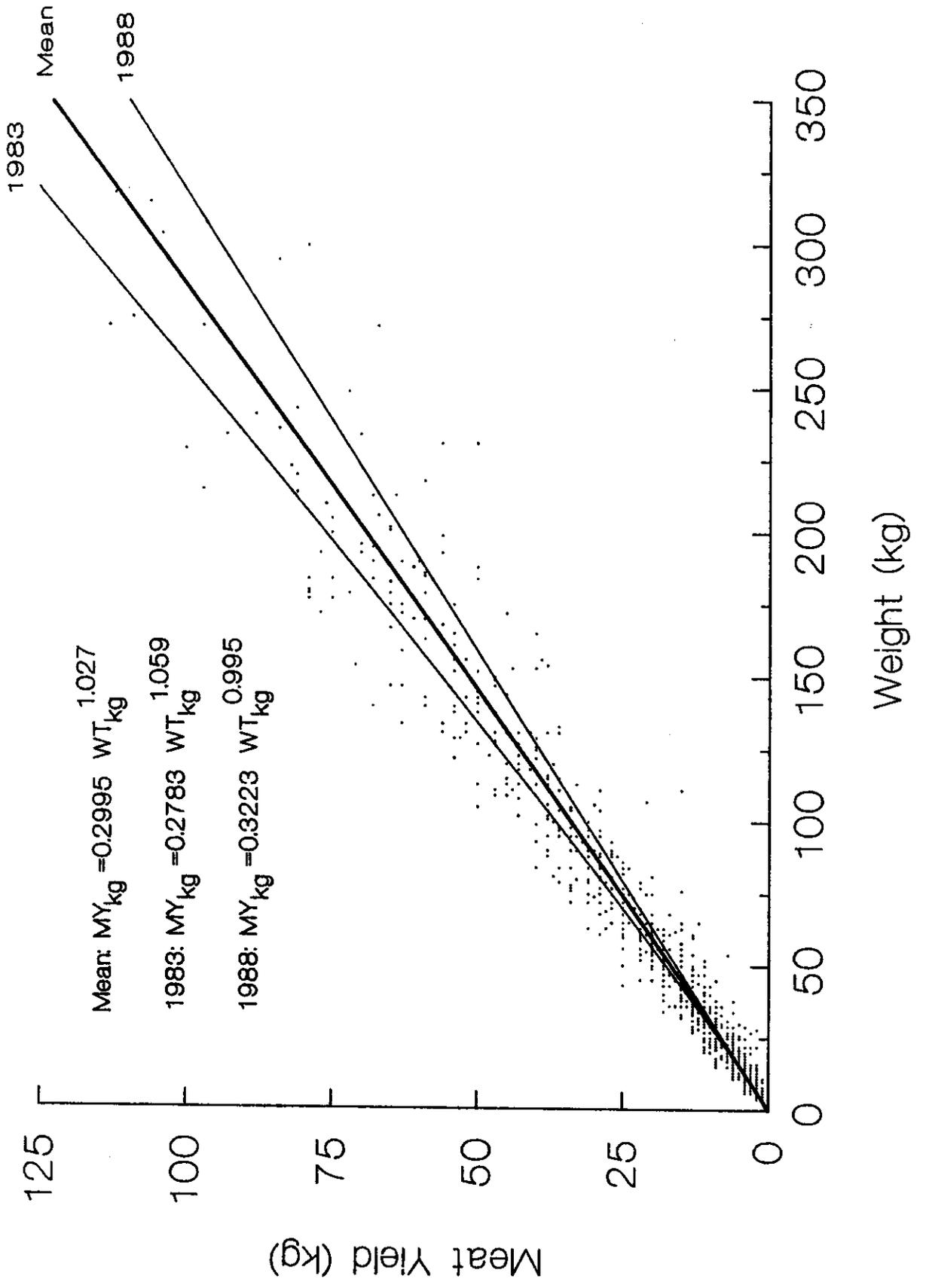


Fig. 16. Relationship between meat yield and weight for alligators on all harvest areas estimated for years 1983, 1988, and overall for years 1983-88.

Table 8. Comparative estimated weights (Kg) of 122 and 183 cm TL alligators for Florida (this study), Louisiana (Chabreck and Joanen 1979), North Carolina (Fuller 1981), and South Carolina (Brandt 1991) alligators.

Total Length	
122 cm	183 cm
5.893 (N.C.)	22.620 (La.)
5.091 (La.)	19.612 (N.C.)
4.746 (S.C.)	19.450 (Newnans)
4.736 (Newnans)	18.915 (Lochloosa)
4.567 (Orange)	18.181 (Orange)
4.548 (Lochloosa)	17.371 (S.C.)

Hide Length - Total Length

Reliable hide length data is available for all wild alligators harvested in Florida, whereas accuracy of carcass lengths reported by hunters can be highly variable. *HL* can be converted to *TL* for analysis of harvest yields and size class composition for use in monitoring the effects of management programs (Taylor and Neal 1984, Woodward et al. 1987a).

HL was strongly associated with *TL* (pooled $R^2 = 0.9926$; Fig. 19). We found no AREA \times SEX interaction ($P = 0.896$) in power coefficient means, nor were SEX and AREA main effects important ($P = 0.726$) in the model. The overall power coefficient ($b = 0.9798$, SE = 0.0069) indicated that the degree of linear hide stretching decreased as *TL* increased (Fig. 17). Thus, hides ranging from 122-396 cm *TL* stretched 5.4-2.9%. The *HL-TL* relationship is described by the equation:

$$HL_{cm} = 1.161 (TL_{cm})^{0.9798}$$

$$HL_{in} = 1.139 (TL_{in})^{0.9798}$$

The following equation should be used to predict *TL* from *HL* in English units:

$$TL_{in} = (HL_{in}/1.139)^{1.0206}$$

Alligator hides usually stretched to a greater length than carcass length, but the degree of stretching depended on storage method and moisture content of the hide (David 1987). Our findings are similar to the findings of Woodward et al. (1987a) and Taylor and Neal (1984), who found 6-2% and 4% hide stretch factors.

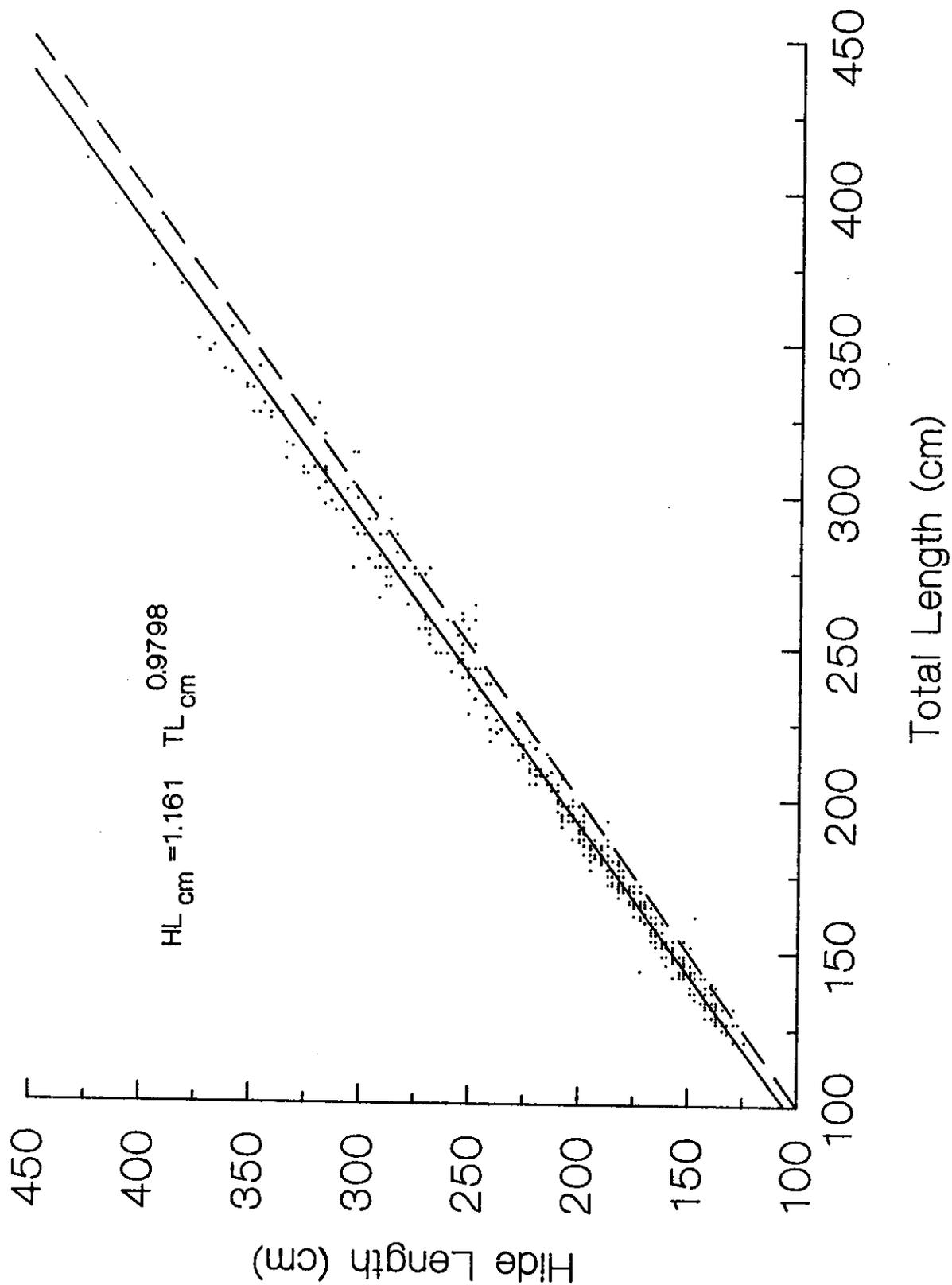


Fig. 17. Estimated relationship between hide length and total length (solid line) for alligators on combined harvest areas during 1987-88. Dashed line represents a 1:1 relationship.

Weight - Total Length \times Tail Girth

Frequently, it is difficult to weigh large alligators because equipment or personnel are lacking. Weights are important for comparing physical condition among populations or for evaluating other biological relationships, e.g., the relationship of clutch weight to female weight (Hall 1991). Predicting *WT* from *TL* and *TG* provides an effective and easy method of obtaining such data.

WT was strongly associated with the joint effects of *TL* and *TG* (pooled $R^2 = 0.9938$). Lack of annual replicates of *TG* data prevented us from testing trend in estimated coefficients *b* (for *TL*) and *c* (for *TG*). We found no AREA \times SEX interaction ($P > 0.355$), nor did we find any AREA or SEX effects in the overall model ($P = 0.140$). *WT* was roughly proportional to the product of *TG* and TL^2 . The equation for this relationship is:

$$WT_{kg} = 7.198 \times 10^{-6} (TL_{cm})^{1.948} (TG_{cm})^{1.251}$$

$$WT_{lb} = 3.125 \times 10^{-4} (TL_{in})^{1.948} (TG_{in})^{1.251}$$

POPULATION TRENDS

We could detect no evidence ($P > 0.05$) that trends differed among areas for either the harvestable or adult size classes, and therefore, all areas were pooled for trend analysis of those size classes. Thus, we concluded that trends of harvestable and adult alligator populations on the control area, Woodruff, did not differ those on harvest areas. The harvestable alligator population showed no evidence of annual trends ($b = -0.0023$, $P = 0.9198$) but we saw some evidence of a negative trend for adult alligators ($b = -0.0509$, $P = 0.0552$). Count densities of both harvestable and adult alligators increased with decreasing water levels ($P < 0.05$). A YEAR \times DMWL interaction was observed ($P < 0.05$) for both harvestable and adult alligators indicating that trends were more detectable when water levels were low. Low relative counts during high water levels apparently decreased our ability to detect changes.

Increases in numbers of ≥ 30 cm alligators were observed on both Orange and Lochloosa, but these were primarily due to increases in the 30-122 cm segment (Table 9, Fig. 18). No trends were observed in count densities of ≥ 30 -cm or juvenile alligators on Newnans and Woodruff (Table 9, Fig. 18). Count densities of harvestable alligators were relatively stable on all areas (Table 9).

Estimated 10-year declines of 45% and 63% for adults counted on Orange and Lochloosa appeared biologically important but were not statistically significant at the $P = 0.05$ level. However, considering the lack of power (low replication and high variation) in our data, the $P = 0.152$ detected on Orange could be considered significant (Burger and Kock 1989, Peterman 1990). Estimated count density of adult alligators on Woodruff declined 18%; though not statistically significant, the decrease suggested that factors other than harvest may have influenced observed declines of adults. Intense capture and release activities in 1990 corresponded to a sharp dip in count densities (Fig. 19) and suggest increased alligator wariness. Greater than expected declines (46-86%) in adults counted on hunted areas after the first hunt-year exceeded estimated harvest rates (13%) and were followed by relative stability (Fig. 19), thereby suggesting wariness. Durbin-Watson statistic values for harvested area were negative (Lochloosa = -1.639, Newnans = -1.914, and Orange = -1.529) indicating strong negative correlation of counts during the first 2 years, whereas the Durbin-Watson value for Woodruff indicated weak autocorrelation. Durbin-Watson values differed ($P = 0.049$) between harvested areas and the control area. The negative correlation indicates that counts were higher than expected during the first year (pre-hunted population) and lower than expected during the following post-hunt year. We attribute this response to wariness.

Increasing water level negatively affected counts of juvenile alligators on Orange and Woodruff, positively affected counts of adults on Newnans, and had no detectable effect on harvestable or adult alligators on Lochloosa, Orange, or Woodruff (Table 9). Percent hydrilla coverage positively affected counts of juvenile and harvestable alligators on Orange but negatively effected juvenile alligator counts

Table 9. Estimated % population change during study, estimated trend (annual % growth rate), partial correlation coefficients (r) for covariates (water level and % hydrilla coverage), and overall adjusted R^2_{adj} for model describing observed alligator densities from night-light surveys on 4 Florida lakes 1981-90.

Study area (n)	Est.		Year		Water level		Hydrilla		R^2_{adj}
	pop. change (%)	trend	P	r	P	r	P	r	
Lochloosa Lk. (18)									
≥30 cm	+284	14.4	0.046	-0.355	0.177	0.052	0.848	0.798	
30-122 cm	+976	26.8	<0.001	-0.278	0.298	0.224	0.404	0.918	
≥122 cm	- 10	-1.1	0.902	-0.380	0.146	-0.155	0.566	0.328	
≥183 cm	- 63	-9.4	0.374	-0.312	0.240	-0.175	0.516	-0.078	
Newnans Lk. (17)									
≥30 cm	+ 60	5.4	0.217	-0.113	0.688	-0.556	0.031	0.374	
30-122 cm	+ 69	6.0	0.440	-0.381	0.161	-0.536	0.039	0.519	
≥122 cm	+ 72	6.2	0.227	0.244	0.382	-0.362	0.185	-0.036	
≥183 cm	+ 47	4.4	0.452	0.613	0.015	-0.019	0.947	0.483	
Orange Lk. (15)									
≥30 cm	+ 88	6.5	0.035	-0.650	0.016	0.577	0.039	0.756	
30-122 cm	+169	10.4	0.002	-0.730	0.005	0.489	0.090	0.868	
≥122 cm	+ 5	0.5	0.908	-0.170	0.579	0.568	0.043	0.191	
≥183 cm	- 45	-5.8	0.153	-0.105	0.734	0.495	0.085	0.315	
Lk. Woodruff (18)									
≥30 cm	+ 26	2.3	0.583	-0.680	0.003			0.537	
30-122 cm	+ 49	4.1	0.396	-0.785	<0.001			0.032	
≥122 cm	- 1	-0.1	0.870	-0.347	0.173			0.032	
≥183 cm	- 18	-2.0	0.673	-0.044	0.86			-0.119	

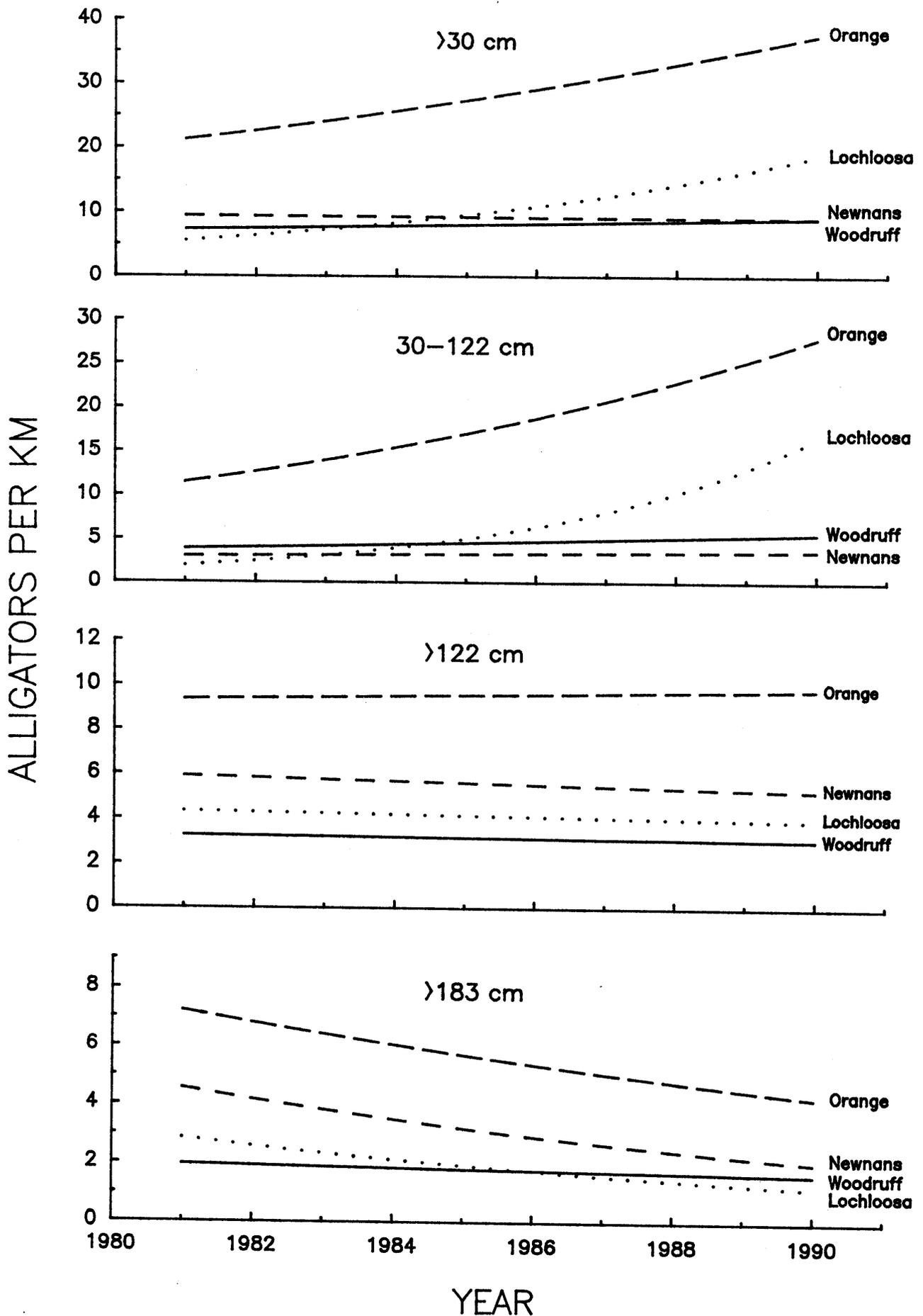


Fig. 18. Estimated trends from night-light surveys of 4 size classes of alligators for harvested lakes Lochloosa, Newnans, and Orange (broken lines) and for control area, Lake Woodruff (solid line) during 1981-90.

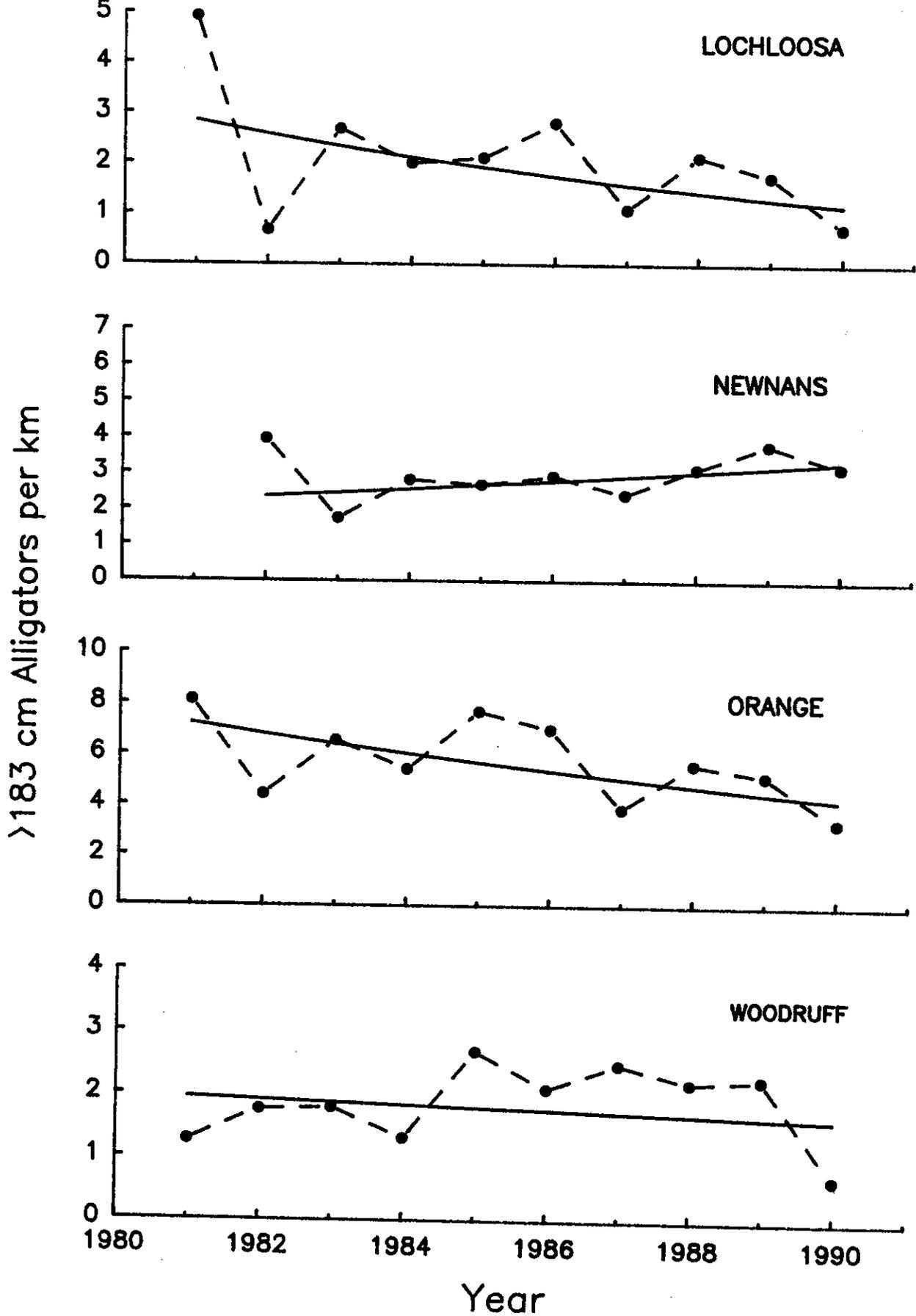


Fig. 19. Estimated trends and water level-adjusted point estimates of adult alligators population densities from night-light counts on 4 Florida lakes during 1981-90.

on Newnans (Table 9). Low water level tended to force smaller alligators into open water and enhanced counts. For this reason, size class distributions estimated during low water years probably provided the least biased representation of alligator population structure (Fig. 20).

Apparently stable populations of harvestable alligators on harvest areas during 1981-90 indicated that an approximate 13% harvest had no measurable effect on their densities. Increasing juvenile alligator populations on Orange and Lochloosa provided strong evidence of increasing alligator production and/or juvenile survival. Evidence of declines in adult alligator counts on Orange and Lochloosa may be partly attributed to increased wariness. Reduced approachability was attributed to increased wariness of alligators during intensive surveying on Newnans during the mid-1970's (A. Woodward, unpubl. data). Similarly, Webb and Messel (1979) and Bayliss et al. (1986) found learned wariness of night-light survey boats in saltwater crocodiles in Australia, but they also found evidence of some natural increase in wariness with age. Although hunting may have contributed to depressed counts on Lochloosa and Orange, our data suggest that wariness had a greater influence.

Stable population densities among the various size classes on unharvested Woodruff may indicate population equilibrium. The possibility of substantial emigration from Woodruff exists, but we view net population loss through dispersal as unlikely because we have no reason to believe population densities on neighboring Lake Dexter and the St. Johns River changed during the study.

In accessible habitat, night-light counts can be used to provide an index of crocodylian population changes (Wood et al. 1985, Brandt 1989, Webb et al. 1990, Woodward and Moore 1990). However, varying environmental conditions can influence night-light counts. Accounting for major sources of variation and reducing random experimental error lowers overall variation and reduces both minimum detection size of trends and number of years of data needed to discern trends (Harris 1986). We detected a 6.5% annual increase in ≥ 30 -cm alligators on Orange over 10 years but were not able to detect a trend for adult alligators on Orange and Lochloosa where estimated observed densities declined by annual rates of 5.8% and 8.6%. We attribute this outcome to the high variability and small densities of large alligators and to the failure of external covariates (MWL and hydrilla coverage) to appreciably control sources of variation. This suggests that unknown or uncontrollable factors influence adult alligator observability and that increased replication is the best solution for increasing the power for detecting trends.

Environmental variables, water level and hydrilla coverage, were least effective in describing variability in counts of harvestable and adult alligators. We suspect that long-term rather than short-term water availability in adjacent marshes and swamps associated with lakes, influenced alligator distribution. Water availability in those habitats did not always coincide with water levels in the open lake where measurements are normally taken and, therefore, the association of water levels and counts was erratic.

NEST PRODUCTION AND SURVIVAL

Nest Observability

Of all nests eventually observed, mean percent of nests sighted during initial aerial searches ranged from 94% on Orange Lake to 98% on Paynes Prairie and averaged 96% for 4 areas (Table 10). However, replicate surveys on Orange Lake indicated that only 77% of all nests were observed during an initial aerial survey (K. Rice, pers. commun.). Therefore, nest surveys did not detect all nests, a result substantiated by observations of hatchling pods in areas where nests were not sighted.

Nest Production and Densities

Mean total nests observed varied among areas ($P < 0.001$) but was greatest on Orange (91.1/year) and least on Lochloosa (12.5/year) (Table 10). Because of a dense tree canopy, we found only 1 nest from the air on Newnans from 1981-1983. Aerial surveys on Newnans were subsequently discontinued, but ground surveys (by boat) located 3 more nests (1985-1990). For Newnans, we estimated minimum production based on both aerial and ground searches for nests and from evidence of

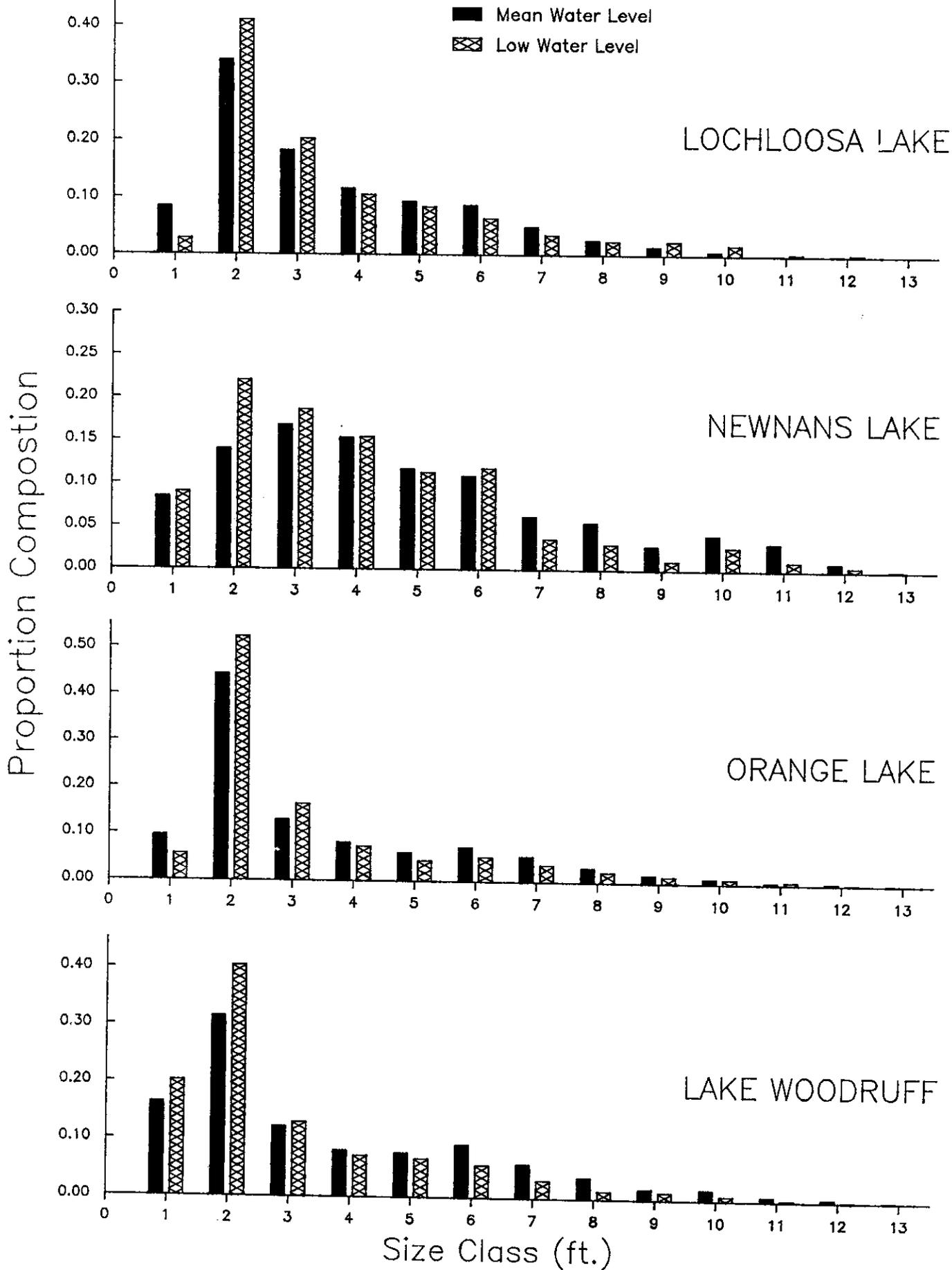


Fig. 20. Size distribution, in 1 ft. (30.5 cm) size classes, of 4 alligator populations during average water years (1981-90) and during an extreme low water year (1990).

other nesting indicated by observations of pods not associated with known nests (Appendix C).

Mean estimated ha of nesting habitat (emergent marsh or wooded swamp) per nest for study areas were: Lochloosa = 77.5, Newnans = 204.1, Orange = 19.6, Paynes Prairie = 35.8, and Woodruff = 85.5. Woodward et al. (1984) and Jennings et al. (1987) found inconsistent annual use of successful nesting sites on Orange. This suggests that nest sites were not a limiting factor on Orange. Nesting was more likely limited by number of reproductively capable females or by separation of breeding territories by females.

Table 10. Mean annual aerial observations of total nests, % false nests, true nests, and % of total nests during first search (% first). Estimated rates of nest depredation (dep), flooding (flood), and survival for 4 Florida wetlands for the mean year (1985.5) of the study.

Area	Nests obs.	% false nests	True nests obs.	% first	Est. mortality rates		Est. survival rate
					dep	flood	
Lochloosa Lake	12.9	2.8	12.5	95.3	0.242 ^a	0.010 ^a	0.747
Orange Lake	94.9	3.7	91.1	93.6	0.510	0.038 ^a	0.452
Paynes Prairie	103.7	3.8	100.2	97.8	0.363 ^a	0.107 ^a	0.530
Lake Woodruff	50.5	3.7	48.6	95.7	0.379 ^a	0.038 ^a	0.583

^aNo differences were found among rates with similar letters at the Bonferroni-adjusted level of ($P = 0.08$).

^bPaynes Prairie was greater than Orange Lake at the Bonferroni-adjusted level of $P = 0.08$.

False Nests

Nests identified from the air as false constituted 2.8-3.8% of the mean observed nest production (Table 10). False nests were typically smaller than (<0.5 of volume) and located within 20 m of true nests. However, we occasionally found nests of normal size and shape that contained no clutches (means for 1986-90: Orange = 2.8%, Paynes Prairie = 0.6%, Woodruff = 7.2%) during nest inspections. Occasionally, the normal-sized false nests were attended and maintained by alligators. We speculate that attended false nests indicated premature oviposition or egg resorption by females (Taylor et al. 1991). False nests were commonly used by Florida redbelly turtles (*Pseudemys nelsoni*) as nesting sites and were frequently depredated by raccoons. Unattended false nests were probably abandoned by female alligators in favor of an alternate site (Joanen 1969, Wilkinson 1983).

Factors Affecting Nest Production

Of 8 monthly combinations, MAY and SEPTEMBER MWL's provided the overall greatest reduction in variability in nest production due to water level (mean rank = 6.0, Table 11). A model with AREA, YEAR, MAY, SEPTEMBER, AREA × YEAR, AREA × MAY, and MAY² effects best described variation in square root-transformed counts ($R^2 = 0.917$). The positive influence of mean May water level varied by area ($P = 0.028$), but a negative quadratic effect of May water level on nest

production ($P = 0.017$) was observed on all areas. This relationship indicated that nesting increased with water level to a point of maximum productivity then declined as flooding conditions occurred. We also detected an increase in nest production with mean September water level ($P = 0.050$). Nest counts, adjusted for water level, increased ($P < 0.05$) during the study on Orange and Woodruff, but showed no evidence of change on Lochloosa and Paynes Prairie (Fig. 21). Nest counts, adjusted for year, increased with water level on all areas except Woodruff, where water level did not seem to influence counts.

Population harvest models predicted that reduced densities of adult female alligators would result in declining alligator nest production (Nichols et al 1976; Abercrombie, unpubl. data). However, nest production remained stable on Lochloosa and increased on Orange during the study, indicating a compensatory response to depressed adult densities. Although water levels for all months during the periods Sep-Oct and Mar-Jun affected nest production, May water levels were most influential. This relationship appears to be widespread throughout the range of the alligator. Depressed nesting during

Table 11. Ranking and R^2 value of pairs of fall and spring monthly water level measurements used in the alligator nest production regression model, averaged over 4 Florida wetlands 1981-90.

Month pair	Mean rank	R^2
Sep, May	6.00	0.75
Sep, Apr	5.25	0.66
Sep, Mar	5.00	0.63
Oct, May	5.00	0.63
Oct, Mar	4.00	0.50
Oct, Apr	4.00	0.50
Oct, Jun	3.50	0.44
Sep, Jun	3.25	0.41

very low and very high Mar-Jun water levels was observed on Rockefeller Refuge, Louisiana (Joanen and McNease 1989), and coastal impoundments in South Carolina (Wilkinson 1983).

The mechanism relating water level fluctuation to variability in nest production is unclear. Physical stress induced by drought conditions may reduce lipid reserves, decreasing the likelihood of vitellogenesis and ovulation (Fischer et al. 1991). Low water conditions may also increase social stress and associated corticosterone levels, which have been tied to depressed vitellogenesis in adult female alligators (Elsey et al. 1990). How high water level reduces nest production is more uncertain. We doubt that vitellogenesis and egg production are affected by high water levels. However, we suggest that, depressed nest counts associated with flooding may result from females (1) resorbing eggs (Taylor, et al. 1991; P. Cardeilhac, pers. commun.) or (2) releasing eggs into the water because of a lack of suitable nest sites, and/or (3) nests built prior to flooding may be obscured by water, and/or (4) a greater

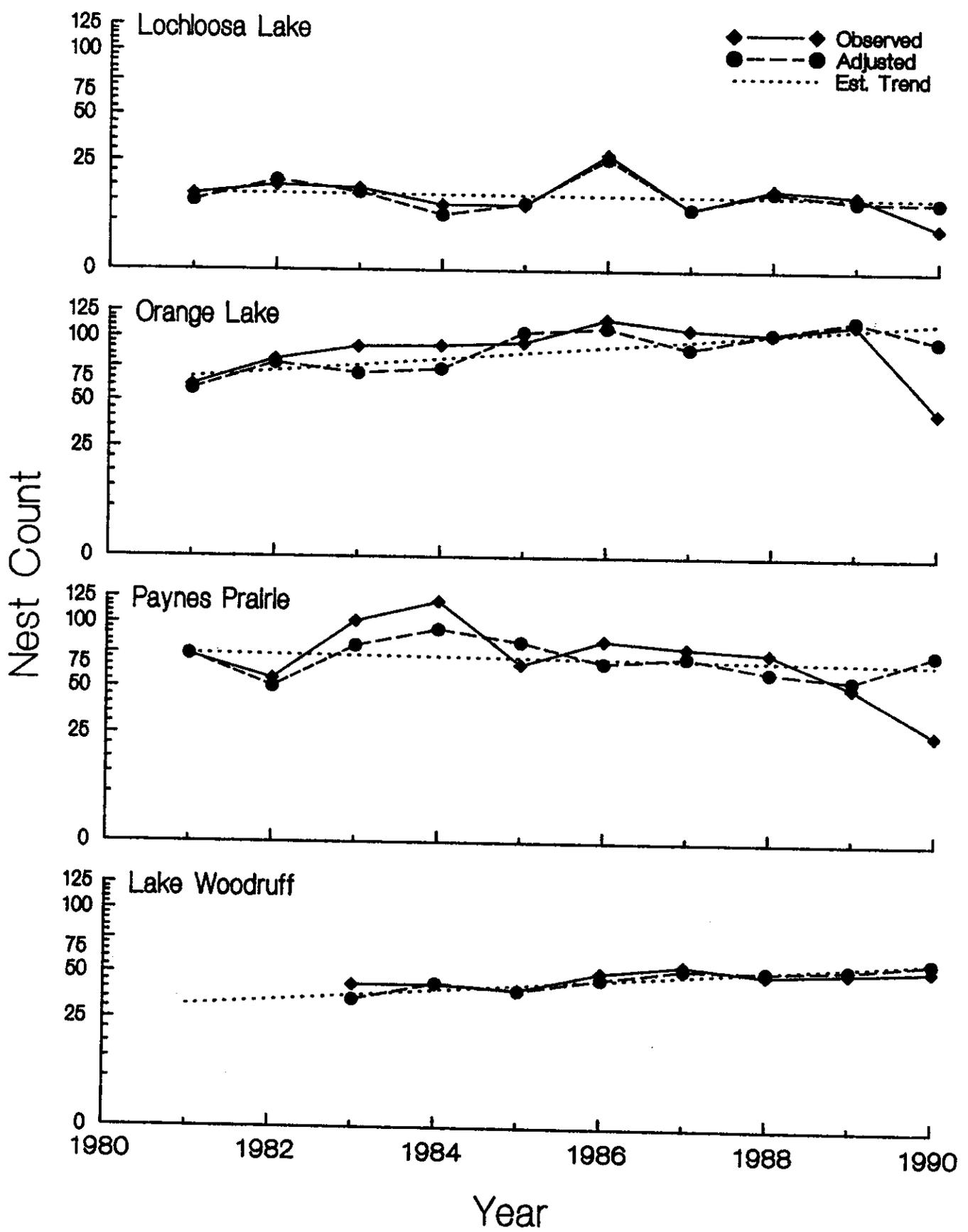


Fig. 21. Observed and water level-adjusted nest counts and estimated trends for Lochloosa Lake, Orange Lake, Paynes Prairie, and Lake Woodruff during 1981-90.

proportion of nests may be built in higher areas with dense tree canopy and concealed from aerial view.

Nest Survival

Overall survival. -- Mean proportion of nests with uncertain final status ranged from 0.017 on Woodruff to 0.092 on Orange and 0.078 on Lochloosa. Likely reasons for undetermined fates were: (1) nests were located under tree canopy and were very difficult to see, (2) nests were located in habitat without nearby landmarks and were difficult to relocate, and (3) depredated nests frequently became overgrown with green vegetation and were difficult to distinguish from surrounding vegetation. We suspect a slight bias may have occurred from reason (3), but we could not quantify the amount, and we believe that the bias was negligible.

Many clutches were inspected during this study, involving human activity at the nest site and nest opening. All survival analyses assumed no difference in predation rate between opened and unopened nests, even though Deitz and Hines (1980) concluded that opened nests were more likely to be depredated. We were not able to repeat their experiment but found variable results when we compared predation rates of opened vs. unopened nests. Opened nests were about as likely to be depredated as unopened on Orange, more likely on Paynes Prairie, and much less likely on Woodruff (Table 12). These comparisons may be biased because nests opened were not randomly selected and had already survived for approximately 1/3 of incubation. Thus, our sampling procedure may have selected nests more likely to survive. However, the variability of predation rates for opened nests, provided us no evidence to conclude that opening of nests had an effect on probability of nest predation.

Overall nest survival increased with year ($P = 0.001$) (Fig. 22), although the observed survival rates were too variable to fit the estimated trend closely ($P < 0.001$). Jun-Aug MWL affected nest survival differently by area ($P = 0.027$), and these differences resulted in no net water level effect ($P = 0.747$). Because Jun-Aug MWL interacted with AREA, comparisons of nest survival probabilities among areas depended on water level.

Table 12. Mean predation rates of nests opened for clutch inspections and unopened nests for 3 alligator populations during 1983-90.

Area	<i>n</i> years	Treatment			
		Opened		Unopened	
		\bar{x}	(SE)	\bar{x}	(SE)
Orange Lake	7	0.476	(0.117)	0.525	(0.132)
Paynes Prairie	4	0.423	(0.299)	0.328	(0.244)
Lake Woodruff	8	0.072	(0.065)	0.509	(0.279)

Nest Predation. -- We found no yearly trends in predation rates ($P = 0.280$, Fig. 22), but the predation rate was greater on Orange than other areas at the 1985.5 study midpoint ($P < 0.001$). No differences were found among predation rates on Lochloosa, Paynes Prairie, and Lake Woodruff (Table 10). The AREA \times MWL interaction for nest survival was due to varying dependence of predation rate on water level. Though we could not statistically detect differences among areas, estimated predation rates on

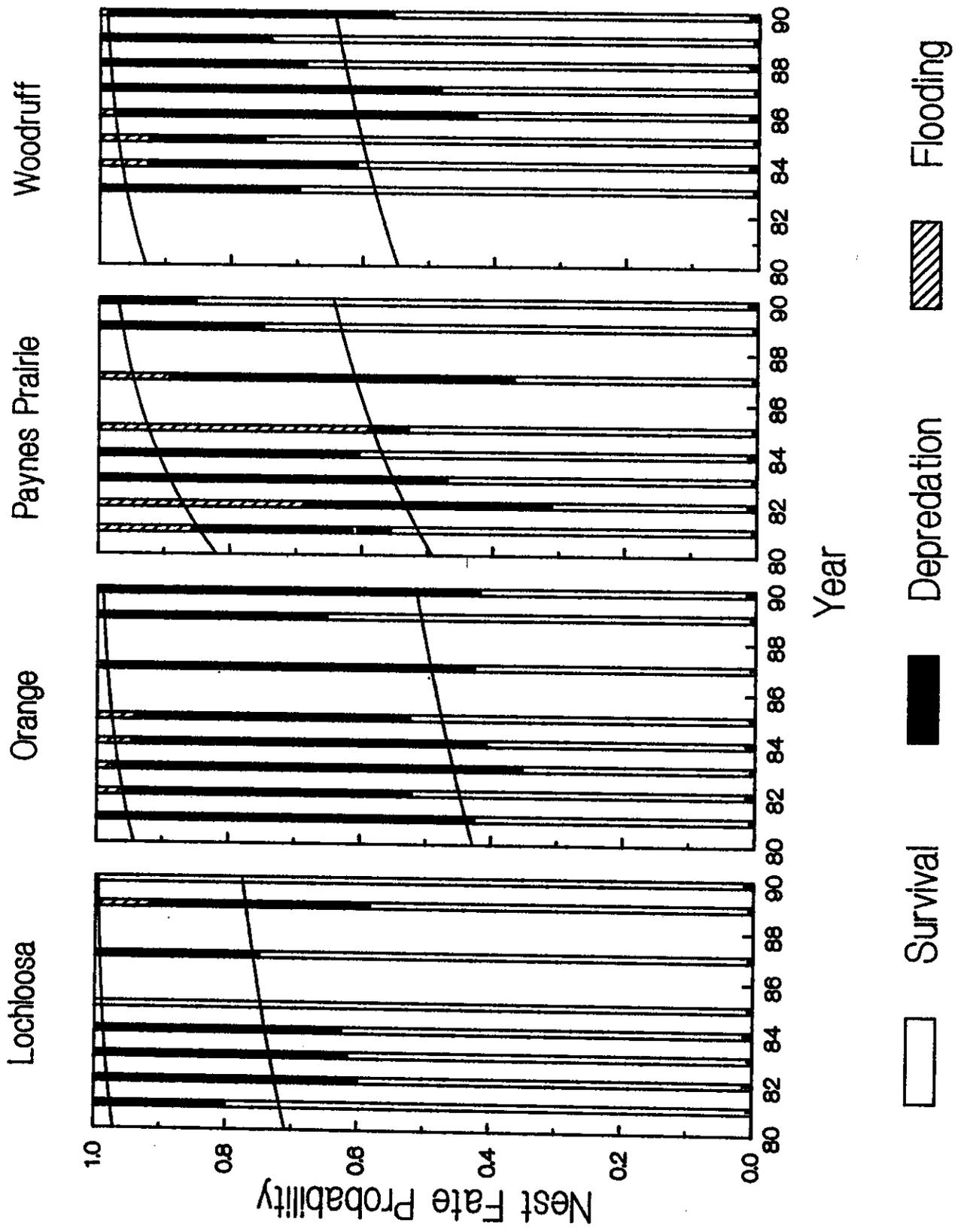


Fig. 22. Observed survival, depredation, and flooding rates of nests, and estimated trends of the rates during 1981-90 on Lochloosa Lake, Orange Lake, Paynes Prairie, and Lake Woodruff.

Paynes Prairie and Lochloosa increased with higher summer water level, but decreased on Woodruff. Predation rates on Orange were not affected by water level.

Nest depredation was common on all areas and we attributed most of it to raccoons (*Procyon lotor*). We never observed raccoons depredating a nest, but we occasionally found tracks confirming their presence. After initial visits by raccoons, nests typically had numerous small penetration holes, apparently made as raccoons probed for eggs. Eventually, the entire nest was flattened, presumably during subsequent visits by raccoons. One nest at Orange was clearly depredated by wild hogs (*Sus scrofa*), as evinced by extensive rooting and hoof-prints around the nest. We saw no specific evidence of other predators. We found, as did Joanen (1969) and Wilkinson (1983), that clutches were completely destroyed within several days after initial excavations. Disturbance of the clutch cavity by nesting Florida redbelly turtles occasionally damaged or exposed eggs.

Nest predation is common for most alligator populations throughout the range, but rates are variable and may be dependent on habitat types and local raccoon population densities. Goodwin and Marion (1978) found 31% of 15 nests depredated on a small wetlands in northcentral Florida. Deitz and Hines (1980) attributed 50.9% and 62.8% depredation rates for Orange Lake and Paynes Prairie during 1974-77 mostly to raccoons, although they credited river otters (*Lutra canadensis*) with 7% of the predation. The predation rate reported for Orange Lake by Deitz and Hines (1980) agreed closely with our findings, but their higher estimated rate for Paynes Prairie was possibly a result of the inclusion of a greater proportion of levee nests in their sample. Fogarty (1974) also attributed a 16.5% predation rate for Everglades nests to raccoons. Raccoon predation was an important source of alligator clutch losses on some wetlands in Louisiana (Joanen 1969, Fleming et al. 1976) and Georgia (Ruckel and Steel 1984), and to a lesser extent, on coastal impoundments in South Carolina (Wilkinson 1983). However, Carbonneau (1987) found relatively little depredation at Lacassine Nat. Wildl. Refuge, Louisiana during 1986-87. Metzen (1977) and Hunt and Ogden (1991) reported extremely high depredation rates (90% and 69%) in the Okefenokee Swamp, Georgia, and reported black bears (*Ursus americanus*) as the primary nest predator, with raccoons accounting for substantially less predation. Feral hog depredation was also observed by Ruckel and Steel (1984) in Georgia and by Fogarty (1974) in the Everglades.

Fleming et al. (1976) attributed lower depredation during a high-water year at Rockefeller Refuge, Louisiana, to raccoons avoiding marsh and using levies and berms. Hunt and Ogden (1991) found a similar relationship between predation rate and water level in the Okefenokee Swamp and hypothesized that low water limited the defensive capacity of attending females. Jennings et al. (1987) found that predation distribution was affected by water level and suggested that this was caused by water level-dependent foraging strategies by raccoons. During our study, the relationship between water levels and predation rates was area-specific. We suspect that variation in proximity of alligator nesting habitat and raccoon habitat, water level-related changes in raccoon foraging efficiency, and raccoon population density fluctuations within areas influenced the relationship between predation rates and water level.

Time of Predation. -- We detected a linear decline ($P < 0.05$) in survival of non-flooded nests throughout the incubation period for 4 of 10 years on Orange; The direction of the trend in the other 6 years was also negative, but small sample sizes each year precluded their statistical detection. The quadratic term estimates were positive for all 10 years, indicating that the downward trend in survival followed a concave trajectory rather than either straight or convex trajectories ($P < 0.005$). This type of trajectory is consistent with the hypothesis of constant mortality (constant proportion dying at each time interval). The estimated non-flooded nest survival was 77% at 15 July and 65% at 1 Aug (Fig. 23).

We found no evidence to support the contention that depredation increases during late incubation. This finding is contrary to those of Joanen (1969), Fleming et al. (1976), Goodwin and Marion (1978), and Wilkinson (1983), who ported predation to be largely confined to the final 2 weeks of incubation. Joanen and McNease (1989) attributed late-incubation predation to possible odors emitted by eggs as they swell and crack. Wilkinson (1983) suggested that hatchling vocalization during pipping attracted raccoons. Conversely, Metzen (1977) attributed early incubation predation by black bears to odors from decaying nest material. Only Ruckel and Steel (1984) reported predation throughout incubation, as we found in our study. Why our depredation pattern differed from those of other alligator populations is

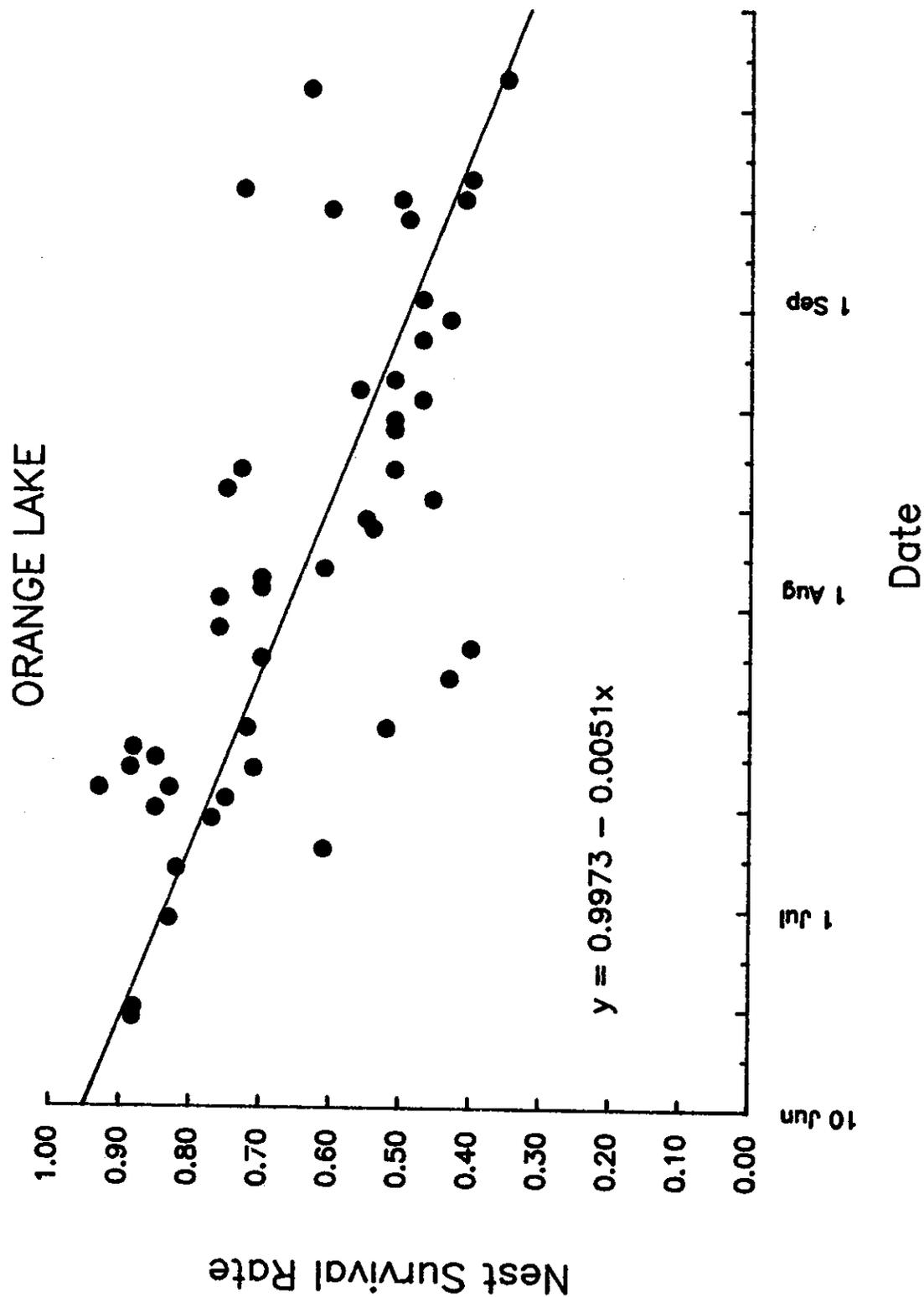


Fig. 23. Proportion of alligator nests surviving through incubation and associated linear trend for non-flooded nests on Orange Lake during 1980-90.

unknown. P. Wilkinson (pers. commun.) has suggested that timing and site for alligator nest searches is a learned behavior by local raccoon populations and may be passed on to succeeding generations.

Time of predation is important when determining optimum collection time for egg harvest programs (Joanen and McNease 1987b, Jennings et al. 1988, Woodward et al. 1989). A constant rate of survival supports the concept of collecting clutches early in incubation to preclude losses to predation.

Nest Flooding. -- The increasing trend over years in nest survival was attributed to decreasing occurrence of nest flooding ($P < 0.001$) on all study sites (Fig. 22). Compared at area means of water level, estimated flooding rate was greater on Paynes Prairie than on any other area, but only the comparison with Orange was detectable ($P = 0.004$; Table 10; Fig. 22). Increased occurrence of nest flooding with greater water level was not detected ($P = 0.444$). Flooding is a major cause of nest losses in some habitat types, especially shallow marshes or wet prairies with little physical relief (Hines et al. 1968, Joanen 1969, Wilkinson 1983, Joanen and McNease 1989, Kushlan and Jacobsen 1990). In Florida, water levels tend to rise gradually through the incubation period from low levels in June (Kushlan and Jacobsen 1990, Fig. 4), exposing eggs to continually increasing flooding risk.

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Clutch Characteristics

Clutch Size. -- Clutch size distribution was symmetrical on Orange, left-skewed on Woodruff, and right-skewed on Paynes Prairie (Fig. 24). We found no AREA \times YEAR interaction in the analysis of either clutch size median or skewness. Mean median annual clutch size was greater for Woodruff ($P < 0.001$) than for Orange and Paynes Prairie (Table 13). Mean clutch size skewness differed among areas ($P = 0.011$), and mean skewness for Paynes Prairie was greater than that for Woodruff ($P = 0.003$, Fig. 24). We detected no trends in median clutch size ($P = 0.428$) or distribution skewness ($P = 0.662$).

Average clutch sizes were similar to those found for Orange Lake and Paynes Prairie during 1974-77 (Deitz and Hines 1980). Joanen (1969) found no association between clutch size and female size for Rockefeller alligators, nor did Deitz and Hines (1980) for Orange Lake and Paynes Prairie alligators. However, Wilkinson (1983) observed a positive relationship between the 2 parameters for South Carolina alligators. Clutch weight may more precisely reflect female size (Deitz and Hines 1980, Hall 1991), but we had insufficient data on clutch weight (1988-90) to test for trends over the study period. We suspect that clutch size is controlled by a combination of female size and condition. In either case, we found no evidence to indicate that harvest affected the biological processes controlling clutch size.

Clutch sizes for Orange and Paynes Prairie were smaller than those reported for other Florida lakes (Woodward et al. 1989, 1993), but comparable to those reported for the Everglades (Kushlan and Jacobsen 1990) and for small isolated wetlands in northcentral Florida (Goodwin and Marion 1978). Although some evidence suggests that clutch size is a function of female size (Ferguson 1985, Hall 1991), other factors such as nutrition and residual lipid supplies (Fischer et al. 1991) may also influence clutch size. Mesotrophic-eutrophic wetlands with highly fluctuating water levels (Orange Lake, Paynes Prairie, and the Everglades) may have lower fish biomass (kg/ha) relative to hypereutrophic wetlands such as lakes Apopka, Griffin, Jessup, Okeechobee, and Woodruff (Kautz 1980) which have greater clutch sizes than Orange and Paynes Prairie (Woodward et al. 1989). Of particular interest was the relatively high phosphorus level on Woodruff compared to Orange (Table 1). Phosphorus is considered the most important element limiting primary productivity on Florida lakes (Canfield 1981), and is closely associated with fish biomass. Food (fish) availability may affect energy available for egg production. We were not able to further examine this hypothesis, but investigations into the relationship of nutrient levels of wetlands and alligator clutch size and weight are recommended.

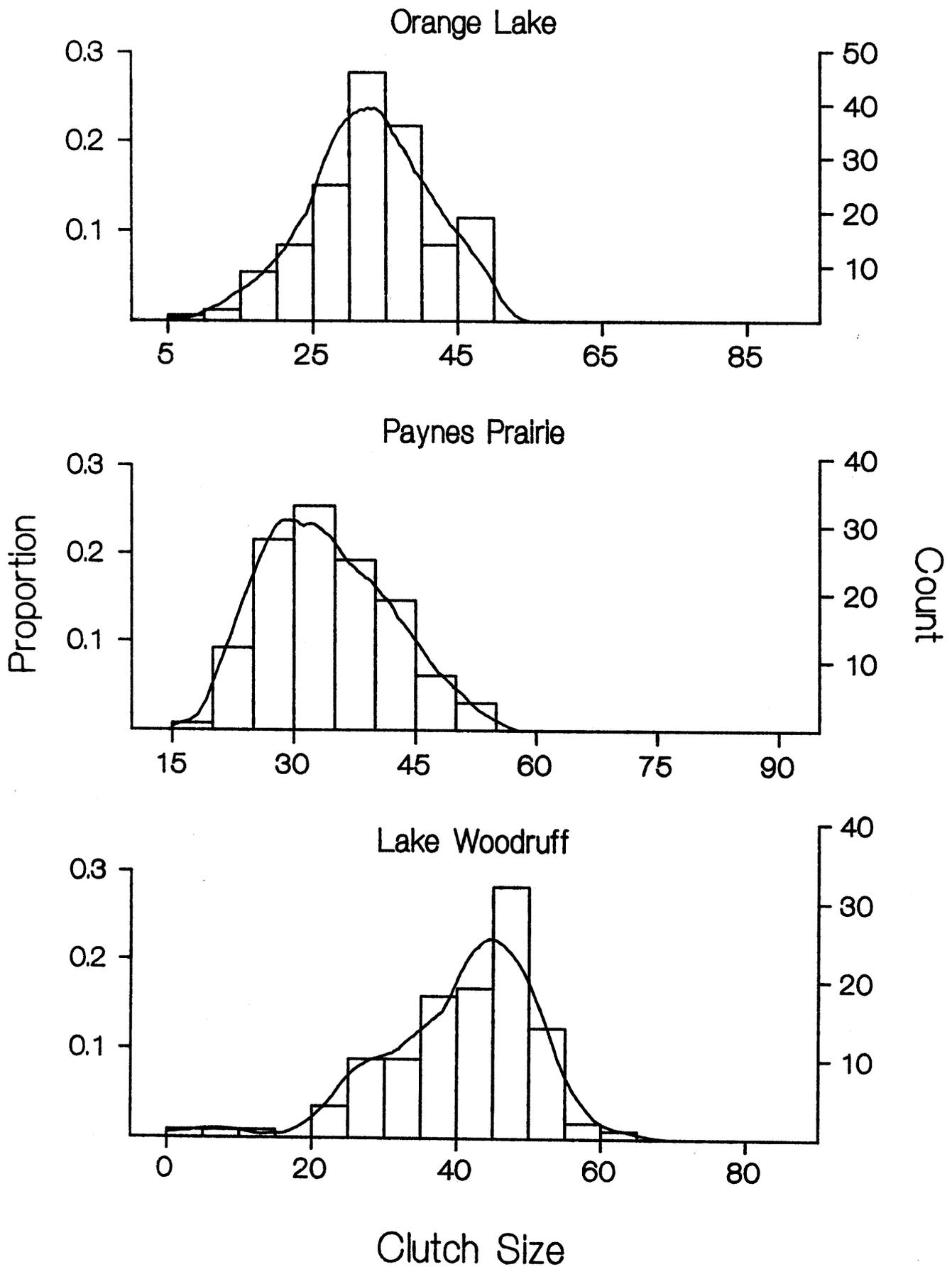


Fig. 24. Clutch size distributions for 3 alligator populations from 1983-90. A smoothed, nonparametric estimate of the distribution shape is overlaid on each histogram.

Table 13. Median number of clutches inspected/yr (n_{md}); and minimum (min), maximum (max) and mean^a estimated clutch sizes at mean year (1986.5) for 3 Florida alligator populations during 1982-90. Median banding rate and proportion (Pr) of clutches with perfect (1.0) banding are also reported.

Parameter		Study area		
		Orange	Paynes Prairie	Woodruff
Clutch size	n_{md}	22.5	14.0	12.5
	min	14	21	21
	max	49	52	61
	\bar{x}	32.8	33.8	42.9
	SE	0.77	0.86	0.95
Banding rate	n	156	115	104
	median	0.975	0.968	0.973
	Pr = 1.0	0.55	0.43	0.52

^aDerived from mean of annual median values.

Banding Rate. -- Distributions of banding rate observations were strongly left-skewed (most data points were equal to or in the vicinity of 1.0) for all areas (Table 13). Probability of complete banding success varied over time (Fig. 25), but at rates that differed by area ($P = 0.020$). During 1983-90, the estimated declines in probability on Orange and Woodruff were different from the estimated increase on Paynes Prairie ($P \leq 0.017$, Fig. 25). For clutches with banding rates < 1.0 , we found no evidence of differences among areas (Table 13) and detected only a weak increasing trend. For both banding rate analyses, we found no consistent evidence of differences in banding rates among areas, although differences may have occurred in specific years. Apparent declines in complete banding success for Orange and Woodruff were caused by an increase, over years, of frequency of clutches with 1-several unbanded eggs. Although this would have reduced the proportion of complete banding successes, it also would have increased the incidence of high banding rates for clutches with less than complete banding success, thus producing apparently conflicting results. The net result is a smaller decrease in banding rate. Median banding rates (Table 13) were somewhat higher than the combined Orange Lake and Paynes Prairie "fertility" rate (89.1%) reported by Deitz and Hines (1980) for 1976-77. However, higher rates in our study may reflect an improved ability to distinguish bands on eggs. Banding rates for our study areas were slightly greater than published banding rates for other populations in Florida (Woodward et al. 1989, 1993) but comparable to those reported for Rockefeller Refuge, Louisiana (Joanen and McNease 1987b, 1989).

Viability Rate. -- Viability rate observations were limited ($n = 59$) and restricted to the period 1988-90. We found no evidence of AREA \times YEAR interaction ($P = 0.328$), differences in viability rates among areas ($P > 0.872$), or trend over years ($P = 0.982$). Median viability rate for all areas combined was 0.875. The viability rate was greater than those for other Florida wetlands reported by Woodward et al. (1989, 1993) and Percival et al. (unpubl. rep., Fla. Coop. Fish and Wildl. Res. Unit, Gainesville, 1991) and comparable to viability rates reported for Louisiana (Joanen and McNease 1987b, 1989). Our viability rate measured survival rate of embryos to time of inspection, usually prior to day 40 of

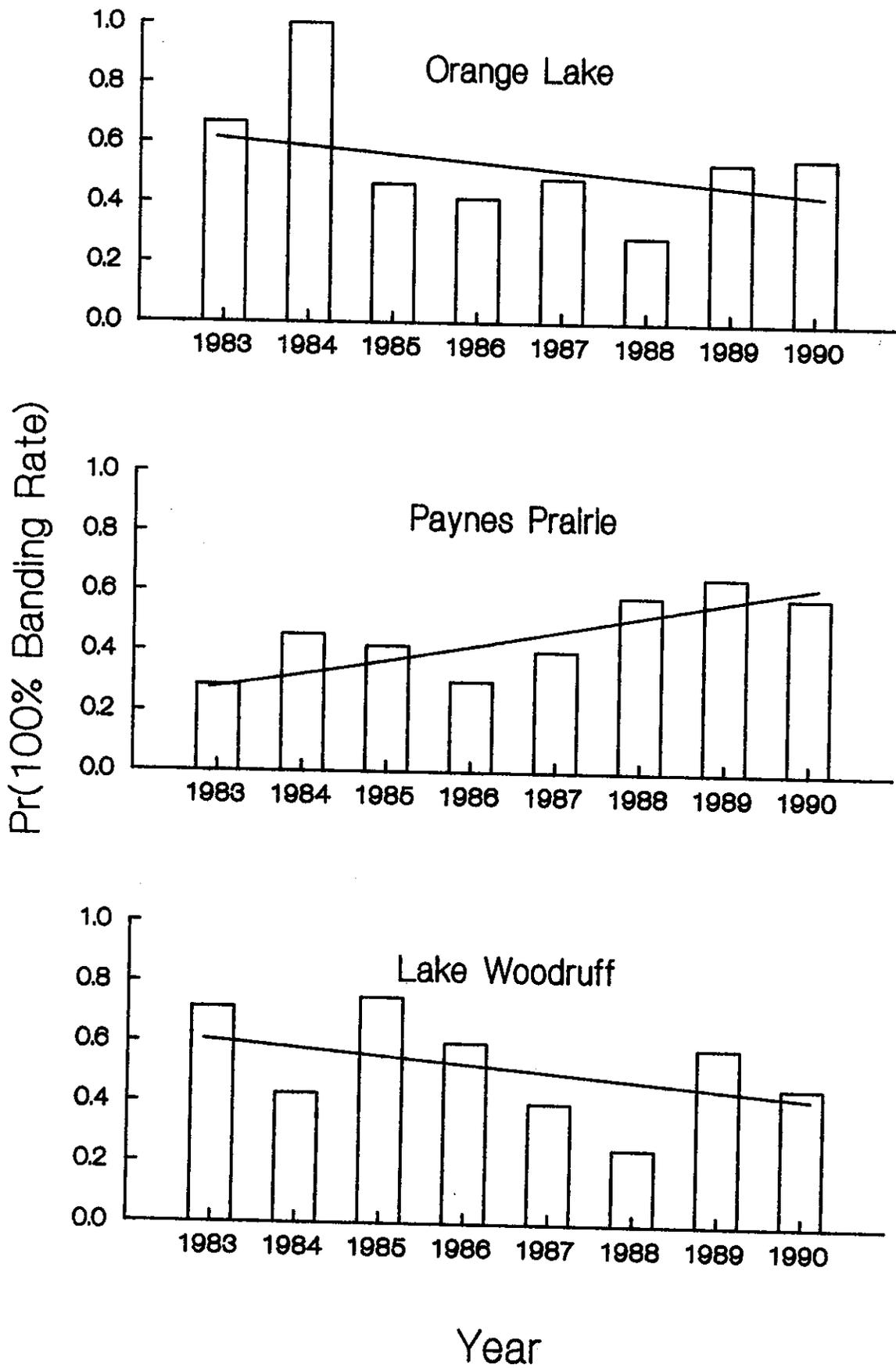


Fig. 25. Observed proportion and estimated trends in probability of encountering alligator clutches with 100% banded eggs for 3 alligator populations during 1983-90.

incubation. Percival et al. (unpubl. rep., 1991) found 15% embryo mortality occurring after day 40 of incubation. Our use of viability rate almost certainly overestimated embryo viability to hatch, but the difference should not have altered our conclusion that the viability rate for Orange, Paynes Prairie, and Woodruff represents a marked departure from other rates reported for Florida. Tests of viability rates under controlled incubation conditions would provide added insight into viability rate variation among Florida wetlands and possible factors affecting clutch viability.

Oviposition Time. -- We found an AREA \times YEAR interaction ($P < 0.001$) for estimated mean oviposition date, which indicated that dependence of oviposition date on year varied by area. Estimated mean annual oviposition dates were similar among areas in 1984 (pooled mean = 27 June), but departed and were different among all pair-wise area combinations by 1990 ($P < 0.003$; Table 14). Estimated mean oviposition date declined ($b = -1.394$, $P = 0.002$) on Woodruff during 1984-90, but did not change over that same period on Orange and Paynes Prairie. Pooled mean year (1987) oviposition date for all areas was 26 June (Table 14). Estimated oviposition dates ranged from 30 May on Orange to 16 July on Paynes Prairie (Fig. 26). Hatching ranged from 3 August on Orange to 19 September on Paynes Prairie; 53.5% of hatching was completed by 1 September, 85.8% by 7 September, and complete by 19 September (Fig. 27).

Mean oviposition dates for our study area were similar to those reported by Woodward et al. (1989) for lakes in central and south Florida. Oviposition date ranges were similar to those reported for Orange Lake and Paynes Prairie by Deitz and Hines (1980) but were more protracted than oviposition dates reported for Rockefeller Refuge, Louisiana (Joanen and McNease (1979), and for South Carolina (Wilkinson 1983). Joanen and McNease (1979) concluded that Mar-May air temperatures determined oviposition timing, but Wilkinson (1983) found no clear relationship between spring air temperatures and oviposition time. We hypothesize that mean oviposition dates are similar throughout the range of the alligator but that range in oviposition dates varies with spring air temperatures. This is supported by a comparable mean but greater range in oviposition dates for clutches from Lake Okeechobee (Woodward et al. 1989), the most southerly reported, compared with clutches from other Florida populations.

Harvested Females

Size at Maturity. -- Minimum size at maturity was 94 cm SVL (180.5 cm TL) for Orange (Table 15). Therefore, we considered alligators ≥ 94 cm SVL as reproductive-size females, a measurement of reproductive potential rather than reproductive success. Smallest and largest sizes at puberty were 90 cm SVL (175 cm TL) on Orange and 124.5 cm SVL (245 cm TL) on Newnans.

Probabilities of immaturity were strongly and sigmoidally associated with size ($P < 0.001$; Fig. 28). No interactions among AREA, time group, or SVL were detected. Maturity occurred at smaller sizes for Orange alligators than Newnans alligators ($P = 0.013$), but Lochloosa alligators did not differ in this respect from other areas. Specifically, the estimated proportion of alligators undergoing puberty increased ($P = 0.042$) at the expense of both immature and mature alligators (Fig. 29). Therefore, in later years, puberty began at a smaller size and maturity commenced at a larger size. The extended range of sizes for pubescent alligators may reflect increased growth rates through puberty, although our growth rates analysis could not confirm this (See GROWTH RATES below). Predicted proportion of mature females at 213 and 244 cm TL varied by area (Table 15).

We found minimum size at maturity (180.5 cm) to be comparable to the 1.8 m TL observed by Joanen and McNease (1980). However, the average size at maturity among areas was associated with growth rate; Newnans alligators grew faster and attained sexual maturity at greater lengths than Orange alligators. This indicates that onset of sexual maturity may be partly controlled by age as well as size.

Our findings on age at maturity differ from those of Wilkinson (1983) who found maturity to commence at 203 cm TL, and attainment of maturity by most females at 220 cm. Wilkinson (1983) attributed the larger size to the generally cooler spring temperatures in South Carolina and the inability of smaller females to store adequate heat to begin and sustain vitellogenesis. Our data suggest the

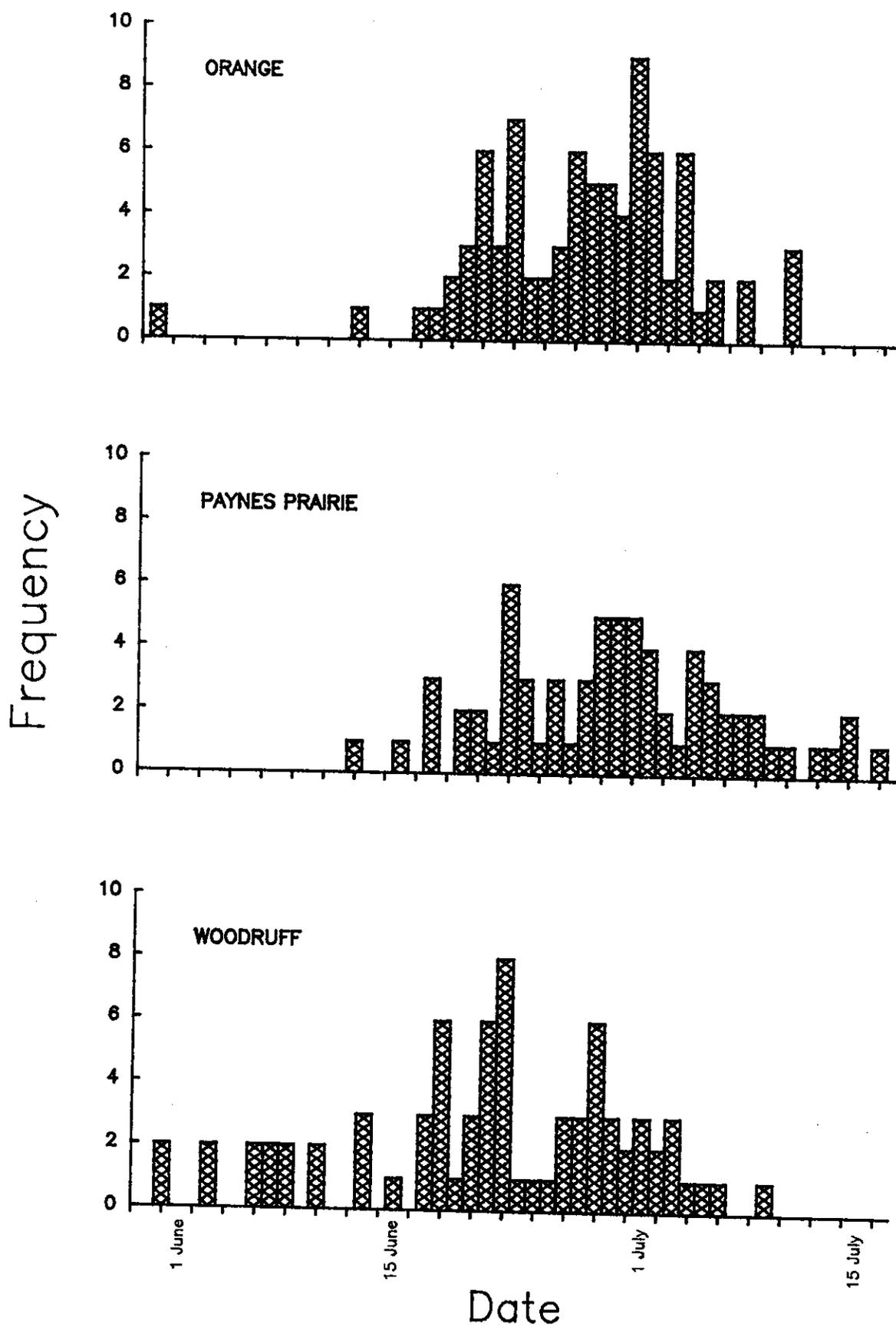


Fig. 26. Frequency distributions of oviposition dates for 3 alligator populations during 1984-90.

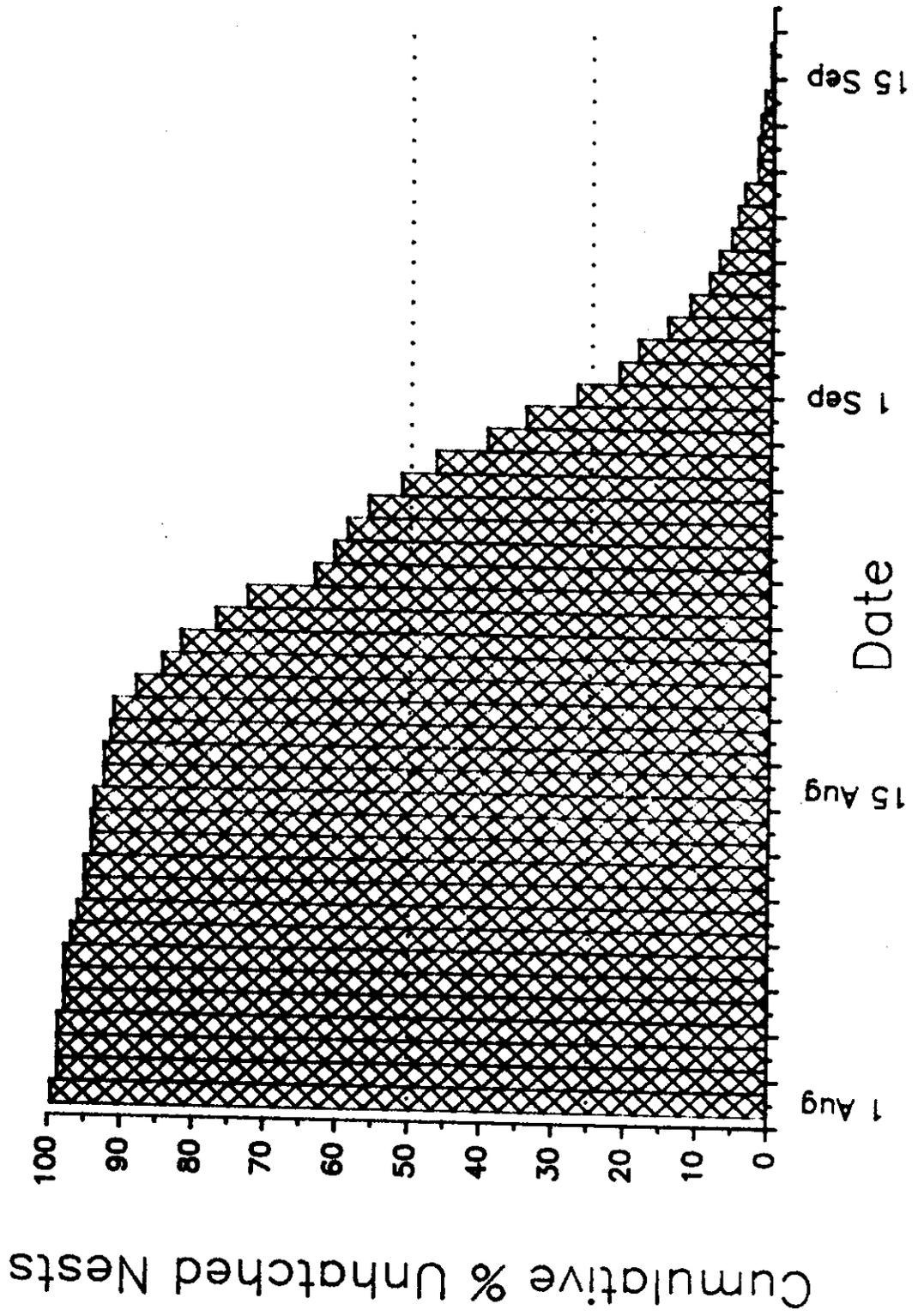


Fig. 27. Pooled cumulative frequency distribution of proportion of unhatched alligator nests for Orange Lake, Paynes Prairie, and Lake Woodruff during 1984-90.

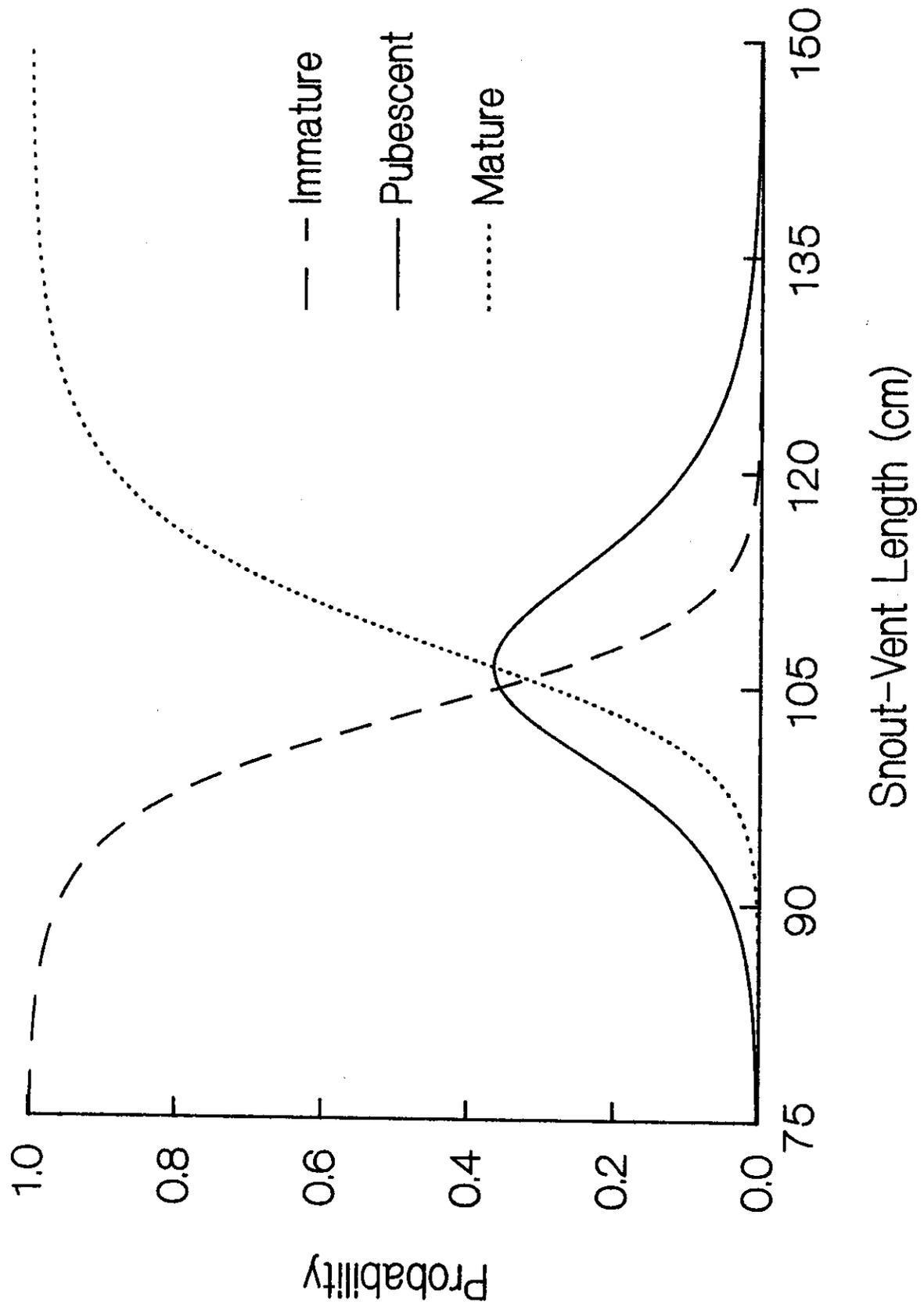


Fig. 28. Estimated relationship of maturity status probability to snout-vent length for female alligators on Lochloosa, Newnans, and Orange lakes, 1981-90.

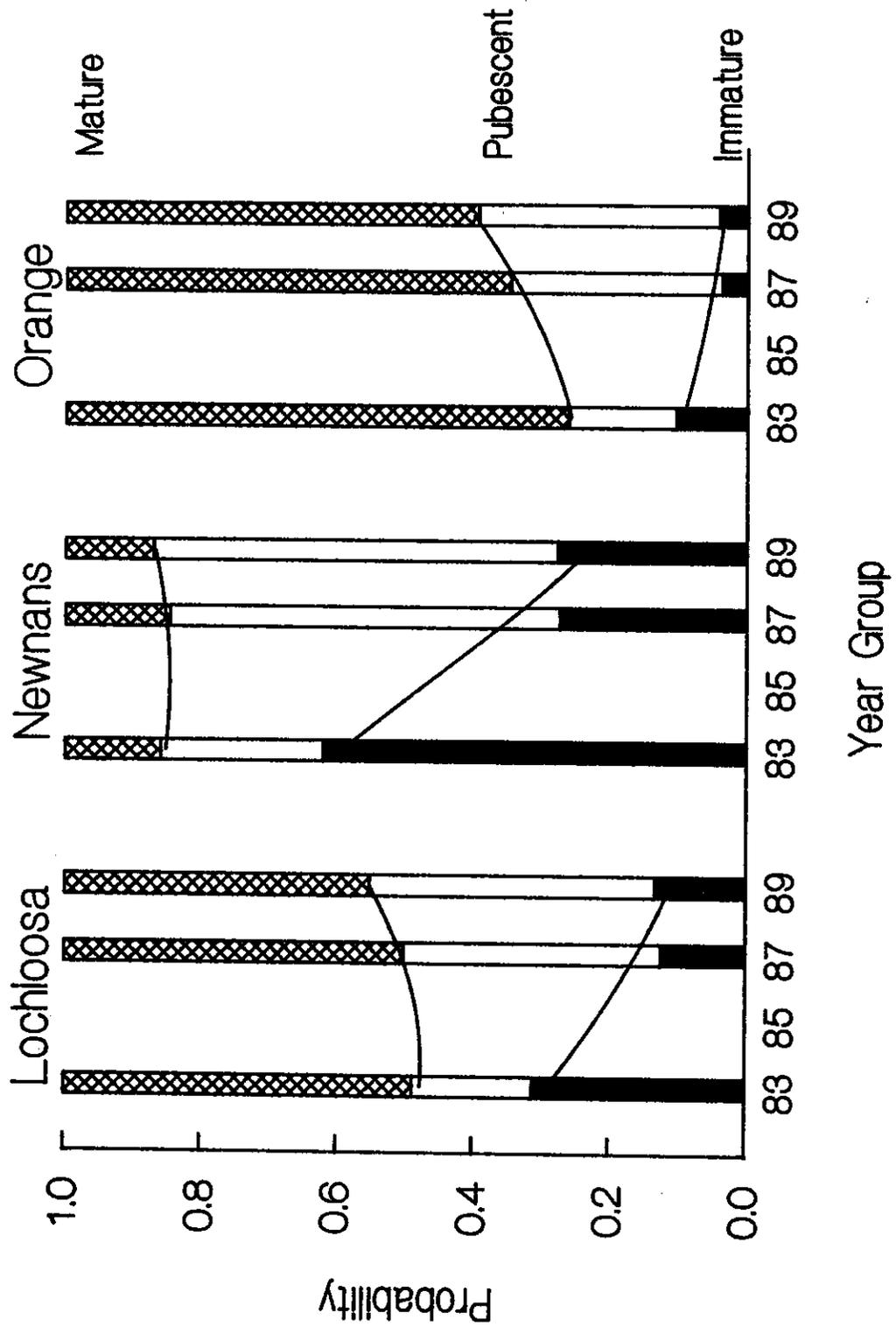


Fig. 29. Trends over years in 3 estimated maturity status probabilities for a 107 cm SVL (209 cm TL) female alligator in each of 3 Florida alligator populations.

possibility that female alligators sampled by Wilkinson (1983) grew relatively fast, similar to Newnans alligators.

Table 14. Mean oviposition dates for 3 alligator populations during 1984-90. Mean oviposition dates were not different among populations at the Bonferroni-protected level ($P = 0.008$) in 1984 but were different in 1990.

Area	<i>n</i>	Year		
		1984	1987	1990
Orange Lake	83	28 June	26 June	24 June
Paynes Prairie	68	25 June	29 June	2 July
Lake Woodruff	75	26 June	22 June	18 June
Pooled areas	226	27 June	26 June	25 June

Proportion of Mature Females Ovulating. -- No interactions among AREA, time groups and SVL were detected in analysis of postpartum status probability. We found no overall differences among areas ($P = 0.106$), nor did we detect any differences in postpartum probability in pair-wise comparisons between specific areas. However, we found weak evidence ($P = 0.035$) of a greater postpartum probability for Orange than for Newnans alligators at any SVL or time group (Table 15). We found no evidence that probability of postpartum condition changed with SVL of mature females ($P = 0.431$), nor did we detect a trend in proportion of postpartum females over time ($P = 0.281$). In the analysis of the Orange sample by year, neither year trend ($P = 0.519$), water level ($P = 0.603$), nor hunter effort ($P = 0.788$) influenced proportion of postpartum females.

Prior to the hunts, we speculated that postpartum females would be under-represented in the take of mature females because they: (1) preferred less-accessible marsh habitat for brooding hatchlings and (2) hunters might not take females with pods on ethical grounds. We thought increased water levels would expose a greater proportion of brooding females to harvest by allowing access to marsh. However, we saw no evidence of this relationship. As hunts progressed and hunter effort increased to maintain success, we hypothesized that hunters would be less likely to pass over brooding females. Again, we saw no evidence of an increase in proportional take of postpartum females. Failure to detect associations may have been due to inadequate sample size, our inability to accurately measure water level and hunter effort variables, or our failure to consider other external influences on proportional take of postpartum females. Furthermore, if females from unsuccessful nests left nest sites and joined other non-reproductive females in less protected habitat, a greater proportion of the postpartum population would have been exposed to hunting. Questions concerning female vulnerability to hunting may only be resolved through further investigations using radio-telemetry.

Studies of female crocodylian reproductive tract morphology have largely focused on development prior to and regression immediately after oviposition (Graham 1968; Joanen and McNease 1980; Kofron 1987, 1990; Lance 1987, 1989; Taylor et al. 1991). Only Guillette et al. (1994) have produced a detailed study of the September reproductive tract morphology of female crocodylians when an ample supply of specimens is available for evaluation from harvests in Louisiana and Florida.

Table 15. Observed size of smallest mature female alligator sampled, estimated probability of maturity at 3 TL sizes (cm), and proportion of postpartum (*PP*) mature females for 3 harvested areas during 1983-90.

Area	<i>n</i>	Obs. size		<i>P</i> mature			<i>PP</i>
		SVL	TL	≥ 183	213	244	
Lochloosa	13	96.5	(193.0)	0.621	0.601	0.943	0.385
Newnans	19	112.0	(211.0)	0.667	0.204	0.834	0.158
Orange	88	94.0	(180.5)	0.627	0.749	0.978	0.398
Overall \bar{x}					0.497	0.947	0.314

Corpus luteum size was the only reliable indicator of past reproduction (Guillette et al. 1994). However, corpora lutea regress relatively quickly in crocodylians (Graham 1968, Guillette et al. 1994) and, by September, are less than 30% of their original size, making classification of postpartum females difficult. Guillette et al. (1994) followed the regression of corpora lutea by examining a sequence of reproductive tracts removed from nesting and brooding females from late June to late November, thus providing us with a high level of confidence in our ability to determine past reproductive status.

We found no relationship between nesting probability and mature female size. This does not support the findings of Joanen and McNease (1980) and Taylor et al. (1991), who found a higher nesting rate among larger (>228 cm) than smaller mature female alligators. Low sample size and biased sampling may have contributed to our inability to find a relationship. However, lower densities of large females as a result of hunts may have reduced competition for reproductive resources and permitted increased nesting rates for smaller adult females. This phenomenon has been observed for captive adult alligators in Florida (Cardeilhac 1989) and Louisiana (Elsie et al. 1990).

GROWTH RATES

Maximum Size

Harvest size distributions (Fig. 10) provided an indication of the mean estimated maximum length of alligators. Appendix D provides sizes for the 10 largest male and female alligators taken from harvest lakes. The largest male alligator was 423 cm (13 ft. 10 1/2 in.), weighed 473 kg (1043 lbs.), and was taken from Orange as a nuisance alligator in 1989. The only larger Florida alligator measured by biologists since nuisance alligator harvests began in 1977 was a 427-cm (14 ft. 1/8 in.) alligator from the Apalachicola River in Gulf County, Florida in 1989. The largest female alligator taken during our study [TL = 297 cm (9 ft. 9 in.), WT = 115.5 kg (255 lbs.)] was from Orange. The record female alligator [TL = 304.8 cm (10 ft. 0 in.)] was taken during an experimental harvest on Lake George in 1986.

Based on the size frequency curve generated from our harvest data, we predict 430 cm as the mean maximum size for male alligators and 300 cm for females on our study areas.

Growth Rates

Seasonal Growth Rate Variability. -- Relative to summer-fall growth rates, alligator growth was slow in the winter and rapid in the spring ($P \leq 0.001$; Fig. 30), but the specific pattern of seasonal growth varied by area-sex cohort. For all areas and both sexes, a compromise model of seasonal growth featured a zero winter growth rate, a spring growth rate 2.8 times that of summer-fall, and onset dates of 1 Nov, 15 Apr, and 15 Jul for the winter, spring, and summer-fall growth phases (Fig. 30). For the model results that follow, we smoothed out seasonal growth spurts and dormancies by relating size to growing time rather than to calendar time.

Growth Curve Estimation. -- Over the period 1975-90, we obtained measurements on 439 female, 965 male, and 1,984 indeterminate-sex, known-age alligators. The majority (69%) were recorded on Orange (Table 16). Ranges of size (10.2-114.5 cm SVL) and age (0.0-12.0 yr) were limited relative to known ranges reported for *A. mississippiensis* (Joanen and McNease 1987a, Woodward et al. 1987a).

We recorded 655 female, 1,156 male, and 398 indeterminate-sex capture-recapture occasions for which the time between captures did not fall entirely in 1 winter growth period (1 Nov-15 Apr of successive years, see below). Most records (81%) were from the Orange study area (Table 17). Time range between captures was wide (1 day-13.5 yr), and we observed a greater size range (12.2-176.4 cm mean capture SVL) among MC than among KALC alligators. Because of unavoidable measurement error which is magnified on smaller alligators recaptured over short periods of time, raw growth rate (size increase/time) varied wildly (-29 - 256 cm/yr) and was sometimes (4.2%) negative or zero. Because variability was greatest among hatchlings recaptured ≤ 75 growing days of first capture, and because growth rate values ≤ 0 cm/yr cannot be utilized in growth rate curve estimation, we excluded data for such captures from further analysis.

We successfully fit the power growth model to MC data for both sexes from each area, but we could not fit the more complex Richards model to the limited data from Newnans. Quality of each fit varied by area and sex but tended to be greater for the power (R^2 range: 0.4046-0.7667) than for the Richards model (R^2 range: 0.2869-0.6685). We lacked sufficient data to fit growth models to KALC data from Newnans (Table 16, Fig. 30). However, the models fit the data from the remaining samples well, and the quality of the fit was about the same for both the power (R^2 range: 0.8698-0.9869) and the Richards (R^2 range: 0.8703-0.9880) models. Weighted R^2 for each model type fit to MC and KALC data simultaneously was typically greater for the power (range 0.7490-0.8516) than for the Richards (range 0.7005-0.7965) model.

Several studies of crocodylians, mostly of known-age juveniles, have documented seasonally varying growth (Webb et al. 1978, 1983; Chabreck and Joanen 1979; Hutton 1987; Jacobsen and Kushlan 1989; Brandt 1991). However, attempts to incorporate this variability into models of adult growth differed among studies. Brisbin (1990) and Jacobsen and Kushlan (1989) did not model or adjust for seasonal growth variability. Others (Webb et al. 1978, 1983; Chabreck and Joanen 1979; Fuller 1981; Hutton 1987) adjusted for seasonal growth variability by calculating, either directly or in essence, a growth time interval as the portion of time between captures falling in a predetermined growing season.

No growth was assumed to occur outside of the growing season, and growth within the season was assumed to be constant, although Chabreck and Joanen (1979) and Jacobsen and Kushlan (1989) offered evidence contradicting these assumptions. Ours is the first attempt that we are aware of to test these assumptions and to estimate onset, rate, and duration of seasonal growth from the data.

Estimated growth curve shapes differed between sexes ($P < 0.001$) and among Lochloosa, Orange, and Woodruff areas ($P < 0.001$; Newnans curves were not statistically compared for lack of data). As a result, alligator growth rate differed by area, sex, and size (Table 18, Fig. 31). Growth was slow for Woodruff alligators < 122 cm relative to those on other areas (Table 18). Between 122 and 183 cm, growth rates of Lochloosa and Newnans alligators were greater than those of Orange and Woodruff

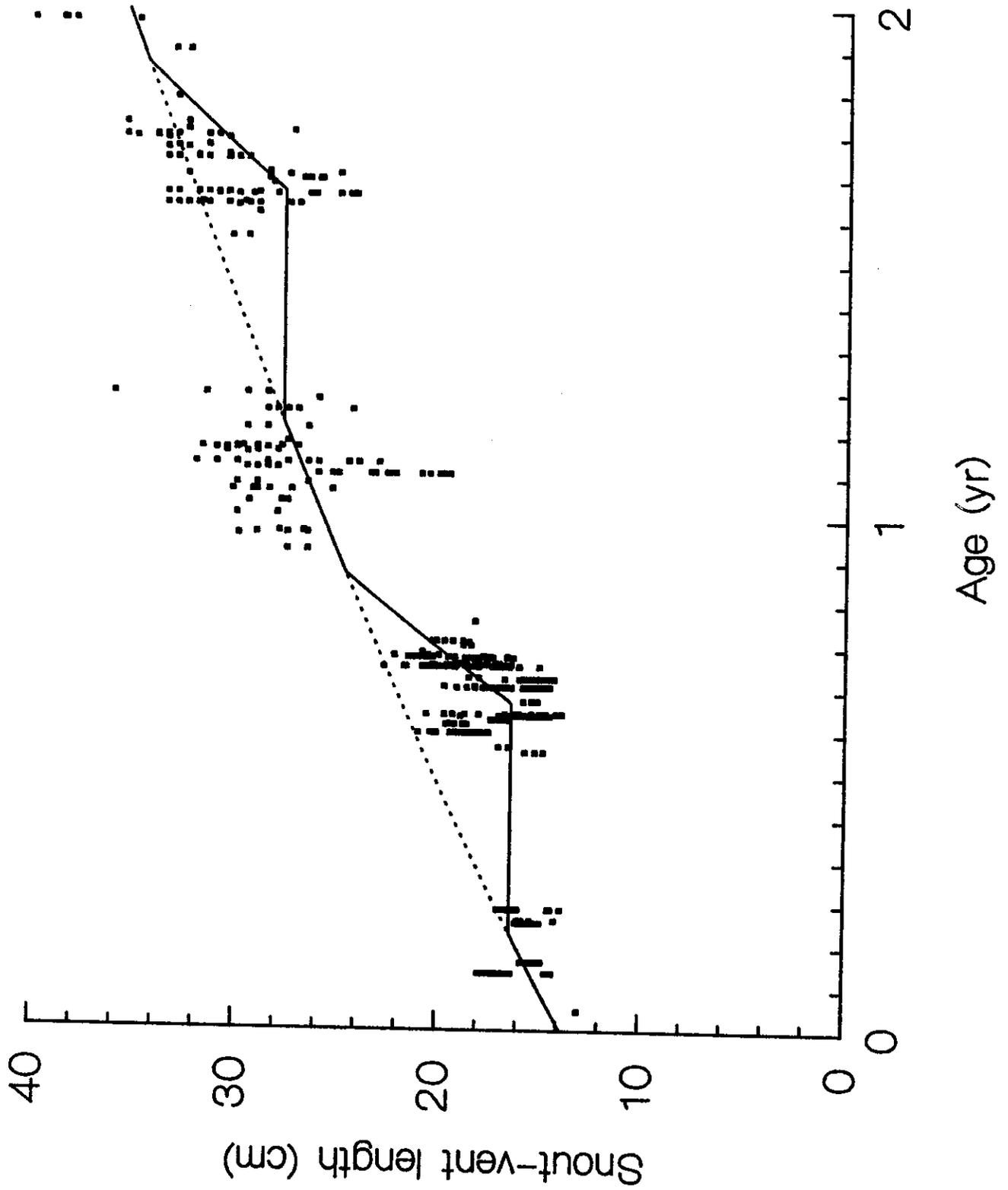


Fig. 30. Snout-vent length versus age for male Orange Lake alligators <2-yr old. Estimated seasonal pattern of growth deceleration and acceleration is displayed as a solid line. To make use of smooth, uninterrupted growth curves, we assigned growing ages to alligators. Growing age of an alligator was that value on the age axis corresponding to the intersection of a horizontal line drawn through predicted size of the alligator (a line connecting the Y-axis and the solid line) and the smooth growth curve (dashed line).

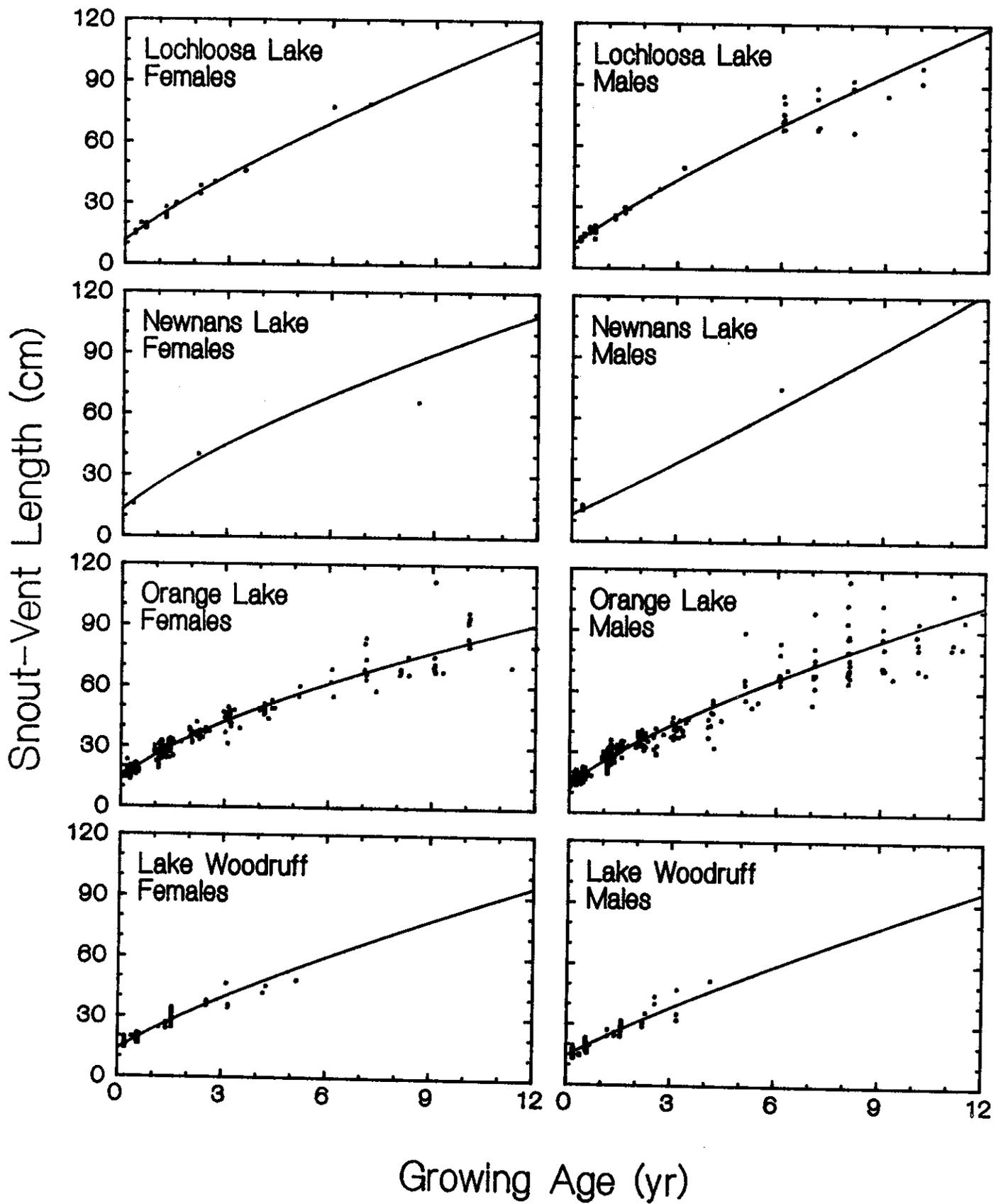


Fig. 31. Growth of snout-vent length for male and female alligators from 4 alligator populations. Estimated power curves were derived from known-age and multiple-capture data but data points are displayed for the known-age component only.

(Table 18). On all areas, males grew faster than females in the 122-183 cm size range (Table 18). For females, estimated time to attain minimum reproductive size (180 cm for Lochloosa and Orange and 211 cm for Newnans) ranged from 8.9 yr on Lochloosa to 12.4 yr on Orange (Table 18). Range of time to estimated median reproductive size was 10.9 yr (Lochloosa) to 15.0 yr (Orange).

Because captures of old, known-age crocodylians are rare, some models of size growth using KALC-type data limited inference to juveniles of known age (Murphy 1981, Brandt 1989, Jacobsen and Kushlan 1989) or to those animals that could be aged approximately via skeletochronology (Graham 1968, Hutton 1987). Brisbin (1990) fit growth curves to McIlhenny's (1934) 64 measurements of Louisiana alligators observed at 0-11 years of age. However, most studies employed MC-type data (Webb et al. 1978, 1983; Chabreck and Joanen 1979; Fuller 1981; Hutton 1987; Jacobsen and Kushlan 1989) or distance between femur annuli (Craig et al. 1990, unpubl. rep.) to relate the growth interval to animal size. Two approaches to analyzing alligator capture-recapture data have been taken. Chabreck and Joanen (1979) and Fuller (1981) modelled size at recapture as a function of size at initial capture and the time interval (Fabens 1965). Jacobsen and Kushlan (1989) modelled growth rate between captures as a function of average capture size (White and Brisbin 1980, Kaufmann 1981), as we have done.

Growth curves estimated from KALC-type data are said to be in integral form, and those estimated from MC-type data that provide growth rate at capture size are in derivative form (White and Brisbin 1980, Kaufmann 1981). The form chosen in growth studies is dictated by the type of data available. This mathematically-based nomenclature for curve form implies that although the algebraic expressions of the integral and derivative forms of a curve may differ, all curve parameters found in the derivative form are also found in the integral form. For example, parameter b in the linear growth model represents growth rate in both the model's derivative ($dy/dx = b$) and integrated ($y = a + bx$) forms. Likewise, unless the 2 types of data differ in some manner that would affect inference on growth (e.g., different age ranges represented in the 2 data types), the group of curve parameters estimated in either model form is an independent set of estimates of a common group of parameters. Therefore, most efficient use of KALC and MC data would combine both data types for joint estimation of parameters common to both growth model forms. To our knowledge, this has not been attempted for crocodylian data.

Our selection of the power (Kaufmann 1981, Jacobsen and Kushlan 1989) over the Richards (Richards 1959, White and Brisbin 1980, Brisbin 1989) model implied that alligators do not grow to a determinate, or asymptotic, size. Among crocodylian studies that investigated adult growth, most earlier ones assumed determinate growth (Webb et al. 1978, 1983; Chabreck and Joanen 1979; Fuller 1981; Hutton 1987; Brisbin 1990), although Graham (1968) and later studies by Jacobsen and Kushlan (1989) and Craig et al. (1990, unpubl. rep.) allowed the possibility of growth to indeterminate size. Brisbin (1990) argued that alligator growth may be intrinsically determinate but that the phenomenon is more likely observed in long-lived captive animals than in wild animals exposed to a wider range of mortality factors: the conclusion of indeterminate growth is but an artifact of the lifespan of the studied population. Jacobsen and Kushlan (1989) rejected growth models with size asymptotes in favor of a model having no size limit. They pointed out that confidence in their model selection was constrained within the size range of their data (<170 cm SVL) and that uncontrolled sources (e.g., seasonal, yearly, and age-dependent) of growth variability in long capture intervals and high measurement variability in short capture intervals may have obscured selection of other models. However, Jacobsen and Kushlan (1989) offered bioenergetics rationale and morphological evidence supporting the hypothesis of indeterminate growth in alligators. Our sample limits (oldest KALC animal = 12.0 yr, largest MC size = 176.4 cm SVL) matched or exceeded that of contemporary alligator growth studies yet fell substantially short of reasonable life span estimates (30-50 yrs) and the size range of the largest alligators sampled (211-226 cm SVL, Appendix D). Although our conclusion that the power model best fits our data was consistent with that of Jacobsen and Kushlan (1989), our sample limits were much too small to conclusively reject either hypothesis of determinate or indeterminate growth.

Alligator growth on Orange may best be modelled by a growth curve with distinct phases. The overall growth pattern can be summarized by: (1) a 2-yr period of fast growth, (2) a 4-yr slow down

Table 16. Sample statistics for known-age at last capture alligators used in growth rates analysis.

Study Area - Sex	n	Age (yrs)			SVL (cm)		
		min	median	max	min	median	max
Lochloosa - female	39	0.68	0.79	7.09	14.6	19.4	78.7
Lochloosa - male	76	0.18	0.79	10.07	13.2	19.0	99.0
Lochloosa - indet. ^a	175	0.04	0.19	1.06	11.0	14.0	22.0
Newnans - female	4	0.68	1.43	8.77	15.8	28.2	66.0
Newnans - male	11	0.68	0.68	6.05	15.1	16.0	74.9
Newnans - indet. ^a	32	0.19	0.69	0.91	13.5	16.0	22.5
Orange - female	272	0.11	1.16	12.03	13.7	27.8	112.0
Orange - male	665	0.04	0.73	11.73	13.0	20.5	114.5
Orange - indet. ^a	1385	0.00	0.13	1.97	10.2	14.6	37.0
Woodruff - female	122	0.20	0.77	5.16	14.4	19.1	48.5
Woodruff - male	209	0.20	0.58	4.16	13.1	16.8	52.0
Woodruff - indet. ^a	256	0.18	0.60	0.81	12.5	15.0	20.4

^aUnable to determine sex.

Table 17. Sample statistics for multiple capture alligators of unknown age used in growth rates analyses.

Study Area - Sex	n	Elapsed Time (yrs)			\bar{x} SVL (cm)			Growth rate (cm/yr)		
		min	median	max	min	median	max	min	median	max
Lochloosa - female	46	0.05	1.64	9.14	16.0	29.0	89.2	-2.3	6.6	21.9
Lochloosa - male	104	0.05	1.32	9.97	13.0	36.0	115.8	-0.9	9.1	30.0
Lochloosa - indet. ^a	35	0.08	0.37	0.92	12.3	14.3	27.8	-1.9	-0.5	1.1
Newnans - female	23	0.26	4.31	11.83	26.5	64.0	123.1	2.4	8.2	24.7
Newnans - male	30	0.29	3.61	11.30	34.6	58.7	155.0	4.8	9.2	24.1
Newnans - indet. ^a	1	0.19	0.19	0.19	19.0	19.0	19.0	36.0	36.0	36.0
Orange - female	521	<0.01	1.00	12.03	13.6	27.9	113.8	-3.3	7.7	49.4
Orange - male	935	<0.01	0.71	13.51	12.4	24.9	176.4	-29.2	8.6	255.7
Orange - indet. ^a	331	0.05	0.48	6.14	12.4	15.9	49.3	-0.9	7.8	57.8
Woodruff - female	62	0.01	1.08	3.89	14.0	24.1	41.3	-7.8	9.3	36.5
Woodruff - male	83	0.01	1.01	3.49	14.5	26.1	57.8	-0.2	8.6	21.2
Woodruff - indet. ^a	16	0.11	0.42	0.42	13.6	14.1	14.7	-2.6	-1.9	3.6

^aUnable to determine sex.

Table 18. Size-specific average growth rates (TL, cm/yr)^a and years to attain harvest size (122 cm), estimated minimum reproductive size (R_{min})^b, and estimated median reproductive size (R_{50})^c, as predicted from power growth models of 4 alligator populations.

Area	Sex	Growth rates				
		Size range		Years		
		0-122	122-183	122cm	R_{min}	R_{50}
Lochloosa Lake	M	19.7	15.9	4.97	8.61	-
	F	19.5	15.1	5.03	8.86	10.88
Newnans Lake	M	17.6	17.9	5.58	10.52	-
	F	19.5	13.3	5.03	11.97	13.04
Orange Lake	M	18.3	11.9	5.34	10.19	-
	F	16.2	9.2	6.06	12.35	14.99
Lake Woodruff	M	15.3	11.7	6.39	-	-
	F	15.6	11.0	6.27	-	-

^aHatch - 122 cm growth rate = $(122\text{cm} - 24\text{cm}) / \hat{A}_{SVL|TL=122}$, 122 - 183 cm growth rate = $(183 - 122\text{cm}) / (\hat{A}_{SVL|TL=183} - \hat{A}_{SVL|TL=122})$, where $\hat{A}_{SVL|TL=x}$ = age predicted from area and sex-specific power growth model for size SVL, the predicted SVL value for TL = x from the overall TL-SVL allometric relationship (Table 7).

^b R_{min} is 180 cm for Orange and Lochloosa and 211 cm for Newnans; estimated age is $\hat{A}_{SVL|TL=R_{min}}$.

^cSize at which estimated probability of maturity is 0.50 (see FECUNDITY); R_{50} is 208 cm for Lochloosa, 201 cm for Orange, and 223 cm for Newnans; estimated age is $\hat{A}_{SVL|TL=R_{50}}$.

(Fig. 32), (3) a second period of accelerated growth to sexual maturity, and (4) continued but diminished growth by both sexes, with growth of females decelerating at a faster rate than that of males (Fig. 33).

We hypothesized that the juvenile growth slow-down on Orange represents a transition period in alligator diets, coupled with increased energy demands for dispersal and possible avoidance of larger alligators. We had insufficient data to determine if this pattern occurred in other populations. The second slow-down phase for females at sexual maturity is likely associated with the high energy demands of egg production and nesting.

Alligators have a relatively long maximum life span and may pass through several growth phases depending on size and habitat. Several studies have documented early growth patterns in alligators (Hines et al. 1968, Bara 1975, Murphy 1977, Fuller 1981, Jacobsen and Kushlan 1989, and Brandt 1991), but extrapolation of resulting curves can lead to faulty assumptions of long-term growth patterns, age at maturity, and asymptotic size (Jacobsen and Kushlan 1989). Although Joanen et al. (1987) demonstrated that juvenile growth rate is linked to conditions during embryonic and neonatal development, absolute linear growth rates may change throughout life in response to environmental conditions, changes in prey availability, and morphological changes in alligators.

Data for growth rates and the resulting age-size relationships of alligators are essential for developing meaningful population models. The only long-term (> 7 yrs) growth studies of wild alligator populations were conducted in southwestern Louisiana (Chabreck and Joanen 1979) and in a thermally altered reservoir in South Carolina (Brandt 1991). Bara (1975) and Murphy (1981) presented growth rates for juvenile alligators in South Carolina, and Fuller (1981) reported growth rates for juvenile North Carolina alligators. Most published information about Florida populations is for juvenile alligators (Hines et al. 1968, Deitz 1979, Jacobsen and Kushlan 1989), and only Jacobsen and Kushlan (1989) provided data on growth of large individuals. There are no published comparisons of SVL growth between sexes or among populations within Florida. Evidence suggests that climate (relative annual growth period) and nutrition significantly affect alligator growth rates (Coulson and Hernandez 1983, Joanen and McNease 1987b). In areas with similar ambient temperatures, we would expect nutrition to be the more important influence on growth rate. We saw some evidence of this on Newnans, which had a higher trophic level (Kautz 1980, Canfield 1981) and faster growth rate than Orange. Jacobsen and Kushlan (1989) attributed slow relative growth of Everglades alligators to sparse prey populations and high metabolic costs. Periodic droughts in shallow wetlands such as the Everglades may temporarily increase available prey (fish and reptiles) in remaining ponds and canals (Kushlan 1974), but severe droughts followed by flooding may reduce prey availability for extended periods. Prey availability in lake habitat is less likely to be affected by droughts and floods, and alligator growth may respond positively under those conditions. We suspect that nutritional quality accounted for higher reported growth rates for Louisiana alligators (Chabreck and Joanen 1979). Further investigations are needed to validate the relationship between wetland trophic level, prey availability, and alligator growth.

Growth Rate Trends

Recaptures. -- For females, positive growth rate trends were detected for alligators with 1 and 2-yr capture intervals (Table 19). Mean trends for all and 2,..., 11-yr capture intervals tended to be negative but were not statistically detectable (Table 19). For males, a negative trend was detected for 1 and 5-yr capture intervals, but positive trends were found for 2, 3, and 4-yr intervals (Table 19). Overall, the growth trend for males was weakly positive, but the 2,...,11-yr mean trend was strongly positive (Table 19). Growth trends may have been biased because of unequal size distribution among capture intervals; smaller alligators were more likely to be caught in short capture intervals.

Skeletochronology. -- For individual growth ring classes, the only detectable trend was for 10-ring females (Table 20). A negative trend was detected for the mean of females with 6-10 rings. No trends were found for males.

Growth rate trend analyses disclosed no clear propensity for female growth rates to increase or decline during the hunt. Sample size of femur sections were adequate to detect a 10% change in SVL,

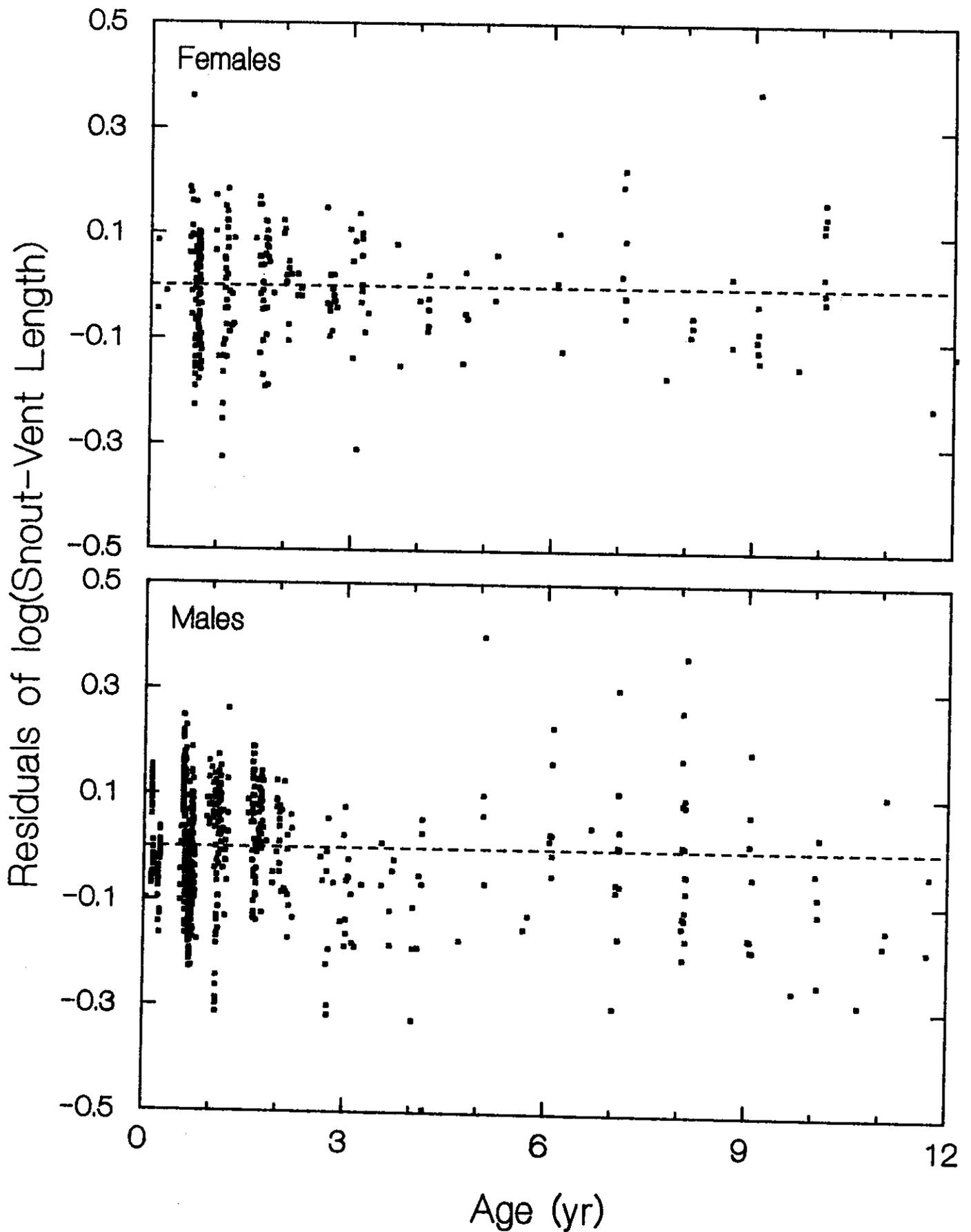


Fig. 32. Residuals (differences between observed and predicted SVL from growth model) for known-age Orange Lake alligators. Evidence of depressed (less than predicted) growth during ages 2-5 years may indicate more than 1 phase of growth.

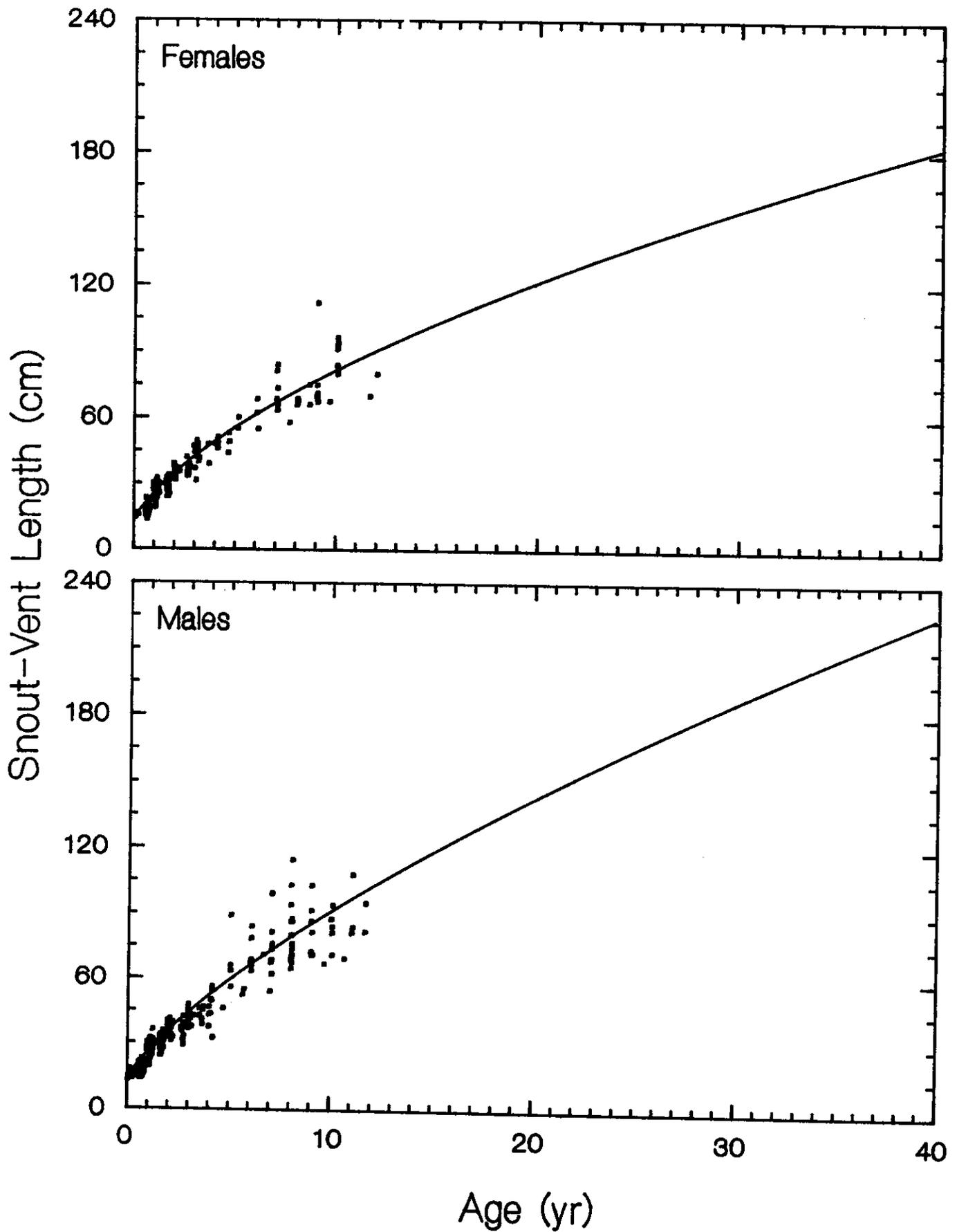


Fig. 33. Growth of snout-vent length for known-age male and female Orange Lake alligators. Estimated power curves are extrapolated to 40 years.

given ring count, over the 10-year period (C. Moore, unpubl. data). The direction of the overall trend in mean growth rates was negative, though not statistically detectable, for female alligators; however, a negative trend was detected for females with 6-10 rings. This suggests that female growth rates declined slightly over years. Although overall mean male alligator growth rates from growth rings did not appear to change over time, recapture data showed some evidence of an increasing trend. Capture data may have been somewhat biased toward smaller alligators, and resulting trends could disproportionately reflect increased growth rate among those sizes. When only the youngest (5-7 ring) male alligators from the bone analysis were evaluated, a positive trend was apparent. This indicated that growth rates increased only for the smallest (122-152 cm) male alligators.

Drawing firm inferences on trend from recapture and growth ring data is difficult, because time effects cannot be completely separated from age effects; that is, if mean size does vary among annual samples of equal-aged alligators, then variability would be less detectable among groups of older alligators, which have been exposed to more years of temporal effects, than among younger alligators. Therefore, we may have failed to detect real trends because comparisons involving older alligators or alligators not recaptured for many years incorporated much temporal variability. Conversely, growth changes measured during our harvest may have resulted from environmental or density-related factors that occurred prior to the hunt. We conclude that growth rates of female alligators did not respond to harvests. Thus, the rate at which they reached both harvest and reproductive size did not change. However, growth rates of smaller males did appear to increase during the hunt, indicating that they reached harvest size more quickly. Sex-related differences in growth rate trends during the harvest may reflect a disproportionately greater alligator density reduction in open water habitat preferred by subadult males than in marsh habitat preferred by females (McNease and Joanen 1974).

A positive response in growth rates to reduced density was the only density-dependent component of our preliminary population harvest model. Yet, estimated annual change in growth rate observed for 122-194 cm male alligators on Orange was almost negligible (0.15 cm SVL/yr, or, an estimated 3 cm TL/10 yrs). These changes in no way approximated the growth rate changes predicted by our harvest model, which achieved highest growth rates in a 6-year period. It is likely that on wetlands such as Orange, growth rates are affected more by changes in prey availability due to water levels (see ECOLOGICAL EFFECTS below), rather than the relatively small reduction in densities imposed during our experiment. Our findings indicate that detection of potential density-dependent changes may require more than 10 years of monitoring.

SEX RATIOS

Sex Classification

A covariance model with variables SEX ($P = 0.018$) and SIZE ($P = 0.065$) best described the probability of incorrect sex classification of alligators. Females were more likely to be misclassified than males, but as alligator size increased, misclassification probability decreased for either sex (Fig. 34). We did not find a TIME effect, which indicated that we could no better classify alligators 1982 and thereafter, than before.

Distinguishing between the external genitals of crocodylians can be difficult, especially for neonates (Joanen and McNease 1978, Webb et al. 1984). The female clitoris superficially resembles, and can be confused with, a penis in younger alligators. We suspect that misclassification of females as males occurred when no males were available with which to compare genitalia during a capture event. Males were occasionally misclassified as females when inexperienced handlers were unable to protrude a male's penis. In some cases, we observed alligators with ambiguous sex organs that could not be confidently assigned to either sex.

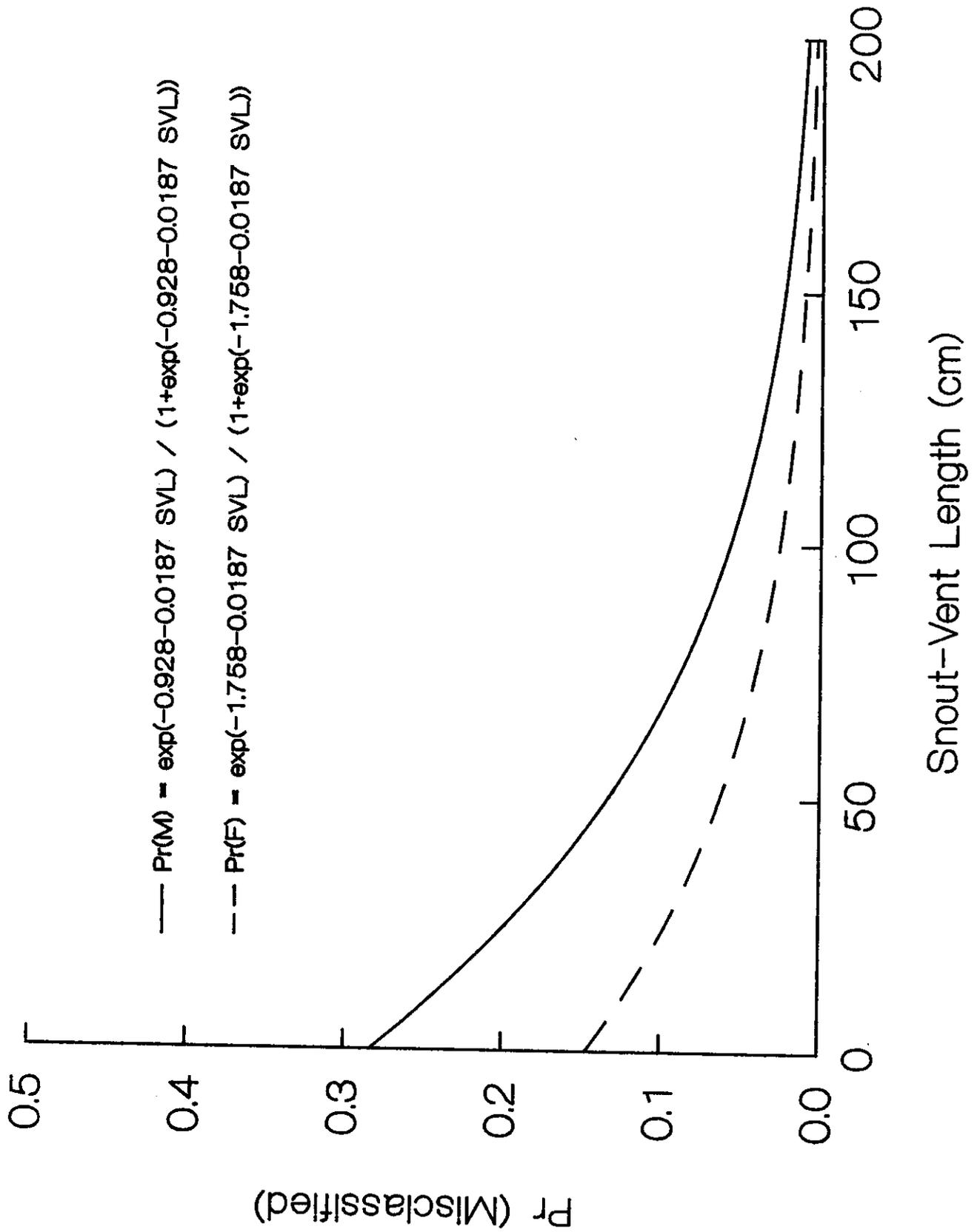


Fig. 34. Relationship of estimated probability of incorrectly classifying the gender of alligators to length (SVL), given alligator gender.

Sex Ratios

Sex ratios of live-captured alligators varied by area ($P < 0.001$) and general size class ($P < 0.001$; Table 21). The interaction between area and size class ($P = 0.035$) implied that although males

Table 19. Annual trend in size increase ($\log [SVL_R/SVL_c]$) at fixed intervals between successive captures of Orange Lake alligators during experimental hunts, 1981-90. Time interval represents whole years between initial capture and recapture.

Time interval (yr)	Female				Male			
	<i>n</i>	trend	SE	<i>P</i>	<i>n</i>	trend	SE	<i>P</i>
1	36	0.066	0.031	0.037	87	-0.059	0.029	0.041
2	11	0.289	0.137	0.037	11	0.120	0.075	0.110
3	9	-0.032	0.128	0.800	15	0.137	0.072	0.057
4	15	-0.025	0.037	0.503	14	0.153	0.076	0.046
5	12	0.025	0.040	0.539	24	-0.058	0.028	0.041
6	7	-0.026	0.078	0.743	24	0.029	0.038	0.458
7	8	-0.064	0.055	0.244	20	-0.003	0.038	0.932
8	10	-0.108	0.124	0.384	17	0.011	0.045	0.807
9	12	-0.070	0.056	0.209	8	0.028	0.075	0.710
10	4	-0.412	0.487	0.400	6	0.061	0.114	0.594
11	0				5	0.086	0.162	0.598
mean	124	-0.036	0.055	0.517	231	0.046	0.024	0.055
mean 2-11	88	-0.138	0.113	0.226	144	0.151	0.053	0.005

less severely outnumbered females in increasing size classes on each area, the rate of change varied by area. Sex ratios of 61-121 cm alligators were imbalanced for Lochloosa, Orange, and Woodruff but nearly proportional on Newnans and Paynes Prairie (Table 21). Sex ratios of alligators 61-121 cm may most closely represent the sex ratio at birth for the following reasons: (1) our findings and experiments conducted by Joanen and McNease (1978) indicating that alligators can be reliably sexed at 61 cm, (2) growth rates of male and female alligators are relatively equal through 122 cm, and (3) we sampled juvenile alligators in, or proximal to, major nesting areas.

Subadult female alligators tend to prefer marsh to open water habitat in Orange Lake (T. Goodwin, pers. commun.) and coastal marshes of Louisiana (McNease and Joanen 1974). Low water

Table 20. Annual trends in size (SVL) at fixed counts of femur growth rings for Orange Lake alligators taken during experimental hunts, 1981-90. Ring counts represent number of growth rings observed in sections of femurs.

Ring count	Female				Male			
	<i>n</i>	trend	SE	<i>P</i>	<i>n</i>	trend	SE	<i>P</i>
5	10	0.75	1.44	0.606	20	0.18	0.74	0.804
6	27	-0.05	0.47	0.910	25	0.09	0.57	0.881
7	50	-0.35	0.35	0.315	53	0.57	0.38	0.140
8	55	-0.13	0.35	0.708	54	-0.16	0.43	0.708
9	54	-0.29	0.32	0.365	26	-0.23	0.70	0.747
10	49	-1.11	0.40	0.006	14	-2.52	1.51	0.096
11	19	0.35	0.48	0.462	5	0.11	1.93	0.956
12	14	0.74	0.76	0.329	0			
13	5	-0.86	1.13	0.449	0			
mean	283	-0.11	0.25	0.668	197	-0.28	0.40	0.478
̄ x 6-10 (female)	235	-0.39	0.17	0.024				
̄ x 6-9 (male)					158	0.07	0.27	0.805

levels force females out of marshes and into open water. Compared to adults, sex ratios of harvested subadults (Fig. 12) during flooding (1988) or drought years (1989-90) were probably less biased samples of the population sex ratio and yielded more balanced sex ratios.

Sex compositions of harvested alligator populations have been predominantly (> 60%) male (Giles and Childs 1946, Hines and Woodward 1980, Joanen and McNease 1987a, Woodward et al. 1987a) but were probably biased because hunting was conducted in habitat preferred by males (Joaanen and McNease 1970, 1972; McNease and Joanen 1974; Goodwin and Marion 1979; Taylor 1984). Taylor et al. (1991) found a balanced sex ratio (49:51) for adult alligators at Marsh Island, Louisiana, following intense hunting in all habitat types, supporting the notion of sex-related differences in habitat use. Similarly, we found, as did Joanen and McNease (1987a), that sex composition harvest bias was minimized under flooding conditions when hunters accessed preferred female habitat, or during droughts when females moved into habitats accessible to hunters.

Live-captured adult alligators yielded similar sex imbalances. Murphy (1977) and Brandt (1989), using trip-snare traps (Murphy and Fendley 1973) to live-capture alligators, found adult sex ratios of 79:21 and 71:29 in a South Carolina reservoir. Wilkinson (1983) found a more balanced ratio of 60:40 for adult alligators in South Carolina coastal impoundments, as did Fuller (1981) in North Carolina. Wilkinson's (1983) captures of 1549 alligators of all sizes and 402 adults from both female and male habitat on coastal marshes in South Carolina probably represent the least biased and best substantiated sex ratio information published.

Nichols and Chabreck (1980), considering growth, survival, and habitat preference, concluded that juvenile sex ratios probably provide the best indication of natural sex ratios. They found sex ratios of 60-150 cm alligators skewed toward males in Louisiana. Bara (1975) found a more balanced sex ratio (57:43) in alligators <91 cm in South Carolina, and Fuller (1981) found a 60:40 ratio for alligators <183 cm. Murphy (1977) and Brandt (1989) found juvenile sex ratios weighted toward males at Par

Table 21. Male:female alligator ratios by general total length size class, for live-captured alligators from 5 populations studied during 1975-90.

Area	Size class (TL)			
	0 < 61	61-121	122-182	183-274
	ratio (n)	ratio (n)	ratio (n)	ratio (n)
Lochloosa	59:41 (171)	59:41 (121)	44:56 (16)	
Newnans	46:54 (59)	54:46 (109)	44:56 (25)	42:58 (12)
Orange	72:28 (1106)	63:37 (928)	55:45 (188)	53:47 (53)
Paynes Prairie	52:48 (60)	46:54 (118)	25:75 (4)	
Woodruff	60:40 (554)	62:38 (424)	61:39 (67)	43:57 (58)

Pond, South Carolina. Hines et al. (1968) reported an unbalanced sex ratio (80:20) for juvenile Florida alligators but stressed that inaccurate sex determination and non-random sampling may have biased their findings. Ferguson and Joanen (1983) reported the only predominantly female sex ratios for alligator populations and argued the possibility of an unbiased wild sex ratio as 17:83. Deeming and Ferguson (1988) used data reported by Ferguson and Joanen (1983) to conclude that adult populations of all wild crocodylians (including alligators) are heavily weighted toward females. Their extrapolation of 2 years of data collected at a single location in Louisiana, based on untested assumptions, to sex ratios for all alligator populations was misleading. Consequently, their conclusions depart from other reported findings, including Nichols and Chabreck (1980), Wilkinson (1983), and Taylor et al. (1991), all of whom thoroughly sampled alligators in habitat similar to that of Rockefeller Refuge. Ferguson and Joanen (1983) and Deeming and Ferguson (1988) based their assertions, in part, on constant-temperature incubation experiments that did not mimic the 1.2 C natural diurnal temperature cycles in alligator clutch cavities (Chabreck 1973). Our findings and most other studies on the American alligator indicate either proportional sex ratios or a preponderance of males.

Ferguson and Joanen (1983) and Ferguson (1985) presented a case for temperature-dependent sex determination in alligators, and it is likely that incubation temperature directly influences population sex ratio in all size classes. In alligators, females are produced at lower temperatures and males at higher temperatures. A gender gradient is found in a clutch from top (warmer and more likely males) to the bottom (cooler and more likely females) (Ferguson and Joanen 1983). Nest flooding after sex has been determined would cause greater mortality on female embryos, which are more likely to occupy bottom levels of the clutch, and influence sex ratios. Wilkinson (1983) reported 14% of eggs were lost to flooding in totally and partially flooded nests. A loss of 14% of predominantly female embryos would yield a predominantly male sex ratio.

Differing juvenile sex ratios among our study areas may reflect nesting habitat. Alligator nests on Lochloosa, Orange, and Woodruff were constructed on relatively high, dry, and unshaded sites,

perhaps resulting in warmer nests and a greater proportion of males. In contrast, alligators on Newnans frequently nested under dense canopy (Goodwin and Marion 1979), providing cooler incubation conditions and possibly resulting in the production of more females (Ferguson and Joanen 1983).

SURVIVAL

Survival Estimates

Woodward et al. (1987b) incorporated a Jolly-Seber recapture model to estimate alligator survival on Orange Lake to 2 years of age. They found survival rates to 1 and 2 years to be 41% and 8%. The 2-year survival rate may have been biased low due to lower recapture probabilities of marked relative to unmarked animals resulting from dispersal during their second summer. Mortality appeared to be highest during warmer months, corresponding to the dispersal period for young alligators and the accelerated feeding and growth period for larger alligators (Woodward et al. 1987b).

Few objective survival studies have been conducted on crocodylians, largely because of the difficulty in recapturing animals past their first few years of life, and because of the inherent biases of unequal probabilities of capture resulting from wariness (Woodward et al. 1987b). Mark-recapture studies have attempted to monitor minimum-known-alive (MKA) survival for hatchling alligators (Deitz 1979), but Woodward et al. (1987b) found that the MKA method underestimated survival. For 4 pods on Par Pond, South Carolina, Brandt (1989) found 63% and 19% MKA survival to 1 and 3 years using MKA estimation, and 60% survival to 2.5 years using Jolly-Seber.

Mortality

Nuisance alligators were removed from all 3 harvest lakes during the study. Nuisance complaints (Hines and Woodward 1980) were most frequent for alligators in Cross Creek and residential waterfront on Lochloosa. Records were only available for 1981-82, and 1987. Mean nuisance alligators harvested per year were 4.7 for Lochloosa, 1.0 for Newnans, and 0.1 for Orange. We considered alligator mortality from nuisance removals as influential only on Lochloosa.

Delany and Abercrombie (1986) found evidence of substantial cannibalism on Orange from tag recoveries from stomachs of harvested alligators. Tags were found in 12% of adult alligator stomachs sampled. Estimated median retention time of tags force-fed to alligators and monitored for 588 days was 8.0 years. Band recovery models that related tag recovery probabilities to annual probabilities of juvenile survival, cannibalism, tag retention, adult survival, and adult harvest indicated that cannibalism may account for 6.3-8.1% of the young (<91 cm) alligator population annually (Delany et al., in prep.).

Mortality from cannibalism and intraspecific fighting continued as alligators grew. Delany et al. (in prep.) found a tag for an alligator of last-known-size of ≥ 140 cm in an alligator stomach from Orange. GFC biologists observed subadult alligators in the jaws of ≥ 274 -cm alligators in 1983 on Woodruff, in 1987 on Paynes Prairie and in July 1991 on Orange. We frequently found alligators with broken jaws and other major wounds that probably resulted from intraspecific fights. From these observations, we suspect that mortality resulting from wounds is a major component of mortality in larger alligator.

Evidence of non-cannibalistic mortality for alligators is sparse. At least 3 alligators died on Paynes Prairie in January 1990 following 36 hours of -9-0 C air temperatures exacerbated by drought. Reports of mortality in other alligator populations have been anecdotal. Fogarty (1974) listed wading birds, black bass (*Micropterus salmoides*), common hawks, larger water snakes, raccoons, and river otters as potential predators of juvenile alligators in the Everglades. Allen and Neill (1952) suspected "otters, mink, raccoons, cottonmouth moccasins, larger alligators, bullfrogs, black bass, herons, and other creatures..." as predators of small alligators. Wading birds were observed to prey upon juvenile alligators on Paynes Prairie (W. Murdich, Univ. of Fla., pers. commun.). Neill (1971) observed large leopard frogs (*Rana utricularia*) eating hatchling alligators. Prolonged freezes and ice formation can kill alligators through suffocation and disease (pneumonia) as has been reported in Louisiana (Chabreck 1965;

T. Joanen, pers. commun.) and South Carolina (Brisbin et al. 1982). Droughts may also increase desiccation-related mortality (Nichols et al. 1976), but this has not been well documented.

Disease may be responsible for a considerable amount of natural mortality in alligators. We rarely observed dead alligators during this study, but substantial mortality could have been overlooked. Shotts et al. (1972) attributed mortality of alligators stressed during a drawdown of a Florida lake to pneumonia caused by *Aeromonas sp.* infections. Alligators are often the definitive host of a pentastome, *Sebekia mississippiensis*, and high rates of infection and disease (sebekiosis) have been reported in captive alligator populations (Boyce et al. 1984). Pentastomes were not found in hatchlings, but prevalence increased from 20% for alligators 41-60-cm to 60% for alligators 61-80 cm on Orange, indicating a gradual accumulation. Moreland et al. (1989) suggested that alligators may accrue a resistance to sebekiosis. We suspect that sebekiosis-induced disease may increase when alligators are in high densities, when exposed to drought-related stress, or when injured.

MOVEMENTS

Mark-recapture records indicated that some alligators moved between study areas. As expected, most movement was between Orange and Lochloosa, probably through 1.5-km Cross Creek. Recaptured alligators moved from Orange to Lochloosa at least 35 times, from Lochloosa to Orange 23 times, and from Orange to Lochloosa and back to Orange 2 times. Two alligators moved 12 km from Orange to Newnans. Although the small amount of tagging on Paynes Prairie limited our probability of recapturing tagged alligators, one alligator was recaptured after moving about 1 km from Paynes Prairie to Newnans. We suspect that substantial movement occurs from Paynes Prairie, a high nest production area, to Newnans, a low nest production area, especially during droughts, as alligators seek permanent water, and during flooding in search of greater prey densities.

We found limited evidence of emigration. A large (> 335 cm) alligator marked on Newnans was hit by an automobile on Highway 301 approximately 10 km north of the lake. A 340-cm alligator tagged on Woodruff was killed as a nuisance alligator at the State Road 40 bridge over the St. Johns River, approximately 20 km from the original capture site.

The above observations indicate at least a small amount of interchange among areas and some emigration out of the general study areas. We interpret this as negligible, and it may have been compensated for by immigration. We believe that this interchange did not compromise the findings of our study, except possibly for survival estimates.

DIETS

Fall (Sep-Oct) alligator diets were similar among harvest lakes but differed by alligator size (Delany and Abercrombie 1986). On Orange, insects were the primary food of alligators 25-60 cm (Delany 1990). The proportion of invertebrates (crustaceans and snails) and vertebrates (fish and reptiles) increased and insect prevalence decreased as alligators grew to 121 cm, but no single taxonomic group dominated the diet (Delany 1990). Fish became a major component of alligator diets on all harvest areas as alligators attained 122 cm, and they were predominant in diets of all but the largest (≥ 300 cm) alligators, which tended to eat more turtles (Delany and Abercrombie 1986). Delany et al. (in prep.) found evidence of substantial cannibalism based on marking tags found in stomachs from harvested alligator.

Delany (1990) and Delany and Abercrombie (1986) concluded that diets were probably influenced by habitat, prey availability (and vulnerability), prey size, and alligator size. As alligators grew they took larger prey, suggesting increased efficiency and the physical ability to take such prey (Dodson 1975, Delany 1990).

Diets of alligators on our study lakes comprised more fish and reptiles (turtles) than did those of nuisance alligator diets in northcentral Florida (Delany et al. 1988) and probably reflected differential

prey availability. We did not sample seasons other than fall but could see no reason why prey availability would change seasonally. Florida alligator diets contrasted with Louisiana coastal marsh alligator diets, which consisted predominantly of crawfish (*Procambarus clarkii*), nutria (*Myocastor coypus*), and muskrat (*Ondatra zibethicus*) (Chabreck 1971, McNease and Joanen 1977, Wolfe and Bradshaw 1987, Platt et al. 1990). Crawfish were a predominant food in both juvenile and harvestable alligators, whereas nutria and muskrats were eaten primarily by larger alligators. Diets of alligators in a cypress lake in Louisiana consisted predominantly of mammals, turtles, and fish (Taylor 1986). Nutrition affects growth rates and reproductive success (Joanen and McNease 1987a) of captive alligators and probably affects wild alligators in a similar manner.

Quality and, to a lesser extent, quantity of diet may explain the relatively slow growth rate experienced by Orange alligators 61-122 cm as compared to Louisiana alligators. Alligator populations may be regulated by hydrological conditions that influence food (fish) availability.

ECOLOGICAL EFFECTS

Estes et al. (1990) found a positive linear relationship between standing crop (biomass) of fish and percent coverage of aquatic macrophytes on Lochloosa and Orange. Changes in fish species composition commonly occur when water levels are stabilized (Kautz 1980), and some evidence of this phenomenon was found on our harvest lakes (Krumrich et al. 1989, Estes et al. 1990). Estimated standing crops of fish tended to cycle in response to macrophyte changes, which varied with water level fluctuations and aquatic weed management regimes (Krumrich et al. 1989, Estes et al. 1990). Because alligator populations were relatively stable and fish populations fluctuated, we concluded that harvests had no direct effect on fish populations. Alligators are opportunistic feeders and eat a variety of fish species (Delany and Abercrombie 1986). It is likely that alligators take advantage of booms in fish populations and may limit maximum population densities of certain species of fish, but data were not available to support that hypothesis.

Florida redbelly turtles were the primary alligator nest parasite, although 1 clutch of Florida softshell turtle (*Apalone ferox*) eggs was found in an alligator nest. Florida redbelly turtles were also a major part of the diet of larger alligators (Delany and Abercrombie 1986). Therefore, we hypothesized that harvest-related changes in alligator populations might positively affect turtle populations through reduced predation or negatively affect turtles through reduced nesting sites. Although adult alligator populations declined, nest production was stable or, in the case of Orange, increased. Nest parasitism rates averaged 14.0% for the 7 years in which turtle nesting was noted, but we were not able to discern a trend. The highest incidence of nest parasitism (25%) was during a relatively wet early incubation period (1989), but nests were searched more thoroughly that year. The lowest incidence of parasitism (0%) was in 1990 during drought conditions. We suspect that turtle population densities fluctuate in response to densities of aquatic macrophytes, which provide the bulk of their diet (Allen 1939). As with fish, alligator predation on turtles may limit the upper limits of turtle densities.

In some situations, prolonged crocodylian harvests can conceivably reduce nutrient levels of aquatic ecosystems. The ecological implications of nutrient removal from the Amazon River basin via caiman harvests have been discussed by Fittkau (1970). Harvests on Lochloosa, Newnans, and Orange resulted in a substantial removal of nitrogen, phosphorus, and calcium, and possibly other nutrients. We were unable to model nutrient flow on our harvest areas but could make some general observations. All 3 lakes are naturally rich in nutrients, but phosphorus apparently limits primary productivity (Canfield 1981, Gottgens and Montague 1987). Nitrogen, phosphorus and calcium levels remained fairly stable during 1970-1990 (Brezonic and Shannon 1972, Canfield 1981, Estes et al. 1990). Total phosphorus level was elevated in 1990, but this probably resulted from a nutrient release following macrophyte decomposition and increased suspended bottom solids induced by drought (J. Estes, pers. commun.). Increased nutrient loads and eutrophication are thought to be caused by reduced nutrient export through flushing and incorporation into aquatic macrophytes resulting from stable water levels (Gottgens and Montague 1987). Given the relative stability of nutrients during our study, we conclude that it is unlikely that alligator harvests affected the nutrient regime on harvest lakes.

Well developed alligator holes or dens, as described by McIlhenny (1935), Craighead (1968), Hines et al. (1968), and Kushlan (1974) were not readily discernible on any of our study areas. This may be because of relatively stable water levels and ready access by alligators to permanent deep water. Therefore, the importance of alligator holes to these ecosystems is minor compared to areas such as the Everglades or Louisiana coastal marshes.

AESTHETICS AND PUBLIC OPINION

Daylight visibility of alligators dropped 25% following the 1982 harvest season (Table 22). The decline was probably caused by a combination of 3 factors: (1) reduction in the number of alligators (10.2%), (2) increased wariness because of hunting, and (3) reduced alligator activity resulting from cooling water temperatures (27.9 - 26.3 C). Immediately after the hunt, most (52%) residents and fishermen on Newnans also noticed a decline in alligators observed (Delany et al. 1986). Little change in daylight visibility in pre-hunt surveys 1982-85 (Table 22) suggested that observability had recovered by the following season.

Table 22. Alligator visibility survey results, 1982-85, Newnans Lake, Florida. Surveys in 1983-85 were conducted prior to that year's harvest.

	Year				
	1982		1983	1984	1985
	Before	After			
Obs. time (hrs.)	19.0	16.3	19.0	10.2	14.7
No. obs.	146	94	149	86	91
Obs./hr.	7.7	5.8	7.8	8.4	6.2

The majority (60%) of people polled immediately after the hunt in 1982 enjoyed seeing alligators (Delany et al 1986). Most respondents (76%) approved of harvests, although 20% perceived the experimental harvest to be a nuisance alligator harvest (Delany et al. 1986).

ECONOMICS

Average annual wholesale value of hides and meat produced by the harvest was \$107,476 (Appendix E). Harvest value increased during the study, primarily because of increases in hide and, to a lesser extent, meat prices (Fig. 35). Orange yielded the most alligators and produced a greater annual mean total harvest value (\$71,867) than did either Newnans (\$19,441) or Lochloosa (\$16,167). Hide value comprised 62% of the overall value but varied by area from 66% and 65% on Lochloosa and Orange to 48% on Newnans. Meat value was more important on Newnans relative to Lochloosa and

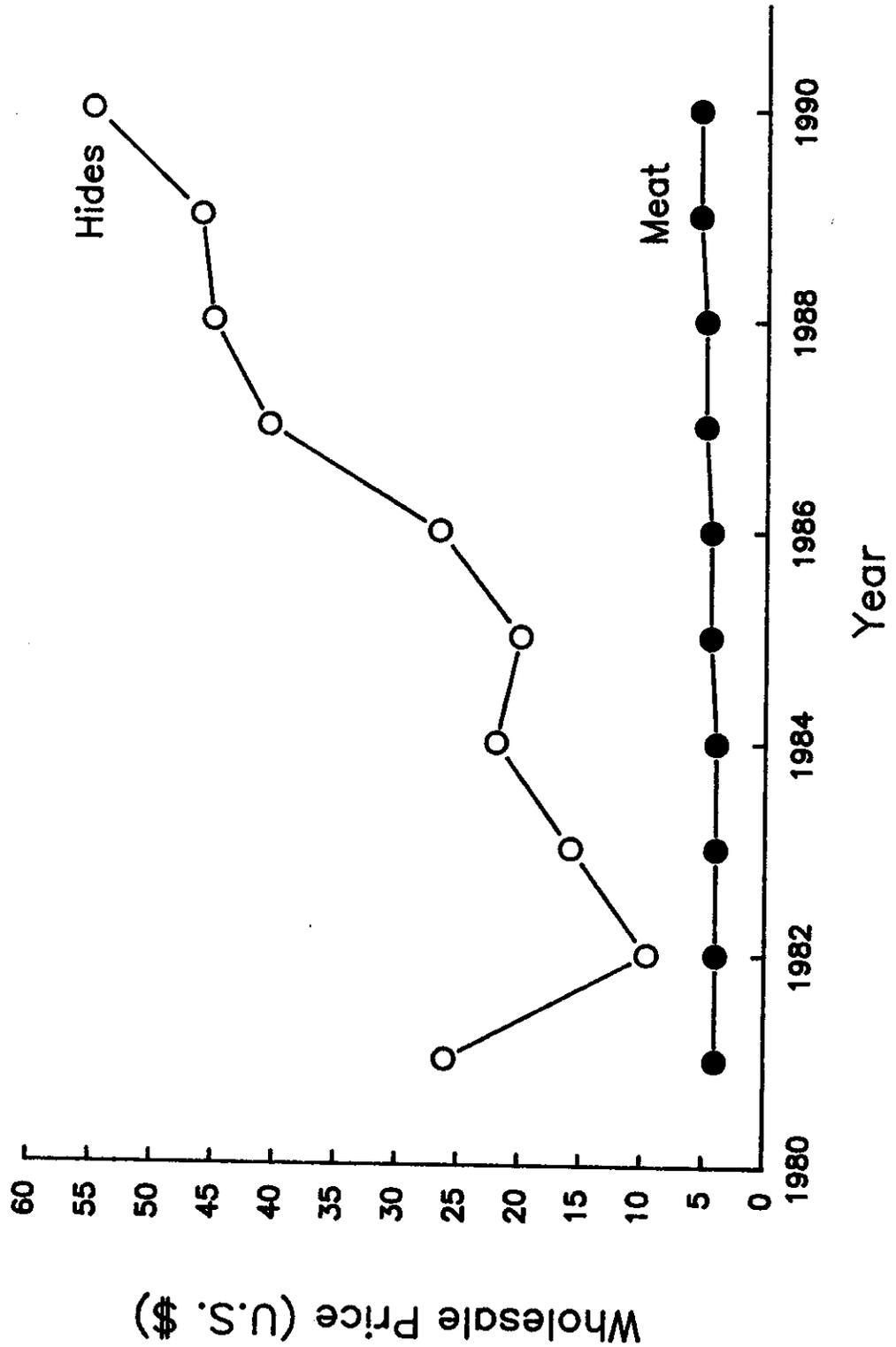


Fig. 35. Wholesale prices of alligator hide (\$/ft.) and meat (\$/lb.) for alligators harvested during 1981-90 harvests on Lochloosa, Newnans, and Orange lakes.

Orange because proportionally more larger alligators were taken (Table 4), with corresponding greater meat yields.

For all years, the mean value of each alligator was \$332 (Appendix F). GFC fees for harvesting alligators averaged \$48 per alligator and represented 15% of the gross wholesale value (Appendix F). Mean annual aggregate net hunter income for all years was \$87,415. Individual gross hunter income (adjusted for GFC fees) averaged \$4,183 for a mean annual take of 15.8 alligators/hunter. Net incomes were as high as \$8,250 for 1 hunter who took 11 larger ($TL_{\bar{x}} = 301$ cm) alligators in 1987, but several hunters failed to take any alligators.

Hunters desired to hunt for a combination of income and recreation, although the emphasis shifted from income to recreation when hunts were expanded statewide (D. David, GFC, unpubl. data). The average net income generated by the hunt (\$4,183) appeared to be sufficient compensation for a hunter and assistants for 10-15 nights of hunting. Most hunters reapplied for the hunt each year and felt strongly about being selected (or not selected) to participate. Hunters were satisfied with the recreational qualities of the hunt, particularly with the preferred method of take (harpoon). However, many hunters complained that lakes, especially Newnans, were too crowded with other hunters. During this study, the entire group of hunters selected for all 3 lakes was permitted to hunt each night, resulting in as many as 37 boats on Newnans during 1 night in 1989. Hunters also complained that hunt hours and season length were too short. We allowed all hunters to hunt on all areas and limited hunt hours and season length to facilitate data collection during our study. Under statewide hunt regulations (GFC Wildlife Code Book, 1991-92 - Rule 39-25.042 F.A.C.) these problems should be alleviated.

Hunter Composition

Commercially-oriented hunters (those that obtain 25% or more of their income from commercial fishing, frogging, or alligator hunting) represented 40.9% of the hunters during 1981-87. For 1989, the only year after 1987 for which hunter background information was available, the proportion of commercially-oriented hunters dropped to 3.6%. This decrease was probably due to the change from a restricted eligibility area that included only 1 major population center (Gainesville) to an unrestricted statewide area and increased publicity of the statewide program. Many commercially-oriented hunters were not selected in the statewide program, which has received 5,000-20,000 applications each year, and could only be involved in the hunt as agents or processors. This caused some dissatisfaction, especially among commercial fishermen who lived near harvest lakes.

During the development of this study we viewed the involvement of commercially-oriented hunters as an important part of a VAC harvest program for 3 reasons: (1) they would tend to maximize utilization of alligators, (2) they might have an greater vested interest in the conservation and protection of the alligator resource because they derived a substantial portion of their income from nearby harvest lakes, and (3) most owned or had access to boats, equipment, and local processing facilities, which would be an efficient use of those resources.

Meat

Processing alligators at county health department inspected facilities helped insure that meat was properly handled and stored. No instances of human illness arising from consumption of alligator meat were reported to us during the study. We also tested meat samples for environmental contaminants in 1985 to provide preliminary information on the potential public health hazard for consumption (Delany et al. 1988). Eight metals and various chlorinated hydrocarbons were detected. Although there were no U.S. Food and Drug Administration action levels established for alligator meat, mean residue concentrations were below action levels for fish and major livestock species (Delany et al. 1988).

CONCLUSIONS

Population Response to Harvest

Prior to our study, we assumed that alligator populations were at or near equilibrium and that age distribution was stable. We hypothesized that reproduction, growth, and survival parameters of alligator populations responded to population density. Specifically, we postulated that population density was limited by (1) food availability, (2) intraspecific competition for reproductive resources, (3) disease, and (4) cannibalism. We considered annual population density reductions from harvest as sufficient to evoke a response in population parameters. Although we were able to measure the response of some parameters directly, most had to be evaluated through indirect associations.

We found that a sustained mean annual proportional harvest rate of 13% had few negative effects on 3 alligator populations. Densities of harvestable alligators fully recovered from annual reductions by the following season, indicating increased recruitment into the subadult size class, perhaps through enhanced juvenile survival or physical growth rates. Night-light count densities of juvenile alligators remained stable or increased, supporting our contention of sustained recruitment of harvestable alligators. Counts of adult alligators exhibited some evidence of decline on Lochloosa, Orange, and, to a lesser extent on control area, Woodruff. However, we attributed these count decreases primarily to increased wariness resulting from hunting and live-capture activities, rather than actual population declines.

Nest counts remained stable or increased, suggesting that adult female productivity was not adversely affected, and may have been enhanced, by harvests. However, we found no evidence of increased nesting frequency by adult females. This suggests an increase in the adult female population, even though night counts suggested stable to declining adult populations. We were not able to separate adult female population trends from overall adult trends but assumed they were equivalent. It is possible that undetected population increases of adult females occurred during the study but were obscured by declining counts of large males. Minimum maturation size did not change, nor did we observe changes in clutch size or fertility rates, which might have signaled a change in the demographic profile of the adult female population.

We observed no consistent response of growth rates or physical condition to harvest. Any response of these parameters would have been confounded by factors not directly related to the harvest, such as influence of early development and food availability, and by water level and aquatic vegetation fluctuations. The size and sex distributions of harvested alligators changed, but these changes were likely due to increased wariness (and reduced vulnerability) of larger alligators and increased take of smaller subadult and female alligators.

Because the above responses may or may not have been directly tied to reduced densities, we were unable to demonstrate cause and effect. However, they do provide evidence that: (1) alligator populations are resilient to long-term proportional harvest and (2) population parameters such as fecundity and survival fluctuate and respond positively to harvest.

Ecological effects of harvests appeared negligible because of the low harvest rate relative to the overall population and the enriched nutrient state of study lakes. The standing crop of fish fluctuated independently of alligator populations during the study and was closely tied to changes in aquatic macrophyte availability brought about by water level fluctuations. We were not able to monitor turtle populations, but incidence of Florida redbelly turtles nesting in alligator nests did not change appreciably throughout the study. Stable levels of indicator nutrients (P, N, and Ca) during the study indicated that removal of alligators had little measurable effect on the nutrient regime of harvest lakes.

Alligators on Newnans showed little annual change in daylight observability. Daylight alligator observability declined immediately after a season but recovered by the following season. People living near to or using Newnans Lake accepted the seasonal decline in observability that resulted from this harvest.

Area differences were pervasive throughout the analysis. In designing the experiment, we thought that populations on all 3 harvest areas were sufficiently similar to respond in a like manner to

treatments. However, we found area differences in responses of virtually every demographic parameter evaluated.

Median TL of harvested alligators decreased over years. Nightly hunter success was variable over years, but increased hunter effort was necessary to maintain or reduce the rate of decline in harvest success. The increased difficulty in harvesting alligators may have been, in part, due to slightly reduced densities of adult animals, but wariness undoubtedly contributed to reduced hunter success. Wariness may be a natural safeguard against overharvest and may provide insight into how Florida's "endangered" 1960's alligator populations "recovered" so rapidly during the early 1970's following protection (Hines 1979).

Based on our findings, we suggest that water levels may be the major underlying factor affecting alligator populations. Water levels affected nesting effort and survival, which affected population recruitment. Fish population densities, which may ultimately affect alligator growth rate and survival, fluctuated with water level changes. Water level gauge stations on open water fail to reflect availability of marsh and, therefore, do not provide an accurate indication of alligator distribution in relation to water levels. The overwhelming effects of water level and our inability to accurately measure changes in population parameters limited our detection of direct responses of populations parameters to hunting.

In our experiment, population changes were difficult to detect and were more gradual than the model predicted. This may have resulted from 3 factors: (1) populations were well below equilibrium when hunts were initiated, (2) population growth potential was underestimated, and (3) the model failed to include all density-dependent functions affecting alligator population growth and response levels.

Management Considerations

Managing alligator hunts through quotas requires population estimates which are inherently difficult to obtain. We used night-light surveys as a basis for estimates and adjusted counts for factors that might affect counts. Population estimates from these counts showed high annual variability for Orange Lake. Long-term averages closely corresponded with population estimates from mark-resight studies, but differed from nest count-based populations estimates by 44%. Population estimates from night-light counts and nests counts were similar on Lochloosa Lake but did not agree on Lake Woodruff, possibly because of differences in population size structures and under-estimation of adult alligators. Quotas estimated from nest counts on Lake Woodruff would have been 214% higher than those from night counts. These differences might be explained by variation in the number of adult alligators/nest resulting from size-class distributional differences among areas.

Night counts provided a reasonably good index of long-term changes despite considerable unexplained annual variation. Yearly spikes and dips in night-light counts probably reflected changes in observability caused by difficult-to-measure variables such as water availability in marshes and swamps rather than actual population changes. Although night counts varied considerably, actual population densities probably changed in a more gradual manner, as would be expected for a species with relatively low natural adult mortality and protracted longevity.

Based on our findings, nest counts can be used to estimate alligator populations on wetlands where nest production can be estimated and the underlying population size distribution is known. Therein lies a problem; unbiased night-light counts are needed to establish the underlying size distribution for the Chabreck estimator to work effectively. Therefore, values for parameters in the Chabreck (1966) or Taylor and Neal (1984) nesting-based population estimators are only valid for populations with specific population size distributions.

Harvest quotas estimated from annual night-light counts resulted in sizeable fluctuations in quotas despite relatively stable underlying populations. Stability in harvest quotas would allow more consistent hunt effort on individual areas and would facilitate projecting annual hunt quotas, number of hunters, and license revenues for long-range planning. The practice of using estimated rather than actual count data has been applied to waterfowl populations to stabilize trend lines (Johnson 1989). This method, the Empirical Bayes Approach, bases current year estimates on a weighted average of counts in the current year and in previous years. A modification of this approach, using predicted values based on regression

lines, should work well for harvested alligator populations because of relatively low ($\leq 15\%$) harvest rates and gradual population density changes.

Our findings on population response to harvest are based on an estimated average harvest rate of 13% on populations with specific size and sex compositions. Harvest rates reported in this study may not be sustainable for populations with different demographics. Similarly, hunting vulnerability may change for habitats with differing amounts of marsh or swamp that can be used as refuge from hunters. Learned wariness by larger alligators apparently increased with decreasing density and may have limited harvest rates of larger alligators. However, under the comparatively liberal season length and hunt hours currently applied to statewide alligator hunts, risk of overharvest of adults is elevated. Hunters tend to select for large alligator for both economic and recreational reasons. Excessive adult harvest of both sexes may lead to reductions in nesting effort, observability, and long-term economic yields, ultimately failing to optimize harvest yields.

The maximum sustained yield harvest concept assumes that population parameters such as survival and fecundity respond inversely to population density (*compensation*) (Nichols 1987, Kautz 1990) and that populations follow logistic growth (Caughley 1977:178-185, Abercrombie 1989). Under this principle, all members of the population are assumed to be limited by the same resources and maximum sustained harvest yields are obtained when populations are 1/2 carrying capacity (Caughley 1977, Getz and Haight 1989). In crocodylians, this is not the case, because diet, predators, and habitat utilization change with size. Hence, 1 size class may prosper while another fails. Our pre-harvest population model considered response of a single compensatory parameter, growth rate, to alligator population densities and prey availability. We assumed that the Orange Lake population was at or near carrying capacity because of low growth rates relative to Louisiana alligators. However, carrying capacity, in all likelihood, fluctuated with changing environmental conditions. Pre-harvest simulations suggested cycles of immediate population declines followed by recoveries.

Computer simulations of Louisiana alligator harvest dynamics by Nichols et al. (1976) indicated that a sustained harvest rate of 9% was optimum if alligators were taken in proportion to their size- and age-specific abundance, but that a 15% harvest rate caused a long-term population decline. Harvest simulations conducted prior to this experiment projected that harvests of 15% all-male or 7% both-sexes could be sustained if alligator growth rates responded positively to reduced densities, but that a 15% proportional harvest of both sexes could not be sustained. Population models by Nichols et al. (1976) and C. Abercrombie (pers. commun.) did not include several possible compensatory effects such as response of female fecundity and survival to decreased densities. More importantly, our population harvest model did not account for the subtle effects of extrinsic phenomena, such as water level, on alligator population dynamics. We did not observe declines as predicted by Nichols et al. (1976) and C. Abercrombie (pers. commun.), which suggests that their models underestimated population growth potential and the full extent of density-dependent mechanisms.

Declines in count densities of adult alligators may reflect the inability of recruitment to replace the adult hunting mortality of 13% annually. This may be most applicable to bull alligators, which grow at a much slower rate than do smaller adults or subadults. Proportional harvests with respect to size classes are disproportionate with respect to levels of growth rates and, therefore, result in underharvest of smaller, faster growing alligators relative to larger, slower growing individuals. Proportional harvest rates applied in this study may be too great for sustained harvest of adult alligators. However, harvests may be sustainable by progressively weighting the harvest toward smaller alligators. Immediate drops in count densities of adult alligators following the initial hunt year may have reflected wariness. Trends after the initial drop may have actually reflected actual population changes. Aerial basking surveys have proven effective at counting adult alligators, seem robust to alligator wariness and may prove useful in quantifying wariness.

Hunters preferred to take larger (> 214 cm) alligators because of the geometrical increase in value per lineal increment. Increased alligator wariness resulted in increased hunter effort required to maintain average TL of harvested alligators.

Alligator hunts were conducted in September to avoid taking reproductively active females and to maximize yearly growth gains. Findings from this study tend to support this rationale. Physical

growth of alligators in northcentral Florida ceases during November-March and growth does not fully recover until April. Maximum yearly length and weight are attained in the fall (Sep-Nov). However, cooling weather conditions may limit effectiveness of hunts in north Florida beyond September. Hatching was 53.5% complete by 1 September, 85.8% complete by 7 September, and complete by 19 September. Because neonates depend on attending females for liberation from the nest, killing reproductive females prior to completion of hatch may result in some hatch failure. However, the demographic consequence of hatch failures is dependent on the proportion of brooding females killed prior to completion of hatch and the importance of non-liberated hatchlings to the population. For populations with either a ranching harvest or cropping harvest, effects would be minimal. Consequences would be more critical for populations with simultaneous (ranching and cropping) harvests.

The commercial value of alligators represented a substantial economic value to some people near harvest lakes. Prior to converting to statewide regulations, hunt participants were strongly represented by commercial fishermen and frog hunters who derived some of their income from harvest lakes. If not selected to hunt, local residents frequently participated in hunts as agents of licensees. Most alligators were processed and hunting equipment and supplies were purchased and maintained in the vicinity of harvest lakes. Alligator hunting was a small but important component of the economy of lake shore communities such as Lochloosa and Cross Creek.

We surmise that harvests provided some value-added-conservation. The commercial value of the alligator populations on harvest lakes was considerably improved, and local economies were enhanced, especially prior to 1988, when local hunters and processors handled a larger portion of the harvest. The economic, ecological, and aesthetic importance of alligators accounted at least in part for designation of Orange Lake as an Outstanding Florida Water (OFW) in 1987. OFW designation will prevent lowering of existing water quality through more restrictive permitting of water discharge into the lake and will elevate the level of state agency review regarding regional development (Allen 1986). Alligator hunting represents a low intensity industry that enhances rural economies with a minimum of environmental degradation.

MANAGEMENT RECOMMENDATIONS

A 13% proportional harvest of ≥ 122 cm alligators is sustainable for populations with size structures and population dynamics similar to areas studied in this investigation.

Use of biologist judgements to estimate the proportion of the population not accounted for in night-light counts can provide more accurate population estimates and can be used effectively to achieve maximum harvest quotas. Judgements can be calibrated by conducting aerial basking surveys of unsurveyable habitat.

September is the optimum time to harvest alligators. To maximize hatchling production, hunts should be initiated after 95% of the hatch is complete (7 September) or shortly thereafter.

Adult alligator wariness should be calibrated by conducting aerial basking counts in conjunction with night-light counts on a representative sample of harvest areas.

A technique similar to the Empirical Bayes Approach, using predicted values from regression analyses for areas with ≥ 3 independent night-light counts should be used to stabilize quotas. To reduce the probability of a Type II error (not detecting a decline when there really was one), we recommend relaxing the Type I error rate (alpha level) from 0.05 to 0.20. Although this would increase the probability of detecting a trend when one did not occur, a Type I error (detecting a trend when there was none) would be preferable to a Type II error when concern about negative effects of a treatment is a priority.

An aggregate length limit as used in this study, a slot limit that would limit the size of alligators taken for certain tags issued, or reduced area quotas should be imposed to minimize the likelihood of overharvest. However, the latter approach may fail to optimize harvest yields.

More precise measures of water level are needed to accurately reflect marsh water availability. To account for a greater amount of variation in night-light counts and nest counts, we recommend establishing supplemental water level gauges in marsh habitat.

Intensive management may require a knowledge of population dynamics for individual areas or groups of areas with similar population dynamics. The applicability of this approach will be dependent on a benefit-cost analysis - at some point costs of studying the population may exceed the commercial value of the resource. However, recreational value of hunts should be considered when evaluating benefits. For areas that do not have sufficient alligators to warrant evaluation of population dynamics, the only other option may be to apply a conservative harvest strategy.

To optimize the value of alligators and provide a broader distribution of the resource, the constituency of hunters could be expanded by instituting a sport or recreational hunt. Our recommendation is to permit a special recreational hunt prior to commercial hunts with quotas of 2-3 alligators per hunter. This would increase the opportunity for participation in alligator hunting by the public. A limit of 2-3 alligators would allow hunters to participate in the commercial hunting aspect of alligator harvests, but would accommodate a constituency with limited equipment, time, and experience in alligator hunting. Providing increased recreational opportunities is consistent with the purview of the mission of the GFC, and may significantly enhance the conservation of alligators.

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Appendix A.1. Analysis methods for seasonal growth rate variability.

Each popular integral growth model form (i.e., size at age) includes a term $b \cdot t$, the product of t and growth rate b (Kaufmann 1981, Brisbin 1989). If growth rate varies during a specific time of the year by factor k , then whether the resulting product is expressed as $(k \cdot b) t$ or as $b (k \cdot t)$ is irrelevant. In other words, growth rate variability may instead be expressed as a constant rate applied to a varying time unit. We called this time unit growing age, or t_g . We arbitrarily defined growth rate occurring on 23 Aug of each year as the constant growth rate around which seasonal slow-downs and accelerations might occur. Therefore, we required $t = t_g$ on 23 Aug each year, but we relaxed this requirement between birthdays to permit seasonal variability. How t and t_g differed depended only on season. A growing day represented the number of calendar days required to attain an arbitrary size increase at a rate of growth specific to a particular time of the year. Therefore, a growing day could be longer, shorter, or the same length as a calendar day.

From plots of size vs age for each of the first 3 age classes, we hypothesized that growth rate might diminish in the winter relative to the 23 Aug mean value, exceed the mean value for a short period in the spring, then return to the mean value in summer and fall. We modelled seasonal variability in growth rate through a piecewise linear function of age and Julian date:

$$t_g = \text{int}(t) + \frac{1}{365} \cdot \begin{cases} J, & J < J_1 \\ J_1 + r_1(J - J_1), & J_1 \leq J < J_2 \\ J_1 + r_1(J_2 - J_1) + r_2(J - J_2), & J_2 \leq J < J_3 \\ J, & J_3 \leq J \end{cases}$$

Model parameters J_1 , J_2 , and J_3 were respective Julian onset dates of slow winter

growth, rapid spring growth, and mean summer-fall growth. Parameters r_1 and r_2 were ratios of winter and spring growth relative to summer-fall growth: values <1.0 indicated slower growth than in summer-fall, and values >1.0 indicated faster growth. The expression $\text{int}(t)$ represented the alligator's age in whole years. J varied between 0 and 364, thus the model created a growing age value by adding a fraction of a year to the number of birthdays the alligator had lived. Growing age equalled calendar age when $r_1 = r_2 = 1.0$ or when $J = 0$ (23 Aug). The model as written above involved 4 equations and 5 unknown parameters, thus 1 parameter was redundant with the rest of the system. We reformulated the model prior to its estimation by expressing J_3 in terms of the other parameters.

We substituted the t_G function in place of t in integrated forms of the power (Kaufmann 1981) and Richards (Brisbin 1989) models. The power curve contains a parameter a that determines the shape of the curve, a growth rate parameter b , and a parameter t_0 related to size of the alligator at hatching:

$$SVL = [ab(t_G + t_0)]^{1/a}.$$

In Brisbin's (1989) formulation of the Richards curve, m controls the shape of the curve, S represents asymptotic size, S_0 is size at hatching, and T measures growth rate as the time necessary to complete the majority of growth:

$$SVL = \{S^{1-m} - (S^{1-m} - S_0^{1-m}) \exp[-2 t_G (m+1) T^{-1}]\}^{1/(1-m)}.$$

Both models were fully specified by adding a random error component to each. We fit the models to the KALC data via nonlinear least squares, performing the analyses by sex for each of the Orange, Lochloosa, and Woodruff study areas. Data from hatchling alligators we could not confidently sex were combined with each known-sex set of data. For each model, we calculated an approximate Wald F ratio (Gallant 1987:47-55) for testing the hypothesis of no season effect on growth rate ($H_0: r_1 = r_2 = 1.0$). We overlaid plots of estimated t_G vs J from each model to select, by eye, a compromise growing age function having "round"

values of J_1 , J_2 , and J_3 . Parameters in the compromise model were tested for equality with parameters estimated in each area-sex model (Wald test). We used the compromise model to predict growing age, t_g , for each alligator in the KALC databases. Just as determining a time interval between successive captures of an animal does not depend on knowing the animal's age, we could also calculate a growing time interval, i_g , for observations in the MC database.

Appendix A.2. Development of models for integrated form growth analysis.

Plots of SVL vs. t_g for each area-sex cohort indicated that SVL variability increased with age. By cohort, we broke SVL into quantiles containing approximately 5 observations each. Quantile standard deviation increased when we plotted it against quantile mean. Both plots suggested that SVL prediction error was multiplicative rather than additive. Because least squares estimation methods require the assumption of additive errors for unbiased estimation of parameter variances, we log-transformed (\log_e) both SVL and the growth model. For each cohort, we fit values of \log_e SVL in the KALC database to nonlinear, integrated forms of the power

$$\log_e \text{SVL}_i = a^{-1} \log_e [ab(t_{g_i} + t_0)] + \epsilon_i$$

and Richards

$$\log_e \text{SVL}_i = (1 - m)^{-1} \log_e \{S^{1-m} - (S^{1-m} - S_0^{1-m}) \exp[-2 t_{g_i} (m+1) T^{-1}]\} + \epsilon_i$$

models.

Appendix A.3. Development of models for derivative form growth analysis.

For each pair of captures in the MC database, we calculated specific growth rate (Kaufmann 1981) as

$$\text{SGR} = i_g^{-1} (\log_e \text{SVL}_2 - \log_e \text{SVL}_1)$$

where the subscripts on SVL represent order of capture. As Jacobsen and Kushlan (1989) discovered, variability in SGR increased as time between captures decreased.

We fit SGR to $\overline{\text{SVL}}$, the arithmetic mean of SVL at both capture occasions (McCallum and Dixon 1990), in a reparameterized (Brisbin et al. 1986) derivative form of the Richards growth model (White and Brisbin 1980):

$$\text{SGR}_i = 2 (m + 1) (S^{1-m} \overline{\text{SVL}}_i^{m-1} - 1) [T(1 - m)]^{-1} + \epsilon_i.$$

We estimated parameters in the power model by fitting $\log_e \text{SGR}$ to $\log_e \overline{\text{SVL}}$ in a nonlinear regression:

$$\log_e \text{SGR}_i = \log_e b - a \log_e \overline{\text{SVL}}_i + \epsilon_i.$$

Ordinarily, one would treat the expression $\log_e b$ as a parameter and estimate the resulting model in a linear regression (Kaufmann 1981, Jacobsen and Kushlan 1989). However, doing so would not have preserved parameter consistency between integral and derivative forms of the power model, therefore we estimated b directly through nonlinear means. We conducted analyses for each cohort.

Appendix A.4. Joint estimation of parameters common to both derivative and integral growth model forms.

Kirkwood (1983) described a maximum likelihood procedure to jointly estimate parameters common to 2 forms (age-at-size and time interval-at-size increase) of a von Bertalanffy growth model. He also provided a likelihood ratio test of the hypothesis that parameters estimated separately for each data set are equal. Because the procedure estimates a residual variance term specific to each data type, dissimilar data types, like those represented in the KALC and MC databases, may be simultaneously modelled. We adapted Kirkwood's (1983) methodology to our formulations of the power and Richards models. Allowing θ to represent the set of parameters for a growth model, $Y_i = I(X_i, \theta) + \epsilon_i$ to represent the integral form of the model on n_I observations of Y_i and X_i , and $y_j = D(x_j, \theta) + \delta_j$ to represent the derivative form of the model on n_D observations of y_j and x_j , we maximized the nonlinear function

$$L(\theta, \sigma_I^2, \sigma_D^2) = -\frac{n_I}{2} \log_e(2\pi\sigma_I^2) - \frac{1}{2\sigma_I^2} \sum_{i=1}^{n_I} [Y_i - I(X_i, \theta)]^2 \\ - \frac{n_D}{2} \log_e(2\pi\sigma_D^2) - \frac{1}{2\sigma_D^2} \sum_{j=1}^{n_D} [y_j - D(x_j, \theta)]^2$$

to find the maximum likelihood estimates of θ , σ_I^2 , and σ_D^2 for each curve and cohort. We tested the hypothesis of equality of corresponding parameters estimated separately in integral and derivative model forms. Kirkwood (1983) provided more detail on analytical techniques for model estimation and testing.

Appendix A.5. Methods for selection of growth model shape.

The quantity R^2 measures the quality of fit of a nonlinear model to data values W_i :

$$R^2 = 1 - \left[\sum_{i=1}^n (W_i - \hat{W}_i)^2 / \sum_{i=1}^n (W_i - \bar{W})^2 \right].$$

Here, \hat{W}_i represents the predicted value of W_i and \bar{W} represents the mean of all W_i . Following joint estimation of model parameters, we calculated a weighted average of R^2 values obtained from the integral and derivative parts of the joint model:

$$\bar{R}^2 = (n_I + n_D)^{-1} (n_I R_I^2 + n_D R_D^2).$$

We treated $\bar{R} = (\bar{R}^2)^{0.5}$ as a correlation and applied Fisher's Z transformation to \bar{R} (Steel and Torrie 1980:279). For each cohort, we calculated an approximate test of equality of transformed \bar{R} (Steel and Torrie 1980:280) from the power and Richards models. We chose the growth form that consistently provided the better fit (greater \bar{R}) as the curve shape appropriate for alligator SVL growth. We verified our selection by evaluating parameter estimates and residual plots for reasonableness and correctness.

Appendix A.6. Methods for growth model comparisons among cohorts.

We tested for area, sex, and area x sex differences in each of the estimated parameters of the chosen growth curve (Wald test). Significance was declared at the 0.05 probability level in all tests except those that compared individual study areas. For the 6 pairwise comparisons among areas, significance was declared at the Bonferroni-protected probability level of 0.0083.

We inspected residual plots to assess the fit of all growth models. We used the SYSTAT software (NONLIN module, Wilkinson 1990) to estimate nonlinear models. Because many models were discontinuous, we employed a derivative-free direct search procedure (option SIMPLEX) which slowly but reliably found likelihood function maxima if they existed.

Appendix B. Number of night-light surveys conducted (n), alligators observed (\bar{V}), proportion composition of observed alligators (pr \bar{V}), proportion of population surveyed (A), survey conditions coefficient (C), population estimates (N_t), and estimated aggregate length (AL) and densities of ≥ 122 cm alligator population for 4 Florida lakes, 1981-90.

Study area	Year	n	\bar{V}			pr. \bar{V}			N_t		Est. ≥ 122 c m		Est. ≥ 122 c m	
			≥ 30 (c m)	≥ 122 (c m)	≥ 183 (c m)	≥ 122 (c m)	≥ 183 (c m)	A	C	≥ 122 (c m)	≥ 183 (c m)	pop. AL (m)	/km	density /ha
Lochloosa														
	Sep 1981	1	188.0	129.0	78.0	0.69	0.41	0.80	0.90	511.9	309.5	998.2	19.9	0.146
	Aug 1982	1	64.0	27.0	10.0	0.42	0.16	0.60	0.80	160.7	59.5	313.4	6.3	0.046
	Aug 1983	2	113.5	61.5	46.0	0.54	0.41	0.70	0.90	278.9	208.6	543.9	10.9	0.080
	Aug 1984	2	132.5	61.0	39.5	0.46	0.30	0.70	0.80	311.2	201.5	606.9	12.1	0.089
	Aug 1985	2	309.0	139.5	64.5	0.45	0.21	0.90	1.00	442.9	204.8	863.6	17.2	0.126
	Aug 1986	2	370.5	147.5	60.5	0.40	0.16	0.80	0.90	585.3	240.1	1141.4	22.8	0.167
	Aug 1987	2	258.5	86.0	28.0	0.33	0.11	0.85	0.80	361.3	117.6	704.6	14.1	0.103
	Aug 1988	2	589.0	247.5	81.0	0.42	0.14	0.95	1.00	744.4	243.6	1451.5	29.0	0.213
	Aug 1989	2	544.5	139.0	52.5	0.26	0.10	0.95	1.00	418.0	157.9	815.2	16.3	0.119
	Aug 1990	2	636.0	126.0	36.5	0.20	0.06	0.90	1.00	400.0	115.9	780.0	15.6	0.114
	\bar{x}		320.6	116.4	49.7	0.42	0.20	0.82	0.91	421.5	185.9	821.9	16.4	0.120
Newnans														
	Jul 1981	1	391.0	189.0	112.0	0.48	0.29	1.00	1.00	540.0	320.0	1053.0	25.2	0.182
	Aug 1982	1	204.0	163.0	134.0	0.80	0.66	0.80	0.90	646.8	531.7	1261.3	30.2	0.218
	Aug 1983	2	157.5	83.5	83.5	0.53	0.53	0.80	0.90	646.8	331.3	646.1	15.5	0.112
	Aug 1984	2	204.0	132.0	92.0	0.65	0.45	0.90	1.00	419.0	292.1	817.1	19.6	0.141
	Aug 1985	2	174.0	120.0	80.0	0.69	0.46	0.80	0.80	535.7	357.1	1044.6	25.0	0.181
	Aug 1986	2	130.5	97.0	66.0	0.74	0.51	0.90	0.80	384.9	261.9	750.6	18.0	0.130
	Aug 1987	2	157.5	103.0	52.5	0.65	0.33	0.95	0.95	326.1	166.2	635.9	15.2	0.110

Appendix B. (continued).

Study area	Year	n	V			pr. V			N _h		Est. ≥122 c m	Est. ≥122 c m density		
			>30 (c m)	>122 (c m)	>183 (c m)	>122 (c m)	>183 (c m)	>122 (c m)	>183 (c m)	pop. AL (m)			/km ² /ha	
Newmans (continued)														
	Aug 1988	2	232.0	138.5	54.5	0.60	0.23	1.00	0.95	416.5	163.9	812.3	19.5	0.140
	Aug 1989	2	263.5	131.0	40.5	0.50	0.15	1.00	0.95	394.0	121.8	768.3	18.4	0.133
	Aug 1990	2	219.0	116.0	51.5	0.53	0.24	0.95	0.95	367.2	163.0	716.1	17.2	0.124
	\bar{x}		213.3	127.3	76.7	0.60	0.36	0.91	0.92	436.2	270.9	850.5	20.4	0.147
Orange														
	Sep 1981	1	1108.0	507.0	339.0	0.46	0.31	0.80	0.80	2263.4	1513.4	4413.6	87.1	0.431
	Aug 1982	1	774.0	363.0	259.0	0.47	0.33	0.70	0.70	2116.6	1510.2	4127.4	81.4	0.403
	Aug 1983	1	662.0	275.0	220.0	0.42	0.33	0.70	0.60	1870.7	1496.6	3648.0	72.0	0.356
	Aug 1984	1	496.0	190.0	141.0	0.38	0.28	0.70	0.60	1291.5	959.2	2520.4	49.7	0.246
	Aug 1985	2	1199.0	514.0	365.0	0.43	0.30	0.80	1.00	1835.7	1303.6	3579.6	70.6	0.349
	Aug 1986	2	1497.0	587.0	306.5	0.39	0.20	0.80	0.90	2329.4	1216.3	4542.3	89.6	0.443
	Aug 1987	2	984.5	282.5	144.0	0.29	0.15	0.65	0.85	1460.9	744.7	2848.7	56.2	0.278
	Aug 1988	2	1814.0	619.5	250.5	0.34	0.14	0.85	1.00	2082.4	842.0	4060.6	80.1	0.396
	Aug 1989	2	1378.0	388.0	214.0	0.28	0.16	0.80	0.95	1458.6	804.5	2844.4	56.1	0.278
	Aug 1990	2	2103.5	343.0	144.0	0.16	0.07	0.80	1.00	1225.0	514.3	2388.8	47.1	0.233
	\bar{x}		1201.6	406.9	238.3	0.34	0.20	0.76	0.84	1793.5	1090.5	3497.4	69.0	0.341
Woodruff														
	Jun 1981	1	570.0	163.0	68.0	0.29	0.12	0.90	1.00	517.5	215.9	1009.0	15.9	0.079
	Jun 1982	1	211.0	117.0	90.0	0.55	0.43	0.80	0.90	464.3	357.1	805.4	14.2	0.071
	Jun 1983	2	162.0	105.5	82.5	0.65	0.51	0.60	0.90	558.2	436.5	1088.5	17.1	0.085
	Jun 1984	2	281.5	127.5	69.0	0.45	0.25	0.80	0.90	506.0	273.8	986.6	15.5	0.077

Appendix B. (continued).

Study area	Year	n	Y		pr. Y		N ₁		Est. ≥ 122 c m pop. AL	Est. ≥ 122 c m density				
			≥ 30 (c m)	≥ 122 (c m)	≥ 183 (c m)	≥ 122 (c m)	≥ 183 (c m)	≥ 122 (c m)			≥ 183 (c m)	/km	/ha	
Woodruff (continued)														
	Jun 1985	2	531.5	225.0	142.5	0.42	0.27	0.90	0.90	793.7	502.6	1547.6	24.3	0.121
	Jun 1986	2	419.0	181.0	108.5	0.43	0.26	0.90	0.90	638.4	382.7	1245.0	19.6	0.097
	Jun 1987	2	714.0	255.0	131.5	0.36	0.18	0.90	0.90	899.5	463.8	1754.0	27.6	0.137
	Jun 1988	2	612.5	216.5	115.0	0.35	0.19	0.90	0.90	763.7	405.6	1489.2	23.4	0.117
	Jun 1989	2	1000.0	258.0	122.5	0.26	0.12	0.90	0.90	910.1	432.1	1774.6	27.9	0.139
	Jun 1990	2	325.5	83.5	37.0	0.26	0.11	0.90	0.95	279.0	123.6	544.1	8.6	0.043
	\bar{x}		482.7	181.5	101.1	0.38	0.21	0.85	0.91	668.6	377.6	1303.7	20.5	0.102

Appendix C. Population estimates (N_t), harvest quotas (Q), take, harvest rate, and success rates ($[S]$ % of Q taken) in number (No.) and aggregate length (\overline{AL}^1) of >122 cm alligators during experimental harvests on Lochloosa, Newmans, and Orange lakes, 1981-90.

STUDY AREA	N_t		Q		Take		% Harvest rate		% S		Mean TL (cm)	% males
	No.	\overline{AL} (m)	No.	\overline{AL} (m)	No.	\overline{AL} (m)	No.	\overline{AL}	No.	\overline{AL}		
LOCHLOOSA LAKE												
1981	512	998	88	172	67	125	13.1	12.5	76.1	72.7	186	70.2
1982	161	314	20	40	22	41	13.7	13.1	110.0	102.5	188	68.2
1983	279	544	55	107	39	80	14.0	14.7	70.9	74.8	206	66.7
1984	311	606	48	94	32	81	10.3	13.4	66.7	86.2	253	96.9
1985	443	864	67	131	62	128	14.0	14.8	92.5	97.7	206	74.2
1986	585	1141	88	172	90	172	15.4	15.1	102.3	100.0	191	67.8
1987	361	704	54	105	56	98	15.5	13.9	103.7	93.3	176	76.8
1988	744	1451	101	197	44	81	5.9	5.6	43.6	41.1	184	70.4
1989	418	815	63	123	73	125	17.5	15.3	115.9	101.6	171	60.3
1990	400	780	60	117	47	77	11.8	9.9	78.3	65.8	163	66.0
Total	421.4	821.7	644	1258	532	1008	13.1	12.8	86.0	83.6	192.4	71.8
\bar{x}			64.4	125.8	53.2	100.8						
NEWMANS LAKE												
1982	647	1262	86	184	66	174	10.2	13.8	76.7	94.6	264	84.8
1983	331	645	66	129	52	140	15.7	21.7	78.8	108.5	269	75.0
1984	419	817	60	117	46	112	11.0	13.7	76.7	95.7	243	76.1
1985	536	1045	78	152	45	124	8.4	11.9	57.7	81.6	276	71.1
1986	385	751	58	113	41	103	10.6	13.7	70.7	91.2	252	85.4
1987	326	636	49	96	45	111	13.8	17.5	91.8	115.6	247	66.7
1988	416	811	62	122	21	51	5.0	6.3	33.9	41.8	242	66.7
1989	395	770	59	116	51	90	12.9	11.7	86.4	77.6	177	64.7
1990	367	716	55	107	50	97	13.6	13.5	90.9	90.7	193	80.0
Total	424.7	828.1	573	1136	417	1002	11.3	13.8	73.7	88.6	240.3	74.0
\bar{x}			63.7	126.2	46.3	111.3						

Appendix C. (continued).

STUDY AREA	N _T		Q		Take		% Harvest rate		% S		Mean TL (c m)	% males
	No.	AL (m)	No.	AL (m)	No.	AL (m)	No.	AL	No.	AL		
ORANGE LAKE												
1981	2263	4413	373	728	283	550	12.5	12.5	75.9	75.5	194	67.8
1982	2117	4128	303	600	291	589	13.7	14.3	96.0	98.2	202	68.4
1983	1871	3648	386	753	186	366	9.9	10.0	48.2	48.6	197	66.1
1984	1293	2521	204	398	193	422	14.9	16.7	94.6	106.0	219	73.1
1985	1836	3580	277	540	229	515	12.5	14.4	82.7	95.4	225	73.8
1986	2329	4542	349	680	284	516	12.2	11.4	81.4	75.9	182	68.3
1987	1461	2849	219	427	202	380	13.8	13.3	92.2	89.0	188	57.4
1988	2082	4060	312	609	185	340	8.9	8.4	59.3	55.8	184	52.4
1989	1459	2845	219	427	345	634	23.6	22.3	157.5	148.5	184	58.6
1990	1225	2389	184	359	160	337	13.1	14.1	87.0	93.9	211	60.0
Total	1793.6	3497.5	2826	5521	2358	4649	13.5	13.7	87.5	88.7	198.6	64.6
\bar{x}			282.6	552.1	235.8	464.9						
ALL LAKES												
1981	2775	5411	461	900	350	675	12.6	12.5	75.9	75.0	190	69.0
1982	2925	5704	409	824	379	804	13.0	14.1	92.7	97.6	218	73.8
1983	2481	4837	507	989	277	586	11.2	12.1	54.6	59.3	224	69.3
1984	2023	3944	312	609	271	615	13.4	15.6	86.9	101.0	238	82.0
1985	2815	5489	422	823	336	767	11.9	14.0	79.6	93.2	236	73.0
1986	3299	6434	495	965	415	791	12.6	12.3	83.8	82.0	208	73.8
1987	2148	4189	322	628	303	589	14.1	14.1	94.1	93.8	204	67.0
1988	3242	6322	475	928	250	472	7.7	7.5	52.6	50.9	203	61.6
1989	2272	4430	341	666	469	849	20.6	19.2	137.5	127.5	177	61.2
1990	1992	3886	299	583	257	511	12.9	13.2	86.0	87.7	189	68.7
Total	2597.2	5064.5	4043	7915	3307	6659	13.0	13.4	84.4	86.8	208.8	69.9
\bar{x}			404.3	791.5	330.7	665.9						

¹Based on estimated 1.95 m total length.

Appendix D. Size statistics in descending order of SVL, for 10 largest alligators of each sex harvested on study lakes during 1981-90. Two males were taken through the nuisance alligator control program.

Sex	TL (in.)	SVL (in.)	WT (lbs.)	Date	Study area	Comments
Males	164.0	89.0	700	25 Sep 84	Orange	
	165.0	88.3 ^a	676 ^a	22 Jul 83	Orange	Nuisance
	166.5	86.0	1043	17 Apr 89	Orange	Nuisance
	161.0	85.0	650	13 Sep 84	Orange	
	156.0	84.0	695	26 Sep 85	Orange	
	157.5	84.0	715	26 Sep 88	Orange	
	161.5	83.5	670	7 Sep 87	Orange	
	153.0	83.0	600	13 Sep 82	Newnans	
	159.0	83.0	605	25 Sep 84	Orange	
	159.0	83.0	645	11 Sep 84	Orange	
Females	117.0	61.0	255	24 Sep 85	Orange	
	110.0	57.0	142	18 Sep 89	Orange	
	110.5	56.5	168	14 Sep 87	Newnans	
	107.0	56.0	195	18 Sep 85	Newnans	
	107.0	56.0	200	16 Sep 86	Newnans	
	90.0	55.0	165	16 Sep 82	Newnans	Bobtailed
	107.0	55.0	150	9 Sep 85	Orange	
	107.0	55.0	185	17 Sep 85	Newnans	
	106.0	55.0	210	19 Sep 85	Newnans	
	108.0	55.0	165	22 Sep 86	Orange	

^aSVL and WT estimated from allometric relationships (Table 7).

Appendix E. Yields and estimated values (U.S. \$) of aggregate feet of linear hide length (AHL) and pounds of boneless meat production (meat), for alligators harvested on 3 Florida lakes, 1981-90.

Year	Lochloosa			Newmans			Orange			All areas		
	AHL	Meat	Total	AHL	Meat	Total	AHL	Meat	Total	AHL	Meat	Total
1981	Yield	422	1,580				1,861	6,427		2,283	8,007	
	Value	10,993	6,320	17,313			48,479	25,708	74,187	59,472	32,028	91,500
1982	Yield	139	322		589	4,348	1,989	5,323		2,717	9,993	
	Value	1,334	1,288	2,622	5,654	17,392	19,094	21,292	40,386	26,083	39,972	66,055
1983	Yield	264	1,330		460	3,739	1,201	4,123		1,925	9,912	
	Value	4,179	5,320	9,499	7,282	14,956	19,012	16,492	35,504	30,473	36,768	67,241
1984	Yield	277	1,992		382	2,871	1,440	7,350		2,099	12,213	
	Value	6,083	7,968	14,051	8,389	11,484	31,622	29,400	61,022	46,094	48,882	94,946
1985	Yield	419	1,816		407	3,685	1,691	8,933		2,517	14,434	
	Value	8,380	8,172	16,552	8,140	16,583	33,820	40,199	74,019	50,340	64,953	115,293
1986	Yield	564	2,065		340	2,471	1,758	5,175		2,662	9,711	
	Value	15,138	9,293	24,430	9,126	11,120	47,185	23,288	70,472	71,448	43,700	115,148
1987	Yield	342	981		383	2,446	1,314	4,524		2,039	7,951	
	Value	13,875	4,905	18,780	15,538	12,230	53,309	22,620	75,929	82,722	39,755	122,477

Appendix E. (continued)

Year	Lochloosa			Newmans			Orange			All areas		
	AHL	Meat	Total	AHL	Meat	Total	AHL	Meat	Total	AHL	Meat	Total
1988	Yield	276	882	173	1,108	1,160	2,902	1,609	4,892			
	Value	12,467	4,410	16,877	7,814	5,540	13,354	52,397	14,510	66,907	72,679	97,139
1989	Yield	425	882	307	799	2,164	5,929	2,896	7,610			
	Value	19,610	4,851	24,461	14,165	4,395	18,559	99,847	32,610	132,456	133,621	175,476
1990	Yield	261	496	330	1,174	1,150	4,462	1,741	6,132			
	Value	14,355	2,728	17,083	18,150	6,457	24,607	63,250	24,541	87,791	95,755	129,481
1981-90	Yield	3,389	12,346	3,371	22,641	15,728	55,148	22,488	90,135			
	Value	106,414	55,255	161,668	94,258	100,156	194,414	468,016	250,659	718,674	668,687	1,074,756
\bar{x}	Yield	339	1,235	337	2,264	1,573	5,515	2,249	9,014			
\bar{x}	Value	10,641	5,525	16,167	9,426	10,016	19,441	46,802	25,066	71,867	66,869	107,476

Appendix F. Number (\bar{n}) of alligators taken, mean wholesale value of harvested alligators, GFC fees, fees on a % of \bar{x} value of alligator (% tax), aggregate net hunter income (ANHI), number of hunters participating, and mean potential income/hunter (\bar{x} PI) for alligator harvests on Lochloosa, Newmans, and Orange lakes, 1981-90.

Year	\bar{n}	\bar{x} value / \bar{n}	GFC ¹ fees	GFC fee / \bar{n}	% tax	ANHI	No. hunters	\bar{x} PI
1981	350	\$ 261	\$ 17,842	\$ 51	19	\$ 73,659	14	\$ 5,261
1982	379	174	7,825	21	12	58,230	20	2,912
1983	277	243	9,142	33	14	58,099	20	2,905
1984	271	350	13,828	51	15	81,118	20	4,056
1985	336	343	15,102	45	13	100,191	20	5,010
1986	415	277	21,434	52	19	93,713	20	4,686
1987	303	404	24,817	82	20	97,661	20	4,883
1988	250	389	13,000	52	13	84,139	22	3,824
1989	469	374	22,820	49	13	152,656	35	4,362
1990	257	504	12,210	48	9	117,271	18	6,515
Σ	3307		\$158,020			\$916,736	209	\$44,413
\bar{x}	330.7	332	\$ 20,061	\$48	15	\$ 87,415	20.9	\$ 4,183

¹Based on the retention of 30% of the sale price of hides by the GFC from 1981-87, and charging \$250/hunter license and \$30/hide validation fees from 1988-90.