POPULATION ECOLOGY OF THE LEOPARD FROG,

Rana pipiens pipiens SCHREBER

AT DELTA MARSH, MANITOBA

by

SUSAN BATES EDDY

A thesis

submitted to the Faculty of Graduate Studies

in partial fulfilment of the requirements for the

degree of Master of Science

Department of Zoology

University of Manitoba

Winnipeg, Manitoba

Canada

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ABSTRACT

Population parameters and various aspects of the life history of

the leopard frog, Rana pipiens pipiens, were studied at the University of

Manitoba Field Station at Delta Marsh, Manitoba over three summers.

Stomach samples contained a wide variety of animals, including

tadpoles and frogs of their own species. Empty stomachs were found during

cold and cloudy weather, and during migration and breeding periods.

Spring migration from the lake to breeding areas in the marsh took

place as soon as it was physically possible and breeding occurred

immediately. Fall migration seemed to be triggered by a combination of

internal and external mechanisms although the weather controlled the

intensity of activity on any evening.

Tadpole growth varied between sites and between years, probably

because of the amount of food available.

There are at least three year classes of frogs, but following the

fourth summer more than one year class can form a size class - growth is

fastest in the second summer, and extremely slow following the third.

Females grow faster than males, but the difference is not significant.

Although mortality is normally high in the tadpole stage, low water

levels resulted in even higher mortality. This was probably because of

algae toxins and lack of oxygen rather than predation.

During the study there was a shift in the size structure of the

population due to selective mortality on younger frogs. Unusually heavy

ice and north winds following the beginning of the thaw killed younger

frogs, which stayed in or near the lake in early spring. By the spring

of 1974 there were very few frogs left and most of these were of the

largest size class.

INTRODUCTION

The northern leopard frog, Rana pipiens pipiens Schreber, breeds in shallow, temporary ponds, spends the summer in meadows, often relatively far from water, and overwinters under water in bodies of water that are not frozen to the bottom and are not subject to oxygen depletion during the winter. Its range extends over most of North America as far north as the Northwest Territories. It is replaced by R. pipiens sphenocephala and R. pipiens berlandieri in the southeastern United States. The species does not occur on the Pacific Coast.

In Manitoba it is abundant in the marshes on the southern shores of Lakes Winnipeg and Manitoba. Leopard frogs are found in lower density throughout the Interlake area and the rest of southern Manitoba. There is probably only one population of leopard frogs along the southern shores of Lake Manitoba, and this may not be genetically isolated from leopard frogs throughout southern Manitoba.

Thorough population studies have been carried out on other anuran species, some closely related to Rana pipiens. Tadpole survival has been estimated in R. aurora by Calef (1973a), in R. clamitans by Martof (1956a), in R. pretiosa by Turner (1960), in R. sylvatica by Herreid and Kinney (1960) and in both R. pretiosa and R. aurora by Licht (1974). Adult population structure has been studied in most of these species by Calef (1973b), Martof (1956b), Turner (1960), and Licht (1974).

Very little is known about the size distribution and production and growth rates of leopard frogs. Force (1933) did a brief study of growth rates in the middle of one summer. Ryan (1953) measured growth

in marked and recaptured frogs of three ranid species including R. pipiens. Merrill (1968) measured egg production and estimated total and breeding populations in conjunction with a study on occurrence of the Burnsi and Kandyohi genes, unspotted and speckled skin patterns, in Minnesota leopard frogs. The remaining information on growth and mortality is derived from laboratory studies.

The leopard frog in southern Manitoba is within 300 miles of its northern limit for this longitude. It is subjected to more severe climatic conditions than in other areas where it has been studied, longer winters and frequent dry summers. Despite the severity of conditions, the leopard frog is very abundant in this area, and apparently is an important link in the marsh food chain. It is also being increasingly exploited by man.

The objective of this study was to determine the size structure of the leopard frog population at Delta Marsh, rates of production and growth, and mortality rates at various stages in the life history. In order to harvest these frogs without endangering the population, it is necessary to know these parameters and the factors which influence them. It was also important to study feeding migratory behavior, aspects of the annual cycle which influence population parameters.

METHODS

The Study Area

This study was conducted on the University of Manitoba Field Station property at Delta Marsh, Manitoba. General descriptions of the entire marsh area are available in Hochbaum (1944, 1955), Sowls (1955), Olsen (1959), and Walker (1959, 1965). Maps and descriptions of the field station property are given by Hlynka (1970), McNicholl (1971), and Acere (1971). Fig. 1, a map of the University of Manitoba Field Station, shows the sites described below in relation to Lake Manitoba and other prominent local features.

Egg production and tadpole development were studied in specific areas where mating was observed and eggs were found. These sites varied with yearly water levels. Site I is a wet meadow area near the west dyke of the Assiniboine River Diversion. It is surrounded by Scolochloa festucacea with emergent Typha sp. and Scirpus sp. bordering directly the deeper water in the area. In 1972 the water, continuous with the Blind Channel via small furrows, was as deep as 1 m in May. Egg deposition was observed carefully in an area approximately 100 m by 200 m in that year. As the water level dropped, tadpoles moved into a larger, deeper area. The water level dropped gradually throughout the summer. A few small ponds were isolated; most of the area dried completely.

During the summer of 1973 there was no water in Site I and it was abandoned as a study area. In 1974 water in the area was comparable to 1972 levels. Male frogs were heard calling there during the breeding season, but no eggs or tadpoles were found, and the site was again

FIGURE 1.   Map of the University of Manitoba Field Station area.

Roman numerals denote sites for tadpole study.

LAKE MANITOBA

BEACH RIDGE

BLIND CHANNEL

DIVERSION

I

III

ASSINIBOINE RIVER

N

UFS BOUNDARY

PERMANENT WATER

0   KM   1
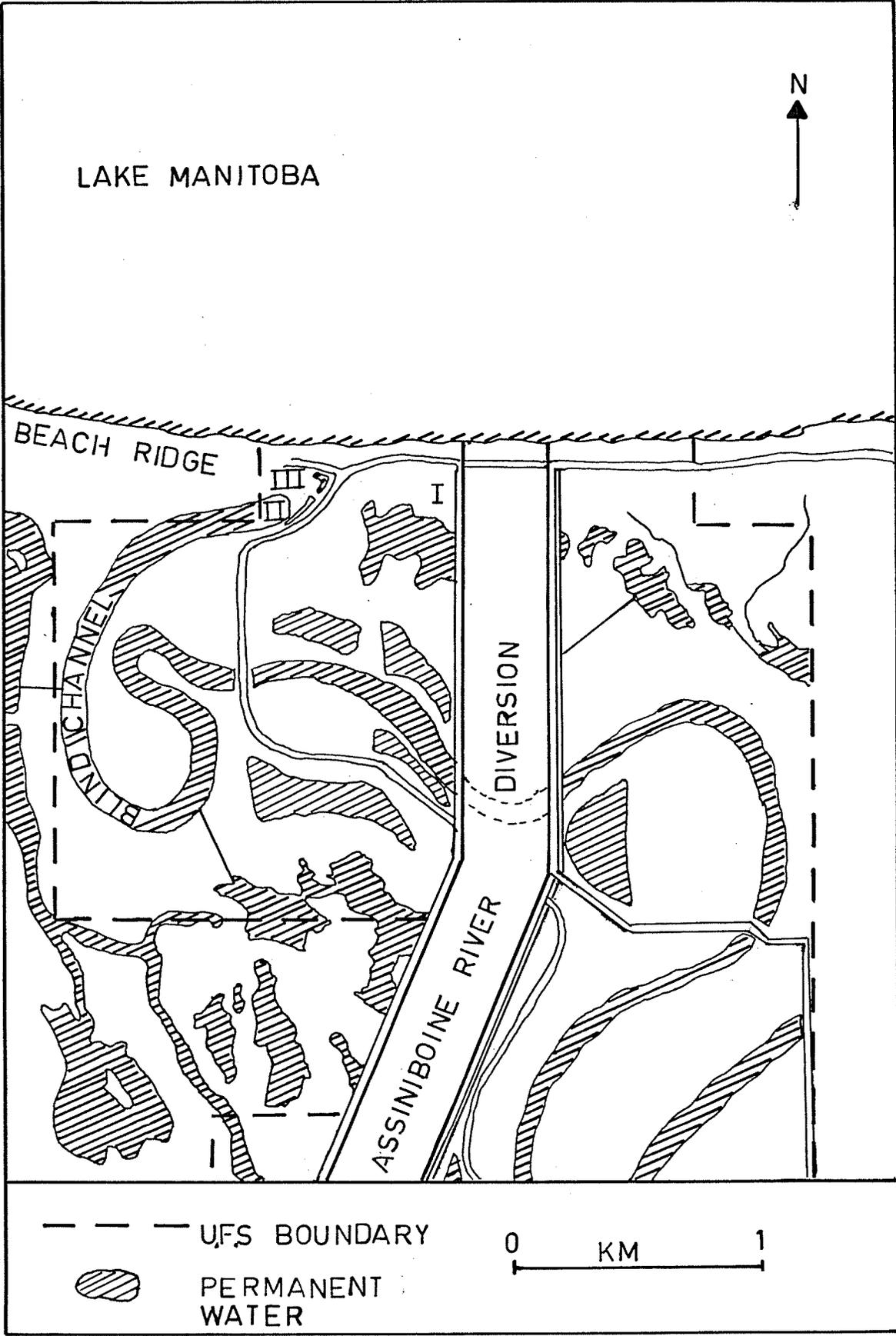
abandoned.

Site II, which was used more extensively to study larval development, was the northeast end of the Blind Channel, which is connected to Lake Manitoba via Cram Creek and man-made ditches. The easternmost 2 km of the channel was monitored for eggs and tadpoles in 1972 and 1973, but none were found past the easternmost 150 m, where the width is 80 m and the water relatively shallow. The channel is bordered mainly by Typha sp where breeding activity occurred. By the time the tadpoles had moved away from egg deposition sites, the bottom of the channel was covered by Myriophyllum sp. In 1974 a scant growth of Potamogetan richardsonii was found on the bottom of the channel by the last week of June, but there was no other vegetation, and no tadpoles were found by that time.

Site III was a small L-shaped ditch with a total length of 195 m and width between 3 and 6.7 m, connected by a culvert to a ditch continuous with the Blind Channel. A description of the site by Acere (1971) includes a map and faunal description. The vegetation in and around the ditch is more varied than for the other two areas. Phragmites communis, Typha sp., Urtica dioica, Agropyron repens, Cirsium arvense, and Salix sp. are among the most frequently occurring plants along the banks of the ditch. Myriophyllum sp., Potomogetan pectinatus, and P. richardsonii cover most of the bottom, and Lemna trisulca and L. minor are found in the water.

Collecting Methods

Eggs

In order to estimate production in a study area, egg masses were

located by visual search every two or three days throughout the breeding season. In 1972 the volume of every egg mass found was determined. In 1973 only a sample of the egg masses was measured. In 1974 no determination of egg mass volume was made. Samples from the masses gave an estimate of the number of eggs per ml of egg mass and percentage of fertilized eggs. From these samples a total number of viable eggs in a study area could be estimated.

Tadpoles

Both growth and numbers of tadpoles were followed. Tadpoles were caught for both purposes mainly by dipnet. Growth of tadpoles was followed in all study areas from a few days after hatching until most of the population had transformed, a period of about six weeks. Body length and total length were measured with dial calipers to the closest 0.1 mm on a sample of 50 or 100 tadpoles, when it was possible to catch that many, and the mean lengths were calculated for each day. The tadpoles were returned to the population. In 1972 search was abandoned when it became difficult to obtain samples of 10 or more. In 1974 tadpoles were not found at all in the first two weeks after hatching, nor were any found before July in Site II, so samples were taken only in Site III, and the sampling period was brief.

Numbers of tadpoles were estimated by a marked recapture experiment, which is described later, and by trapping on a grid. In 1973 funnel traps made of polyethylene bottles, a modification of Calef's (1973a) method, were anchored just below the surface of the water in Site II where eggs had been found. These traps were placed 15 m apart on a 75 m^2 grid. No trapping was possible in 1972 and 1974 because eggs were not deposited

in great numbers in areas extensive enough for such a grid.

Transformed Frogs

Juvenile and adult frogs were collected throughout the marsh for measurements of size frequency and for enumeration, but mainly within the University Field Station property. During spring and fall migrations between the lake and the marsh frogs were found on the beach and wooded ridge. Following the spring migration, they were collected in the shallow water where they were breeding. Collections were made either by hand or with the aid of a dipnet, mostly at night during the breeding season, and during both day and night for the rest of the summer. In 1972 the June and July samples were confined to 100 frogs each over a 24-hour period. Otherwise no restrictions were placed on sample size. August and September samples were biased intentionally towards adult frogs because of the extremely large proportion of the population represented by juveniles. Daily samples of all catchable frogs were taken several times during this period in order to obtain a true size frequency distribution.

To increase the sample size during spring and fall migrations, a drift fence was built between two of the field station buildings at the top of the beach ridge. Five gallon cans were sunk into the ground at the ends of the drift fence as shown in Fig. 2 and served as pitfall traps. One trap (outgoing) was used in the spring and two (outgoing and incoming) in the fall.

All frogs were measured and, if possible, sexed externally. Most frogs were then released approximately where they had been captured. In 1972 frogs being released were marked to aid in enumeration by cutting

FIGURE 2.   Arrangement of pitfall traps.

SPRING

N

LAKE MANITOBA

BEACH

BUILDING

DRIFT
FENCE

TRAP 1
INCOMING

~0.5 M
HIGH

BUILDING

|← ~6 M →|

DELTA MARSH

FALL

N

LAKE MANITOBA

BEACH

TRAP 1
OUTGOING

TRAP 2
INCOMING

DELTA MARSH
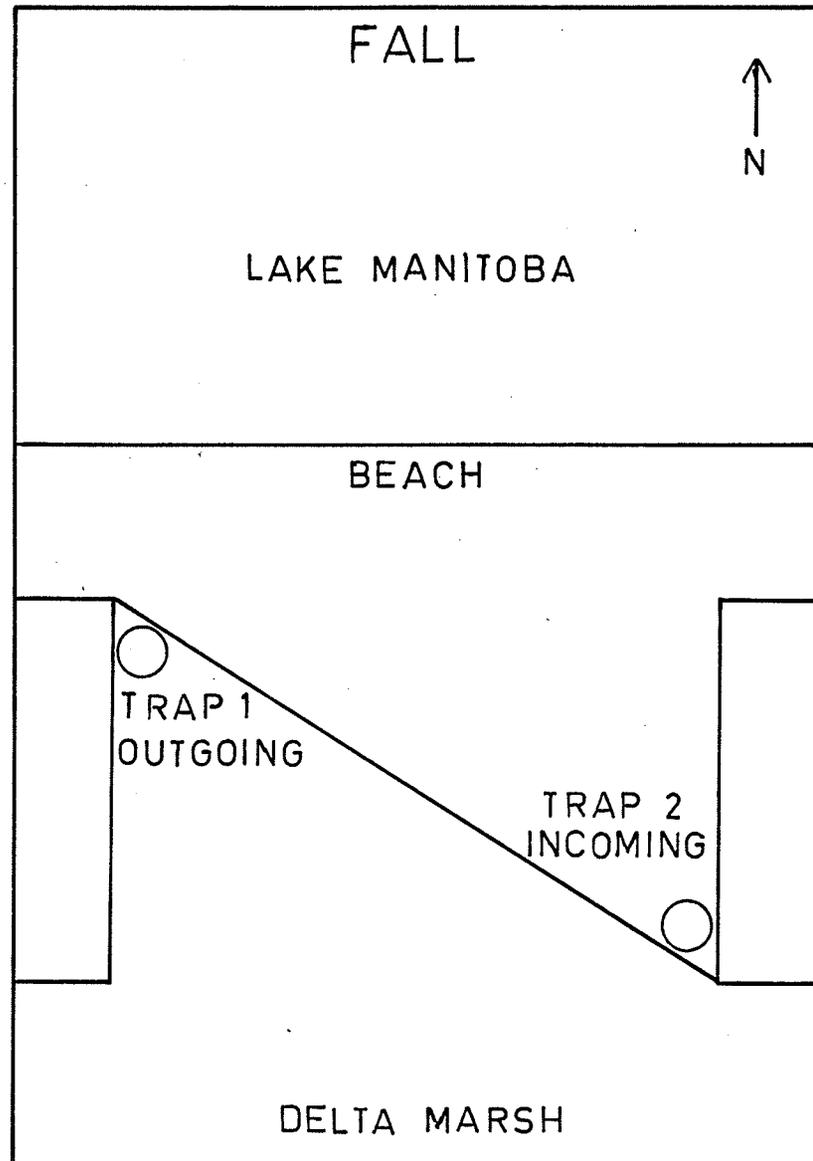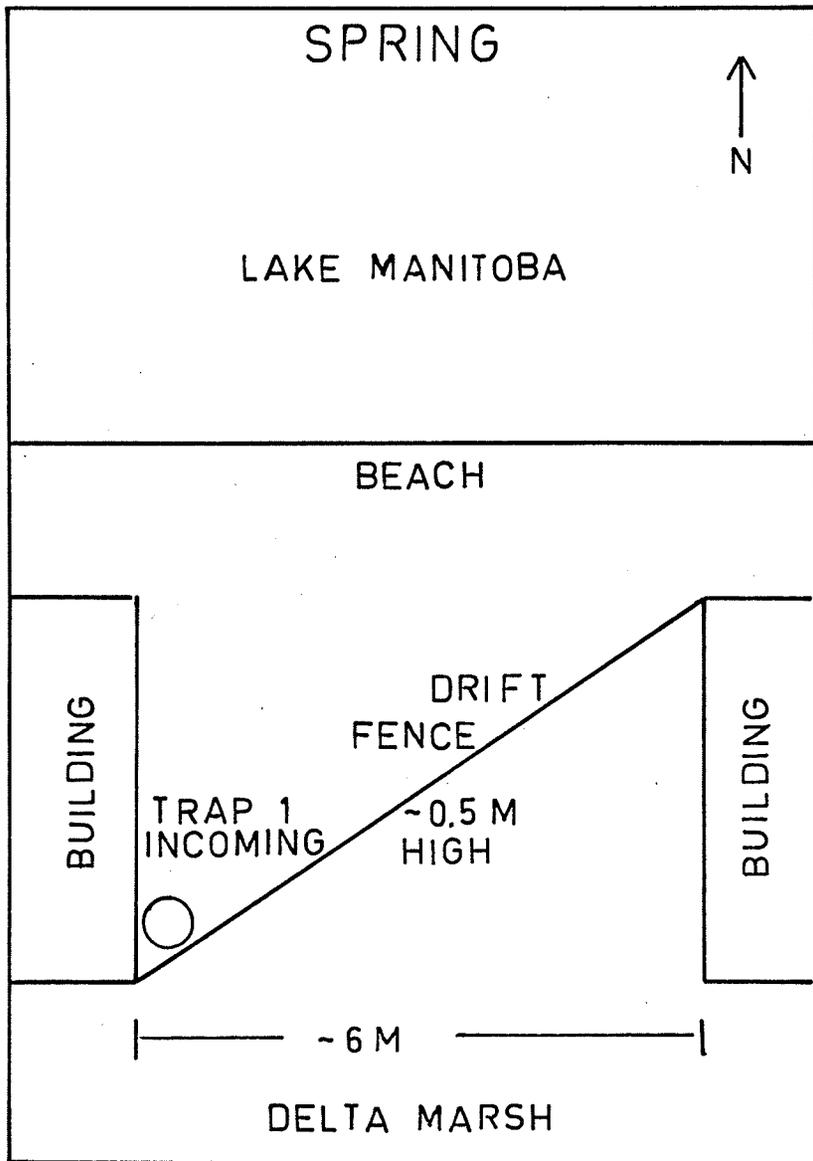
the distal joint off   a single digit.   A different digit was used for each month, and frogs were marked only the first time they were caught. In 1973 and 1974 each frog was given an individual mark, using a marking system similar to that described by Martof (1953a).   Up to 2 digits per foot were clipped.   Front toes were numbered 1-8 from the outer right toe to the outer left toe, and rear toes 1-10 in the same manner.   This gave a total of 27,994 combinations, and by July, 1974, 4,014 had been used.

A sample of frogs was saved from each month's collection for stomach content analysis throughout the summer during all three years.   The sample was distributed as uniformly as possible among both sexes and all size classes.   Intact insects were identified to order, and insect parts were identified to order when possible.   Arachnids were identified to order.   Other invertebrates were identified to class.   Amphibians and mammals were identified to species.

Data Treatment

Tadpole Growth

In order to measure the effect of temperature on growth, I plotted body length against cumulative degree-days since hatching, as reported by Calef (1973a).   Four degrees Celsius was subtracted from each temperature on the assumption that there is no growth at temperatures below 4°C.

Water temperatures were taken from the meteorological record kept at the field station.   Maximum and minimum temperatures are recorded daily in an evaporation pan which is approximately 2 m in diameter and the same depth as water in which leopard frog eggs were

deposited. The mean of the two temperatures was used to calculate degree-days during egg and tadpole development. The record was incomplete for May, 1974 because of unusually low temperatures and flooding of the field station.

Growth of Transformed Frogs

Relative frequency of snout-vent lengths was plotted for transformed frogs caught in May, June and September of each of the three years of the study (see Figs. 8-13). Since sampling effort varied with time of year and between years, each month's sample was normalized independently. With the exception of the September samples, males, females, and juveniles were caught randomly and approximately in the ratio in which they occurred in the population, so the frequencies of all three groups add to one for each sampling period. In September samples more effort was expended in trying to catch adult frogs because the young of the year were far more numerous. For this reason relative frequencies of the young of the year add to one, and relative frequencies of all older frogs add to one.

In order to separate size frequencies into classes, cumulative percent frequency was calculated separately for males and females of each month's sample and plotted on probability paper (Cassie, 1954). Inflection points on the resulting curve may indicate troughs between normal distributions. The normal distributions, which represent age classes, can be separated at these inflection points, and cumulative percent frequencies recalculated for each distribution. Plotting these points on probability paper again changes the normal curve to a straight line, with a mean size at 50%. Since 68.26% of the points in a normal

distribution fall within one standard deviation of the mean in either direction, the standard deviation is equal to the distance between the sizes at 50% and 15.87% (or half the distance between sizes at 84.13% and 15.87%).

Since in many cases the trough between the distribution represents an overlapping of two size classes, the distributions have been truncated in defining the ranges of the size classes. In these cases the standard deviations cannot be used for statistical tests, and it is more meaningful to make qualitative comparisons of the size classes between years.

It is also possible to find inflection points on the probability curve which do not represent real troughs between two component normal distributions, but are chance events due to small sample size. Comparisons should be made between the resultant size classes and size frequency distributions given by Figs. 8-13 in order not to create artificial size classes.

Growth rates were calculated by two methods. In the first the difference in means of each year class for May and September were compared for each year of sampling. The second method was the calculation of daily growth rates from measurements of marked and recaptured frogs.

Difference in size over the recapture period and the average amount of change per day were calculated for each of 485 frogs marked and recaptured in 1973 and 46 marked and recaptured in 1974. Size differences were divided into recapture periods by daily intervals. I assumed that apparent net increase in size is due to sampling error until growth greater than that of a one-day recapture period is reached. This occurred

at 7 days (see Appendix 1).

Recapture results for 7 or more days were split into sexes and size classes. Because the captures occurred throughout the summer, size classes defined by size frequency analysis could not be assigned. Five mm intervals were used instead, pooled if necessary to give a usable sample size. These are as follows:

I	<50 mm	V	80.1 - 85 mm
II	50.1 - 60 mm	VI	85.1 - 90 mm
III	60.1 - 75 mm	VII	>90 mm
IV	75.1 - 80 mm		

Pooling the results of growth of frogs over various time intervals creates three problems. Mean growth rates for successive intervals are correlated if an individual frog is used more than once in obtaining a mean. This presents problems in performing tests of significance on size changes based on these means. Second, the time between captures could not be controlled, so growth rates, though standardized to rates of mm/day, are actually averages of the slopes of secants of differing lengths and hence, differing slopes. Thus Fig. 16, where growth rate (rate of change of size) is plotted against size gives only an approximation of how growth rate (tangent to the growth curve) changes with size. Third, growth rates are averaged for various times of year, and seasonal differences in growth rate are lost.

For these reasons growth between actual times in the season is also presented. In order to dampen error due to measurement, sizes of frogs captured and recaptured on the same two days were averaged. Since

decrease in size is probably due entirely to measurement error, negative growth was ignored in this presentation. Values for recaptures within 7 days were also left out.

Tadpole Enumeration

Enumeration of tadpoles by mark and recapture was attempted only in 1972, this being the only year in which tadpole density was high enough in an enclosable area for recovery of marks. The population was contained in Site III by a 1/4 inch mesh net tied securely over the end of the culvert which connected the site to the Blind Channel. The mark used during the early part of the development period consisted of a methylene blue solution injected into the caudal fin. At the beginning of transformation a hind toe was clipped as a second mark in order to estimate survival. Recaptured tadpoles with dyed fins were not marked with a toe clip, so only the original capture time was known in subsequent sampling times.

It was not possible to mark a large enough number of tadpoles in one day to recapture a meaningful number of marks, so samples were marked every second day for the last 2 weeks of the development period. Samples were treated as if all tadpoles marked with a given mark had originally been caught on the same day.

The total number of tadpoles in the population at various times was estimated by two methods. The Petersen estimate (Cormack, 1968) was used, treating each mark separately and comparing the two estimates to estimate survival. The assumptions on which this estimate is based are the following:

1. Marked and unmarked animals suffer the same natural mortality.
2. Marked and unmarked animals are equally catchable.
3. Marks are not lost before the recapture period, and remain recognizable.
4. Marked animals become randomly mixed in the population by the time of recapture.
5. Recruitment is negligible.

A laboratory holding experiment that tested these assumptions is discussed in Appendix 2.

Since the distribution of the estimates for N is severely assymetrical, the reciprocal, which is more symmetrically distributed, is estimated by m/Mn, where n is the sample size at the second sample time, m is the number out of n that is marked, and M is the number of marks released into the population at the first sample time. The variance of the reciprocal is estimated by $1/nM\hat{N}(1-M/\hat{N})$. Confidence limits for N can be calculated from the confidence limits for $1/N$. A death rate which is the same for marked and unmarked animals does not affect these estimates if the number of both marked and unmarked animals is large (Cormack, 1968). $\hat{N}$ now estimates the population size at the first sample time.

A Jolly-Seber estimate of the tadpole population can be used if there are at least three sample times and if the time of the most recent capture time can be determined for each recaptured tadpole. This was possible with the two methods of marking tadpoles. The sampling dates used were 15-29 June for time 1, the period during which the dye injection was used as a mark, 30 June as time 2, when a hind toe was clipped for a mark, and 2 July as time 3, the first day on which both

marks were recovered in the sample. Marked tadpoles caught on 30 June would have been seen most recently at time 1, (n_{21}) by Jolly's notation (Jolly, 1965). On 2 July tadpoles marked with dye would probably have been seen most recently at time 1 (n_{31}) and tadpoles marked with a toe clip would have been seen most recently at time 2 (n_{32}).

The assumptions for the Jolly-Seber model are similar to those for the Petersen estimate except that recruitment is permitted and all animals that leave the population must do so permanently. Since marking was begun late in the development of the tadpoles, and the net containing the population was watched carefully for rips, recruitment was unlikely anyway. The estimation equations used when there is death but no recruitment are the following (Jolly, 1965):

$$\hat{N}_i = s_i Z_i! / R_i + n_i \quad (i=1,2,\ldots L-1)$$
$$\hat{\Phi}_i = \hat{N}_{i+1} / (\hat{N}_i - n_i + s_i) \quad (i=1,2,\ldots L-2)$$
$$V(\hat{N}_i) = (\hat{N}_i - n_i)(\hat{N}_i - n_i + s_i)(1/R_i - 1/s_i) + \hat{N}_i = \hat{N}_i^2 / \hat{N}_i$$

N_i = Total number in the population when the ith sample is captured.

L = Number of samples

n_i = Number captured in the ith sample.

M_i = Total number of marked animals in the population at time i.

A_i = M_i / N_i.

m_i = Number of marked animals in the population at time i.

s_i = Number released from the ith sample after marking.

Φ_i = Probability that an animal alive at the moment of release of the
     ith sample will survive till the capture time of the i+1st sample.

Z_i = The number marked before time i which are not caught in the ith

sample but are caught subsequently.

$Z_i' = Z_i + \sum_{k+i+1}^{L} n_{k0}$. This includes animals captured for the first time

after time i.

R_i = The number of the s_i animals that are caught subsequently.

Enumeration of Transformed Frogs

Mark recapture results of adult and sub-adult frogs in 1973 were

used in an attempt to estimate total population for the sampling area.

A modification of Jolly's (1965) and Seber's (1965) method to obtain a

"pooled" estimate (Kreger, 1973; Arnason and Kreger, 1973) was used to

compensate for a low recapture rate. A recapture rate R_i of 10-15% is

necessary for a meaningful population estimate, and by pooling data over

sampling periods it is possible to improve the precision of the estimate

at the expense of sensitivity to short-term fluctuations.

The statistics s_k, R_k, m_k, and n_k are pooled over k=i, i+1, i+2,

...i+c-1, where c is the number of sampling times being pooled. The

Jolly-Seber estimates and variances are then formed in the usual way

using these "pooled" statistics. The pooled estimates have the following

meanings:

N_i is the size of the population at time i, the time the

ith sample was captured.

ϕ_i is the probability that an individual alive at time i

survives to time i+c.

B_i is the number of new entries between sample times i and

i+c.

The pooling interval chosen for this study was three weeks, and the total sampling time was 19 weeks.

In addition to the usual assumptions of the Jolly-Seber estimate is the assumption that the proportion of marks in the population is changing only slowly so that the ratios m_k/n_k and R_k/s_k have about the same expected values within each pooling interval. Movement appeared to be slow in the frogs except during spring and fall migrations, and mortality of adult frogs during the summer was relatively low, so this assumption is met with reasonable certainty. Mortality in newly transformed frogs is quite high, and the recapture rate low, so the estimate was not attempted on young of the year.

The assumption that all migration is permanent is subject to question. In 1972 male frogs disappeared from the population after breeding and became available for capture again later in the summer. In 1973 the sex ratio remained equal throughout the summer, so the assumption was probably met in that year at least until the fall migration. By the time of the migration, recapture rates were too low for meaningful estimates, so bias due to non-permanent migration was irrelevant. Failure of this assumption can produce serious over-estimates of population size but does not seriously affect survival estimates (Cormack, 1972).

RESULTS

Annual Cycle

Leopard frogs emerge from Lake Manitoba in late April or early
May, when the ice first retreats from the lake shore. Emergence was
first observed on 25 April in 1972, 21 April in 1973, and 4 May in
1974. It is possible that a few frogs survive the winter in the marsh
in sections of water that do not freeze to the bottom. Mowbray (pers.
comm.) reported leopard frogs calling in the marsh in 1974 when the
lake was still completely frozen around the shore. It may have been
possible for some frogs to emerge from the lake via the stream channels
which cut through the beach ridge, although this was not observed.

Male frogs cross the beach ridge first and begin calling from
shallow water in the marsh. In the earliest days of the breeding period
the majority of frogs found in the marsh are males. A sample caught on
the beach during the peak of the migration (9 May, 1974) had an equal sex
ratio (38/38/24 immature). Most frogs in the marsh at this time were
males, and most caught subsequently in the trap on the ridge were females.
These observations suggest that the females linger on the beach or in the
wooded ridge until breeding areas are established. In 1973, when the
breeding area was crowded with males before many females had reached the
marsh, multiple males were observed trying to mate single females.

Juvenile frogs appeared in the marsh later than adults in 1972 and
1973. In 1974 the ice was very late in melting, and most frogs emerged
in the 6 days at the beginning of break-up. After 6 days of ice-free
shore a north wind blew the ice onto shore for another 10 days, and many

frogs left on or near the shore were crushed by the ice.

The marsh was extremely dry in the spring of 1973 because of low snowfall during the previous winter and low rainfall during the spring. For this reason the breeding and post-breeding behavior of the frogs was quite different from that of the other two years. In 1972 and 1974 early breeding took place in very shallow bodies of water, many of which were temporary. Some of these dried up before the eggs had hatched, and only later breeding, in roadside ditches, borrow pits, channels, and permanently flooded meadows produced successful tadpoles. In 1973 breeding areas were limited to channels, ditches and borrow pits with permanent water, for example, Site III. Tadpole habitat was crowded, and mortality appeared to be high.

Following breeding in 1972 and 1974, the males dispersed from the breeding areas and were nearly absent from the June sample. In 1973 the sex ratio was nearly equal throughout June. Apparently in normal years the males disperse throughout the marsh to feed near permanent water, but few are found. In July they return to the breeding area, where females have remained, where they feed on the numerous insects in the ditches and to join the females in cannabalizing their own young as they transform.

Hatching occurs between the middle and end of May. Tadpoles remain near the egg masses for two or three days, after which they disperse. They are usually difficult to find for several days.

Feeding of Transformed Frogs

Food items of adult and sub-adult frogs indicate food availability rather than preference (Table 1). Empty stomachs were most often found during migration and breeding periods. All stomachs were empty in May,

TABLE 1.   FOOD ITEMS OF TRANSFORMED FROGS

Organism	% of Stomachs Examined in which Item Occurred									
	MAY		JUNE		JULY		AUG		SEPT	
	1973	1974	1973	1974	1972	1973	1972	1973	1972	1973
Oligochaeta	8.8									
Gastropoda	10.5		22.2	40.0	12.5	30.8	23.3	26.3	27.8	10.0
Arachnida										
Araneae	5.3		29.6	10.0	37.5	3.8	6.7	5.3	5.6	
Opiliones				5.0		3.8				
Acarina					37.5	11.5	10.0		5.6	
Crustacea										
Ostracoda			3.7							
Amphipoda				5.0						
Insects (Total)	96.5		96.5	85.0	75.0	69.5	73.4	68.5	44.4	50.0
Ephemeroptera					12.5					
Odonata	7.0		3.7	10.0	50.0	15.4	20.0	10.5		10.0
Orthoptera			3.7			7.7	3.3	5.3		
Hemiptera						7.7	3.3			
Coleoptera	40.4		63.0	55.0	25.0	30.8	40.0	31.6	16.7	30.0
Trichoptera	1.8			5.0		3.8	13.3	10.5		
Lepidoptera	5.3		18.5	10.0	25.0	23.0	6.7	21.1	5.6	
Diptera (Total)	70.1		55.6	5.0	62.5	30.8	16.7	5.3	5.6	10.0
Chironomidae	70.1		29.6		12.5					
Hymenoptera	1.8		7.4	10.0	37.5	7.7	16.7			
Unidentified										
Insect parts	3.5		33.3	45.0		26.9	6.7	10.5	33.3	10.0
Insect eggs			7.4							

TABLE 1 (cont.)

Organism	% of Stomachs Examined in which Item Occurred									
	MAY		JUNE		JULY		AUG		SEPT	
	1973	1974	1973	1974	1972	1973	1972	1973	1972	1973
Chilopoda					12.5					
Amphibia										
R. pipiens										
Juvenile	1.8				12.5	11.5	23.3	26.3	27.8	10.0
Tadpoles						11.5				
Other				15.0						
Mammalia										
Clethrionomys gapperi							3.3		11.1	
Microtus pennsylvanicus							3.3			
Vegetation	8.8		18.5	15.0	34.6			36.8		
Stones	1.8			5.0	12.5	23.0	10.0			
Empty		100	3.7		12.5	7.7	6.7	5.3	16.7	40.0
Total Sample Number	57	12	27	20	8	26	30	19	9	10

1974, the only time a pre-breeding sample was taken. During a chironomid hatch which lasted for two weeks in 1973, stomach contents examined were 100% chironomid remains.

Cannabalism of newly transformed juvenile frogs by adults was common following transformation. With the exception of a few small samples in 1973, all samples of frogs taken following transformation had whole or partially digested juvenile frogs in at least 10% of the stomach contents examined. Cannabalism occurred with equal frequency in males and females, and although it was most common in very large frogs, it occurred in all size groups representing frogs more than one year old. Most stomachs contained only one frog, but a few contained two or three, in various stages of digestion.

Fall Migration

The fall migration toward the lake begins around the first of August, although frogs are active on the beach ridge and shore at least until October. Movement of the young from the time of transformation is more or less toward the lake. The pitfall and drift fence trap almost always showed some movement from the beach towards the marsh during the fall. On the peak nights of migration, 9 September in both 1972 and 1973, 29.3% and 7.3% respectively of frogs caught in the trap were travelling toward the marsh.

The pitfall trap was not used in the fall of 1974, but migration of large numbers of frogs was reported on the night of 6 September (Gee, pers. comm.). A large sample was taken on the night of 23 September, and a far larger number of frogs was observed at this time than in previous years.

Frogs tended to migrate in large numbers on warm nights, particularly after a cold spell (Figs. 3 and 4). Moisture is probably the most important factor. Many frogs migrated during or after rain showers. Most of an evening's migratory activity occurred in the first hour of darkness unless there was rain later in the evening. Activity during cold weather increased as the autumn progressed. Movement was greater at a given low temperature late in September than earlier in the month.

Throughout the summer, frogs were active on land at temperatures as low as 13°C. In mid-August 8°C was the lowest temperature at which terrestrial activity was observed, although few frogs were active at temperatures below 10°C. In mid and late September frogs migrated in large numbers when temperatures were as low as 4°C.

Tadpole Growth

Tadpole growth rates were similar for all three years in both sites in spite of wide differences in hatching dates and water temperatures (Figs. 5 and 6). Body lengths of tadpoles correlated highly (P = 0.01) with cumulative degree-days since hatching (Table 2, Fig. 7), but analysis of covariance showed that the slopes of the regressions were unequal (Appendix 3). The mean tadpole body lengths at the time of transformation differed significantly between sites and years (Appendix 4). Individual comparisons within sites showed a significant difference in size between years for Site III, but not for Site II. A comparison between years for both sites also showed a significant difference.

FIGURE 3.   Numbers of frogs caught in pitfall trap per night

during fall migration in 1972 with maximum and

minimum daily temperatures.

△   max. temps.

○   min. temps.
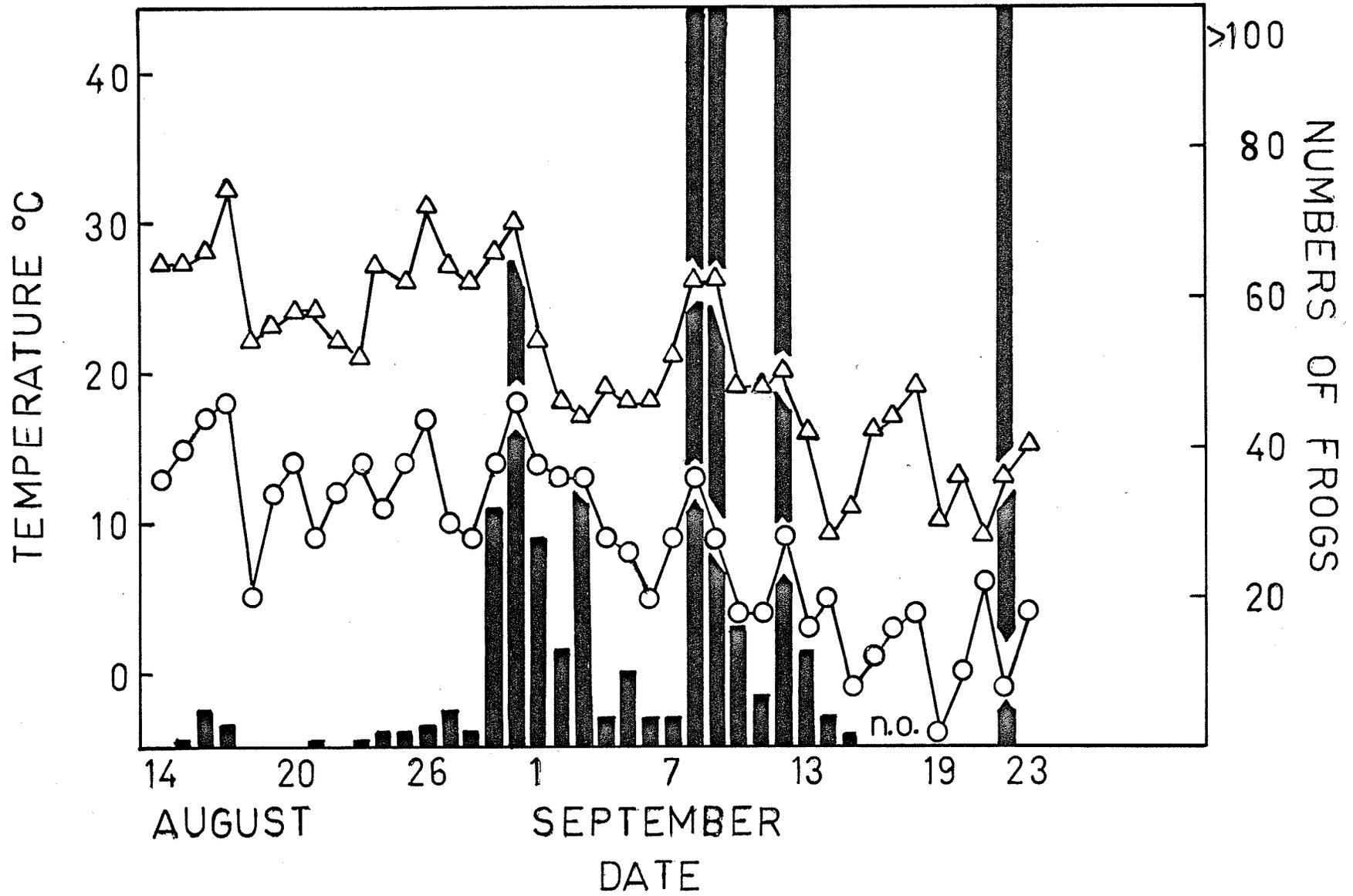
FIGURE 4.   Numbers of frogs caught in pitfall trap per night

during fall migration in 1973 with maximum and

minimum daily temperatures.

△   max. daily temp.

○   min. daily temp.
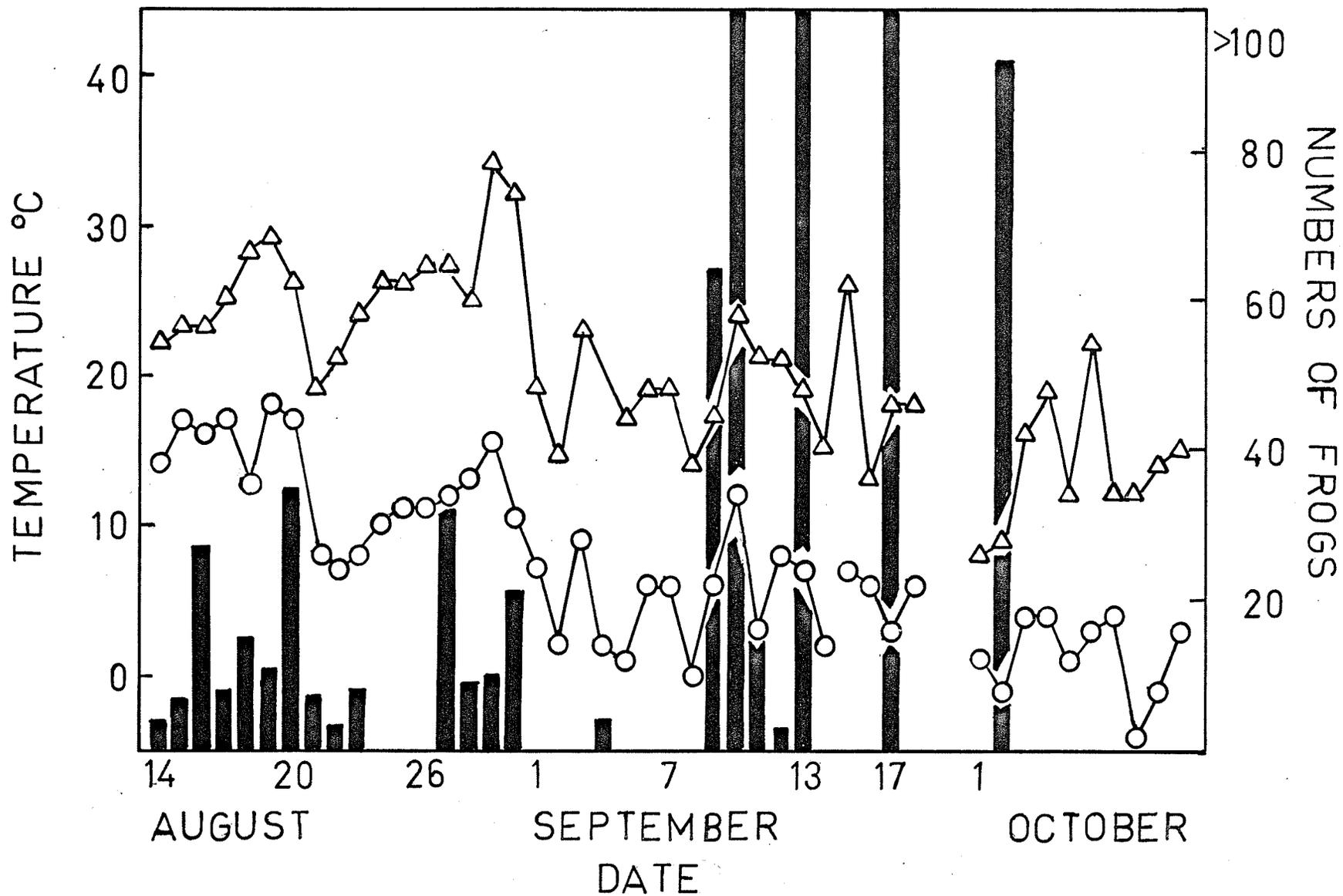
FIGURE 5.   Tadpole growth in Site II.

⊕   1972

✛   1973
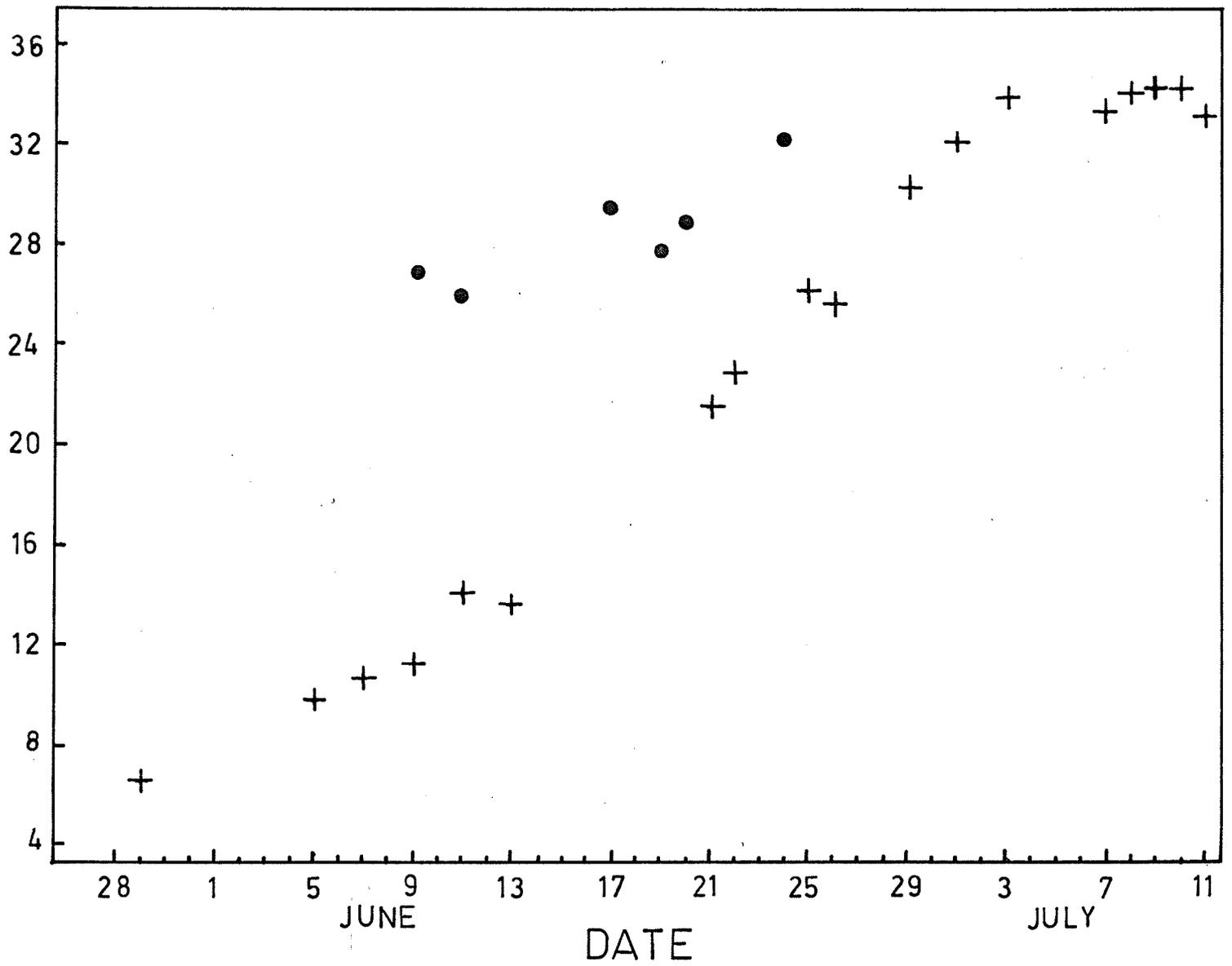
FIGURE 6.   Tadpole growth in Site III.

⊕ 1972

+ 1973

o 1974
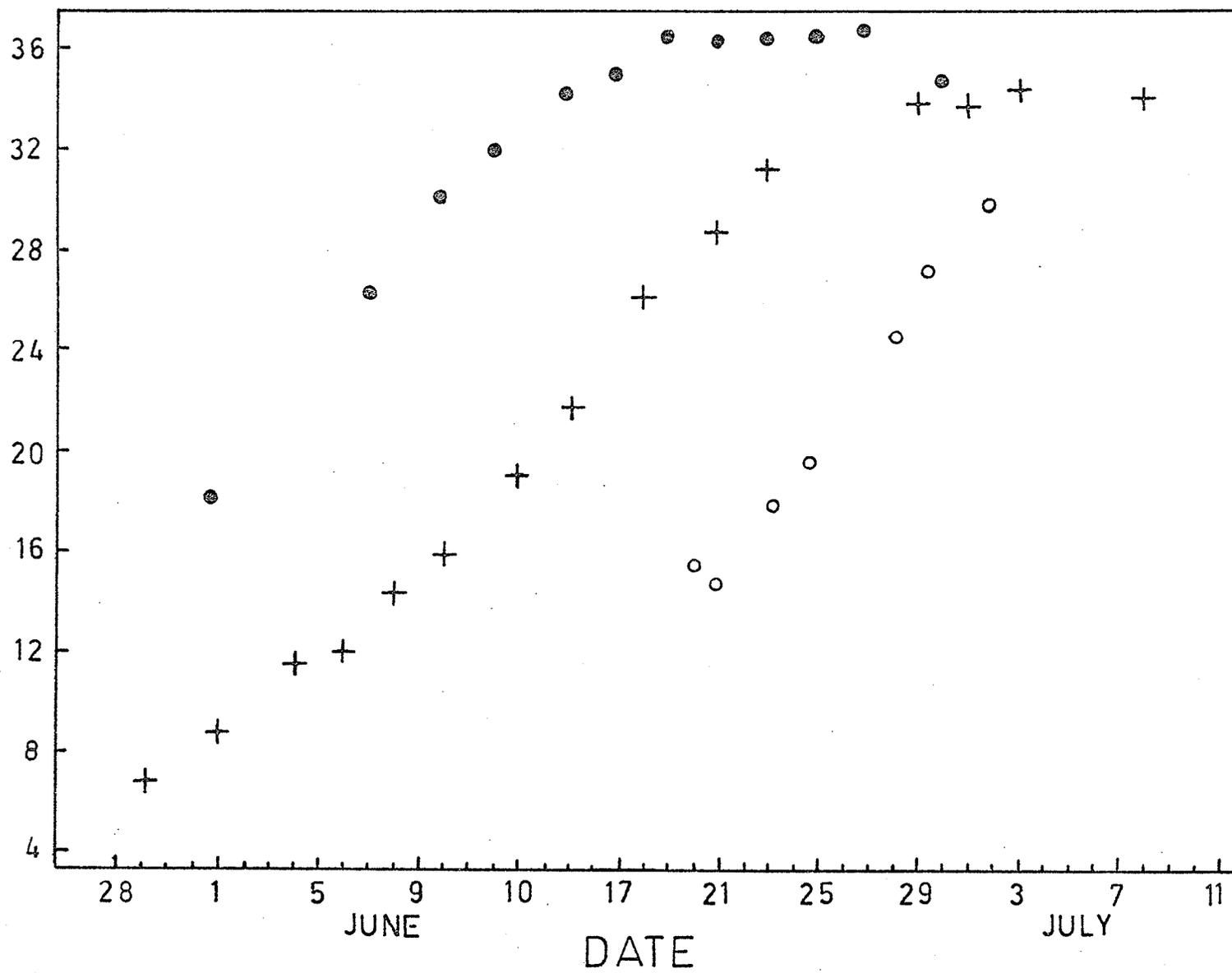
TABLE 2.   BODY LENGTH OF TADPOLES AS A FUNCTION OF CUMULATIVE TEMPERATURE.

	SITE II		SITE III		
	1972	1973	1972	1973	1974
N	6	15	10	15	7
$\hat{\beta}_1$	.025	.051	.044	.056	.0697
$S_{\hat{\beta}_1}$	.0048	.0018	.0054	.003	.003
β_0	15.62	-1.64	10.89	.568	-3.69
$S_{\hat{\beta}_0}$	2.75	.887	2.71	1.27	1.25
$\hat{Y}$	15.62+.025x	-1.64+.051x	10.89+.044x	.568+.056x	-3.69+.070x
F	25.80	753.83	2021.57	331.83	401.42
% reg	86.58	98.30	89.39	98.23	98.77
r	.9336	.992	.9436	.9810	.9940

FIGURE 7.   Body length of tadpoles as a function of cumulative

temperature.
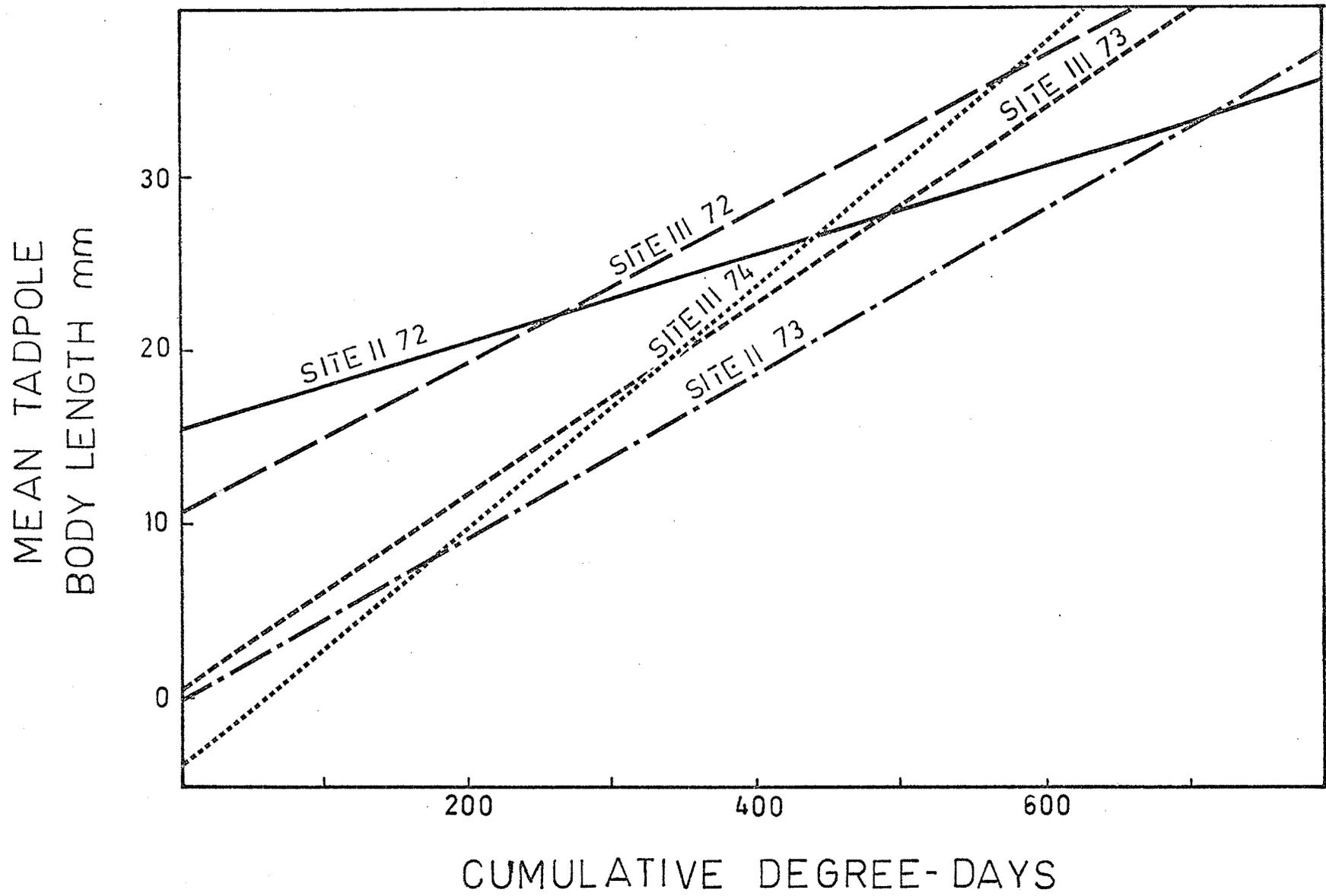
Size Frequency Distribution

Snout-vent length frequencies (Figs. 8-13), in conjunction with separation by probability paper, revealed three size classes for all samples except the one taken in the fall of 1974, when four size classes were present.

The smallest size class, 0, appeared in early July of each year as newly transformed juveniles. This size class remained detectable throughout the summer, when it comprised up to 98% of the population (Fig. 14).

During the following spring and summer this cohort became size class 1, the number indicating that the class had survived 1 winter. By the end of the second summer secondary sex characteristics appeared in some of the males of this class, but it is not known whether this size class was sexually mature.

Size class 2 consisted of frogs which had survived 2 winters. Some appeared to be sexually mature, and others reached maturity during their third summer.

Size class 3 was compared entirely of sexually mature frogs, of which the majority were entering their fourth season. In 1972 this size class decreased in relative abundance toward the end of the summer and was replaced by size class 2. Some survival beyond three years of age was indicated by the infrequent occurrence of extremely large frogs in large samples.

In 1973 and 1974 the summer mortality of the third size class was not as evident, and very large frogs made up an increasing proportion of the samples, with a resulting increase in the mean size for the size

FIGURE 8.   Size frequency histogram, 1972.

Immature frogs are divided arbitrarily equally between
the sexes.
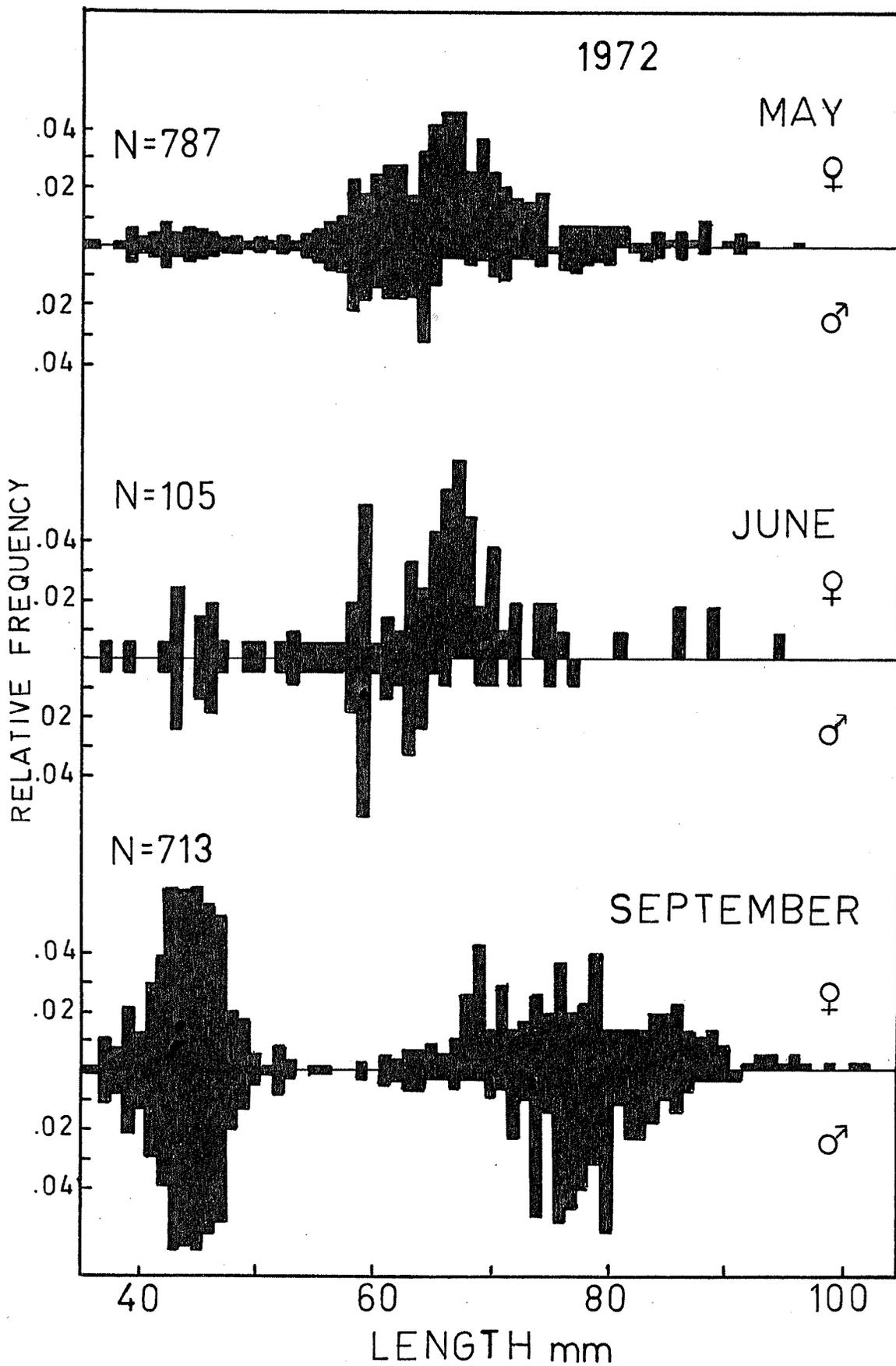
FIGURE 9.   Size frequency histogram, 1973.

Immature frogs are divided arbitrarily equally between
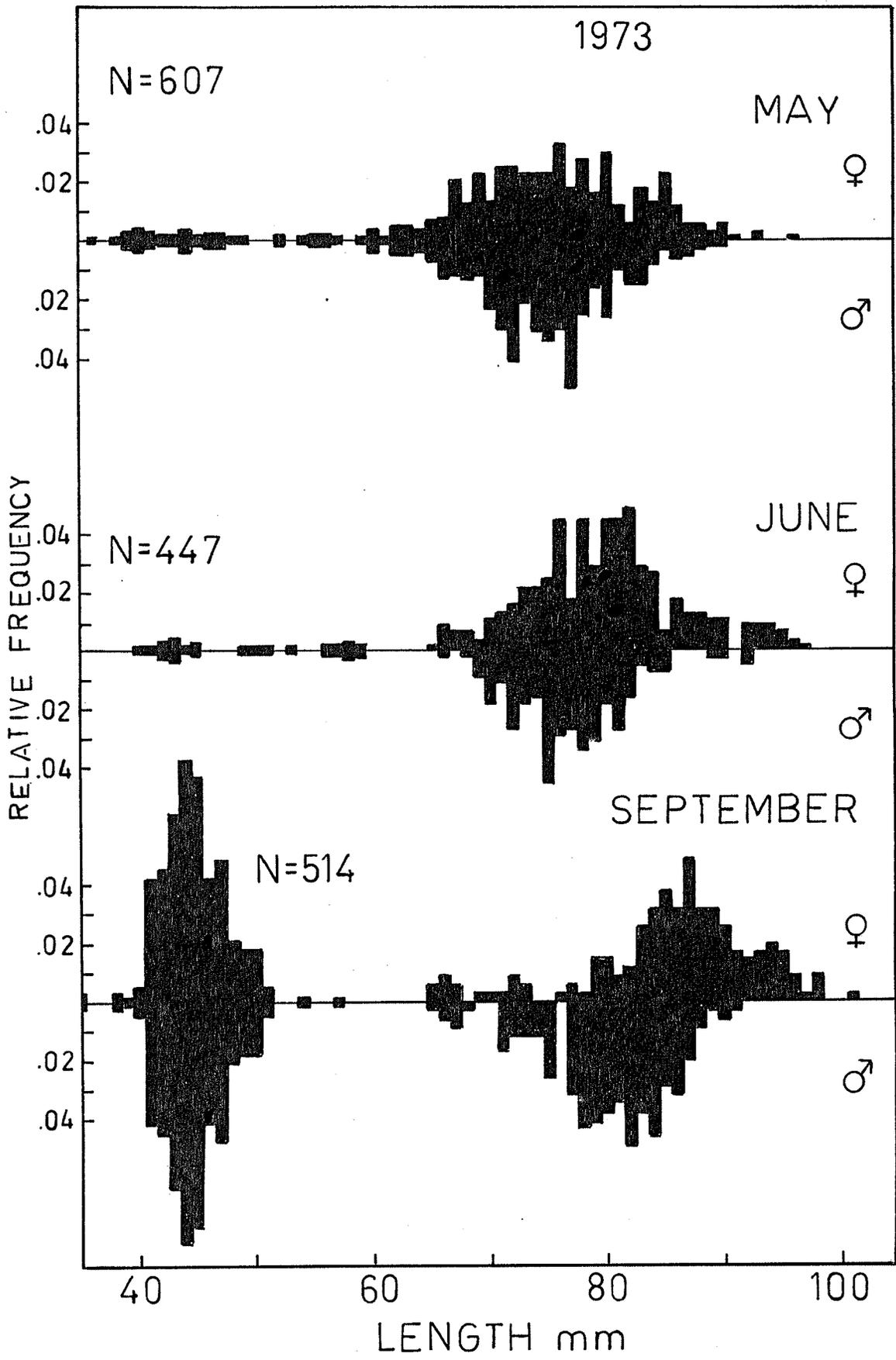
the sexes.

FIGURE 10.   Size frequency histogram, 1974.

Immature frogs are divided arbitrarily equally between

the sexes.

1974

N=193

MAY

♀

♂

JUNE

N=514

♀

♂

SEPTEMBER

N=669

♀

♂

RELATIVE FREQUENCY

.04
.02
.02
.04
.04
.02
.02
.04
.04
.02
.02
.04

40   60   80   100

LENGTH mm
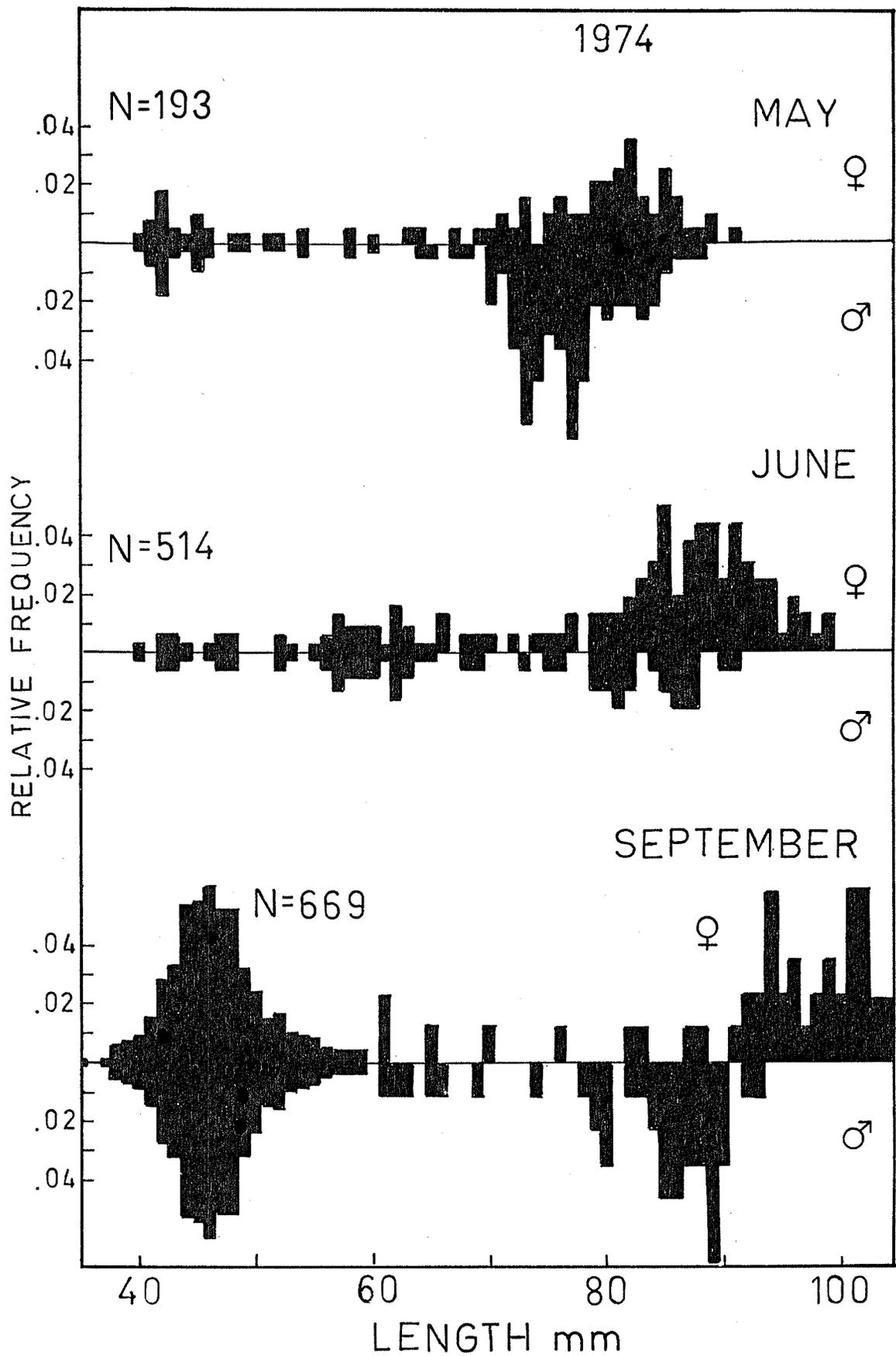
FIGURE 11.   Size frequency histogram for May, 1972, 1973, and 1974.
Immature frogs are divided arbitrarily equally between
the sexes.
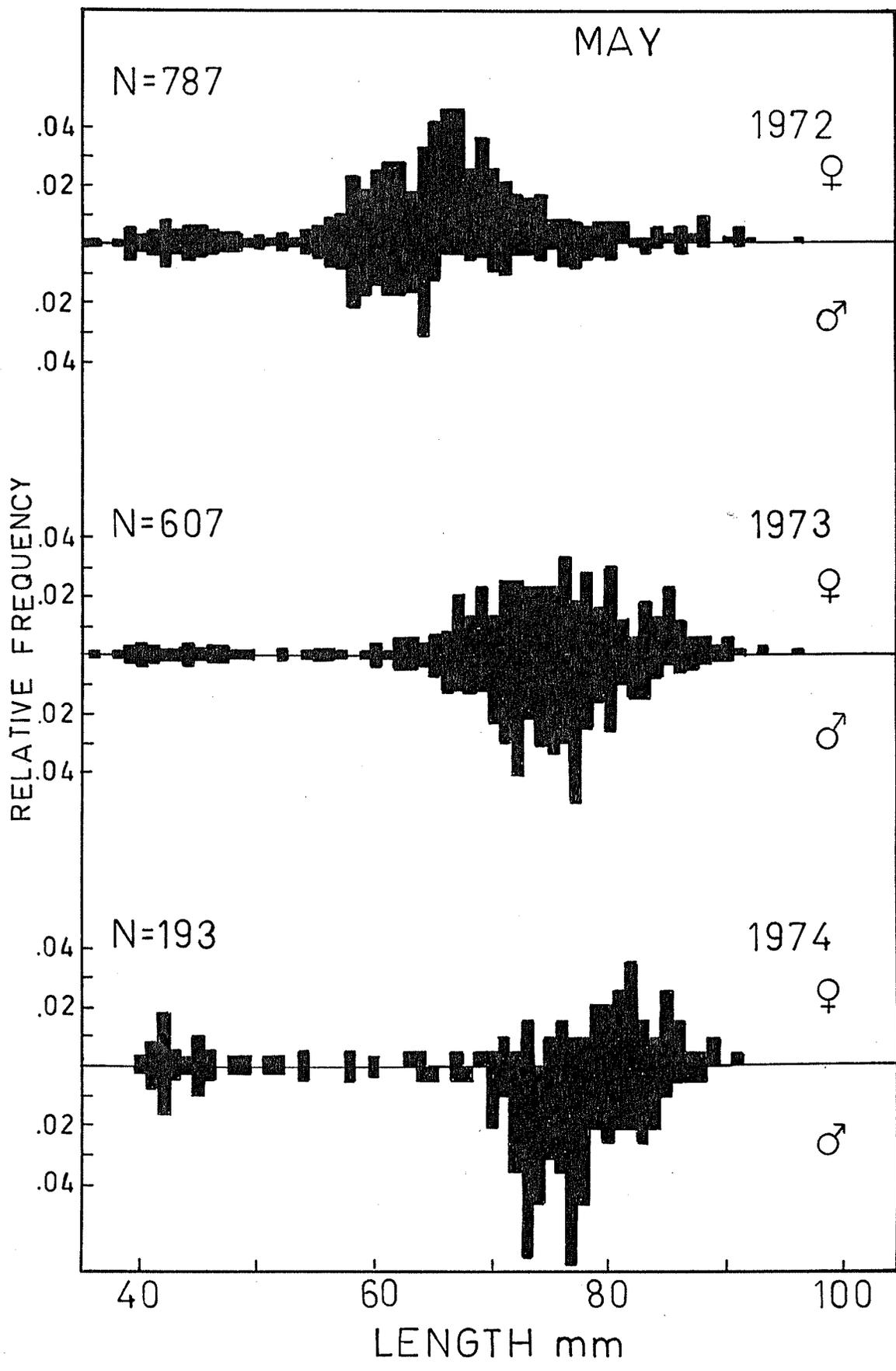
FIGURE 12.   Size frequency histogram for June, 1972, 1973, and 1974.

Immature frogs are divided arbitrarily equally between

the sexes.

JUNE

N=105

1972

♀

♂

N=447

1973

♀

♂

1974

N=514

♀

♂

RELATIVE FREQUENCY

LENGTH mm
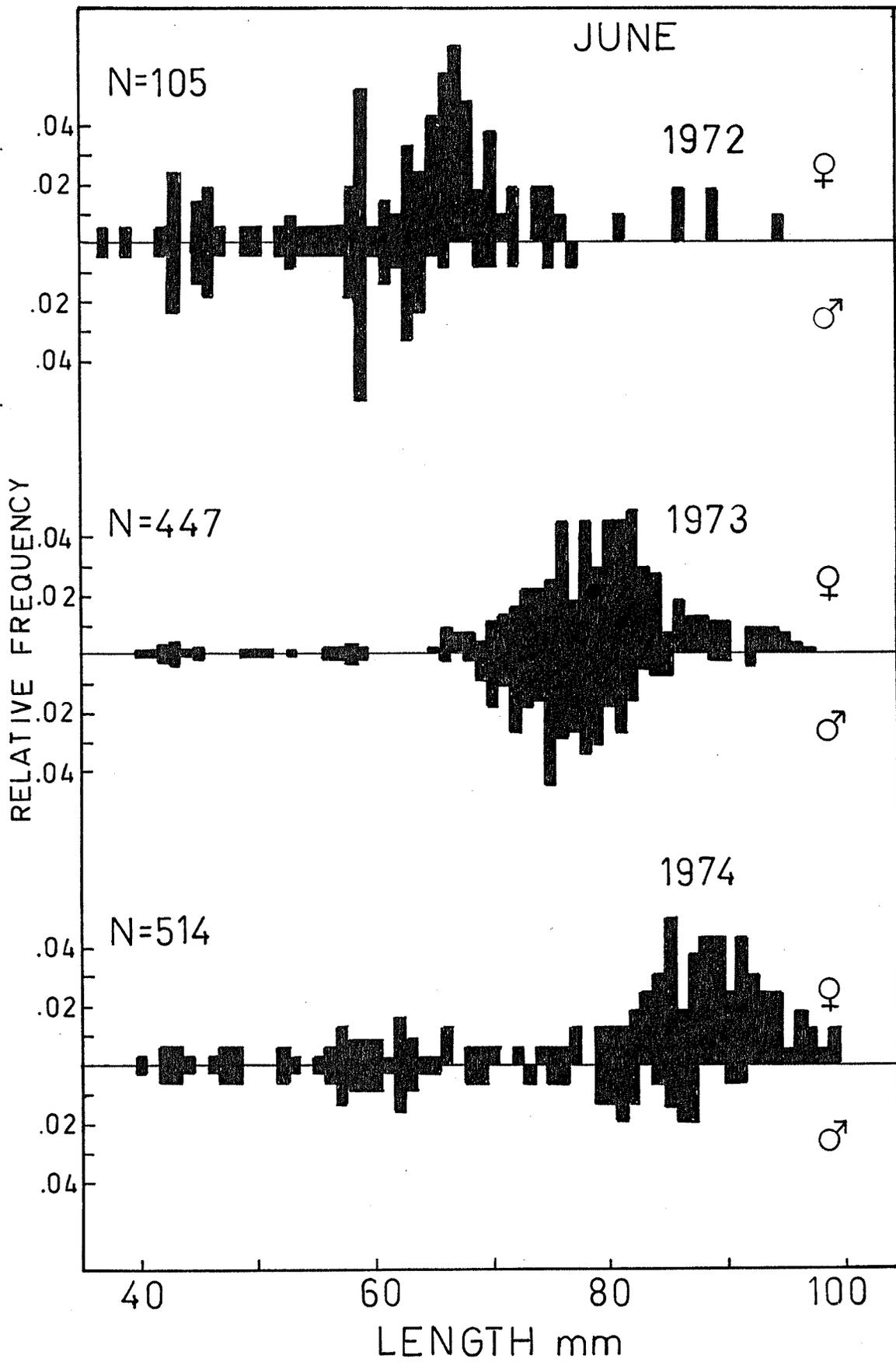
FIGURE 13.   Size frequency histogram for September, 1972, 1973

and 1974.

Immature frogs are divided arbitrarily equally between
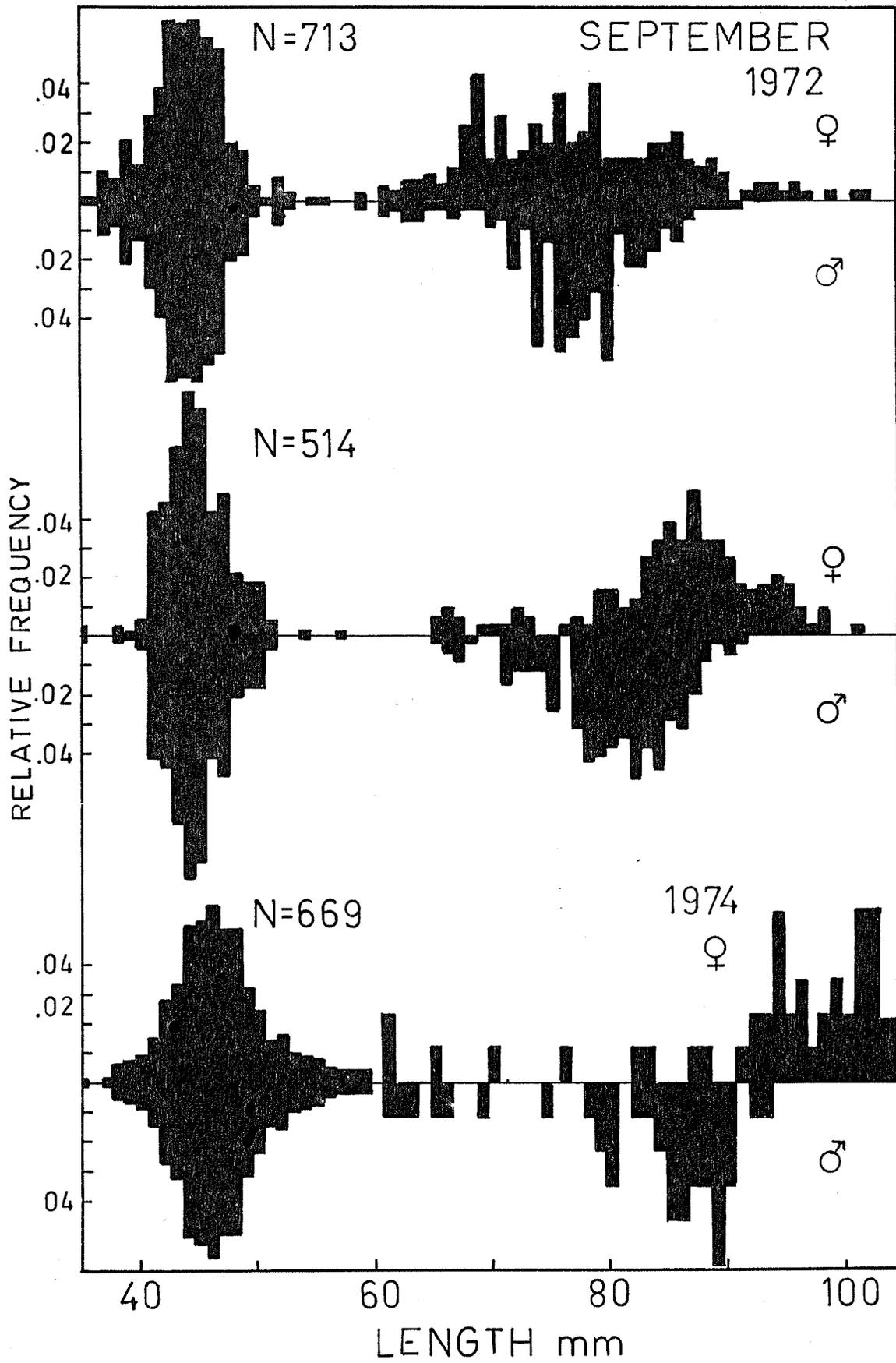
the sexes.

FIGURE 14.   Size frequency histograms for 15 August, 1973.

Immature frogs are divided arbitrarily equally between

the sexes. All frogs possible were caught on this

night by four people over a period of several hours.

15 AUGUST, 1973

38
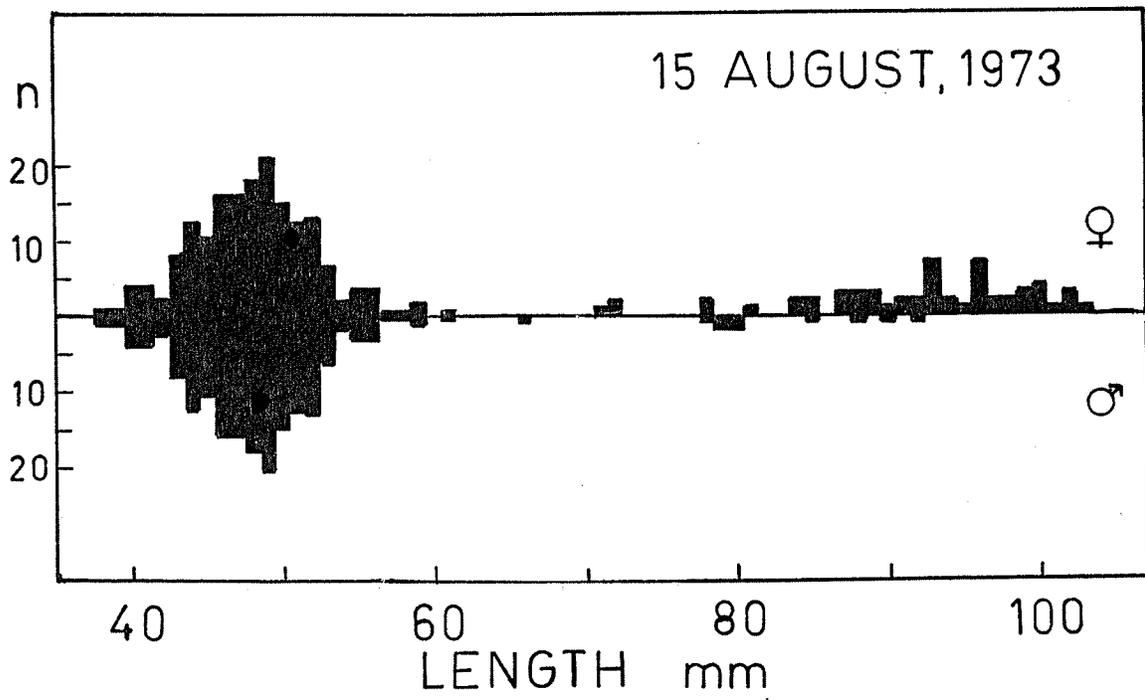
class. In 1974, for the first time, a fourth size class became separable. In both years the apparent survivorship of mature frogs was greater than in 1972. Because of the small sample size of larger frogs, both the third and fourth size classes probably consist of more than one year class.

Separation of size classes using probability paper gives a nearly identical range in snout-vent length for three size classes for both May and September of each year (Table 3). In June of each year, in spite of a large difference in sample sizes among the three years, size class 1 seemed to split in half.

Size class 2 decreased in abundance from year to year, as is shown in the May sample, taken before the dispersal of males (Fig. 15). The young of the year were larger in mean snout-vent length in the fall of 1974 than in previous years. Several frogs were found that had grown nearly to the size of mature frogs in one season. External male sex characteristics, nuptual pads and vocal sacs, were found in a few young of the year, although there was no obvious gonad development.

Growth of Transformed Frogs

Growth of each size class, as calculated from histogram mean sizes, varied between years, but showed a tendency for slow growth in the summer of transformation and after maturity, and rapid growth in the second and third summers (Table 4).

Daily intervals to 6 days, weekly intervals to 4 weeks, and all recaptures after 4 weeks were compared for 1973 and 1974. Comparison between the two years at the various time intervals showed no significant

TABLE 3.　　SIZE CLASSES DERIVED FROM HISTOGRAMS

Year		MAY						JUNE						SEPTEMBER			
		Female		Male				Female		Male				Female		Male	
		Range mm	$\bar{x}$	Range mm	$\bar{x}$			Range mm	$\bar{x}$	Range mm	$\bar{x}$			Range mm	$\bar{x}$	Range mm	$\bar{x}$
	I	35-50	43	35-50	43		IA	37-49	43	37-49	43		I	35-59	43.5	35-47	43.5
							IB	50-59	58	50-59	58						
1972	II	51-74	64	51-65	60		II	60-76	67.5	60-76	67.5		II	60-69	67.5	61-70	65
	III	75-106	82	66-92	73		III	80-99	85.5	----	----		III	70-97	86.5	71-92	78
	I	36-50	42.5	36-50	42.5		IA	40-47	43	40-47	43		I	35-57	44.5	35-57	44.5
							IB	48-60	52	48-60	52						
1973	II	52-66	62	52-70	65		II	61-84	77	61-85	75		II	66-73	69	66-73	69
	III	67-104	76	71-91	76		III	85-97	88	86-92	79.5		III	74-103	86.5	74-92	82
	I	40-49	45	40-49	45		IA	40-48	44.5	40-48	44.5		I	35-60	47	35-60	47
							IB	52-64	58.5	52-64	58.5						
1974	II	51-72	61	51-68	56		II	65-75	69	65-76	70.6		II	61-83	68	61-69	65
	III	74-96	84.5	69-94	81		III	77-99	87.5	79-91	83		III	87-96	92	74-80	78
													IV	98-103	100	83-93	87

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FIGURE 15.   Percentage of relative abundance of size classes.

	FEMALE			MALE			
SIZE CLASS	I	II	III	I	II	III	%
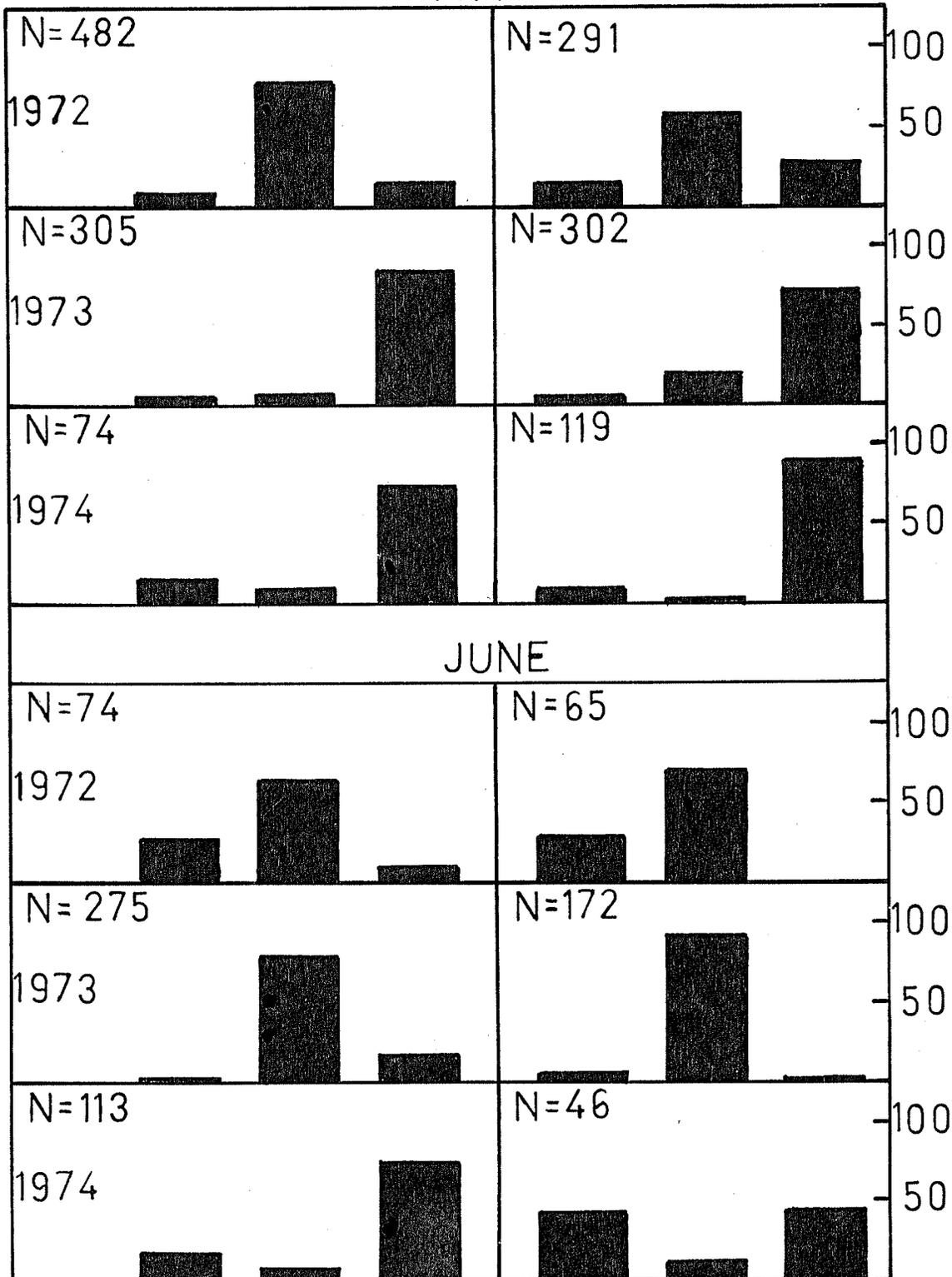
TABLE 4.   GROWTH OF TRANSFORMED FROGS DERIVED FROM HISTOGRAMS.
DIFFERENCE IN MEAN SIZE BETWEEN JULY AND SEPTEMBER FOR NEWLY
TRANSFORMED FROGS.*
DIFFERENCE IN MEAN SIZE BETWEEN MAY AND SEPTEMBER FOR FROGS
BEYOND THE FIRST SUMMER.

FEMALES

Year	1972	1973	1974
Year class			
1970	16.0 mm	-----	-----
1971	24.5 mm	24.5 mm	15.5 mm
1972	10.6 mm*	26.5 mm	31 mm
1973	-----	6.2 mm*	23.0 mm
1974	-----	-----	no July sample

MALES

1970	18.0 mm	-----	-----
1971	23.5 mm	17.0 mm	6.0 mm
1972	10.6 mm*	27.5 mm	22.0 mm
1973	-----	6.2 mm*	20.0 mm
1974	-----	-----	no July sample

differences (Appendix 5), so results for the two years were pooled.
Results of recaptures within 6 days were pooled to place a 95% confidence
interval (±3.92 mm) around all measurements.

Recaptured frogs were not represented in all size classes derived
from size frequency analysis. Of the yearling frogs (II), none were
recaptured in 1973 and only 2 were recaptured in 1974. No male frogs
in VII were recaptured. Since the variance in growth rate was large
between them, the 2 yearlings were omitted from Fig. 16 and the comparison
to growth calculations from the histograms. Mean growth rates for the
other size groups (Fig. 16, Appendix 6) were extrapolated to estimate
seasonal growth, using a 66-day season after transformation for young of
the year and a 130-day season for all other frogs.

In the young of the year and two-year olds, growth predicted by the
two methods compared closely (Table 5). Using the growth rate of re-
captured young of the year to predict growth of yearlings entering their
second summer gives a much slower growth, 15.7 mm, than is seen in sub-
tracting spring and fall mean sizes of the year classes. Young of the
year are still in the process of transformation, so it is not surprising
that their growth rate is low. The frogs which have been designated as
three-year olds are undoubtedly a mixture of age classes. Both methods
of calculating growth indicate that it is slow after maturity.

Averaging the growth of frogs over time intervals rather than within
size classes and omitting negative size increments changes somewhat the
apparent growth rates (Figs. 17-19). Young of the year grow more rapidly
than they would appear to from means of the size class. The growth rate
is similar to that of females. The growth rate of males appears to be

FIGURE 16.   Mean growth rates of recaptured frogs.

O   Females

●   Males

✕   Juveniles

Mean growth rate $\pm$ 2 S.E.
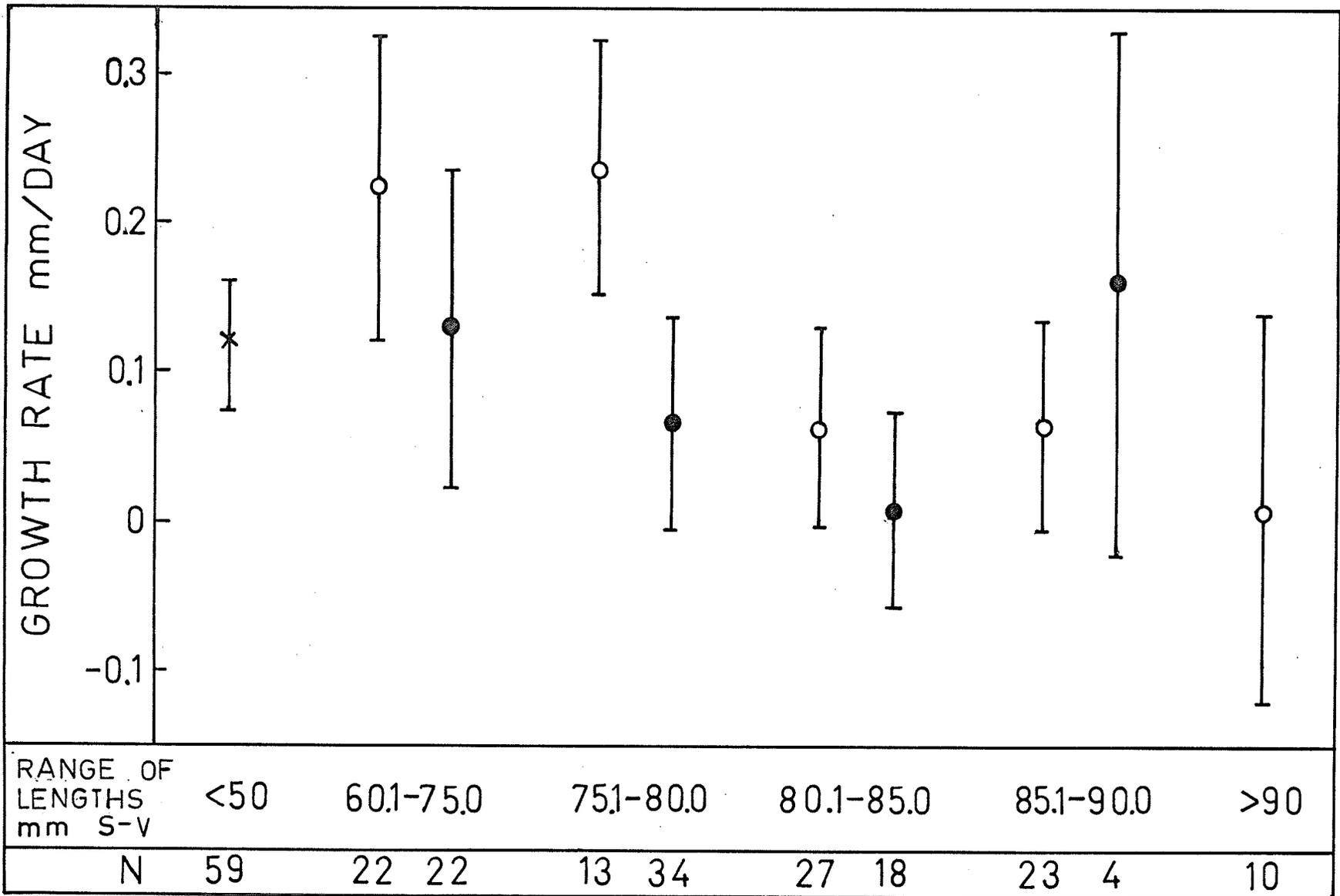
TABLE 5.   COMPARISON OF GROWTH CALCULATIONS FROM RECAPTURE DATA
AND HISTOGRAM SIZE CLASS MEANS.

	Mean increment calculated from histogram means		Mean increment of recaptured frogs	
	FEMALES	MALES	FEMALES	MALES
Young of Year				
1972	10.6 mm	same		
1973	6.2 mm		8.0	same
1-Year Olds (<50 mm)				
1972	24.5 mm	23.5 mm		
1973	26.5 mm	27.5 mm	15.7 mm	15.7 mm
1974	23.0 mm	20.0 mm		
1973/74 ave.	25.1 mm	24.4 mm		
2-Year Olds (60-75 mm)				
1972	16.0 mm	18.0 mm		
1973	24.5 mm	17.0 mm	28.6 mm	17.2 mm
1974	31.0 mm	22.0 mm		
1973/74 ave.	26.0 mm	17.3 mm		
3-Year Olds (80-90 mm)				
1973				
1974	15.5 mm	6.0 mm	8.5 mm	

    Numbers in parentheses refer to the size classes constructed
    from recapture data.

FIGURE 17.   Growth of recaptured juvenile frogs. Lengths of

frogs caught on the same two days have been
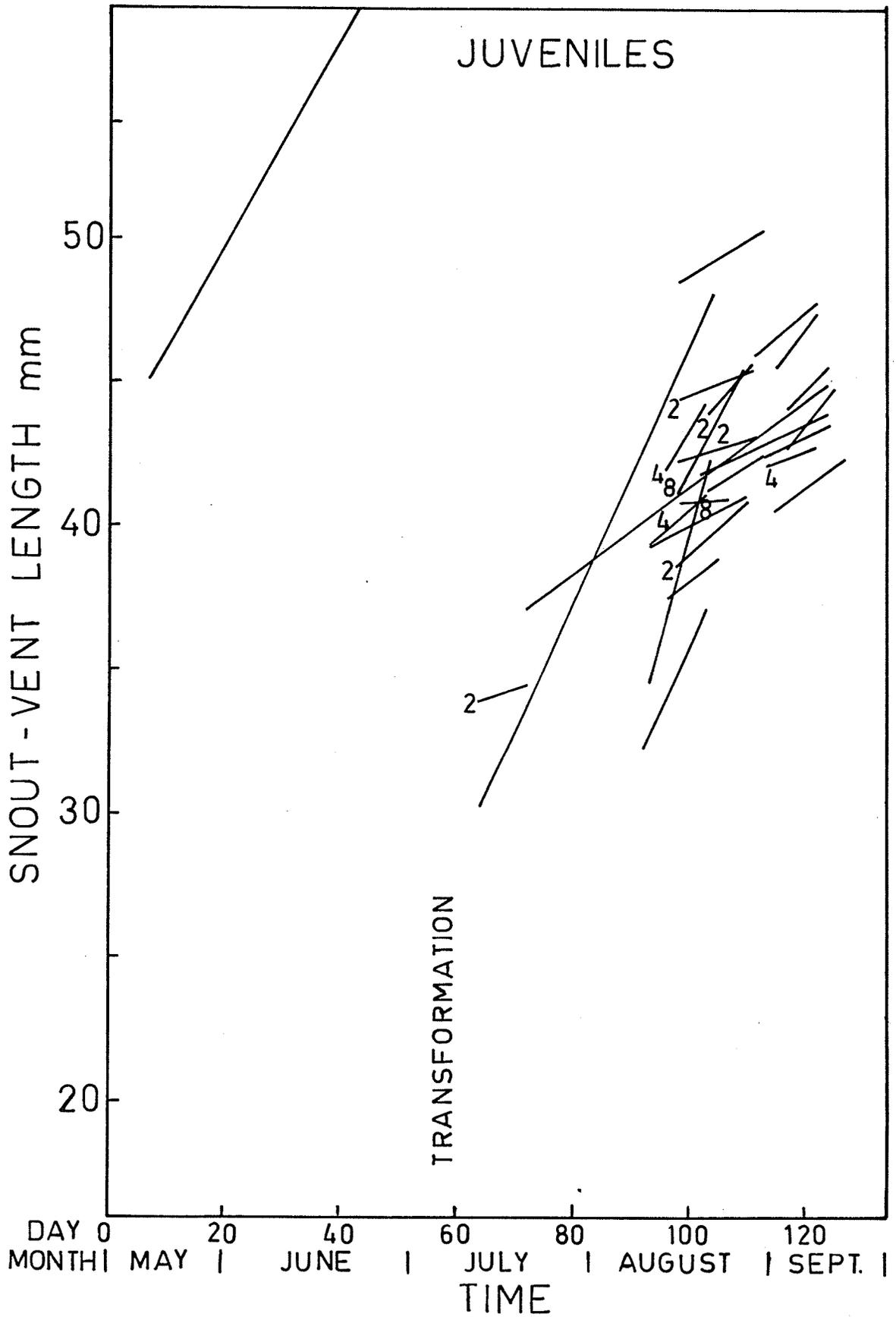
averaged.

FIGURE 18.   Growth of recaptured female frogs.   Lengths of

frogs caught on the same two days have been

averaged.

FIGURE 19.   Growth of recaptured male frogs. Lengths of

frogs caught on the same two days have been

averaged.
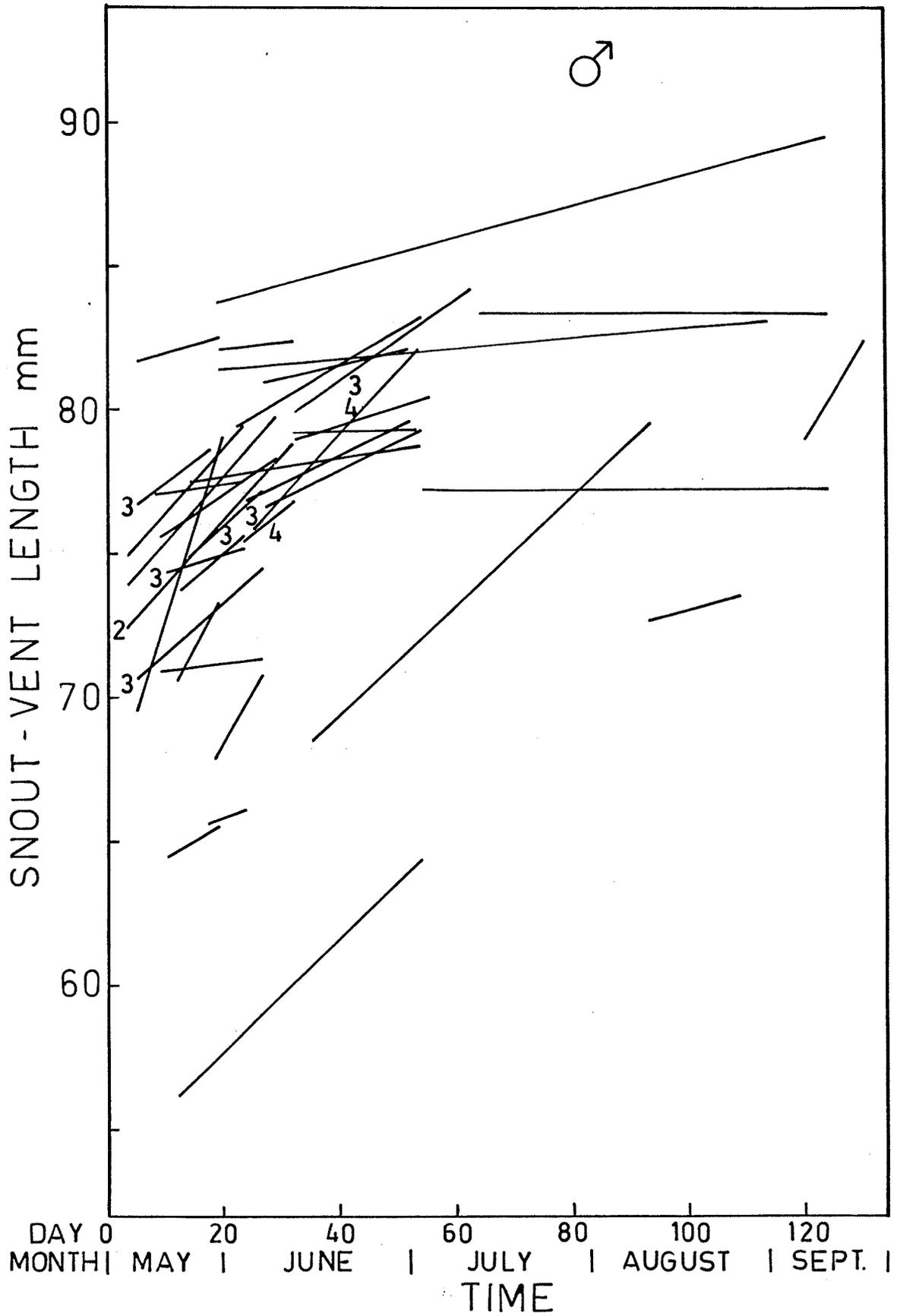
less than that of females. Yearling and two-year old frogs grow rapidly
in the spring, according to the few recaptures in these groups. Both
males and females grow faster in the spring than in late summer. This
observation is also based on a small number of recaptured frogs.

<u>Eggs</u>

Deposition

Egg deposition took place between the last week of April and
21 May in 1972 and between 1 and 23 May in 1973. Breeding was fairly
evenly distributed in time in 1972, but it was nearly completed in the
first 10 days of the season in 1973. In 1974 the first eggs I found
were at the dorsal lip stage (Goin and Goin, 1971) on 17 May, and were
probably deposited 15 or 16 May. Others at the field station reported
seeing eggs about a week earlier, which may have been those of <u>R. pipiens</u>,
or <u>R. sylvatica</u>, which breeds earlier. New clusters were found as late
as 4 June, 1974, and the large variance in tadpole size later in develop-
ment would indicate a long breeding season in that year.

In 1972 eggs were found in the wet meadow (Site I) and in the
Blind Channel (Site II). The egg masses were all adhering to <u>Typha</u> sp.
stems just below the surface of the water. The water in the channel was
too deep at that time for eggs on the bottom to have been visible, but
water depths at which eggs were found in subsequent years were much
shallower than the depth available in Site II in 1972.

In 1973 most egg masses were found at the bottom of Site II at
depths between 31 and 38 cm. Eight egg masses were found in the ditch
(Site III) in water of comparable depths, but these eggs were just below

the surface rather than at the bottom.

In 1974 very few eggs were found. Small flooded clearings within large areas of Phragmites were common calling sites for males, and occasionally clusters of eggs were found in these. These areas probably produced most of the successful tadpoles for the year, but since they were so dispersed, no attempt was made to quantify egg production in 1974.

Production

Numbers of eggs/ml were calculated for 1972, and averaged 21.3 (± 3.06). The figure for 1973 was within the same range, and no volumes were measured in 1974. In 1972 egg masses ranged from 50 to 180 ml, with a mean of 90 ml. The estimated total number of eggs in Site I was 30,700. In 1973 egg mass size in Site II ranged from 50 to 620 ml with a mean of 230 ml. The large numbers of eggs in some of these masses was probably due to several females depositing their eggs within a small area and these clusters adhering to each other. This conclusion is supported by the observation of different developmental stages in eggs from the same masses. A constant number of 230 egg clusters was found in Site II from 8 May to 24 May, when hatching began. The mean size gives a total estimate of 1,086,000 eggs for the 60 by 80 m plot at the end of the channel. The total number of eggs in Site III in 1973, from visual estimates of the size of clusters, was about 13,000, a smaller number than the tadpole estimate near the end of the development period for the same site in 1972.

Development

Mortality in the egg stage was estimated at 50% in Site I in 1972, 20% by failure to develop and 30% by physical displacement and/or breaking up of egg masses. Failure to develop was apparently less frequent in 1973

than in 1972, but was not determined.

Hatching occurred between 7 and 29 May in 1972, with a median date of 18 May. In 1973 hatching occurred between 17 and 25 May, with a median of 21 May. Since few eggs were found in 1974, it is impossible to state the range of hatching dates, but 5 June seemed to be the approximate median date of those eggs which were observed, and 18 May to 8 June the range.

Tadpole Enumeration

The number of tadpoles in Site III for 15 June, 1972 according to the Petersen estimate was 35,838, with a 95% confidence interval of (17,953, 500,000). The recapture data for 21 June was used because estimates remained stable from this date. The lower estimate from recaptures on 19 June probably reflects incomplete mixing of the marked tadpoles. For 30 June, using recapture results for clipped toes on 4 July, is 5,203 with a 95% confidence interval of (4,189, 6,863).

With a median date of 21 June for the first capture period, 15-29 June, the Jolly-Seber estimate of the tadpole population in Site III is 33,000 with a 95% confidence interval of (21, 45) thousand. For 30 June the estimated population is 53.6 with a 95% confidence interval of (34.8, 71.4) thousand. The estimated survival (Φ_1) from time 1 to time 2 is .159. A comparison of the two Petersen estimates gives a ratio of 0.145 (see Appendix 7).

Trapping on the grid in Site II in 1973 gave too low a capture rate for a mortality curve. Results varied from day to day (Table 6). If the total catch of the first three days and that of the last three days are

TABLE 6.   NUMBERS OF TADPOLES CAUGHT PER DAY IN TRAPS IN SITE II ON A 75 m^2 GRID.

DATE	2	3	11	12	13	14	15	16	21	22	23	24	25	26	31	32	33	Total
							TRAP	NUMBER										
7 July	5			2	2	3					1			10		6	7	36
8 July																		
AM	9	1		14	1	6	1	10			3	1		6		13		
PM	8	21		8		5	4							14		5	2	
Total	17	22		22	1	11	5	10			3	1		20		18	2	132
9 July																		
AM	4	6		7							1			8				
PM	3					2		4			1			1		3		
Total	7	6		7		2		4			2			9		3		49
10 July																		
AM								2						1		1		
PM														4		3		
Total								2						5		4		11
11 July																		
AM												1	1					
PM						1								3				
Total						1						1	1	3				6
12 July					2			3						2				7
13 July														9				9
14 July					1	4	6	2						6				19
15 July						1	2							1				4
16 July				1	1													2
17 July					2	2	2											6

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averaged, they show a 94.5% decrease in the last week before transformation.

Enumeration of Transformed Frogs

A Jolly-Seber estimate of the transformed frog population from pooled statistics was fairly precise for the first 6 weeks of the sampling period in 1973 (Table 7). Estimates for N are averaged over three week intervals, the length of the pooling interval. The estimate of B_i would indicate migration into the study area, probably from the wooded ridge. The average $\hat{N}_i$ for weeks 10 to 12 is 2,002.40 $\pm$ 928,55, and this estimate and others following are too variable to be meaningful. Transformation of the young of the year reduced sampling of adults, and results became distorted.

TABLE 7. JOLLY-SEBER POPULATION ESTIMATE OF TRANSFORMED FROGS IN STUDY AREA IN 1973. THESE ARE POOLED ESTIMATES, SO $\hat{\phi}_i$ AND $\hat{\beta}_i$ ARE ESTIMATES FOR THREE WEEK INTERVALS.

Week	$\hat{A}_i = \hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	Ave. N_i	$\hat{\phi}_i$	$\hat{\beta}_i$	SE($\hat{N}_i$)	Ave. SE($\hat{N}_i$)
1 9/5	.0827	0.00	---		.3454			
2 16/5	.1543		593.94	585.46	.4679	623.08	79.22	68.21
3 23/5	2964	171.00	576.98		.8755	1711.00	57.19	
4 30/5	2515	167.83	667.21		.7490	832.03	77.21	
5 6/6	.3086	278.00	900.99	1261.77	.4512	141.30	166.18	251.32
6 13/6	.2176	482.22	2216.17		·3468	994.18	510.57	
7 20/6	2539	338.11	1331.76		1.000	1851.44	265.79	
8 27/6	.2979	160.20	537.81	1210.77	.2204	0.00	102.99	332.48
9	.2803	494.10	1762.73		.2826	2361.88	628.66	

DISCUSSION

Annual Cycle

Feeding

Analysis of stomach contents gave similar results to those of Moore and Strickland (1954) in a study done on leopard frogs in southern Alberta. The major difference is the lack of cannabalism in the Alberta population. Between 10 and 26% of the adult frog stomachs analyzed at Delta Marsh after the period of tadpole transformation contained juvenile leopard frogs. Had cannabalism occurred to this extent in the Alberta study area, it would have been noticed, even in the relatively small sample examined.

Cannabalism occurred most frequently during fall migration, but sample sizes for stomach analysis were small at that time, and there may have been bias for this reason. I only observed adult frogs chasing or catching juveniles on a few occasions, but the variable state of digestion in which juveniles were found would suggest that cannabalism occurred at any time of day or night.

Predation on frogs by birds, mammals, or snakes was never observed, but frogs which had recently consumed juveniles were extremely sluggish and easier to catch than leaner frogs. Sampling was probably biased by the extent to which heavy feeding slowed the frogs, and this sluggishness probably increased predation as well.

Feeding behavior seems to be directly related to weather, and to the availability of prey, which is also directly related to weather. Unlike R. aurora and R. pretiosa in British Columbia, which Licht (1974)

found to have no empty stomachs, many Delta frogs were found with empty
stomachs, most often during cold, rainy weather (Sept., 1973 and May,
1974). Empty stomachs in May suggests that feeding does not commence
until after breeding, probably because of cold temperatures and lack of
prey. In 1972 the early fall was warm and sunny. The fall of 1973 was
cloudy with many days of rain. Frogs were never seen feeding in such
weather.

Migration

Unlike other anurans found in central Manitoba, leopard frogs over-
winter under water. Their migrations at Delta between the overwintering
area, Lake Manitoba, and the breeding area, Delta Marsh, are spectacular,
and the proximal causes are of interest.

Spring migration occurs as soon as the ice leaves the southern
shore of the lake. Since the thaw is later than that in more southern
regions of the range, breeding takes place as soon as frogs reach the
marsh. The similar timing of fall migration in 1972 and 1973, despite
differences in both short- and long-term weather conditions between the
two years suggests that any or a combination of, an internal mechanism,
light intensity, and day length triggers the fall migration. The early
fall of 1972 was warm and sunny, and frogs were active throughout the
day and night on August and September. In 1973 sunny days were infrequent
in August and September, and adult frog activity was slight except at
night at the peak of migration. Although the numbers of migrating frogs
per night were positively correlated with air temperature, the dates of
onset, peak, and termination of the migratory period were nearly the same
in both years.

Holzapfel (1937) showed that external temperature alone did not cause leopard frogs to become dormant, but that there was an endogenous cycle. In experiments in which frogs were kept at 0°C for varying parts of a year, they only became torpid between October and April. At other times of the year they mainly became sluggish. Gonadal changes also occurred at the same time of year regardless of temperature. She concluded that decreasing temperatures were necessary to bring about weight gain and other physiological changes that accompany winter dormancy.

Martof (1953b) found a yearly pattern in the temperatures at which green frogs remained active. Michigan green frogs were active at temperatures above 15°C in summer, leaving the banks for the water at lower temperatures, and hiding in the mud as temperatures dropped further. From mid-August until all frogs were dormant for the winter, frogs remained active at temperatures a few degrees lower.

Frogs remain active at lower temperatures during rain storms (Martof, 1953b), both in summer and during migration. Brattstrom (1963) notes that prevention of evaporation is a method of maintaining a preferred body temperature by preventing cooling.

Activity and migration patterns of leopard frogs at Delta are in agreement with the literature on other Rana species but air temperatures at which Delta frogs were active on land were lower, and dropped from 13°C in mid-summer to 4°C in late September. Migration of large numbers of frogs at low temperatures increased near the end of the migratory period. Many frogs migrated during and after rain showers regardless of air temperatures.

Development of Eggs

The average time from deposition to hatching of eggs seemed more dependent on the number of days since deposition (11 days in 1972, 10 in 1973) than on degree-days since deposition (131.7 in 1972, 104.3 in 1973). Very few individual masses were observed for the whole of their development time in 1974. Time from deposition to hatching varied from 8 to 18 days for those observed. Careful monitoring of daily temperatures in the immediate environment of individual egg masses would perhaps show a stronger relationship of temperature and development rate, but averaging both variables masks any such relationship.

No comparison could be made of egg survival to hatching in 1972 and 1973 because individual egg masses could not be marked in Site II in 1973. The constant number of egg masses after 8 May, 1973 was probably maintained by a combination of at least some additional spawning and loss by displacement by wind, fish, and other agencies. Mammal activity was high in Site I and negligible in Site II, and the eggs were deposited on the bottom of Site II, so they were less vulnerable to wind and birds, and it is likely that displacement was much lower in this site.

Growth of Tadpoles

Growth of tadpoles correlated strongly with cumulative temperature in degree-days since hatching. It is of interest to note that the growth rate was twice that reported for Rana aurora at Marion Lake, British Columbia (Calef, 1973a) in spite of a shorter development time (11-14 weeks for R. aurora and 6-7 weeks for R. pipiens). The amount of food available in Delta Marsh may be considerably more than in Marion Lake.

The tadpole at Marion Lake also had the opportunity to spend time at greater depths than those at which temperatures were taken and the water depths in the tadpole habitat at Delta were more uniform.

The differences in slopes of the regressions of size on cumulative temperature probably reflect differences in productivity between years and between the two sites. Long term weather conditions, particularly water level brought about obvious differences in submerged and emergent vegetation, and epiphytes probably varied along with them.

The concept that the product of cumulative degree-days and development time is constant for fish eggs has been questioned by several workers (Blaxter, 1969). Linearity occurs only over small temperature ranges, and abnormalities in development occur at extreme temperatures. Since the present study of tadpole growth was observational rather than experimental, and the regressions are obviously linear, it must be assumed that the temperatures involved were within normal limits for the species. Moore (1939) reports 6-28°C as temperature tolerance limits for Rana pipiens from Vermont, Quebec, Wisconsin, New York, Indiana, and New Jersey. He later (1949) found the minimum temperature tolerated to be 5°C in frogs from the same areas.

Mean temperatures calculated for the evaporation pan at Delta were approximately halfway between temperatures of Sites II and III at 11:00 a.m. for those days on which field temperatures were recorded. Temperatures of as low as 3°C and as high as 31°C were recorded for the evaporation pan during the tadpole development period, and temperatures as high as 31°C in the field, but no tadpoles were seen on these days. Presumably the tadpoles were sheltering themselves from extreme

temperatures. No minimum temperatures were recorded for the field because all temperatures were taken during the day, but the low temperatures recorded for the evaporation pan all occurred before most eggs hatched.

Growth after Transformation

Results of this study gave very different size classes and growth rates from those in the study of R. pipiens by Force (1933) in Michigan. She found a growth rate of 10-11 mm in the first year after transformation and 7 mm in the second year, with sexual maturity at the beginning of the fourth year. These rates compare with a rate of 5-10 mm following transformation in the Delta frogs, approximately 25 mm in the first full summer and in the second for females, and 17-18 mm for males in the second summer. In further years the growth is less than 10 mm. Force's sample sizes were smaller than mine, about 100 frogs, and what would appear as a single size class in a sample of 500-600, may have appeared as more than one size class in a smaller sample. The frogs in her sample were all very small, with few over 70 mm in snout-vent length. If her measurements were done in the same manner as mine, the population may have had a different size distribution.

Mean increment in length was apparently greater for females than males of all size classes. Turner (1960) also noted faster growth in female R. pretiosa, based on size frequency distribution, but the sexual dimorphism in snout-vent length increment was not significant. Turner also cited reports of dimorphism in R. catesbiena and in some R. clamitans studies. The split in the size class of immature yearling frogs in June is probably sexual dimorphism. By the fall sampling period the sexes are

distinguishable by secondary sex characteristics.

Growth after a year of sexual maturity is apparently slow, and it is impossible to separate year classes. A method of aging frogs independent of size frequency distribution or a much more extensive marked recapture program than the one I carried out is required to determine growth rate beyond maturity and the maximum ages obtained.

There is variability both in relative abundance of size classes and in mean sizes obtained by each size class from year to year. In 1972 almost no three year olds appeared in the fall sample. (The mean size achieved by the largest size class was apparently larger in 1973 than in 1972.) Apparently three year old frogs in 1973 were going to begin at least one more winter and were not separable as a size class from two year olds. In 1974 there was an additional, larger size class of both males and females, indicating either a greater variability in size, or survival of even older frogs.

Many factors probably affect the survival of frogs older than three years. Warm, sunny weather, in which frogs seemed to feed, in 1974 would explain faster growth in 1974 than in 1973, but 1973 showed faster apparent growth than 1972, and there were fewer suitable days for feeding in 1973. Also there is obviously an extra size class in 1974, which may indicate increased survival rather than faster growth. It is possible that predation pressure on the larger frogs has decreased as the frog population declined. If the large 1974 year class has a high rate of survival, predation pressure on larger size classes should increase again by 1976.

In the fall of 1974 young of the year were larger than in other

years and secondary sex characteristics were appearing in some males. Since transformation of tadpoles was later than in the other two years of the study, growth must have been at a much faster rate.

Deferred maturity, that is, sexual maturity occurring later than the minimum age which is physiologically possible for the species, which can be relaxed when the population is low or the food supply abundant, has been documented extensively in birds and fish, as cited by Lack (1968) and Foerster (1968). Many birds stagger egg laying and feed the youngest offspring only if there is surplus food (Lack, 1954, 1966, 1968). In all the cases cited growth is restricted by food, and when more food becomes available, the restriction is relaxed, and either the whole generation matures faster or more of it reaches maturity.

There is no reason for food to be a limiting factor for frogs in a marsh. Insects are plentiful throughout the summer at Delta Marsh, as are most of the other food items which were found in stomach samples. Suitable days for feeding, or the opportunity to feed may by limiting to growth. July and August of 1974 were hot and sunny, suitable feeding weather. Insect production was unusually high because of a wet spring.

A plausable explanation for increased growth of frogs in the 1974 year class is reduced cannablistic pressure from large frogs. Adult and sub-adult frogs were extremely scarce in the spring of 1974, and distributed over a large area. In spite of this, production of eggs and success to transformation were high. As the juveniles transformed there were fewer adults in the area. Decreased pressure from predators of their own species would increase available feeding time for the young of the year and explain faster growth.

Both the survival of older frogs and faster growth and early maturity of young of the year are beneficial to the population as a whole. Two year classes, 1972 and 1973, were severely reduced by climatic conditions; these two phenomena could compensate for the reduction of the breeding population for one or two years.

Regulation of Population

Tadpole Mortality

Mortality at the tadpole stage is high, even in the time required for marked tadpoles to mix with unmarked ones. An 85% estimate for mortality in two weeks in 1972 is probably a more normal rate than 94.5% over one week in 1973. Most of the dead tadpoles found in 1972 were severely injured, but most found in 1973 were not. The 94.5% mortality rate was estimated from trapping results, which may have been biased by trap avoidance behavior.

Tadpole mortality in the wild has been studied in Rana sylvatica by Herreid and Kinney (1966), R. aurora by Calef (1973a), and R. aurora and R. pretiosa by Licht (1974). All these studies showed mortality well over 90% between hatching and transformation, a rapid rate of decline in the first half of the development time followed by a decreased rate in the second half. I was unable to obtain data for the early stages of development, but results for 1972 appear to be comparable to Licht's results for R. pretiosa and to the results in some of Herreid and Kinney's study areas.

If mortality rates in Rana pipiens tadpoles are similar to those of related species, there may have been 300,000 eggs in Site III in 1972,

or 150 egg masses. Although this is not impossible, egg masses would have to have been far more densely distributed in the ditch than they were observed to be in other areas in that year. It seems more likely that tadpoles immigrated to the ditch from its continuation and from the Blind Channel before the barrier net was fastened over the culvert. Immigration into the ditch from other areas was observed in 1974, and since vegetation is lush there early in the summer, it is an excellent area for tadpole feeding, but it is deeper than other areas of egg deposition except around its margin.

Most studies of tadpole mortality allow for density-dependence; the mechanisms are varied. Licht (1967) and Heusser (1972) suggest growth inhibitors released by larger tadpoles under crowded conditions to inhibit the growth of smaller tadpoles of the same species, but slow growth does not explain mortality. Calef (1973a) related mortality to density-dependent predation. Licht (1974) and Calef both performed laboratory experiments in which tadpoles showed high survival for several days without food. Brockelman (1969), however, found a correlation of mortality with density and decreased growth as the cause of mortality. These experiments were all done in enclosures, and it seems unlikely that food could be limiting in natural conditions where tadpoles are mobile.

Predation was probably not the cause of high tadpole mortality in 1973. The giant water bug Lethocerus americanus, dytiscid beetles, Dytiscus sp. and backswimmers, Notonecta sp., have been shown to be predators on tadpoles in other areas (Licht, 1974; Calef, 1973). In spite of the abundance of these species in the study area and many species

of predatory birds, large numbers of dead but uninjured tadpoles were found floating on the water in Site II in 1973, indicating that predation was not the cause of high mortality in that year.

Samples of live and dead tadpoles showed no significant difference in mean size (P=0.05) which indicates that there was no difference in growth. By implication, food must have been equally available to those tadpoles which survived to transformation and those which did not.

Epiphytic algae are abundant in the Blind Channel. Over-productivity of plants is, in fact, a possible explanation of the mortality rate. When high mortality was noted in Site III in 1973, Hach Kit readings of dissolved oxygen were found to be about 3 ppm at the end in which tadpoles had occurred prior to the decline. The channel was choked with vegetation by early June in 1973. Plant growth in 1972 was much slower, and tadpoles had transformed before the area became choked with vegetation. In 1974 there were no submerged plants until July. Measurements taken in the channel over 18-hour periods in late summer 1974 did not show oxygen lower than 7.5 ppm. Toxins produced by blue-green algae may have caused the high mortality.

Density dependent mortality is indirect. Low water levels, which cause overcrowding of tadpoles, also leads to overproduction of vegetation in permanent bodies of water. Since there is less variety of available habitat, most tadpoles concentrate in these overproductive areas, and mortality is high.

Estimation of the Adult Population

The Delta leopard frog population is not well defined, and although an attempt was made to collect frogs uniformly throughout the study area, success was far higher in ditches and on the beach than in wet and dry meadow areas. The effort to collect adult frogs decreased following transformation of the young in order to study growth and dispersal of the young. Long cold spells brought weekly capture rates to almost nothing.

The main problem in trying to estimate the total population is its rapid turnover. The frogs are constantly moving, crossing the beach ridge in May and September, and dispersing following breeding. Mortality is high, predators are numerous, and a road the length of the beach adds automobiles to the natural hazards at migration times. The recapture of the young of the year was so low that they were not included in the estimate.

It seems unrealistic to come to any conclusions based on the Jolly-Seber estimate. The $\hat{N}_i$'s around 1,200 per three-week period are probably fairly accurate for the beach road west of the Assiniboine River Diversion and east of the Portage Country Club. The results do coincide with the life cycle and weather conditions. Recruitment is high in the second week when most of the females migrated into the breeding area. The high "survival" rate in the third and fourth week coincides with a two-week chironomid hatch centered over the beach ridge and road. There was probably no imigration from the study area in this time and juvenile frogs were still emerging from the lake. Pooling probably compensates for variability in sampling effort during the month of June, when tadpole studies took precedent over sampling of transformed frogs. In July and

August following transformation of the young of the year constituted most
of the population, and only occasional attempts were made to catch only
adults. Standard errors were quite high by the end of June and the
estimates were no longer meaningful.

Population Regulation of Transformed Frogs

Unlike anurans of more temperate regions, populations of Rana
pipiens in Manitoba seem to be regulated primarily by weather conditions.
A combination of catastrophic conditions in 1972 and 1973 led to the
prediction of a decline in the adult population. The decline was noticed
both in catch per unit effort and the size frequency distribution. In
1972 the average catch of frogs per day during the spring migration and
breeding period was 49; in 1974 it was 14. The decline in numbers was
also obvious to many long-time residents of the marsh (R. Hancox, L.
Garnham, et al., pers. comm.) and to others trying to collect frogs for
scientific purposes throughout the province.

Licht (1974) stressed the importance of predation on regulating
Rana aurora and R. pretiosa pretiosa, although he admitted that chance
catastrophes, particularly dry weather, could have an immediate effect
on the population. Predators on adult frogs at Delta Marsh are only
evident in large numbers when the frog population is very high. In
August, 1972, great blue herons, Ardea herodias, American bitterns,
Botaurus lentiginosus, garter snakes, Thamnophes radix, and skunks,
Mephites mephites, were numerous along the roadside ditches, where adult
frogs had eaten so much they could escape neither me nor their more
skillful natural predators. Far fewer of these predators were seen in

1973, when the frogs had few warm feeding days and often were not seen for several days at a time. The predators had probably shifted to easier prey and were hunting in other habitats.

Another obvious predator is man. Manitoba leopard frogs are harvested extensively for biological suppliers. Predation is probably regulated again in this case by availability (C. Scott, pers. comm.). Frogs are collected by hand on a part-time basis by casual workers and families, and if the work is not profitable for the time spent at it, these people find other work. It would be possible for man to over-exploit the frog population with more efficient collecting methods, but the danger is probably not great with the present arrangement.

There was no evidence that disease was the cause of declining numbers of frogs. Red-leg, an infection caused by the bacterium Aeromonas hydrophila, was found in a very small number of frogs. The only time large numbers of dead frogs were found was in early spring. In 1973, following a winter with thicker ice than usual on the lake, and in 1974, many small frogs were found dead on the beach. There are several explanations for high spring mortality. When the ice is thick, the lake can be frozen to the bottom for a considerable distance offshore. Small pockets of water between sand bars near the shore may become anoxic. Frogs may be crushed when a north wind blows ice towards shore in early spring, as was obviously the case in 1974.

Early spring mortality seems to be selective on the smaller size classes, perhaps because they spend more time in the lake than breeding adults, and perhaps because they do not go as far from shore to over-winter. Although adult frogs have been caught in gill nets by commercial

fishermen as far as 12 miles offshore, nothing is known of the winter distribution of frogs under the ice.

The combination of poor physical condition for overwintering and early spring wind and ice conditions seems to have the largest effect on the population numbers of transformed frogs.

CONCLUSIONS

The factors which regulate the growth and survival of leopard frogs at the various stages of the life cycle are dependent in some way on climatic conditions.

There is more than enough food available in the marsh, but food availability and the opportunity to feed can limit growth and probably also limit overwinter survival. Neither the frogs nor most of their prey species are active in cool, cloudy weather or in periods of heavy rain. Empty stomachs were observed only in such weather.

Spring migration from the lake to the marsh takes place as soon as the ice first leaves the southern shore and breeding takes place almost immediately. Fall migration seems to be triggered by a combination of internal and external conditions. The intensity of migratory activity is regulated by air temperature and rainfall.

Tadpole growth and development differed between years and sites probably because of differences in water levels and consequent differences in growth of submerged and emergent vegetation and the epiphytes in this vegetation.

Growth of transformed frogs is most rapid in the second summer and very slow in the fourth and following summers. Juvenile frogs grew fastest when the adult population was low in numbers, apparently because predation pressure from adults was reduced and the young frogs had greater opportunity to feed.

Mortality in the egg stage was caused by failure to develop and displacement by wind and other animals. Hatching success varied greatly

between sites.

Mortality in the tadpole state is high, mainly due to predation. Low water levels further increased tadpole mortality, although there were no signs of increased predation or lack of food. Anoxia and toxin from an increased blue-green algae growth were possible causes in two different sites.

High mortality is reflected in changes in the size structure of the transformed population. Thick ice on the lake in combination with north winds caused high mortality in the springs of 1972 and 1973. This mortality was selective on sub-adult frogs because breeding frogs left the lake earlier. The largest size class increased in mean size in the second and third years of the study. This may be explained by a decrease in the population creating decreased predation and a longer survival of the older frogs.

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COMPARISONS OF MEAN GROWTH OF RECAPTURED FROGS BETWEEN INCREASING TIME
INTERVALS.

Time Interval (Days)

	1	2	3	4	5	6	7
Mean increment mm	.334	.135	1.063	-.068	.239	.258	1.78
n:	62	43	30	28	95	23	15
Student's t		.65	1.71	.97	.31	.19	3.06

comparison with

1 day recapture

interval

APPENDIX 2

TEST OF ASSUMPTIONS FOR PETERSEN ESTIMATE

Thirty marked and ten unmarked tadpoles were held in the laboratory for two weeks in order to assess the effects of marking on tadpole survival and mobility and retention of the marks.

No mortality occurred in either group, indicating that marking in itself did not increase mortality. Relative visibility to predators could only be judged by own inability to see whether or not a tadpole was marked before it was removed from the water of the ditch.

Equal catchability was not tested vigorously, but tadpoles held in the laboratory showed no signs of physical impairment when compared with unmarked animals. Most tadpoles had lost at least part of their tails due to matural causes before transformation, and only those with very little tail remaining had trouble swimming. Thus damage to the tail from the injection was not a likely cause of a difference in catchability.

The tadpoles marked with methylene blue dye and held in the laboratory retain their marks for at least two weeks. Many clearly marked tadpoles were still found by the time of transformation. In all cases in which marks were found to be fading in recaptured tadpoles, the animals were remarked by injection of more dye.

The only way to determine when marked tadpoles were mixed with unmarked animals was to continue capturing and marking until the

population estimate stabilized. During the period in which the dye was used as a mark this occurred by 21 June, 6 days after the first sample was released. Later, when toes were clipped as the mark, the number stabilized almost immediately, probably because the tadpoles had become stronger swimmers. For every sampling period the entire ditch was sampled, and marked individuals were released along the entire length of the ditch. Casual observation of each catch did not indicate clustering of marked tadpoles.

Recruitment was unlikely; the experiment started late in the development period when all tadpoles seemed to be uniformly distributed. Only a very long breeding period would allow some tadpoles to be still clustered near their egg masses when others were nearly fully grown and dispersed throughout the area. This could have been a problem in 1974, but in 1972 the breeding period was relatively short.

COMPARISONS OF SLOPES OF REGRESSIONS OF TADPOLE GROWTH ON CUMULATIVE TEMPERATURE.

TABLE 1. CENTRALIZED SUMS OF SQUARES AND CROSS PRODUCTS AND ADJUSTED SUMS OF SQUARES FOR 5 SITE-YEAR COMBINATIONS.

Treatment	d.f.	Σx^2	Σxy	Σy^2	d.f.	$\Sigma y^{1\,2} = \Sigma_j y_{ij}^2 - \dfrac{(\Sigma_j x_{ij} y_{ij})^2}{\Sigma_j x_{ij}^2}$
1. (Site II 1972)	9	147,579.84	6,450.46	316.62	8	1.119
2. (Site III 1972)	5	53,416.01	1,344.67	38.83	4	5.21
3. (Site II 1973)	14	413,430	23,128.99	1,341.36	13	50.55
4. (Site III 1973)	14	538,352.11	27,492.48	1,426.35	13	24.23
5. (Site III 1974)	6	42,929.69	2,993.49	211.25	5	2.60
Total	48	1,195,707.65	61,410.09	3,334.41	43	83.71

TABLE 2.   COMPUTATIONS FOR TEST OF EQUALITY OF SLOPES (FROM STEELE & TORIE, 1960).

$$A = \sum_i \left(\sum_j y_{ij} \right)^{\frac{1}{2}} = 83.71$$

t = number of treatments
(i = 1...t)
(j = 1...n_i)

$$B = \sum_i \left(\sum y_{ij}^2 \right) - \frac{\left[\sum_i \left(\sum x_{ij} y_{ij} \right) \right]^2}{\sum_i \left(\sum x_i^2 {}_j \right)} = 180.46$$

$$F = \frac{(B-A)/(t-1)}{A/\sum_{ni-2t}} = \frac{(B-A)/4}{A/43} = 13.87$$

Critical $F_{4_1 43_1} .05 = 2.58$

Thus, the slopes of these regressions are significantly different.

APPENDIX 4

TADPOLE BODY LENGTH AT TRANSFORMATION.

	II 72	II 73	III 72	III 73
$\bar{X}_i$	34.9	33.16	36.7	34.11
S^2_i	6.66	11.36	6.00	10.96
n_i	50	13	51	21

Source	SS	df	MS	F
Treatment	202.78	3	67.59	11.38*
Error	778.91	131	5.94	
Total	981.64	134		

Critical $F_{.05, \ 3,131} = 2.68$

Comparisons between years

    Site II: $t = 1.91$, $t_{.05, \ 61} = 2.00$

        not significantly different

    Site III: $t = 3.65$, $t_{.05, \ 70} = 1.99$

        Mean sizes at transformation are significantly different in 1972

        and 1973.

Comparison between years for average over both sites

      $\bar{X}_{II} = 34.54$ $\bar{X}_{III} = 35.97$

      $N \ = 63$ $N \ = 72$

      $S_i^{\ 2} = (2.79)^2$ $S_i^{\ 2} = (2.94)^2$

$t = 2.88$ Critical $t_{.05, 133} = 1.96$

The mean sizes are significantly different in 1972 and 1973.

APPENDIX 5

COMPARISON OF GROWTH OF RECAPTURED FROGS BETWEEN YEARS 1973 AND 1974 AT
VARIOUS TIME INTERVALS.

Time Interval (Days)	1	2	3	4	5	6
Mean size increment 1973	.309	.13	1.188	−.110	.224	.157
Mean size increment 1974	.633	.2	−.067	.022	1.85	1.355
Student's t	.687	.077	.796	.143	1.1	.489

Time interval (weeks)	0-1	1-2	2-4	>4
Mean size increment 1973	.203	.954	2.96	5.0
Mean size increment 1974	.485	1.017	5.9	2.78
Student's t	1.85	.055	.81	.848

No differences significant between the two years.

APPENDIX 6

MEAN GROWTH RATE OF RECAPTURED FROGS.

		$\bar{x}$	n	2d	LCL	UCL	$\bar{x}$	n	2d	LCL	UCL
<50	I	.119	56	.040	.079	.159	same	as			
50-60	II	.512	2	.920	-.408	1.432	same	as			
60-75	III	.225	22	.102	.123	.327	.132	22	.106	.026	.238
75-80	IV	.237	13	.086	.151	.323	.068	34	.070	-.002	.138
80-85	V	.064	27	.066	-.002	.130	.009	18	.064	-.055	.073
85-90	VI	.067	23	.070	-.033	.137	.164	4	.184	-.020	.328
>90	VII	.009	12	.130	-.121	.139	-				

MARK RECAPTURE DATA FOR TADPOLE ENUMERATION, 1972.

TABLE 1.   DATA AND ESTIMATES FOR PETERSEN METHOD.

Date	n	M	m	New marks	$\hat{N}$	$1/\hat{N}$	$\sqrt{var(1/\hat{N})}$	95% Confidence Interval about N
15/6				109				
17/6		109	0	204				
19/6	202	313	7	190	9,032.29	11.07×10^{-5}	4.11×10^{-5}	(5,200, 35,000)
21/6	285	503	4	274	35,800.	2.79×10^{-5}	1.39×10^{-5}	(18,000, 500,000)
23/6	281	777	6	245	36,400.	2.75×10^{-5}	1.11×10^{-5}	(20,200, 188,700)
25/6	162	1,022	4	160 .	41,400.			
27/6	117	1,182	6	111	23,000.			
New Mark								
30/6	276							
2/7	557	255	39		3,800	26.05×10^{-5}	4.14×10^{-5}	(2,900, 5,600)
4/7	384	786	58		5,200	19.22×10^{-5}	2.32×10^{-5}	(4,200, 6,900)

TABLE 2.   DATA AND ESTIMATES FOR JOLLY-SEBER METHOD.

Date	n	M_1	M_2	m_i	m_2	u	s
to 29/6	1,189	0				0	1,189
30/6	276	1,189	0	17		259	255
2/7	557	1,189	255	12	27	518	

$m_2 = 17$ $n_{21} = 17$

$m_3 = 39$ $n_{31} = 12$ $n_{32} = 27$

$R_1 = 29$ $R_2 = 27$

$Z_2 = 12$

$Z_1^1 = Z_1 + u_2 + u_3 = 0 + 259 + 518$

$Z_2^1 = 12 + 518 = 530$

$\hat{N}_1 = 33046$

$\hat{N}_2 = 5281.6$

$\sqrt{V(\hat{N}_1)} = 5950.9$

$\sqrt{V(\hat{Na})} = 932.9$

95% Confidence Interval

(21,000, 45,000)

(3,400, 7,200)

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