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THE EFFECT OF ALTERNATIVE LIFE HISTORIES ON POPULATION STRUCTURE IN THE COMMON NEWT NOTOPHTHALMUS V. VIRIDESCENS

by
William Ryder Healy

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The Effect of Alternative Life Histories on Population Structure in the Common Newt *Notophthalmus v. viridescens*

by

William R. Healy

The population structure of the exclusively aquatic life history of the common newt (*Notophthalmus v. viridescens*) was compared with that of the more usual life history which typically contains a terrestrial stage. Populations from the coastal Massachusetts towns of Swampscott, Falmouth and Mashpee were found to manifest the aquatic life history, while the terrestrial-phase life history was examined in populations from inland localities in Central and Western Massachusetts.

In order to evaluate differences in population structure, a method of determining age had to be developed. Size groups delineated on size-frequency histograms constructed from samples taken over a five year period in Swampscott formed the basis for determining age. The presence of a biennial cycle in the abundance of larvae produced distinct size groups on the histograms, and the size groups were found to follow a characteristic pattern of growth from which age estimates could be made. The coherency of each group was established by mark and recapture studies, as well as by correlation with morphologically distinct stages in testis development and mesopodial calcification.

The pattern of testis development in this species proposed by Humphrey was substantiated, and the early stages of development were correlated with groups of known age. Since the testis was found to undergo its first spermatogenesis at the same time in the males of all of the populations studied, the correlation of differences in testis structure with groups of known age in the Swampscott population facilitated the estimation of age in the other populations. A pattern of mesopodial calcification was discovered which reinforced the groupings delineated on the basis of testis structure differences. This pattern, however, unlike the pattern of testis development, could not be used by itself in determining age beyond the first year, since the rate of mesopodial calcification was found to vary among populations.

The three coastal populations were found to possess the same population structure. Similarities were observed in the age at which sexual maturity was attained, the pattern of growth, polymorphism resulting from neoteny, and the response of the populations to environmental changes. The characteristics of the coastal populations were explained in terms of intrapopulation competition and adaptation to the aquatic habitat.

The inland populations were found to vary in the length of the terrestrial stage in their life history. Variations were observed not only between populations from different areas, but also within single populations.

The results of this study showed that population structure differs in the two modes of life history. Members of the inland populations were found to reach sexual maturity a year or two later than individuals from the coastal populations and to grow at a slower rate. Moreover, the size of the inland populations was judged to be larger than that of the coastal ones. The trend toward terrestriality in this species, which distinguishes the two modes of life history, was interpreted as being a mechanism for escaping short term changes in the suitability of the aquatic environment.

The differences in population structure between the two modes of life history were attributed to the post-metamorphic behavior of newly transformed individuals; and, although the cause of this difference in behavior could not be determined, the environment was believed to play a prominent role in its development.

PREFACE

The interaction between environmental and genetic factors in the production of adaptive characteristics is of prime concern to biologists because it offers an insight into the basic mechanisms underlying the process of evolution. Due to the complex relationship existing between these two factors and to the difficulties involved in distinguishing predominantly environmental effects from those which are mainly genetic, an evaluation of the relative roles of each can be made only in situations where one of the two agencies is kept fairly constant.

A considerable amount of success has been achieved in evaluating this interaction in relation to intrapopulation variation. Investigations of polymorphism have demonstrated the effect of a uniform environment acting on genetic diversity in producing changes in the composition of a single population. On the other hand, the production of polyphenic differences in a population has been attributed to the action of diverse environmental agencies on a uniform genotype. In both instances the variation observed resides in the individuals.

Comparatively little work has been directed toward an understanding of the interaction of environmental and hereditary factors in the production of differences in population characteristics, for example, population structure and dynamics, even though such properties are just as subject to

adaptation as are individual characteristics. The reason for this lack of emphasis seems to lie in the greater amount of environmental and genetic variation that exists between distinct populations. Furthermore, population characteristics tend to be more conservative than those of individuals within a single population and, hence, they are less likely to vary.

Differences in population structure and dynamics have been observed between distinct species, but the underlying genetic variability between such distinct populations is too extensive to permit an accurate assessment of the relative roles of each agency, even in instances where environmental variation is somewhat minimized, as, for example, in the study of two closely related sympatric species.

This report describes the occurrence of different population structures within a single subspecies. Because all of the populations belong to the same subspecies, it can be assumed that they possess a fairly similar genetic constitution, therefore, the differences can be attributed largely to environmental influences. Although the results of this study shed some light on the interaction of environmental and hereditary agencies in the control of population characteristics, an extensive analysis of these environmental factors was beyond the scope of this investigation. It is hoped that these results will provide the necessary background for a more detailed evaluation.

In view of the widespread distribution of the common

newt the conclusions drawn from this investigation must be interpreted in terms of the geographical peculiarities of the study area. Undoubtedly similar variations exist elsewhere which have different consequences so that the conclusions reached in this study may not be applicable. The nature and effect of neoteny in the coastal populations of Massachusetts need not be the same as in the newt population from Lake Cayuga in Ithaca, New York. Therefore, caution must be exercised in making comparisons.

I wish to express my sincere appreciation to Richard A. Des Rosiers, Robert M. Giasi, J. David Healy, Donald C. Minnihane, Joseph M. O'Connor, Berton Roffman, and David T. Sullivan for the time and energy they expended in assisting me with the collection of samples. I am deeply indebted to my wife, Gertrude, for her assistance not only in collecting samples, but also in the tedious processes of marking specimens and preparing histograms. Kraig K. Adler, A. Curt Allen, and the late Dr. Norman E. Hartweg generously offered helpful suggestions. Dr. Charles F. Walker and Dr. Ernest E. Williams granted me the privilege of examining preserved material entrusted to their care in the University of Michigan Museum of Zoology and the Museum of Comparative Zoology at Harvard respectively. To all of these I express my gratitude. I also wish to thank Dr. Nelson G. Hairston, Dr. Lois A. Loewenthal, and Dr. Warren H. Wagner, Jr. for critically examining this manuscript and for their valuable advice and comments. Last, but certainly not least, I wish to

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INTRODUCTION

The red-spotted newt, Notophthalmus v. viridescens,[1] has been the object of much study since it was described by C. S. Rafinesque in 1820. In his description Rafinesque distinguished between two closely related species, Triturus (Diemictylus) viridescens and Triturus (Notophthalmus) miniatus, which he separated at the subgeneric level on the basis of a difference in toe structure. The discovery by Kelley (1878) that T. miniatus was the immature form of T. viridescens opened the door for extensive investigation into the curious life history of the species.

Gage (1891) and Pope (1924) presented the most detailed accounts of the life history of the newt and were in general agreement concerning the major aspects of its developmental sequence. Both maintained that after hatching from the egg each individual passes through three morphologically distinct stages: an aquatic larval, a terrestrial immature, and an aquatic adult stage.

The aquatic larvae are characterized by the presence of external gills, gill slits, membranous skin and a large tail fin. In the late summer the larvae metamorphose, leave the water, and acquire certain terrestrial adaptations, for example, rough skin and a rounded tail. During their period

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[1] Smith (1953) has discussed in detail the controversy surrounding the correct scientific name applied to this species.

of terrestrial life, which has been estimated as lasting from one to four years, they possess a distinctive, orange-red color and are referred to as efts. Upon returning to the water to breed the efts undergo a second metamorphosis and develop into olive-green adults which are equipped with a compressed tail and smooth skin.

Exceptions to this general pattern were proposed by Gage, who described larval newts from Ithaca, New York that reached the size of adults, and by Jordan (1893), who mentioned the possibility that some individuals may not pass through the terrestrial stage. Pope discounts Gage's observation as being due to an erroneous identification of the larvae of other salamander species, and he rejected Jordan's reservation as being unsupported by evidence.

Noble (1926) cast serious doubt on the validity of this developmental scheme by suggesting that some Long Island newts omit the terrestrial stage and remain in the water after metamorphosis. Pope (1928) dismissed Noble's evidence by claiming that the aquatic specimens which Noble considered to be in their first year after metamorphosis were actually a year older and had just returned from their stay on land.

This Long Island population, in addition to being geographically separated from mainland populations, was further distinguished by the presence of neotenic specimens. Because of the exceptional nature of this population, Noble attempted to find mainland populations which would support his asser-

tion that the terrestrial stage was not essential to the life history of the newt. In 1929 he described two populations in the vicinity of Woods Hole, Massachusetts which contained a large number of aquatic individuals in the same size range as Pope's efts. These populations also contained neotenic specimens which, according to experimental evidence presented by Noble, could not have spent an extended period of time on land and still have retained their neotenic characters.

Although Noble demonstrated that some populations of newts may omit the eft stage, his choice of Woods Hole as a mainland locality comparable to those used as study sites by other authors was unfortunate because it led to the misinterpretation of data. The fact that coastal plain populations, such as those on Long Island and Woods Hole, participate in a mode of life history that differs from the one observed in more inland areas was not fully grasped until Bishop (1941) made the distinction between the aquatic and terrestrial modes of life history. However, even Bishop could not accept some of Noble's statements.

Most of the confusion and differences of opinion expressed in the literature concerning the life history of the newt stems from the inability of investigators to distinguish age groups with any degree of certitude. As a result some of Noble's conclusions are still not accepted and disagreement concerning the length of the eft stage still exists. Population variation may account for some of the discrepancy, but

individual interpretations must also be considered. Despite the wealth of publications dealing with newt life history, these divergent opinions point out how little is known about the ecology of this salamander.

It is the purpose of the present study to (i) examine in detail the mode of life history expressed in coastal populations, (ii) investigate differences in inland populations concerning the length of the eft stage, and (iii) compare the effect of these alternative expressions of life history on population structure. It is hoped that the results of this study will resolve some of the difficulties still existing in the literature and provide some basis for an evaluation of the evolutionary significance of the terrestrial stage.

MATERIAL AND METHODS

The specimens used in this study were collected in Massachusetts. Populations characteristic of the aquatic life cycle were sampled in Swampscott and in the Cape Cod towns of Falmouth and Mashpee. Inland populations with a terrestrial stage in their life cycle were sampled in Paxton and Charlton in Central Massachusetts and in Adams, Sheffield, and Mt. Washington in the Berkshire Hills of Western Massachusetts.

The Swampscott population was sampled periodically from the spring of 1961 to the spring of 1965. All of the specimens collected in 1961 and 1965 were killed by immersion

in alcohol and preserved for study, while those collected from 1962 to 1964 were examined and then returned to the pond. Specimens from all other areas were preserved.

Measurements

Both total length and snout-vent (tip of the snout to the posterior angle of the vent) measurements were taken and rounded off to the nearest whole millimeter. Total length measurements are used in this report in order to achieve conformity with the presentation of results made by other investigators and to provide a greater range in scale for more graphic representation.

All measurements were taken by the author in order to avoid discrepancies arising from personal judgement. The preserved specimens were measured immediately after killing and before injection and hardening. This step prevented distortions in length arising from prolonged preservation in alcohol. The live specimens were anesthetized with MS-222 - Sandoz (tricaine methanesulphonate) before being measured.

Size-frequency histograms formed the basis on which earlier investigators made their estimates of age, and, unfortunately, most of these estimates were obtained from single samples. Since an isolated sample may not even be a true index of the population from which it was removed, attempts to compare populations on such evidence is open to criticism. Pope (1924) even went so far as to combine data from different populations. Because the determination of age

is an essential prerequisite for the analysis of population structure, several different techniques were employed in an attempt to lend more objectivity to the delineation of age groups.

Periodic Sampling and Mark-Recapture

The objection to the use of isolated samples was removed by the periodic sampling of individual populations. This method made it possible to establish whether or not the populations were stable and also proved valuable in providing a better interpretation of the relationship between age and size. Changes in the size-frequency histograms during the course of sequential sampling reflected the growth of individuals and facilitated the estimation of age based on total length measurements.

The technique of mark and recapture was used on the 1963 and 1964 Swampscott samples, and the results verified the rate of growth estimated from the previous collections. The newts in these samples were marked by means of toe clipping and each individual was marked on two limbs to insure identification, since damage to limbs sustained in the natural habitat is not uncommon. The removal of various toe combinations and the recording of the number of red spots on either side of the dorsal midline provided a means of identifying individual specimens. The presence of unusual markings was also noted as an additional check on positive identification. The regeneration of digits was retarded by the application of a 0.1 N solution of beryllium nitrate as sug-

gested by Heatwole (1961).

Age estimates were made by taking advantage of size-frequency groupings and following the growth of these groups in sequential samples. The mark and recapture technique was used to establish the coherency of these groups. The coherency of each group was also demonstrated by the use of morphological criteria. Successive stages in the development of the testis and mesopodial elements were correlated with size-frequency groups. Since these stages are indicative of a temporal as well as a morphological difference, they served not only to distinguish the different groups, but also to support the estimates of age.

Testis Structure

The newt testis is divided into lobes and each functional (mature) lobe is composed of two clearly defined sections. The caudal or posterior section has a rough surface and a yellow color in fixed specimens, and the cephalic or anterior section is smooth and white. Adams (1940) undertook a histological study of the newt testis and found that the posterior section contained mature sperm, while the anterior section is composed of spermatocytes and spermatids.

Humphrey (1926) demonstrated that spermatogenesis in this species proceeds as a caudocephalic wave and follows a definite pattern. Immature specimens bear a single-lobed testis which has the appearance of the anterior section of a mature lobe. With the onset of gonadal maturity the lobe assumes a divided appearance, and after the evacuation of

sperm during the mating season, the empty lobules in the caudal section do not regenerate immediately. Instead, they form a slender "caudal germ-cell cord" which extends posteriorly from the dorsal end of this section. As the reproductive cycle continues the anterior section of the lobe becomes progressively smaller and the cord increases in length. Eventually a second lobe is formed from a swelling at the posterior end of the cord. This second lobe enlarges and produces its own cord while the anterior (original) lobe becomes smaller and finally disappears. Occasionally three, rarely more, lobes are seen. This occurs when the newly formed cord produces a lobe before the first lobe has completely disappeared. Specimens with three lobes characteristically have a middle lobe which is considerably larger than the other two.

Humphrey believed that the developmental stages leading to the formation of a multiple testis could be correlated with age. In support of this hypothesis he pointed to the increase in total length associated with each of the following stages: one lobe with a short cord, one lobe with a longer cord or a small second lobe, two lobes of equal length, and three lobes.

All of the preserved males were examined and the stages of development described by Humphrey were correlated with the groups delineated on the histograms.

Development of Mesopodial Elements

The major deficiency in Humphrey's scheme is that it does not apply to females. Skeletal differences associated with age have the distinct advantage of being applicable to all members of the population. Moment (1949) failed to correlate growth with the number of caudal vertebrae in individuals of this species. Hilton (1948) noted that all adult members of this species possess carpal and tarsal elements composed of bone, whereas, cartilage is present in the younger individuals. This observation suggested the possibility of a correlation between age and the development of these elements.

In order to explore this possibility, one forelimb and one hindlimb were removed and exposed to the technique of clearing and staining with alizarin red S described by Evans (1948). The presence of stain in the mesopodials indicates that these elements have become either calcified or ossified. Although calcification can often be distinguished from ossification by the appearance of the stain, positive identification of bone requires the use of histological techniques (Uzzell, 1961). Since the large number of specimens examined in this study precluded this confirmation, no attempt was made to distinquish between bone and calcified cartilage, nor, between different degrees of calcification or ossification. Therefore, mesopodials which were stained by alizarin will be referred to in both the text and the tables as being calcified.

The number of calcified mesopodial elements was found to provide a morphological criterion which applied to both sexes and could be used to strengthen the estimates of age based on total length.

Both testis and mesopodial patterns of development rely on the correlation of various morphological stages with total length measurements for interpretation of age. As a result, they are not as definitive as they would be if the proposed stages in the respective developmental patterns were tested against animals of known age (as determined by raising newts in the laboratory or field). Despite this difficulty, the correlation of these data with observations based on periodic sampling produces more objectivity in determining age than was attained by the previous investigators.

COASTAL POPULATIONS

The aquatic life history was studied in three coastal populations. Although it is generally believed that this mode of life history is restricted to coastal plain localities, a population from Swampscott (a suburb of Boston) was discovered which resembled the Woods Hole populations described by Noble. Attempts to locate Noble's ponds met with no success, but two populations were found in the same general area of Cape Cod (Falmouth and Mashpee).

The omission of the eft stage in Swampscott is rather surprising since samples from other areas around Boston indicate that efts are found in this general region. The fact

that the Swampscott pond was located about one-half mile from the ocean may account for the resemblance of this population to those of coastal plain localities.

The aquatic mode of life history was studied most extensively in Swampscott, and the Cape Cod samples were used to reinforce the conclusions drawn from the analysis of the Swampscott population.

History of the Swampscott Population

Samples were taken at various time intervals with the aid of a seine and dip net and the results of these collections, expressed in terms of size-frequency histograms, are summarized in Figure 1. The 1961 samples were preserved and the removal of these specimens had a noticeable effect in reducing the size of the population, but the general pattern of size distribution remained unaltered. From 1962 to 1964 the newts were returned to the pond after examination so that the composition of the population would not be disturbed. The specimens collected in 1965 were also preserved.

The absence of samples for the summer and fall of 1963 was due to a drought which caused the water level in the pond to drop considerably and the temperature of the water to rise. During this period the newts sought refuge in the reeds along the edge of the pond and could not be collected in large numbers.

The water level returned to normal in the winter, and an adequate sample was obtained in the spring of 1964. Although the drought continued throughout the following summer,

Fig. 1 Size-frequency histograms of individuals taken in Swampscott from 1961 to 1965. The black squares represent both males and females.

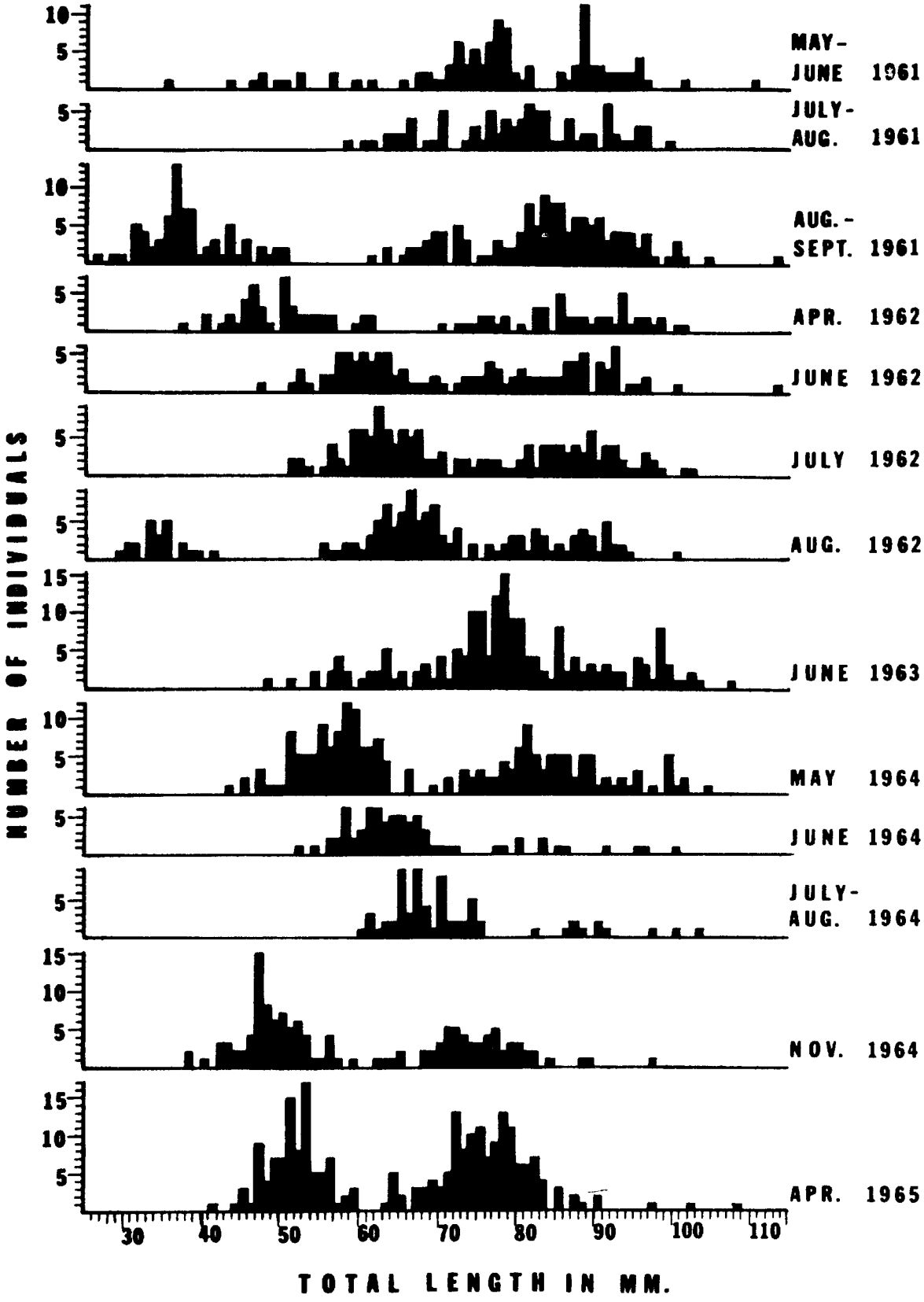

NUMBER OF INDIVIDUALS
MAY-JUNE 1961
JULY-AUG. 1961
AUG.-SEPT. 1961
APR. 1962
JUNE 1962
JULY 1962
AUG. 1962
JUNE 1963
MAY 1964
JUNE 1964
JULY-AUG. 1964
NOV. 1964
APR. 1965
30 40 50 60 70 80 90 100 110
TOTAL LENGTH IN MM.

FIGURE 1

the water level did not drop as drastically as it had in the previous year. Nevertheless, the vegetation in the central region of the pond died, and the newts again moved to the water's edge. This time, however, the water level among the reeds was high enough to permit sampling.

Very few adults were collected during this summer, yet, immature specimens and larvae were numerous. The failure of the adults to reappear in the following spring, when the water level was again high, clearly demonstrated that they were not in the pond and that their absence in the summer of 1964 was not the result of improper sampling techniques. Whether this absence was due to mortality or migration could not be ascertained in this instance, but migration seems to be the more probable reason, since the author did find adult newts hiding under debris around the edge of another drought-stricken pond in Swampscott.

A sample was taken in the spring of 1965 and larvae were observed in July. However, the population had apparently become extinct by September for no specimens were found in the pond.

Estimation of Age from Histograms

An examination of Figure 1 reveals the presence of a biennial cycle in the abundance of small individuals. In 1961 and 1963 the number of small specimens was proportionately low, but in 1962 and 1964 it was high. This phenomenon proved to be of great assistance in the determination of age, because it minimized the effect of overlap in the histograms

so that the extent of growth between successive samples could be determined.

The general conformity of the sequence of histograms for 1962 and 1964, when the small individuals were abundant, and for the spring collections in 1961 and 1963 demonstrates that the growth pattern for this population is relatively stable. The biennial cycle produces a clear distinction between the first two age groups so that the growth of the first year group during the spring and summer of 1962 and 1964 can be followed. Since this growth pattern is stable, samples from different years can be combined to form a progression which is indicative of the average rate of growth for the first two years. This progression (Figure 2) also demonstrates that the rate of growth decreases with age and that little growth is achieved during the winter months. The greatest amount of growth occurs in the spring (between April and June) and in the fall (between September and November).

A demonstration of the growth progression after two years is made difficult by the overlap in the size of members of different age groups, by the slower rate of growth, and by a reduction in the number of individuals due to increased mortality. These factors combine to obliterate representative peaks on the histogram. This difficulty is further complicated by the small size of the third year group in 1961 and 1963 resulting from the biennial cycle, by the low number of adults in 1962 following the removal of the 1961 samples, and by the migration of adults in 1964 and 1965 because of

Fig. 2 Size-frequency histograms of selected samples from Swampscott showing the extent of growth during the first two years. The date of collection, sample size and average total length are given for each group. The black squares represent both males and females.

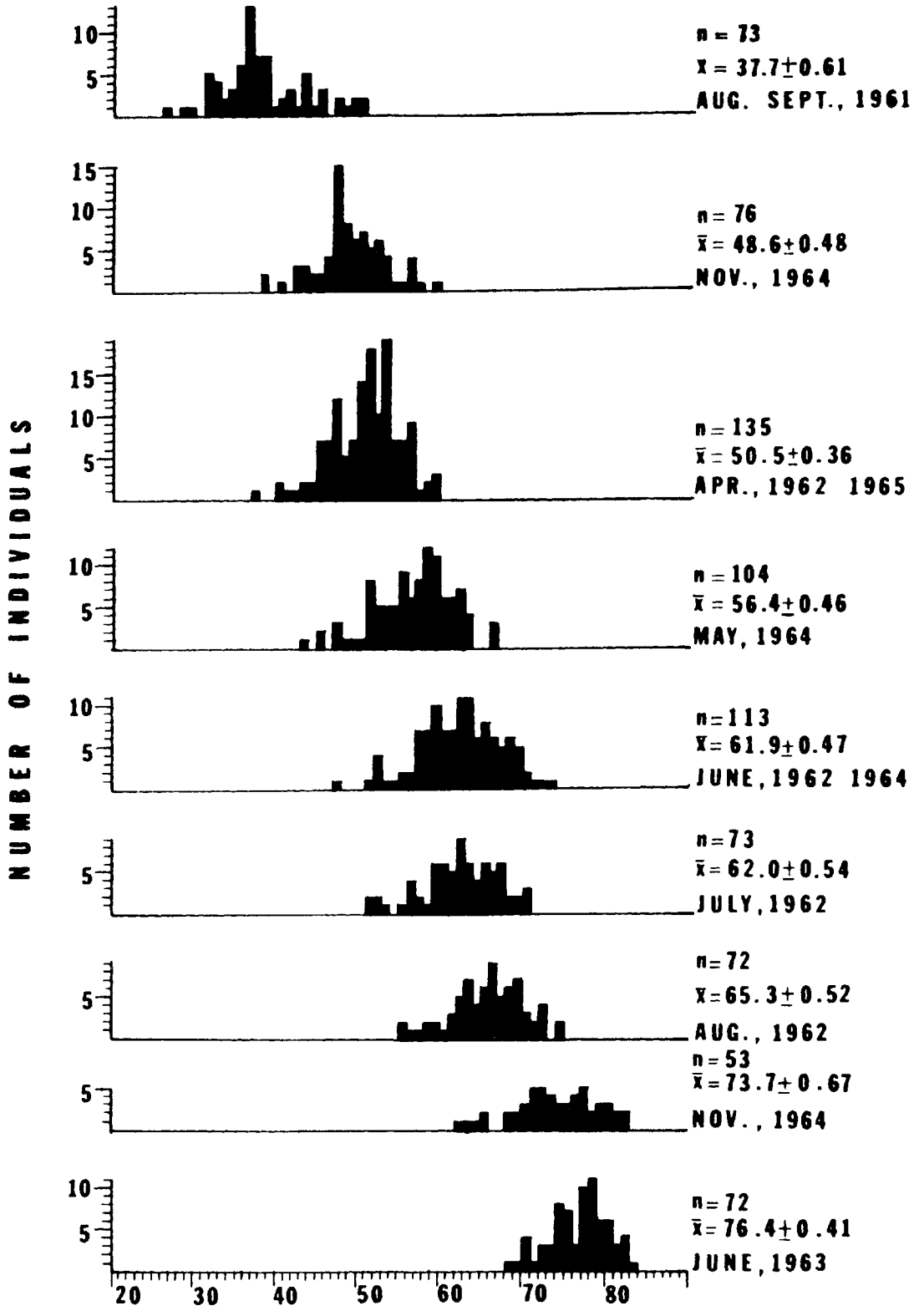

n = 73
x̄ = 37.7±0.61
AUG. SEPT., 1961
n = 76
x̄ = 48.6±0.48
NOV., 1964
n = 135
x̄ = 50.5±0.36
APR., 1962 1965
n = 104
x̄ = 56.4±0.46
MAY, 1964
n = 113
x̄ = 61.9±0.47
JUNE, 1962 1964
n = 73
x̄ = 62.0±0.54
JULY, 1962
n = 72
x̄ = 65.3±0.52
AUG., 1962
n = 53
x̄ = 73.7±0.67
NOV., 1964
n = 72
x̄ = 76.4±0.41
JUNE, 1963
NUMBER OF INDIVIDUALS
TOTAL LENGTH IN MM.

FIGURE 2

the drought.

Despite this handicap some indication of the extent of growth between ages two and three can be observed in the 1961 sequence and in the May, 1964 histogram when the third year individuals were abundant. Correlation of size and age based on growth alone for individuals older than three years was not possible.

Although the drought severely hampered the following of adult growth, it did have its advantages. The effects of the drought on the behavior of the adult newts pointed out that the adults in this population have a greater tendency to leave the pond than have the younger individuals. Another consequence of the drought was an interruption of the biennial cycle in the 1964 generation. According to the previous sequence, this generation was expected to be poorly represented, but the larvae were numerous in the summer of 1964 and they maintained their relative abundance after metamorphosis (as can be seen in the November, 1964 and the spring, 1965 samples).

The low number of adults present in the pond at this time seems to have been responsible for this effect. Whenever the number of transformed individuals was high, the number of larvae was low; and, conversely, whenever the relative frequency of transformed individuals was diminished, the larvae were well represented in the population. This strongly suggests that the size of the larval class is regulated by the number of transformed individuals in the popu-

lation.

The nature of this control has not been determined, but cannibalism seems to be the best explanation. When the author subjected larvae and transformed specimens to conditions of overcrowding, the large newts often devoured the larvae. Other investigators have established the presence of cannibalistic tendencies in this species from the analysis of stomach contents. Smallwood (1928) discovered that newts ate their own eggs, and Morgan and Grierson (1932) found that they preyed on their own larvae. Decreased fecundity induced by conditions of increased population density also may be a factor, but no evidence was found to support this alternative.

Results of Mark and Recapture

Although the mark and recapture technique has been used to estimate population size and survivorship (Green and Evans, 1940), the number of recoveries was so low that such estimates could not be made for this population. However, enough marked specimens were recaptured to show that the growth of individuals was similar to the growth of the group to which they belonged.

All of the specimens collected in June of 1963 were marked individually, and the results of the recoveries in May of 1964 are given in Table 1. Of particular interest is the confirmation of the conclusion that the rate of growth decreases with age, and the establishment of an approximate size range for the third year group. Since the average

TABLE 1

EXTENT OF GROWTH IN THE SWAMPSCOTT POPULATION FROM JUNE OF 1963 TO MAY OF 1964 AS DETERMINED BY THE MARK AND RECAPTURE METHOD. GROUPINGS ARE BASED ON THE JUNE, 1963 HISTOGRAM CONFIGURATION (SEE FIGURE 1).

Group	Marked in June of 1963				Recaptured in May of 1964							
	Number in Sample	Total Length in June of 1963 (mm.)			Number in Sample	Total Length in June of 1963 (mm.)			Total Length in May of 1964 (mm.)			Increment
		Range	Mean	S.D.		Range	Mean	S.D.	Range	Mean	S.D.	
1	30	48- 68	60.5	5.2	2	57, 68	63.0	...	71, 79	75.0	...	12.0
2	95	69- 84	76.8	3.3	10	74- 80	76.6	2.5	79- 85	82.0	1.9	5.4
3	28	85- 93	88.1	2.8	6	85- 93	88.5	3.4	88- 95	91.0	2.7	2.5
4	24	95-103	98.1	2.3	3	98-102	99.7	1.5	99-104	101.0	2.5	1.3

length in June of the recovered specimens is similar to the average length of the entire group, then their average in May may also be taken as a fair approximation of the average for the entire group. Accordingly, the average length of three year old newts in May should be about 82 mm. This figure coincides with the 82.7 mm. average for this same age group as it appears in the August-September collection of 1961 (Table 2).

The unmarked adults collected in May of 1964 were also marked individually and released. Although about fifty percent of the adults collected later in that summer were marked, the total number of specimens (27) was too small to attach any importance to the results.

The first year material collected in May and June of 1964 were marked as a group and not individually. The recovered specimens, though few in number (30), fell into the size range of the group and so established the validity of using histograms from sequential samples to follow growth and determine age.

Correlation between Testis Structure and Size

The samples taken in 1961 provided the preserved material upon which morphological distinctions were made. All of the males in these samples were examined, and the variations in testis structure described by Humphrey were correlated with size (Table 2).

Three distinct size groups appear in the May-June

TABLE 2

CORRELATION OF TESTIS STRUCTURE AND NUMBER OF CALCIFIED MESOPODIALS WITH SIZE GROUPS IN THE 1961 SWAMPSCOTT SAMPLES.

Date of Sample	Estimated Age (Years)	Number in Sample	Total Length (mm.)			Calcified Mesopodials			Testis Structure	
			Range	Mean	S.D.	Range	Mean	S.D.	Number of Testis Lobes	Caudal Germ-Cell Cord
May 25-June 5	1.0	13	35- 67	50.8	8.1	0	0.0	...	1	-
	2.0	55	59- 81	74.6	4.2	5-15	12.4	2.5	1	-
	4.0	36	85- 96	89.9	3.1	15	....	...	1	long
	5.0+	1	101	....	...	15	....	...	2	
July 16-Aug. 7	1.2	24	58- 74	67.0	4.5	0-7	1.3	2.1	1	-
	2.2	37	75- 86	80.2	2.8	10-15	13.7	1.4	1	short
	4.2	25	86- 99	91.5	3.6	15	....	...	2 (1)	(long)
Aug. 20-Sept. 5	1.3	25	61- 75	68.5	3.3	0-11	5.0	3.6	1	-
	2.3	67	73- 89	82.7	3.8	12-15	14.5	0.8	1	short
	4.3	41	85-104	93.1	4.2	15	....	...	2 (1)	(long)

series (Figure 1). Because this sample was taken during the breeding season when the sexual apparatus of reproducing specimens is most fully developed, no difficulty was encountered in recognizing mature individuals. In mature males the testis lobe is divided into distinct caudal and cephalic sections; the wolffian ducts are swollen, convoluted and pigmented; and the secondary sex characteristics are well developed. Mature females possess large oviducts, ovaries containing developed ova, and a small but distinctively shaped cloaca.

The smallest individuals (35-67 mm.) were all immature. No reliable structural differences were found which would differentiate the larger females, but the mature males differed in the extent of testis development. The males in the second size group (59-81 mm.) lacked a caudal germ-cell cord, whereas those in the third group (85-96 mm.) possessed a long cord which in many instances terminated in a bulb-like swelling that was similar in appearance to an immature testis. A two lobed testis was found in just one individual (101 mm.).

Based on the results of sequential sampling, the first two groups were judged to be one and two years old respectively, i.e., they had just completed their first and second years after egg deposition. Although all of the males in these two age classes lacked a caudal germ-cell cord, the difference in the condition of the sexual apparatus provided a suitable method of distinguishing between the two groups.

The third size group was composed of individuals estimated to be four, rather than three, years of age. This estimate was based on the presence of the long germ-cell cord and on the size gap between this group and the two year old specimens. Humphrey's sequence included an intermediary stage between specimens with no cord and those with a long cord. Since no individuals belonging to this intermediary stage, which is composed of individuals possessing a short cord, were found in this sample, the males in the third size group must have been older than three years of age. Furthermore, the size attained by the members of this group greatly exceeded that estimated for three year old specimens (Table 1).

The lone male bearing the two lobed testis was believed to be older than five years because the posterior lobe of its testis was larger than the anterior one.

The developmental changes in testis structure which occur during the summer can be seen in the July-August and August-September samples. After breeding, the two year old males develop a short germ-cell cord which serves to distinguish them from one year old males. The sex apparatus changes in the summer (a detailed account of these changes has been given by Adams, op. cit.) so that most of the characteristics which were used to determine the attainment of sexual maturity have been obliterated. However, the absence of pigment in the wolffian ducts and ovaries can be used in addition to the lack of cord development to identify

one year old specimens. Since all newts which reproduced in the previous spring possess pigmented wolffian ducts or ovaries, the only morphological criterion that can be used to differentiate classes within this large group is the extent of testis development.

Most of the largest males in these two samples have developed a second lobe, and the few which still possess a long cord may be either four year old individuals which were slow in developing the second lobe or remnants of the third year class that was missing in the spring.

The development of a short cord by the two year old males demonstrates that Humphrey's intermediary stage occurs in this population and that the age estimate of the largest group in the spring sample is justified. Since the appearance of the two year old males in the August-September sample will not change drastically over the winter, the characteristics of this group approximate those of the missing three year old specimens. The absence of this group in the May-June sample can be attributed to the effect of the biennial cycle of abundance. Apparently very few, if any, of the individuals which hatched from the eggs laid in 1959 survived until 1961. The discovery that the largest group on the May-June histogram was not composed of three year old specimens serves as an excellent example of the dangers involved in attempting to determine age in isolated samples on the basis of size alone.

Correlation of Mesopodial Development with Size

Table 2 also shows the correlation between size groups and the number of calcified mesopodials. The total number of calcified mesopodials is the sum of the carpal and tarsal elements. Since this species possesses seven carpal and eight tarsal elements, the maximum number of calcified mesopodials is fifteen.

The mesopodials of one year old individuals are completely cartilaginous in the spring. During the summer some of the elements begin to develop so that by the following spring, when these specimens are two years old, at least some calcified elements are present. The number of calcified mesopodials found in two year olds ranges from five to fifteen. However, only twenty-two percent of the entire group possess the full complement of fifteen. Development continues in the summer so that by the next spring almost all of the third year specimens will bear fifteen calcified mesopodials, as will all older individuals. Thus, the number of calcified mesopodials will completely separate the first year specimens from the second year group and will isolate most of the second year specimens. After the second year all elements are calcified and further distinctions cannot be made.

The correlation between testis structure and size groups serves two purposes. It demonstrates that the groups delineated on the basis of size are natural groups and can be morphologically distinguished from other groups. Also,

because the age of these groups is known from the results of sequential sampling, the ages associated with each stage, at least for the earlier stages, in testis development can be ascertained. However, this method does not apply to the first two age groups because variations in testis structure based on germ-cell cord development do not occur until after the first season of reproductive activity. Mesopodial development provides a morphological basis for separating the first two age groups. Since this pattern is independent of sexual activity, it reinforces the distinctions made on the basis of the attainment of sexual maturity and has the same advantage of being applicable to both sexes. Thus, the methods of differentiating specimens by means of stages in testis and mesopodial development complement each other and provide the morphological criteria needed to establish the coherency of the size groups delineated on histograms.

Coastal Plain Populations

Histograms constructed from the Falmouth and Mashpee samples reveal the basic similarity of these two populations (Figure 3). That they share the same life history as the Swampscott population is evidenced by the omission of the eft stage, the attainment of sexual maturity by the second spring following metamorphosis, and the same characteristic growth pattern. The remarkable resemblance of these two populations to the 1964 and 1965 Swampscott samples is a reflection of the severity of the drought in the Cape Cod

Fig. 3 Size-frequency histograms of individuals taken on Cape Cod. The black squares represent both males and females.

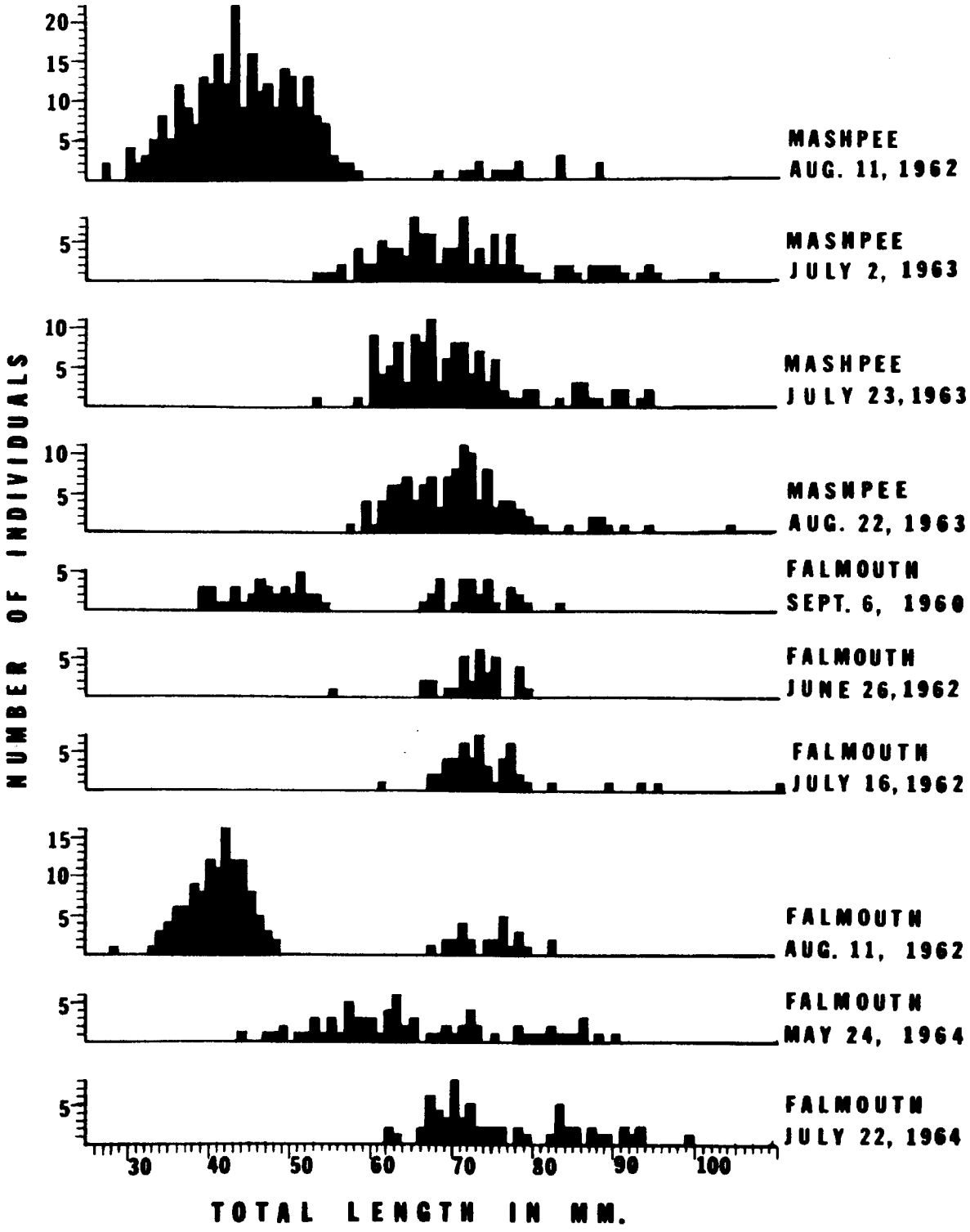

NUMBER OF INDIVIDUALS
MASHPEE
AUG. 11, 1962
MASHPEE
JULY 2, 1963
MASHPEE
JULY 23, 1963
MASHPEE
AUG. 22, 1963
FALMOUTH
SEPT. 6, 1960
FALMOUTH
JUNE 26, 1962
FALMOUTH
JULY 16, 1962
FALMOUTH
AUG. 11, 1962
FALMOUTH
MAY 24, 1964
FALMOUTH
JULY 22, 1964
TOTAL LENGTH IN MM.

FIGURE 3

region. The ponds were quite low during the course of sampling, and collections were halted in the summer of 1964 when the ponds dried up and remained in that state during the next spring.

Sexually mature individuals were scarce and as in Swampscott could be distinguished from the immature first year specimens on the basis of mesopodial development and reproductive ability (Table 3). Because of the limited number of adults, no attempt was made to distinguish separate age groups beyond the first year. However, testis structure studies revealed that the adults were only in their third and fourth years. Only one male was found to possess a two lobed testis.

The 1964 Falmouth samples produced a few specimens whose age could not be exactly determined. These specimens were sexually mature and appeared to be two years old, but the extent of mesopodial development was characteristic of one year old individuals. Four such specimens were found in the May sample and all four lacked calcified mesopodials. Two more individuals appeared in the July sample. Both had reproduced in the previous spring, as judged from the condition of the sexual apparatus, but they possessed only one and five calcified mesopodials. According to size all six individuals could have been included with either age group. The lack of correlation between mesopodial and reproductive development in these six individuals, which were the only deviants in the Cape Cod samples from the pattern described

TABLE 3

CORRELATION OF MESOPODIAL AND REPRODUCTIVE DEVELOPMENT WITH SIZE IN THE CAPE COD SAMPLES.

Locality	Date of Sample	Estimated Age (Years)	Number in Sample	Total Length (mm)			Calcified Mesopodials			Reproductive Organs
				Range	Mean	S.D.	Range	Mean	S.D.	
Mashpee	Aug. 11 1962	0.3	261	27- 58	43.7	6.3	0	....	...	Immature
		1.3	9	68- 83	74.4	4.5	0	....	...	Immature
		2.3+	6	76- 88	82.5	5.2	6-14	10.0	3.0	Mature
Mashpee	July 1963	1.2	200	53- 80	67.8	5.7	0	....	...	Immature
		2.2+	40	75-102	87.5	5.4	8-15	13.4	1.3	Mature
Mashpee	Aug. 22 1963	1.3	115	57- 81	69.1	5.5	....	....	...	.....
		2.3+	9	84-104	90.2	5.9	....	....	...	.....
Falmouth	Sept. 6 1960	0.3	38	39- 54	46.6	4.5	0	....	...	Immature
		1.3	30	66- 83	72.7	4.1	0-9	2.8	3.1	Maturing
Falmouth	June,1962	1.0	33	55- 79	72.3	4.6	0-2	0.1	0.4	Immature
Falmouth	July 16 1962	1.2	43	61- 78	72.3	3.6	0-1	0.0	0.1	Immature
		2.2+	9	71-110	85.3	12.6	5-15	10.6	4.3	Mature
Falmouth	Aug. 11 1962	0.3	119	28- 48	40.9	3.6	0	....	...	Immature
		1.3	27	67- 82	74.3	3.9	0-3	0.4	1.1	Immature
Falmouth	May 24 1964	1.0	43	44- 67	57.7	5.5	0	....	...	Immature
		2.0+	32	60- 90	75.9	8.0	0-15	8.6	5.6	Mature
Falmouth	July 22 1964	1.2	38	62- 75	69.2	3.0	0-3	0.4	0.9	Immature
		2.2+	27	74- 99	84.5	6.3	1-15	12.8	3.4	Mature

for Swampscott, may be explained by either precocious sexual development by one year old individuals, or anomalous mesopodial development in two year old specimens. The latter alternative seems to be the more probable explanation.

A slow rate of summer growth was found in both Cape Cod populations. Since most of the samples were taken in the summer, the extent of growth during the spring was not directly observed, but indications that it was rapid can be seen in a comparison of the August, 1962 Mashpee sample with that taken in July of 1963. The difference in size between the first group on each histogram demonstrates the extent of growth achieved by the larvae from August to the following summer. A better example of this rapid spring growth can be seen by contrasting the size of the first year groups in the May and July samples taken in Falmouth during 1964. It appears that these two populations follow the same growth pattern that was described for the Swampscott population.

Springer (1909) studied the effect of temperature on the growth rate of this species and concluded that the rate of growth diminishes as the temperature increases. Although she used weight as the criterion of size, it may be assumed that similar results would have been obtained if total length measurements had been used instead of weight. These findings explain the slow rate of growth during the summer in the coastal populations as compared with the rate observed in the early spring and fall.

All three coastal populations participated in the same

mode of life history. The scarceness of adults throughout the entire study period in the Cape Cod localities seems to be due to the harshness of environmental conditions produced by the drought. The Swampscott population was less drastically affected in 1961 and therefore contained a good adult representation. As the drought conditions became intensified, this population experienced the same conditions that were observed on Cape Cod with the result that the later population samples from Swampscott displayed the same structural features found in the Falmouth and Mashpee populations.

The Cape Cod populations sampled by Noble in 1929 were essentially similar to the ones described above and differed from them only in having a greater abundance of adults. Undoubtedly this difference is due to the different environmental conditions. The 1961 Swampscott samples, being less affected by the drought, bear the greatest resemblance to Noble's population samples. The occurrence of a biennial cycle in abundance in the Whittemore Pond population described by Noble is evident from the data he presented and further demonstrates the remarkable similarity of the two populations.

Neoteny and the Aquatic Life History

The occurrence of neoteny seems to be an integral part of the aquatic life history for all three coastal populations contained neotenic specimens. The phenomenon of neoteny has often been confused with that of paedogenesis, since both

refer to a change in the relative rates of development of the somatic and reproductive organs during ontogeny. Neoteny results in a retarding of somatic development while the development of the reproductive organs proceeds at the normal rate. Paedogenesis, on the other hand, involves an accelerated rate of reproductive development which results in individuals reproducing while they are still in the larval stage. The fact that the newts bearing larval characteristics in these three populations did not reproduce any earlier than their completely metamorphosed counterparts indicates that these individuals are neotenic and not paedogenetic. However, Noble cited an instance of reproductive development by larvae in one of his Cape Cod populations, and although he referred to this phenomenon as neoteny, it can be more accurately described as an example of paedogenesis.

Although many species of salamanders possess neotenic characters, the expression of this phenomenon in coastal newts is rather unusual because: (i) not all members of the population are neotenic (ii) only certain larval features are retained, hence, these newts are only partially neotenic and (iii) the degree of expression of these larval characters varies among the neotenes. As a result of this last peculiarity, an attempt was made to find some quantitative method which would distinguish the various expressions of neoteny.

The neotenes, as a group, possess three external

characters which readily distinguish them from completely metamorphosed individuals, namely, external gills, the presence of open gill slits, and a failure of the larval gular cleft to completely close. Gill size is so variable due to regeneration and the effect of environmental factors that it offers no hope of a reliable measurement. The presence of open gill slits, on the other hand, seems to vary according to the presence and extent of fusion of the gular cleft. For this reason the extent of gular cleft fusion was chosen as the criterion by which the various expressions of neoteny would be evaluated.

The fusion of the gular cleft always begins in the center of the gular region and proceeds laterally toward the gills. The measurements used to quantify the various degrees of fusion were obtained in the following manner. The markings from a metric scale were carefully transferred to a small strip of paper in order to provide a flexible scale which could follow the curvature of the gular region. The length of this region was taken from the ventral-most external gill on one side to the same gill on the other side. The length of the fusion area was also measured, and the two values were set to the following ratio:

$$\frac{\text{Length of fusion area in mm.}}{\text{Length of the entire gular region in mm.}}$$

This ratio was found to be independent of total length and thus provided a good measure of the expression of neoteny. By means of this ratio and the presence of external gills in cases where the ratio expressed unity all of the

individuals in each population were assigned to one of the following four classes:

Class 1 - completely metamorphosed individuals with no trace of neotenic characters.
Class 2 - neotenes with a fusion ratio above 0.75. Most of the specimens in this class had a completely fused cleft, but they retained traces of external gills.
Class 3 - neotenes with a fusion ratio ranging from 0.45 to 0.75.
Class 4 - neotenes with a fusion ratio ranging from 0.00 to 0.44.

This system of classification provided a means of determining the extent of change in the composition of a population by comparing the difference in the percentage of individuals present in each of the four classes. In the normal process of metamorphosis larvae pass through successive stages corresponding to the four classes. Therefore, the tendency of a population towards neoteny can be evaluated not only by the percentage of neotenes in the population as a whole, but also by the percentage of neotenes displaying the strongest expression of neoteny (Class 4).

The changes found in the yearly samples from Swampscott and Falmouth reveal a definite decline in the tendency toward neoteny (Figure 4). The reasons for this change could not be determined exactly, but the fact that both populations underwent a similar decline seems to be associated with environmental conditions caused by the drought.

Under normal conditions neotenes do not show any tendency to complete their metamorphosis as they grow older. Of the marked specimens which were recaptured twenty were neotenic and during the period between marking and subse-

Fig. 4 Annual proportion of neotenes in the Swampscott and Falmouth populations (all age groups). Consult the text for the Class distinctions.

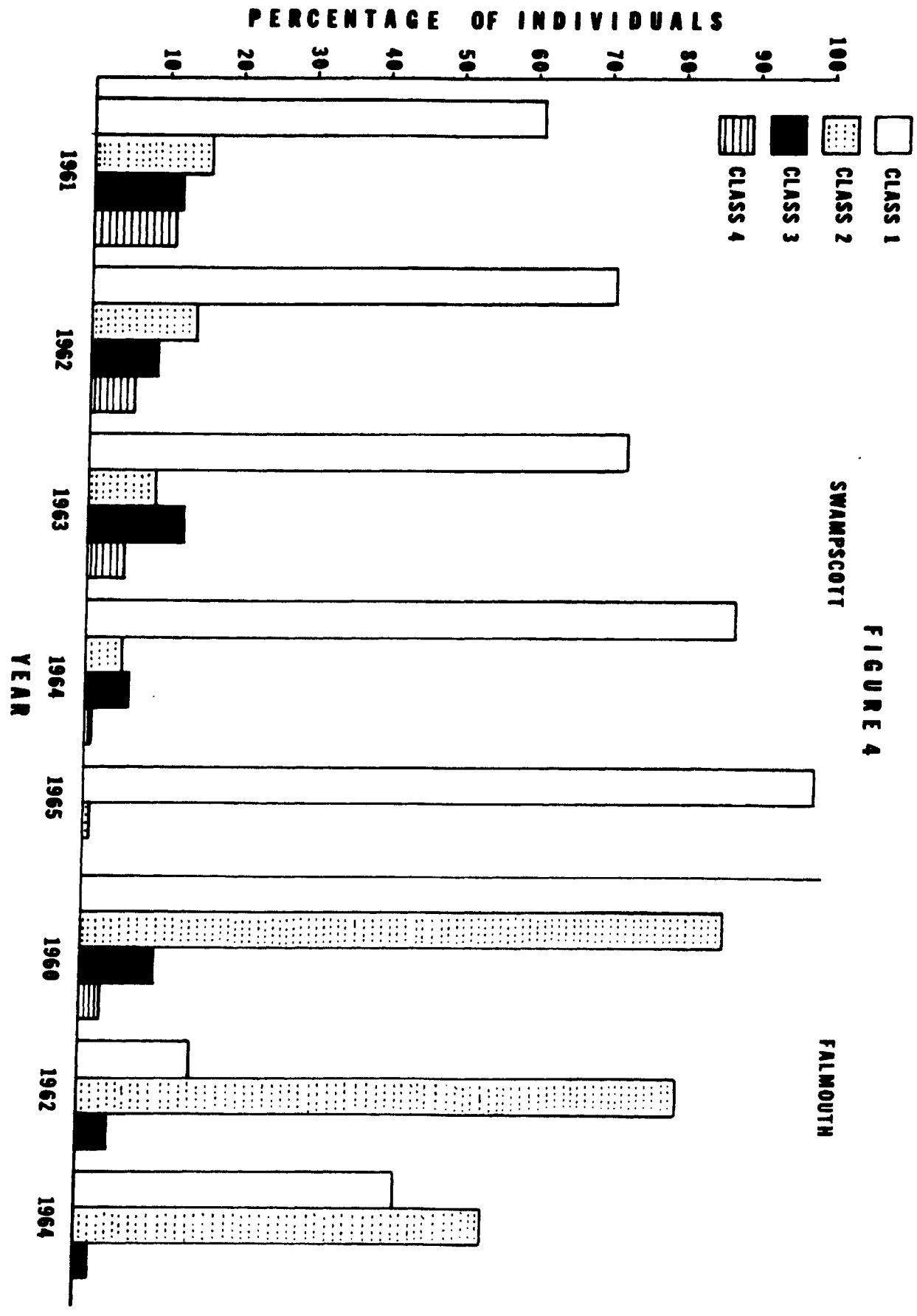

PERCENTAGE OF INDIVIDUALS
10
20
30
40
50
60
70
80
90
100
CLASS 1
CLASS 2
CLASS 3
CLASS 4
1961
1962
1963
1964
1965
1960
1962
1964
YEAR
SWAMPSCOTT
FALMOUTH

FIGURE 4

quent recapture none of them underwent any change in the expression of neoteny. Therefore, while they remain in the pond, neotenes apparently never complete their transformation.

Noble (1929) demonstrated that exposure to a terrestrial environment causes closure of the gill slits and resorption of the external gills. He found that recently metamorphosed forms completely lost their gills when exposed to a land environment, while adults underwent a reduction in gill size. Noble's experiment with the adults was terminated prematurely so that whether or not the adults would have completely lost their gills is unknown.

Morgan and Sondheim (1932) failed in their attempt to induce gill resorption by means of thyroid and pituitary implants and thereby supported the conclusion that neotenic characters tend to be stable. However, these investigators also found that the size of the external gills could be reduced by placing neotenes in a terrarium, but they disagreed with Noble by stating that the change in gill size was only temporary. When they returned the newts to water, the gills regained their normal size. Unfortunately, Morgan and Sondheim gave no indication of the state of sexual maturity of their neotenes.

Neither study mentioned the fate of the gular cleft upon which the expression of neoteny in this study is primarily based. The author repeated this experiment by placing twenty neotenes in a terrarium and observing them periodi-

cally from mid-June until early September. The gular cleft fused rapidly in the immature specimens, but only slowly in the adult neotenes. It was further discovered that the greater the degree of neoteny, the slower was the tendency to transform. In addition to causing gular cleft fusion, the exposure to a terrestrial environment resulted in a closure of the gill slits and a reduction in the size of the external gills. In a few instances the gills disappeared altogether. By the time the experiment was terminated most of the neotenes were well on their way to complete transformation, but gill stubs remained in many individuals.

Because these results indicate that removal of neotenes from the water induces transformation, it is reasonable to assume that the temporary migration of such individuals from the pond under drought conditions can cause a shift in the population composition. Nevertheless, while this may occur, it is doubtful that the transformation of existing neotenes was the main cause underlying the changes observed in the Swampscott and Falmouth populations.

Examination of the first year group alone for each year in Swampscott revealed a dramatic reduction in the number of neotenes and in the extent of expression of neoteny from 1961 to 1965 (Figure 5). This trend was so strong that neoteny was completely eliminated in the generation produced in the spring of 1964. The explanation of this result could not be determined from the data on hand, but two possibilities exist. The environmental changes produced by the

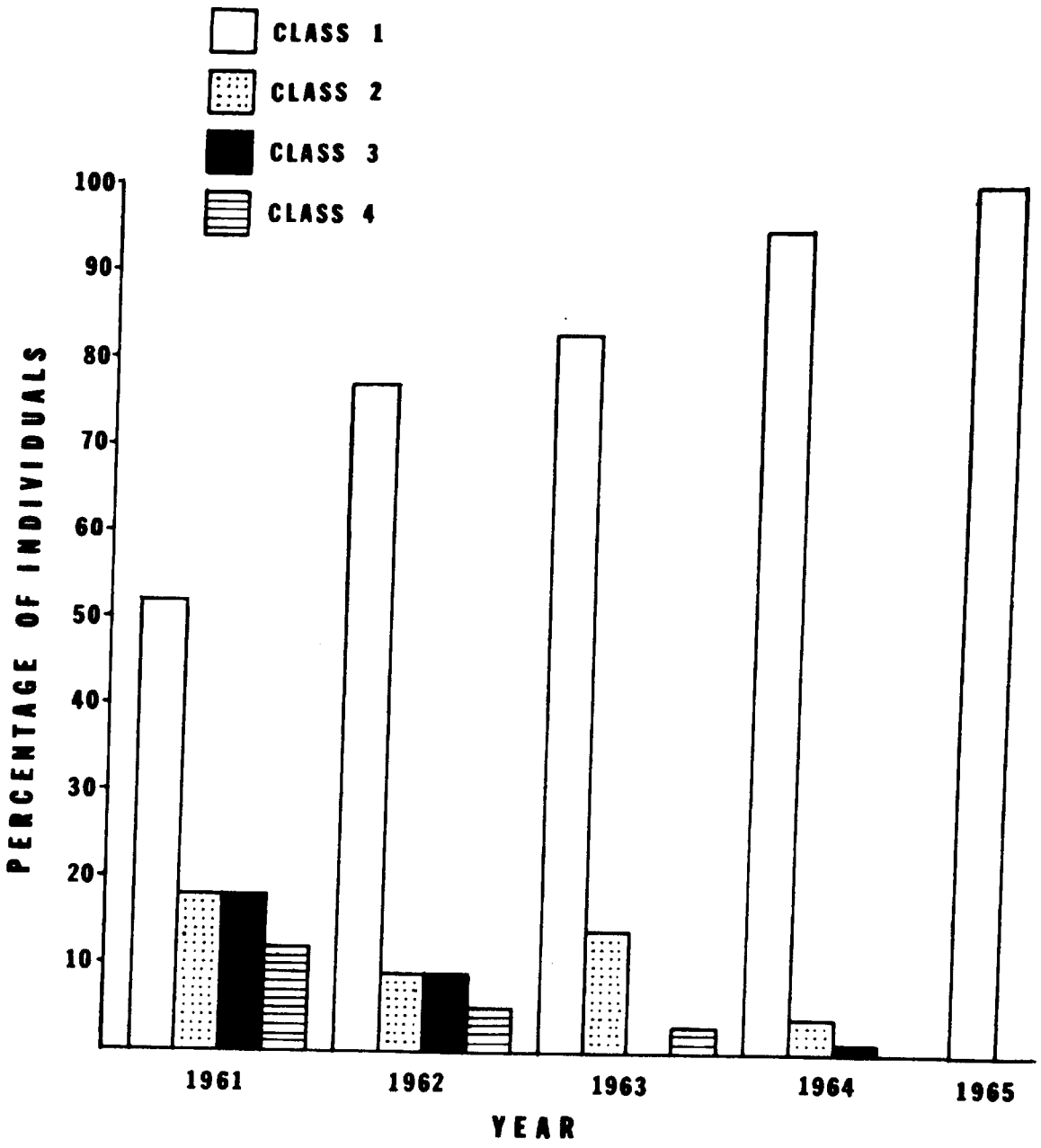


Fig. 5 Annual proportion of neotenes in the Swampscott population (one year old specimens only). Consult the text for the Class distinctions.

drought, e.g., high water temperature, may have caused the complete transformation of those individuals which, under normal circumstances, would have retained some larval characteristics. Premature transformation of larvae has been observed by the author under drought conditions in other, less permanent, ponds in Swampscott. The other possibility which must be considered is the presence of a selective effect operating against neotenes. In either case the environmental influences of the drought seem to have played a prominent role.

INLAND POPULATIONS

All of the inland populations studied were characterized by the inclusion of a terrestrial stage in their life history, but the duration of the eft stage was found to vary. The populations sampled in Central Massachusetts (Charlton and Paxton) contained efts which usually return to the water in the fall of their third year and breed in the following spring, i.e., when they are three years old. The efts from the Berkshire Hills of Western Massachusetts undergo a more extended sojourn on land and do not return to the water until the fall of their fourth year.

The histograms constructed from all of the inland samples are given in Figure 6, but in order to facilitate comparisons, the populations from the two areas of Massachusetts will be treated separately. Because most of the females in these samples could not be aged, the analysis of

Fig. 6 Size-frequency histograms of individuals taken in Central and Western Massachusetts. The black squares represent males and the white squares represent females. Unless otherwise noted, all samples were taken in 1965.

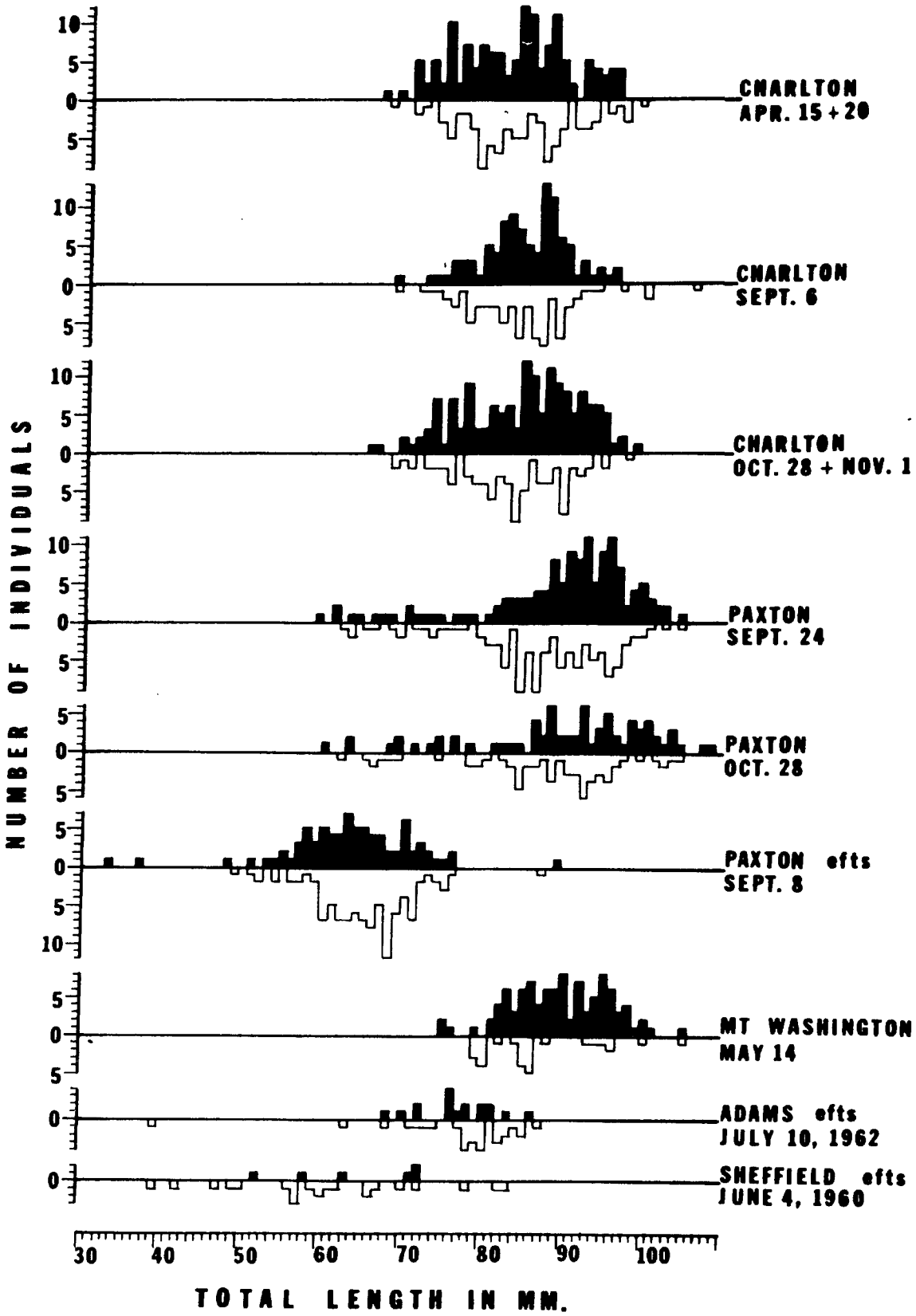

NUMBER OF INDIVIDUALS
CHARLTON
APR. 15 + 20
CHARLTON
SEPT. 6
CHARLTON
OCT. 28 + NOV. 1
PAXTON
SEPT. 24
PAXTON
OCT. 28
PAXTON efts
SEPT. 8
MT WASHINGTON
MAY 14
ADAMS efts
JULY 10, 1962
SHEFFIELD efts
JUNE 4, 1960
30 40 50 60 70 80 90 100
TOTAL LENGTH IN MM.

FIGURE 6

the populations has largely been restricted to the male segment.

Central Massachusetts Populations

The adult population from Charlton was the focal point of the study of the terrestrial life history and was sampled three times during 1965. All of the individuals (male and female) collected in April were sexually mature as was evident from the condition of the sexual apparatus and the presence of secondary sex characters. The males were divided into three morphologically distinct groups on the basis of differences in testis structure (Table 4). The smallest group could be further distinguished from the others by the presence of fewer calcified mesopodials, although some overlapping did occur among individuals possessing the full complement of calcified carpals and tarsals.

Subsequent samples taken in September and early fall demonstrate the extent of growth attained by each of the three groups during the summer. A few returning efts (age 2.3) were collected in September, and a small series of larvae was obtained. The larvae were quite numerous, but since no real attempt was made to secure a large sample, the number shown in Table 4 is not indicative of their relative frequency. A greater number of returning efts appeared in the fall collection, and by this time the larvae had already transformed and left the pond.

The assignment of age to the males in this population was based on the extent of caudal germ-cell cord development

TABLE 4

CORRELATION OF TESTIS STRUCTURE AND NUMBER OF CALCIFIED MESOPODIALS WITH SIZE GROUPS IN THE CENTRAL MASSACHUSETTS POPULATIONS (MALES ONLY).

Locality	Date of Sample	Estimated Age (Years)	Number in Sample	Total Length (mm.)			Calcified Mesopodials			Number of Testis Lobes	Caudal Germ-Cell Cord
				Range	Mean	S.D.	Range	Mean	S.D.		
Charlton	April 15 and April 20	3.0	30	66- 83	75.8	4.4	8-15	13.5	2.2	1	short
		4.0	36	72- 93	82.4	5.2	15	....	...	1	long
		5.0+	22	80- 95	88.5	4.0	15	....	...	2	
Charlton	Sept. 6	0.3	17	33- 38	35.8	1.6	0	....	...	1	-
		2.3	11	68- 78	74.4	2.9	4-15	12.2	4.1	1	short
		3.3	49	73- 89	81.7	4.3	15	....	...	1	long
		4.3+	43	75- 94	85.5	3.8	15	....	...	2	
		5.3+	8	80- 95	89.6	5.1	15	....	...	3	
Charlton	Oct. 28 and Nov. 1	2.5	39	71- 84	75.5	3.3	5-15	12.2	3.3	1	short
		3.5+	39	77- 89	83.7	3.5	15	....	...	1	long
		4.5+	58	79- 98	88.4	4.1	15	....	...	2	
		5.5+	5	85- 93	90.4	3.3	15	....	...	3	
Paxton	Sept. 8	0.3	2	33, 37	35.0	...	0	....	...	1	-
		1.3	43	48- 67	60.3	4.3	0-3	0.3	0.8	1	-
		2.3	34	60- 76	68.6	4.1	4-15	8.5	3.6	1	short
Paxton	Sept. 24 and Oct. 28	1.4	12	59- 70	64.3	4.0	0-2	0.4	0.5	1	-
		2.4	15	64- 78	72.3	4.4	4-15	11.7	3.1	1	short
		3.4+	51	72- 95	87.6	4.8	15	....	...	1	long
		4.4+	109	80-107	93.6	5.2	15	....	...	2	
		5.4+	15	88-108	97.1	5.0	15	....	...	3	

which was already shown to be correlated with age. Since the newly transformed larvae do not acquire gonadal maturity over the winter and since the presence of a short germ-cell cord in males collected in April indicates that gonadal maturity had been achieved in the previous spring, the smallest males in the April series were judged to be three years old. The correlations made in the Swampscott population demonstrate that the males with a longer cord are a year older and those with a two lobed testis are at least five years old.

The age-size correlations discovered in Swampscott males permit the establishment of a relationship between age and testis structure. However, this relationship could only be made up to the initial appearance of the two lobed testis. Although a size difference between two lobed and three lobed males in the inland populations indicates an age difference, the extent of this difference could not be determined. Since two years is required for the development of the second testis lobe, it is reasonable to assume that an additional two years must elapse before the third lobe appears. Variation in the relative sizes of the two lobes and in the extent of development of the second germ-cell cord supports this assumption. Therefore, the males in the inland populations which possess three testis lobes must be at least seven years old.

The relative infrequency of males with three lobed testes should not be taken as an indication that only a few

individuals live to be seven years old. Three lobes are found in a testis only when the original lobe remains until after the third lobe is formed. The fact that some of the largest males collected possessed only a single lobed testis suggests that more often than not the first formed lobe disappears before the third lobe is formed. In such a case only two lobes would be present after the third lobe is formed. Therefore, it is impossible to determine how many cycles have occurred in large specimens, and so no reliable age estimate can be made for individuals with two testis lobes.

No terrestrial newts were found in Charlton, but the testis structure data suggest the existence of a year class intermediate between the larvae and returning efts. Confirmation of the existence of such a class was obtained in a series of efts taken in nearby Paxton on September 8.

One hundred and eighty-four efts were collected as they wandered on land after a rainstorm. The size-frequency histogram for this sample contains three distinct groups. The two smallest individuals, which comprise the first group, were sexually immature and considered to be newly transformed larvae. The two largest specimens displayed adult coloration and advanced reproductive development - the male possessed a two lobed testis and the female had numerous pigment spots in her ovary which indicated previous reproductive activity. Both specimens were adults which had returned to the land during the summer. Brimley (1921)

found that adults in North Carolina usually leave the water during the late spring and return in the fall. Hence, this type of behavior is not uncommon.

The bulk of this sample contained individuals ranging in total length from 48 to 76 mm. All of these efts showed signs of having acquired gonadal maturity - the males possessed a divided testis lobe and the females had large, coiled oviducts and ovaries with developing ova. Although this assemblage would appear to represent a single age class, variation in mesopodial and germ-cell cord development made possible the establishment of two morphologically distinct groups.

Of these two groups the one containing the largest specimens (age 2.3) was similar in cord development and range of calcified mesopodials to the returning efts found in Charlton. The other group represented the age class that was missing in the Charlton samples.

The attainment of gonadal maturity by the smaller efts (age 1.3) is consistent with the appearance of a short germ-cell cord in the larger ones. Humphrey noted a difference in the manner of cord formation between efts bearing mature gonads and sexually mature (breeding) adults. In the latter individuals the cord forms after the evacuation of sperm in the spring, but in the non-breeding efts the cord develops earlier from the degeneration of sperm in the late summer and early fall. This degenerative process had begun in the smaller Paxton efts (age 1.3) since 37% of these males

possessed the rudiment of a cord. The presence of a cord in the larger efts resulted from a continuation of this degenerative process.

The pond bordering the area where the efts were taken was sampled on September 24 and October 28. Of the newly returned efts individuals from both the second and third age classes were found. This occurrence was in marked contrast to the situation in the Charlton population where only efts in their third year returned, and it suggests that the length of the eft stage may vary within a single population.

Western Massachusetts Populations

A collection of breeding adults was obtained during the spring of 1965 in Mt. Washington, which is located near Sheffield in the southwest portion of Massachusetts. None of the males in this sample possessed a short germ-cell cord, and the smallest individuals displayed all of the characteristics of the four year old adults taken in the spring from Charlton (see Table 5). The absence of three year old newts in this aquatic habitat indicated that the eft stage was prolonged in this region, and an analysis of the efts sampled in the Berkshires proved that they do not return to the water until the fall of their fourth year.

Two series of efts were collected in this general area, and both contained individuals which were similar to the three year old adults taken in Charlton. Since both samples were rather small, the males and females were combined in order to provide more data. The scarceness of

TABLE 5

CORRELATION OF TESTIS STRUCTURE AND NUMBER OF CALCIFIED MESOPODIALS WITH SIZE GROUPS IN THE WESTERN MASSACHUSETTS POPULATIONS. MT. WASHINGTON SPECIMENS ARE AQUATIC MALES BUT THOSE FROM THE OTHER LOCALITIES ARE EFTS (MALES AND FEMALES). DUE TO THE SMALL NUMBER OF MALE EFTS, NO TESTIS STRUCTURE COMPARISONS ARE MADE.

Locality	Date of Sample	Estimated Age (Years)	Number in Sample	Total Length (mm.)			Calcified Mesopodials			Number of Testis Lobes	Caudal Germ-Cell Cord
				Range	Mean	S.D.	Range	Mean	S.D.		
Sheffield	June 4, 1960	1.0	6	39- 52	46.5	5.0	0	....	...		
		2.0	11	56- 63	59.1	2.3	0-4	1.7	1.6		
		3.0	11	66- 83	72.6	6.0	5-15	10.9	3.7		
Adams	July 10, 1962	1.2	1	39	....	...	0	....	...		
		2.2	3	63- 68	66.3	2.9	0	....	...		
		3.2	41	70- 87	78.8	4.2	4-15	12.6	2.6		
Mount Washington	May 14, 1965	4.0	27	75- 98	87.2	6.8	15	....	...	1	long
		5.0+	66	81-100	89.9	4.9	15	....	...	2	
		6.0+	4	90-104	97.8	5.9	15	....	...	3	

males prohibited valid comparisons based on testis structure, but in this instance the criterion of mesopodial development proved to be adequate in distinguishing age groups. The Sheffield sample was composed of three groups, the largest of which was similar in both size and range of calcified mesopodials to the three year old newts collected in Charlton in April. The same can be said for the largest specimens in the other series, which was taken on Mt. Greylock in Adams, Massachusetts. This series was predominantly composed of three year old efts which were in the act of migrating to the pond. The low number of individuals in the other two age groups is due to the fact that these groups were not in the process of migration.

COMPARISONS AND CONCLUSIONS

The establishment of two different modes of life history in Notophthalmus v. viridescens is the result of variation in the post-metamorphic behavior of first year individuals. The newly transformed larvae from inland populations leave the water after metamorphosis and develop adaptations for terrestrial life. These adaptations morphologically distinguish the terrestrial efts from the adults which have secondarily acquired modifications for life in an aquatic environment. Coastal newts remain in the water after metamorphosis and immediately assume the adult aquatic adaptations. In some specimens the retention of certain larval characteristics produces even more elaborate adap-

tations for the aquatic mode of life. Therefore, the morphological peculiarities which distinguish the coastal and inland immature individuals stem from specific adaptations to their specific environments.

In addition to affecting individual morphology this difference in post-metamorphic behavior also exerts a noticeable influence on the structure and developmental patterns of the respective populations. Populations expressing the two modes of life history differ in the age at which reproductive activity is achieved, the rate of individual growth, the longevity of the members of the population, and population size.

Reproductive Activity

Coastal newts generally acquire sexual maturity in their second summer (their first following metamorphosis) and reproduce in the next spring when they are two years old. Noble (1926) was the first to suggest this, but his evidence was not generally accepted (Pope, 1928 and Bishop, 1941). Contrary to the findings of other authors, Noble claimed that there was no direct proof that efts required a longer period of time to reach sexual maturity. The more objective age criteria used in this study provided definite proof that efts do not reproduce until they are three or four years old, although individual exceptions to this normal pattern may occur in some populations, e.g., in Paxton.

Testis studies have indicated that spermatogenesis

is initiated at the same time in newts from both life histories, but the temporal relationship of this gonadal maturity to actual reproduction (sexual maturity) differs. The initiation of gonadal maturity coincides with the onset of reproductive activity in coastal newts but preceeds such activity by a year or two in the terrestrial forms.

Growth

Size comparisons of similar age groups between inland and coastal populations show that coastal newts grow at a faster rate. The most striking example of this can be seen in a comparison of the April Charlton collection with the spring series taken in Swampscott (see Tables 2 and 4). The third year inland adults are almost identical in average length to the second year coastal newts. The size differential between coastal and inland newts is most pronounced in the early years after metamorphosis, and despite the small number of efts collected in this study, the greater average length of the coastal newts can be demonstrated (see Table 6). Since all metamorphosing larvae attain the same size, the difference in growth reflects the effects of the different modes of post-metamorphic life.

The transition from an aquatic to a terrestrial habitat involves a number of changes associated with feeding behavior. Pope (1924) noted that newly transformed efts do not eat in captivity and that this refusal to feed may be related to the development of structural modifications which produce a change in the manner of securing food, e.g.,

TABLE 6

SIZE COMPARISON BETWEEN SIMILAR AGE GROUPS FROM INLAND AND COASTAL POPULATIONS. ONLY THOSE SAMPLES WHICH WERE TAKEN AT APPROXIMATELY THE SAME TIME OF YEAR ARE USED FOR COMPARISON.

Estimated Age (Years)	Month of Collection	Inland Populations						Coastal Populations					
		Paxton Total Length (mm.)			Sheffield Total Length (mm.)			Swampscott Total Length (mm.)			Cape Cod Total Length (mm.)		
		Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
1.0	May-June	.....	....	...	39-52	46.5	5.0	43-66	56.4	4.7	44-67	57.7	5.5
1.3	Aug.-Sept.	48-67	60.3	4.3	.....	....	...	61-75	68.5	3.3	57-81	69.1	5.5
2.0	May-June	.....	....	...	56-63	59.1	2.3	68-83	76.4	3.5	.....	....	...
2.3	Aug.-Sept.	60-76	68.6	4.1	.....	....	...	73-89	82.7	3.8	.....	....	...

aquatic newts snap at their prey, whereas efts use their tongues to seize food. A difference in the structure of the tongue between terrestrial and aquatic newts was noted by Breder (1924). Pope also discovered that the sense of smell is less acute in efts than in aquatic individuals (both larvae and adults). Gage (op. cit.) observed a change in the epithelial lining of the mouth associated with a change from aquatic to terrestrial environments. Although this metaplasia is primarily concerned with the manner of respiration, it is not inconceivable that feeding may be interrupted during the transition period.

Aquatic immatures in coastal populations do not undergo such changes and, consequently, continue their normal feeding behavior. Morgan and Grierson (op. cit.) demonstrated that aquatic newts continue to feed and molt during the winter months and, therefore, are active throughout the year. Although the winter growth itself is not extensive, that achieved in the early spring and fall is substantial (see Figure 2). Due to the harsher terrestrial conditions efts are restricted to a shorter period of spring and fall activity and become dormant during the winter. Hence, it is doubtful that they experience much growth during this time. Pope (1928) described a series of efts taken during June in Branchville, New Jersey which included specimens ranging from 31 to 36 mm. in total length. Since this size is identical to that of transforming larvae, little or no growth occurred between September and June.

The interruption of the efts' feeding by the development of terrestrial adaptations and the yearlong activity of aquatic newts seem to be chiefly responsible for the difference in growth rate. Other factors which also may be considered are the greater availability of food in the aquatic environment and the greater mobility of aquatic forms, which gives them an advantage in procuring food.

Besides having a slower growth rate, the inland newts also exhibited a slower rate of mesopodial calcification (see Figure 7). Therefore, unlike the age-testis correlations, no generalized correlations could be made between age and the number of calcified mesopodials.

Longevity

Very few males in the coastal populations possessed a multiple testis, and the majority of those that did were just developing the second lobe; yet, more than half of the aquatic males taken from inland populations bore two or more testis lobes (see Table 7). Since spermatogenesis begins at the same time in both life histories, the more advanced condition of the multiple testis in the inland males demonstrates their greater longevity.

In all inland populations studied the aquatic males outnumbered the females. This observation agrees with the findings of Jordan (op. cit.), Pope (1924) and Bishop (op. cit.). Pope, who made his collections during the breeding season, did not think that this result represented the true sex ratio because he believed that males were more easily

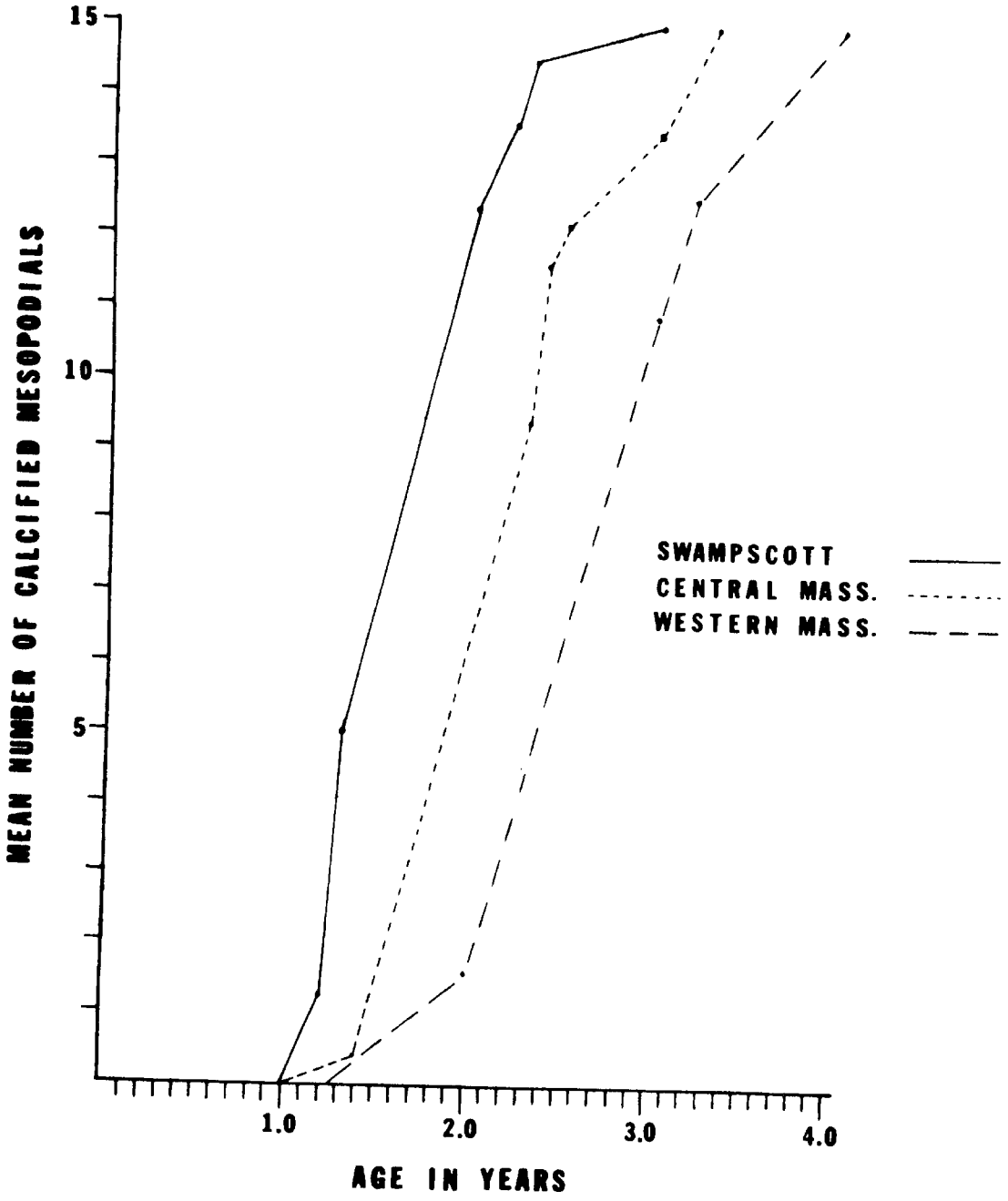


Fig. 7 Interpopulation variation in the rate of mesopodial calcification.

TABLE 7

COMPARISON OF POPULATIONS BASED ON THE PROPORTION OF MALES. ALL OF THE SAMPLES FROM EACH POPULATION (EXCEPT SWAMPSCOTT) WERE COMBINED IN ORDER TO OBTAIN THE PERCENTAGES.

Habitat	Location in Massachusetts	Population	Percentage of Males in the Population	Percentage of Specimens in Male Population with Two or More Testis Lobes
Aquatic	Coastal	Swampscott (1961)	50	20
		Falmouth & Mashpee	52	1*
Aquatic	Central	Charlton & Paxton	58	48
Aquatic	Western	Mt. Washington	79	72
Terrestrial	Central	Paxton	45	0
Terrestrial	Western	Adams	38	0
		Sheffield	25	0

*Because of the effect of the drought on adults, this figure is not representative of the normal population structure.

captured in the breeding season. However, the collections made during the summer in this study revealed the same characteristic numerical superiority of males. Thus, it can be assumed that this difference is real and not a reflection of sampling error due to breeding behavior.

Although actual survivorship calculations could not be made due the lack of criteria for aging females and older males, the greater frequency of aquatic males suggests that females are not as successful as the males. The sex ratios obtained from the eft series show that the terrestrial females are actually more abundant than their male counterparts (see Table 7). Since this is true even for the older migrating efts, it appears that the increased female mortality occurs only after the efts return to the water to breed.

The discrepancy in sex ratio is less pronounced in populations containing a greater percentage of small specimens, e.g., in coastal populations. This further suggests that size plays a major role in determining the extent of female mortality. The data in Figure 6 support the conclusion that the larger females are relatively less successful than males in the aquatic environment. Bishop (op. cit) states that aquatic females are smaller in average length than males, and his data show that the greater the average length attained by the population, the greater is the size differential. This same result can be observed by comparing the Central Massachusetts populations with the

one from Mt. Washington.

Organ (1961) found that the more terrestrial species of the genus Desmognathus had a higher proportion of mature males to mature females. He attributed this result to a greater female mortality related to their aquatic nesting behavior. The trend seems to be similar in newts, but the reasons for increased female mortality appear to be different. The greater weight and smaller tail fin of mature females seemingly results in less mobility in the water (especially during the breeding season) and makes them more susceptible to predators than are males of a similar length.

Population Size

Although density studies were not conducted, the results of sampling may be taken as a rough index of population size. Samples from the aquatic habitat in inland areas were larger and were taken in less time than those from coastal populations. Since these inland samples represented only the adult segment of the population, it seems reasonable to assume that inland populations are larger than coastal ones. It may be argued that the inland populations frequent larger bodies of water which can support more individuals, but the smallest pond sampled in this study was located in Mt. Washington. The specimens from this pond were not only more numerous than those in coastal populations, but, since they all were at least four years old, they also represented only a small proportion of the entire population.

DISCUSSION

The relative abundance of small individuals in the Cape Cod populations and the gradual development of a similar structure in the Swampscott population suggests that the smaller specimens, being more dependent on the aquatic environment, are more suitably adapted to this mode of life. This implies that they can compete more favorably with large individuals for food and space and, consequently, limit the proportion of large adults. The faster growth rate in the coastal populations produces a larger individual size in a shorter period time and thereby reduces longevity, but the acquisition of reproductive activity at an early age compensates for this shorter life span. In order to maintain a sufficient proportion of breeding individuals in the population, the adults regulate the size of the larval class when the number of immature newts reaches a high level. In this manner the size and composition of the population is kept relatively stable.

The Advantage of the Terrestrial Stage

This intrapopulation competition for food and space between sexually mature and immature specimens does not occur in the inland populations because of the spatial segregation of these two segments of the population. As a result the adults enjoy a greater longevity and the population as a whole is larger.

Organ (op. cit.) noted that in Desmognathus the trend

toward terrestriality resulted in a higher proportion of individuals reaching sexual maturity. The absence of survivorship data in this study prevents an accurate assessment of the situation in newts, but it would appear not to be the same. The coastal populations, by virtue of their earlier reproductive activity, would seem to produce a greater proportion of individuals reaching the early stages of maturity, but this advantage is counteracted by the decreased longevity. On the whole the length of reproductive life appears to be approximately the same in both life cycles. This seems true in comparing coastal populations and inland populations with a shorter eft stage, but the increased female mortality in populations having a prolonged eft stage results in a shorter span of reproductive life for these populations as a whole. Prolongation of the trend toward terrestriality would appear to be somewhat disadvantageous.

In view of this possibility the major adaptive difference in the two life histories seems to lie in the greater size of inland populations and in their occupation of two different habitats during ontogeny. Both factors would be of great advantage to the population during short term changes in the suitability of the aquatic environment. The trend toward terrestriality in newts has resulted in the production of an escape mechanism.

Although adult newts can survive for some time on land, they are not as specifically adapted for terrestrial life as are the efts. Small aquatic individuals in the coastal

populations seem even less able to cope with the terrestrial environment. Short term changes in the aquatic habitat would not be as detrimental to the inland populations because one phase of their life history is especially adapted to terrestrial life. Furthermore, the greater size of the inland populations would enable them to withstand more losses during such conditions. Even a few survivors can maintain the population. That a small number of adults can produce an enormous larval class seems evident from the situation in the population sampled in Mashpee in 1962.

Populations which have developed a prolonged eft stage have a better chance of surviving short term changes in the environment than have aquatic populations or even those with a short eft stage. The apparent sacrificing of extended reproductive life in favor of a longer period of terrestrial existence can be explained if the terrestrial life history is viewed as an escape mechanism.

Environmental Influence and Terrestriality

The drought conditions described in the coastal areas provide an excellent example of the type of change in the aquatic environment proposed above. The sequence of events which occurred in the Swampscott population under such conditions offers an insight into the factors governing the development of post-metamorphic behavior in efts.

The increased severity of the drought disrupted the normal environmental conditions of the pond with the result that the newt population became progressively smaller. The

large adults were the first members of the population to be affected, but ultimately the entire aquatic population was depleted. Since neoteny is a specialization for aquatic life, the gradual loss of neotenes in response to the changing environmental conditions indicates that the population was adjusting by ridding itself of its aquatic adaptations.

Sasaki (1924) attributed the co-existence of neotenes and metamorphosed individuals in a population of Hynobius leechi to a difference in microhabitats within a large body of water. The small size of the Swampscott pond suggests that the environment, at least as far as the newts were concerned, was fairly homogeneous. Hence, the polymorphic nature of this population cannot be attributed solely to environmental factors. However, the response of this population regarding neoteny to the changing environment and the occurrence of a similar response in the Cape Cod populations indicates that the environment must play a prominent role in producing neoteny. Whether this environmental role is direct or indirect, e.g., as a selective force, could not be determined, but in either case it must operate in conjunction with genetic factors.

The stimulus for the change in neoteny was strictly environmental and of such magnitude that neoteny was completely eliminated from the life history of the Swampscott population in 1964. Although the members of the 1964 generation had lost all traces of neoteny, they remained in the

water after metamorphosis and did not abandon their aquatic behavior. The disappearance of larvae in late September of 1965 suggests that these individuals changed their mode of life and became terrestrial. The fact that the water level in the pond did not change appreciably between July, when the larvae were abundant, and September militates against the argument that this larval class became extinct. On the other hand, their absence from the pond at the same time when the inland larvae had just begun their terrestrial existence and the gradual tendency away from aquatic adaptation observed in reference to neoteny supports the view that these larvae had changed their life history.

Further evidence in support of this alternative was provided by a small aquatic population from Plymouth, Massachusetts. Although the water level was quite low, both normal individuals and Class 2 neotenes were taken in the pond during August and October of 1964. Almost half of the newly transformed specimens collected in October were found not in the water but under debris along the edge of the pond, and some of these individuals were eft-like in appearance. In May of 1965 the pond was completely dry, and an extensive search for specimens produced a single individual which was definitely an eft. The October collection proved that a change in environmental conditions can cause aquatic newts to leave the pond even though the water level remained high enough to support life, and the eft obtained in May demonstrated that an aquatic population can produce efts under

certain conditions.

Pope (1921), in attempting to explain the greater abundance of efts in hilly regions than in other localities, suggested (with reservations) the possibility that the nature of the environment might affect the habits of the newt. The trend toward terrestriality in Massachusetts' populations seems to be correlated with elevation for the greater the elevation of the land, the longer is the eft stage. This correlation would explain the greater abundance of efts in hilly regions because the prolonged eft stage would increase the relative frequency of such individuals.

Bishop (1943) states that this subspecies of newt reaches its greatest size in the mountains of western North and South Carolina. Since a greater adult size would tend to indicate a long eft stage, Bishop's observation reinforces the previously mentioned correlation.

The trend away from aquatic specialization (and perhaps toward a terrestrial existence) in the coastal populations during the drought conditions and the correlation between the length of the eft stage and elevation suggest an environmental influence over the mode of newt life history. The nature of this influence and its interaction with genetic factors in controlling the life history of the newt still remains a mystery. However, the results of this study seem to indicate that the environment plays a dominant role.

SUMMARY

This study was undertaken in an attempt to resolve discrepancies existing in the literature concerning the life history of the common newt (Notophthalmus v. viridescens) and to compare the effect of alternative expressions of this life history on population structure. Coastal populations similar to the ones described by Noble (1926, 1929) were studied in detail and compared with inland populations which manifested the mode of life history described by Gage (1891) and Pope (1924).

Since the comparisons were based on differences in population structure, a method of determining age which was more objective than that used by previous authors was developed. Size-frequency histograms constructed from samples taken over a five year period in Swampscott, Massachusetts formed the basis for determining age. Size groups delineated on the histograms were found to follow a characteristic pattern of growth from which age estimates could be made. The coherency of these groups was established by mark and recapture studies, as well as by correlation with morphological criteria.

The pattern of testis development in this species proposed by Humphrey (1926) was substantiated, and the early stages of development were correlated with groups of known age. Since the testis was found to undergo its first spermatogenesis at the same time in the males from all of the populations studied, the correlation of differences in

testis structure with groups of known age in the Swampscott population facilitated the estimation of age in the other populations. A pattern of mesopodial calcification was discovered which reinforced the groupings delineated on the basis of testis structure differences. This pattern, however, could not be used by itself in determining age beyond the first year, since the rate of mesopodial calcification was found to vary among populations.

All three coastal populations manifested the aquatic mode of life history and possessed similar population structures. Similarities were observed in the age at which sexual maturity was attained, the pattern of growth, polymorphism resulting from neoteny, and the response of the populations to drought conditions. Except for the low frequency of adults due to the environmental conditions imposed by the drought, these populations resembled the ones described by Noble. A method of quantifying the various expressions of neoteny was devised and was used to demonstrate changes in the tendency of coastal populations towards neoteny. An environmental influence governing such changes was proposed. The characteristics of the coastal populations were explained in terms of intrapopulation competition and adaptation to the aquatic environment.

The inland populations possessed a land stage in their life history, and the duration of this land stage was found to vary not only between populations from different areas, but also within single populations. Efts from localities in

Central Massachusetts underwent a shorter period of terrestriality than did those from the Berkshire Hills of Western Massachusetts. The inland populations were found to differ from the coastal ones in the age at which reproductive activity began, the rate of individual growth, longevity, and population size. The trend toward terrestriality was interpreted as being a mechanism for escaping short term changes in the suitability of the aquatic environment.

The differences in population structure that distinguished the two life histories were attributed to the post-metamorphic behavior of newly transformed individuals; and, although the cause of this difference in behavior could not be determined, the environment was believed to play a prominent role in its development.

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