AGE, GROWTH, AND MORPHOLOGY OF LARVAL REDFISH, SEBASTES SP. (PISCES: SCORPAENIDAE) ON FLEMISH CAP, 1980-1981

RANDOLPH WAYNE PENNEY

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BY

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A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

Dept. of Biology
Memorial University of Newfoundland

February, 1984

St. John's Newfoundland

ABSTRACT

Larval redfish, Sebastes sp., were collected for growth analysis and morphological studies on Flemish Cap, an offshore bank approximately 400-500 kilometers east of the Island of Newfoundland, Canada, using paired Bongo nets. Several cruises were completed during 1980 and 1981. Increments, which are believed to form daily from date of extrusion, were counted from sagittae and measurements of sagittal radii were taken for back-calculation of individual growth histories.

Mean daily growth rates and back-calculated growth histories of over 1200 redfish larvae were determined. Mean daily growth was 0.160 mm per day and 0.109 mm per day in 1980 and 1981 respectively. Total larval length was a linear function of age. A significant non-linear relationship between total length and sagittal, radius, and measurements of sagittal radii at intervals of 5 increments were used to back-calculate the length at extrusion and growth history of each larva.

Growth rates varied considerably over the first 110 days of life. Larvae typically experienced an initial period of reduced growth for 10-15 days following extrusion followed by a sharp increase and a period of relatively

fast growth for 60-70 days before declining as larvae entered the pelagic juvenile stage. Larvae extruded late in the season in 1980 tended to grow faster at all ages than larvae extruded early in the season.

Because of continuing controversies regarding the identification of possibly three species of redfish: S. marinus, S. mentella, and S. fasciatus, a variety of morphometric, meristic, and pigmentation variables were measured and their utility as identification criteria evaluated. Principal Component Analysis could not identify morphometrically distinct groups which might be used to establish species identification criteria. Differences in morphometry, meristics, and pigmentation patterns were closely associated with time of extrusion. Larvae extruded late in the season tended to be more robust and thicker-bodied and developed ossified skeletal elements at relatively smaller sizes compared to earlier-extruded larvae.

The observed morphological differences might be attributable to environmental influences rather than to the presence of larvae of more than one redfish species. The morphological and growth rate differences between larvae extruded at different times have important ecological implications. Due to their relatively earlier ossification of fin rays and supports, coupled with larger head size,

broader gape, and larger gut areas, the later extruded larvae are probably more active predators, capable of capture and ingestion of larger prey which are, energetically, more advantageous for larval growth and survival.

ACKNOWLEDGEMENTS

I would like to express my appreciation to my research committee supervisor, Dr. R. L. Haedrich of the Biology Dept., Memorial University, and the members of my committee, Dr. George Lilly, Dept. of Fisheries and Oceans, St. John's and Dr. Grant Gardner, Biology Dept., Memorial University, for their direction and many useful comments and suggestions during the course of my research work and for providing valuable organizational and editorial advice.

My committee and Mr. John Anderson and Dr. Geoffrey Evans of the Dept. of Fisheries and Oceans, St. John's gave positive criticism and reviewed the manuscript. I also wish to extend my appreciation to Dr. Jake Rice of the Dept. of Fisheries and Oceans, St. John's for his invaluable assistance with the mathematical and statistical aspects of the manuscript. The staff of the Statistics and Computing Section of the Dept. of Fisheries and Oceans, St. John's bailed me out many times from my computer programming errors.

My special thanks to Ms. Kal Lynch without whose kind help I would surely have met defeat at the keyboard of a recalcitrant word processor, to the staff of Fisheries Ecosystems Section for their support and assistance in specimen collection, and to Mr. Herb Mullett and Mr.

Gordon King for their drafting and photography of the figures in this manuscript.

This research project was made possible through the logistical support of the Fisheries Research Branch, Dept. of Fisheries and Oceans, St. John's, to whom I am greatly indebted. Finally, a note of special appreciation to Mr. Scott Akenhead, Experimental Ecology Program, Dept. of Fisheries and Oceans, without whose initial and continuing support this research would never have been begun.

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INTRODUCTION

GROWTH ANALYSIS

The age and growth rate of fish are commonly determined by one of three ways: observation of progression of modes in length frequency histograms, tag-recapture studies, or examination of events recorded in bony structures (Irie 1955, Bagenal 1974). Use of length frequency modes, the simplest of which is the Petersen Method (Tesch 1968), requires a unimodal size distribution of all fish of the same age and is easy to apply if there are no large overlaps in the size of individuals of adjacent age groups. In practice, use of this method requires large sample sizes at frequent sampling intervals when applied to larval fish. This leads to enormous expense because the spawning grounds of most commercially important marine fish species in the Northwest Atlantic are offshore, necessitating the use of large, costly research vessels for larval surveys. Such methods provide only average estimates of growth rates over large areas and cannot provide any information about variation between individuals or growth histories, thus eliminating the possible usage of this method in studies of the causal mechanisms of growth variations.

Most tagging methods are not applicable to small fish or, if they are, may cause great mortality so that recaptures are few and the apparent ratio of marked to unmarked individuals is altered (Tesch 1968), although recent chemical tagging methods (Campana and Neilson 1982) may prove applicable to mark-recapture studies at sea. Tagging studies generally prove problematic when applied to larval fish in that they require, like length frequency methods, expensive multi-cruise surveys and, unless the tag can be individualized, provide only large-scale growth averages. Some mark-recapture methods also suffer from the handicap that marked fish may grow more slowly than unmarked ones and, in the absence of a test of this point, growth rates determined in this way should be used with reserve (Tesch 1968).

Hard bony structures such as scales, vertebral centra, fin rays, operculae, and cleithrae have all been used in age determinations of adult fish but otoliths are used most frequently, especially in marine, temperate species (Bagenal 1974). Although annual marks on otoliths of adult and juvenile fishes have been used for many years in age determinations, their usage is not without problems. One potential problem in the usage of otoliths and, indeed, any calcified structures is the possibility they can stop growing (Liew 1974) or even be resorbed (Pannella and

Weiler 1980.) during periods of stress or starvation.

Fish otoliths consist of an inorganic material, usually calcium carbonate in the form of aragonite crystals, and an organic matrix (Degens et al. 1969). Three otoliths, the sagitta, lapillus, and asteriscus, are found on each side of the brain in the sacculus, lagena, and utriculus of the inner ear (Lowenstein 1971) and the morphology of the calcified structures is usually species-specific (Morrow 1979). Of the three otoliths, the sagitta is usually the largest (Bagenal 1974).

Otoliths grow by the addition of layers of material differing in the relative amounts of otolin and calcium carbonate, resulting in the formation of incremental patterns. An increment represents a cycle of deposition that starts on an organic surface. This is followed by a relatively rapid deposition of calcium carbonate and organic matrix. An increment in completed when calcification slows or ceases and organic material concentrates in a thin layer (Pannella 1980). Under transmitted light, the increments thus appear composed of an inner light zone, representing the area of high calcium carbonate to otolin ratio, and a dark outer zone, representing the area where calcification has slowed and the ratio of calcium carbonate to otolin is lower. Once the periodicity of this cycle of formation and its starting time have been established for a species,

otolith growth increments can be used to estimate a fish's age and past growth history.

Daily growth increments have been known in plants and animals for several decades (Neville 1967), but only recently have they been demonstrated in fish otoliths (Pannella 1971, 1974). Daily periodicity of increment formation has been demonstrated by one or more of several ways: by number of increments within an annulus (Pannella 1971, 1974), by laboratory rearing for a known period of time (Struhsaker and Uchiyama 1976, Barkman 1978, Victor 1982, Campana and Neilson 1982), by examination of otoliths in reared fish of known age (Brothers et al. 1976, Taubert and Coble 1977, Tanaka et al. 1981, Miller and Storck 1982, Radtke and Dean 1982, Marshall and Parker 1982, Victor and Brothers 1982), and by agreement with other data known from field studies (Townsend and Shaw 1982, Laroche et al 1982). The most important application of larval ageing through otolith analysis is the accurate determination of individual growth rates and growth histories of larvae in the sea. This method can also be used to document the timing and duration of spawning events (Townsend and Graham 1981) and changes in life history stages (Victor 1982, Rosenberg 1982).

This technique has been applied to relatively few

species to date in detailed analysis of individual growth histories (Laroche et al. 1982), and much remains to be learned about how growth may change during development and under varying environmental conditions. Because of the potentially large amount of detailed information to be gained concerning larval fish growth and dynamics from otolith growth analysis, more research in this area is advisable. This will also have the effect of greatly increasing the scope and usefulness of larval fish surveys. One aim of this study is to develop an ageing procedure suitable for larval redfish and to use it in a detailed examination of differences in growth during the larval period in 1980 and 1981. Variation during ontogeny of larvae extruded during different times in the extrusion season will also be examined.

MORPHOLOGY ANALYSIS

The redfishes (Family Scorpaenidae), otherwise known as the ocean perches, are perch-like or bass-like in general appearance (Bigelow and Schroeder 1953) but are closely related to the sculpins (Family Cottidae) and sea robins (Family Triglidae) by having bony outgrowths of the suborbital and preopercular bones stretching across their cheeks, giving the head an overall bony appearance.

Furthermore, the top of the head is marked by bony ridges that often terminate in spines. The anterior rays of the dorsal, anal, and pelvic fins are modified as sharp spines.

The Scorpaenidae is primarily a Pacific family, in terms of diversity, with over 100 species in the eastern Pacific alone (Moser et al. 1977), but reaches its greatest commercial importance in the Atlantic Ocean. The family has eight genera, with seven of these occurring in the Atlantic Ocean but only two, Sebastes and Helicolenus, occur in northern latitudes. Only one species of Helicolenus, H. dactylopterus Delaroche 1809, has been reported from the north Atlantic. It ranges from the coasts of Norway south to the Mediterranean in the Eastern Atlantic, and from George's Bank to the coasts of South America in the west. There are no records of its occurrence in the Newfoundland area and it is most abundant off eastern South America from the Caribbean to Brazil.

The genus Sebastes is much more northern in its distribution, extending from shelf break areas off the New England states north into the Labrador Sea, through the mid-Atlantic off Greenland and Iceland into the Irminger Sea, and from northern Norway south to the coasts of Portugal and Spain in the eastern Atlantic. Discussion of the controversies over the taxonomy of the Sebastes genus in the North Atlantic will form part of this paper.

Prior to the late 1940's, the genus Sebastes in the North Atlantic was commonly considered to consist of a single species, Sebastes marinus (Bigelow and Schroeder 1953), although three species had been described taxonomically by 1856. These were S. marinus L. 1758, S. viviparous Kroyer 1845, and S. fasciatus Storer 1856. The general concensus on existence of a single valid species was probably due to the restricted areal coverage of commercial fisheries. Prior to the Second World War, large redfish fisheries were only prosecuted in relatively shallow waters around the coasts of Norway and Iceland, and were practically non-existent in North American waters.

After the war, the European fishery expanded into deep water areas, particularly between Scotland and Iceland, and the North American fishery in the New England states increased considerably. Taning (1949) was apparently the first to assign the names S. marinus to the larger, offshore European redfish, S. viviparous to the inshore, shallow-water redfish and S. fasciatus to redfish caught off New England. In 1951, Travin sub-divided S. marinus into two species, a redefined S. marinus and a new S. mentella (Travin 1951).

The specific status of S. viviparous quickly became generally accepted but its distribution is confined to the European side of the North Atlantic from the coasts of

European side of the North Atlantic from the coasts of Norway and Iceland, through the British Isles and into the North Sea. However, Andriyashev (1954), Kotthaus (1961), Leim and Scott (1966) and Barsukov and Zakharov (1972) all failed to find morphological differences sufficient to warrant the sub-division of S. marinus and Barsukov and Zakharov (1972) were unable to find a single feature which would differentiate S. fasciatus from either S. marinus or S. mentella without often considerble overlap.

When field work for the otolith-based growth analyses presented in this paper began in the Spring of 1980, the generally accepted view among fishery managers, but disputed by some taxonomists, was that the genus Sebastes in the Northwest Atlantic consisted of a single valid species, S. marinus, with recognition of the considerable geographic and depth variation in morphology sufficient to assign the sub-specific names S. marinus marinus and S. marinus mentella. Since then, new work has been published contending that three valid species, S. marinus, S. mentella, and S. fasciatus, should be recognized based on differences in the morphology of the gas bladder muscles and their passage between the ventral ribs (Litvinenko 1980, Ni 1981a and b, Power and Ni 1982). Payne and Ni (1982) differentiated the three putative species of Sebastes by biochemical criteria but McGlade et al. (1983) concluded S. fasciatus is electrophoretically distinct from S. marinus and S.

mentella and individuals of the latter two species cannot be differentiated from each other.

Ni (1981b) also noted differences in numbers of anal fin rays, gill rakers, vertebrae, and dorsal fin rays, fusion of the occipital-nuchal ridge, the angle of the third posterior preopercular spine, and the relationship of the tip of the pectoral fin to the anus were all useful, to varying degrees, in differentiation of S. mentella from S. fasciatus. All three of these putative species do occur on Flemish Cap (Barsukov and Zakharov 1972), but S. marinus is believed to be in low abundance. The main population consists of the sharp-beaked redfishes, S. fasciatus and S. mentella, with S. mentella being the dominant species (Templeman 1976).

This recent rekindling of the controversy over redfish identification in the North Atlantic has arisen from studies on adults. However, since the 1940's, considerable effort has been directed towards larval identification, especially in European waters. Much of this work has stemmed from Taning (1949) who claimed that larvae of the large European redfish (S. marinus) could be differentiated from larvae of the small, inshore redfish (S. viviparous) by the occurrence of caudal pigment spots in the latter which were absent in the former.

Although Taning died in 1958, his drawings and a

discussion were published by Bertelsen at the International Redfish Symposium at Copenhagen in 1959 (Taning 1961). His drawings showed two kinds of larvae, the first with one or two melanophores located in the sub-caudal region of the developing hypural elements, and the second completely lacking in sub-caudal melanophores. Distributionally, the larvae with sub-caudal melanophores were found inshore around the Faeroes and Iceland while those without sub-caudal melanophores were mainly found in offshore areas. Accordingly, he assumed the larvae with the caudal spots were S. viviparous and those without the spots were S. marinus. Taning also noted that larvae of the so-called " American form ", later believed to be S. mentella, also had sub-caudal melanophores. Several studies quickly followed which used the sub-caudal melanophore criterion in analyses of distribution (Corlett 1961a and b, Henderson 1961a and b) and time of extrusion (Einarrson 1960).

Templeman and Sandeman (1959), in a study of pre-extrusion redfish larvae in North American waters, found 97.7% of " mentella-type " larvae and 23.9% of " marinus-type " larvae had sub-caudal melanophores. Consequently, Hansen and Anderson (1961), in a study of larval redfish with sub-caudal melanophores on both sides of the Atlantic, assigned them to S. marinus mentella or S. viviparous based on their distribution.

Doubts as to the reliability of this identification scheme quickly grew (Graham 1962) and several studies reporting results (Raitt 1964, Henderson 1964a and b) conflicting with those of Templeman and Sandeman (1959) were published. Barsukov and Zakharov (1972) suggested Templeman and Sandeman (1959) had mis-identified some of the mentella-type specimens and that they should rightfully be identified as S. fasciatus. Templeman (1980) subsequently reclassified many of these mentella specimens as S. fasciatus indicating that 21% of larvae from mentella parents and 87% of larvae from fasciatus parents had sub-caudal melanophores. Additionally, of those with sub-caudal melanophores, larvae of S. marinus and S. mentella usually had a single melanophore while larvae of S. fasciatus typically had two melanophores.

Thus, to this date, no protocol exists by which redfish larvae of these putative species may be differentiated. Although the taxonomy of the Sebastes genus in the Northwest Atlantic remains a contentious issue, the existence of two or more species on Flemish Cap has important implications for the interpretation of the growth analyses reported in this paper. No detailed study of larval redfish morphology exists for the Newfoundland area. The second aim of this study is, therefore, to detail the morphology of the larval redfish population on Flemish Cap

to determine the existence of morphologically distinct groups which may indicate the presence of or correspond to two or more of these putative species. Possible identification criteria are evaluated and the ecological implications of variation in redfish morphology are examined.

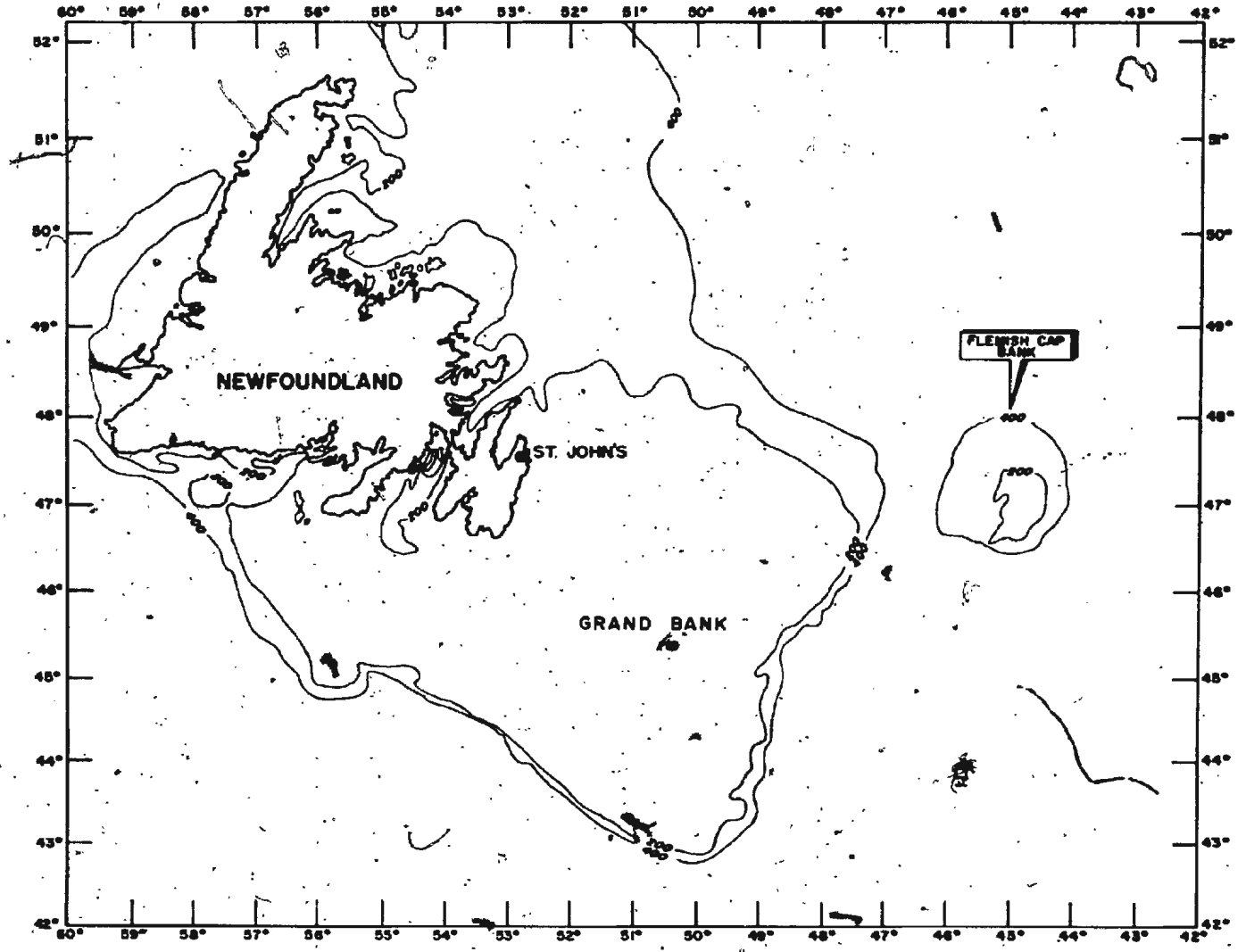
METHODS

II.A. DESCRIPTION OF STUDY AREA

Flemish Cap is a small, offshore fishing bank east of the northern Grand Bank (Fig. 1) from which it is separated by the Flemish Pass, a channel over 1000 meters deep, running roughly north to south between the Flemish Cap and the adjacent Grand Bank. The bank is essentially a submerged mountain with a hard, central granitic core which is smooth and almost devoid of sediment surrounded by younger sedimentary beds that slope outwards (Loncarevic and Ruffman 1972).

The waters of the northwestern part of the Cap are relatively cold and fresh, originating from the offshore branch of the Labrador Current. This current sweeps along the slope of the northern Grand Bank and through Flemish Pass, often washing over considerable portions of the northwestern slopes of the Cap. In the south and southeast, the waters are considerably warmer, being influenced by the northeastward-flowing Gulf Stream Current. Over the Cap itself, the influences of these opposing currents result in the formation of a clockwise gyre (Kudlo and Burmakin 1972).

Figure 1. Location of the study area, Flemish Cap, in relation to the adjacent Grand Bank and the island portion of the Province of Newfoundland and Labrador.


NEWFOUNDLAND
ST. JOHN'S
GRAND BANK
FLEMISH CAP BANK

II.B. SPECIMEN COLLECTION

Larval redfish specimens were collected on seven cruises to Flemish Cap during the Spring and Summer of 1980 and 1981. Actual cruise times are as follows: 6-13 April 1980, 20-26 May 1980, 22-28 July 1980, 27 April-10 May 1981, 22-27 May 1981, 26 June-7 July 1981, 26 June- 5 July 1981.

Larval fish samples were caught by oblique tows of 61 cm paired Bongo nets to 200 meters or to within 5 meters of bottom, whichever was the lesser depth. Nets used were of 0.333 mm mesh, except for the cruise 27 April-10 May 1981 during which some stations were sampled using 0.505 mm mesh nets.

During each cruise, a grid survey pattern of 42 stations was sampled, often supplemented by additional stations within the grid area. Stations from which larval redfish were obtained are indicated in Figures 2 and 3 for 1980 and 1981 respectively.

With each plankton sample, a CTD (conductivity, temperature, depth) profile from surface to 500 meters depth was taken using a Guildline Instruments CTD probe. Profiles of salinity, temperature, and density were subsequently calculated from the data.

II.C. OTOLITH PREPARATION AND INCREMENT COUNTING

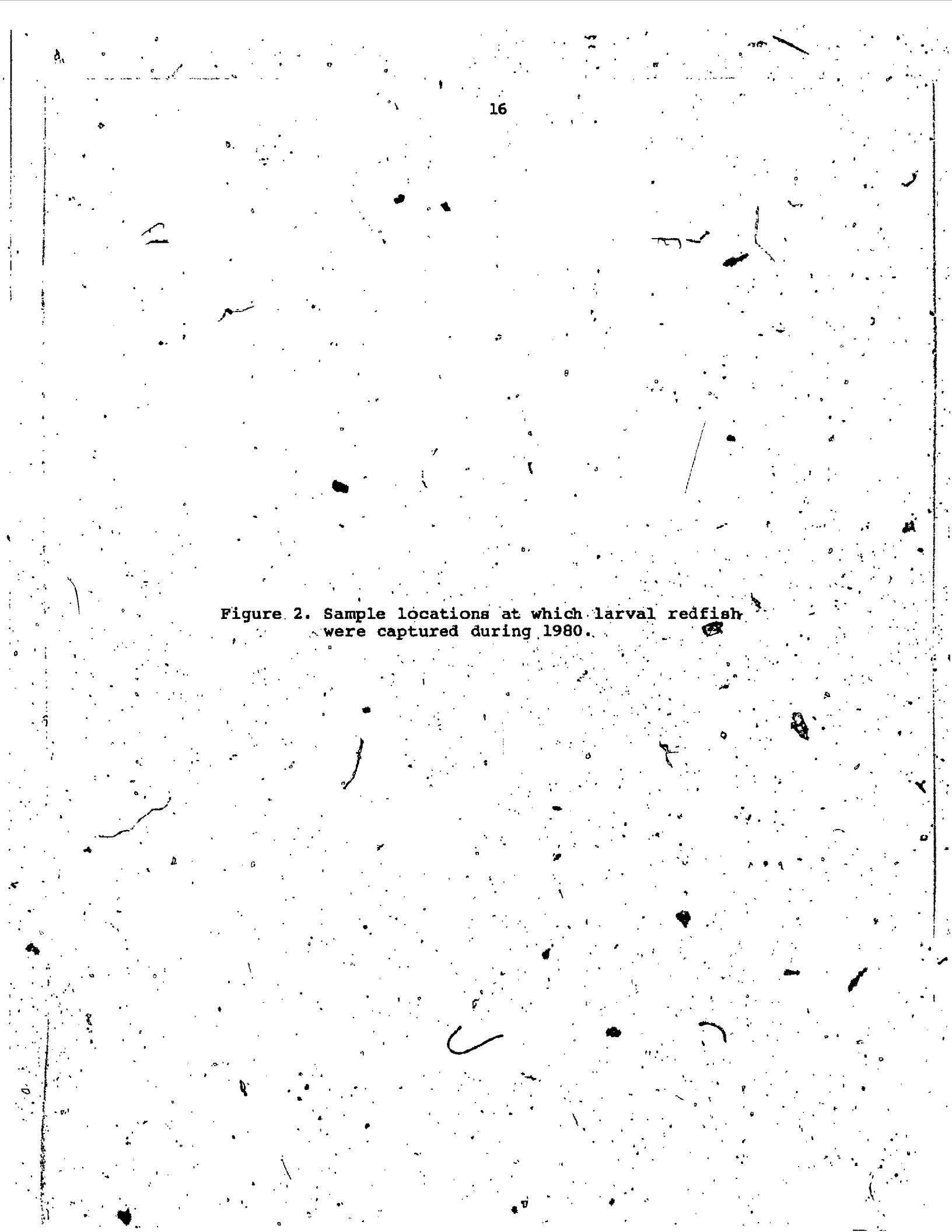
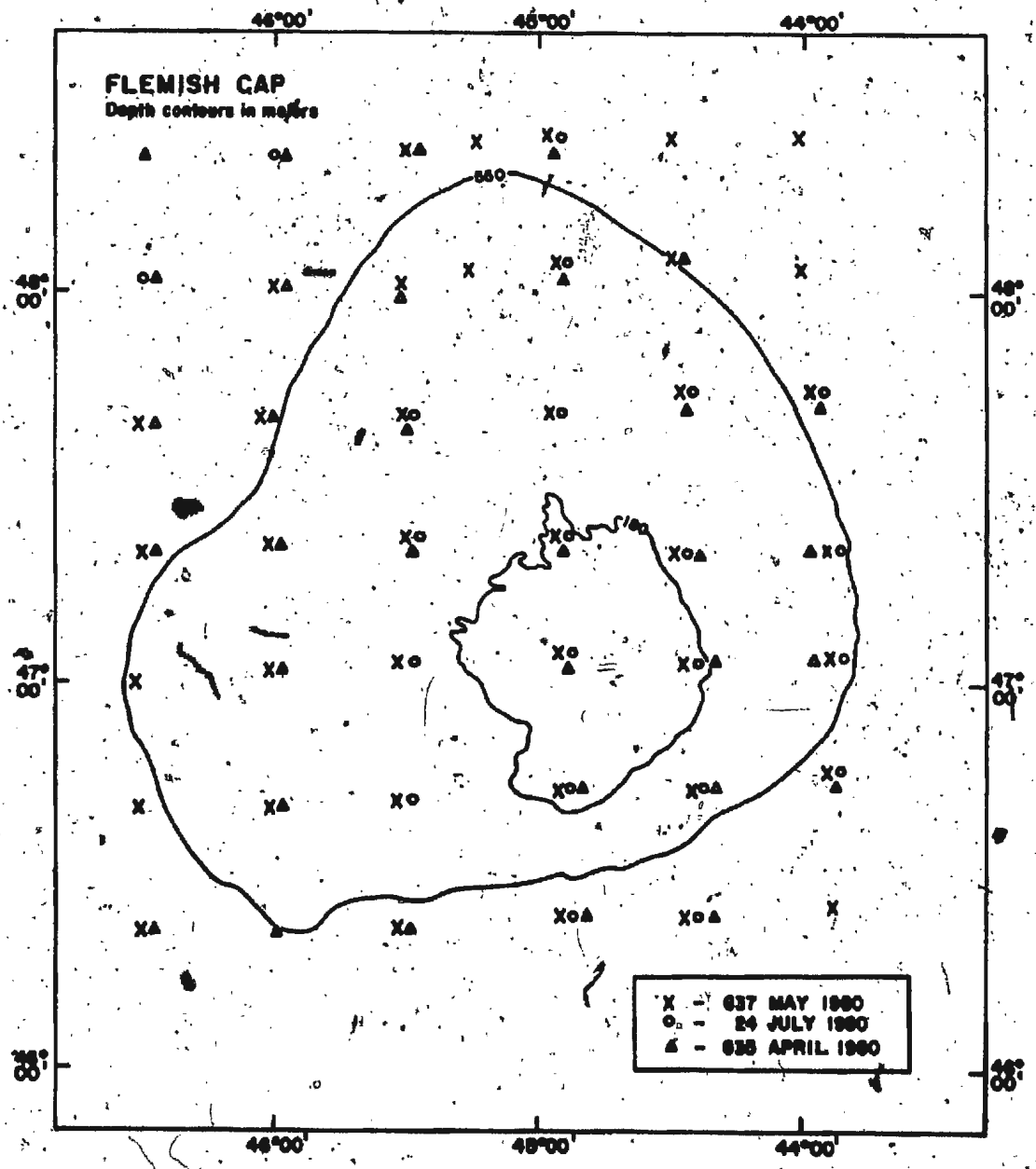


Figure 2. Sample locations at which larval redfish were captured during 1980.


FLEMISH CAP
Depth contours in metres
550
46°00'
45°00'
44°00'
47°00'
X - 637 MAY 1980
o - 24 JULY 1980
Δ - 638 APRIL 1980

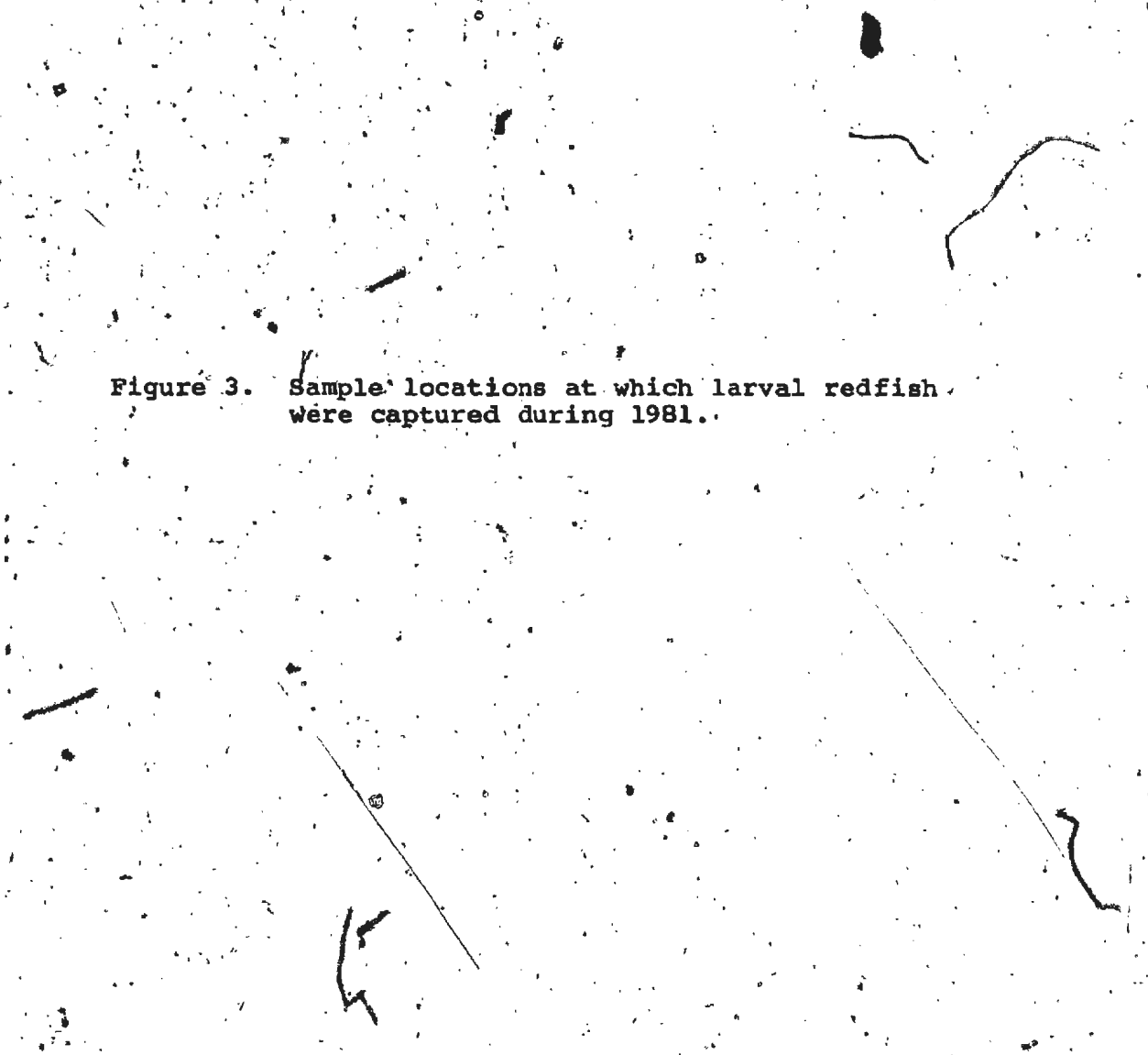
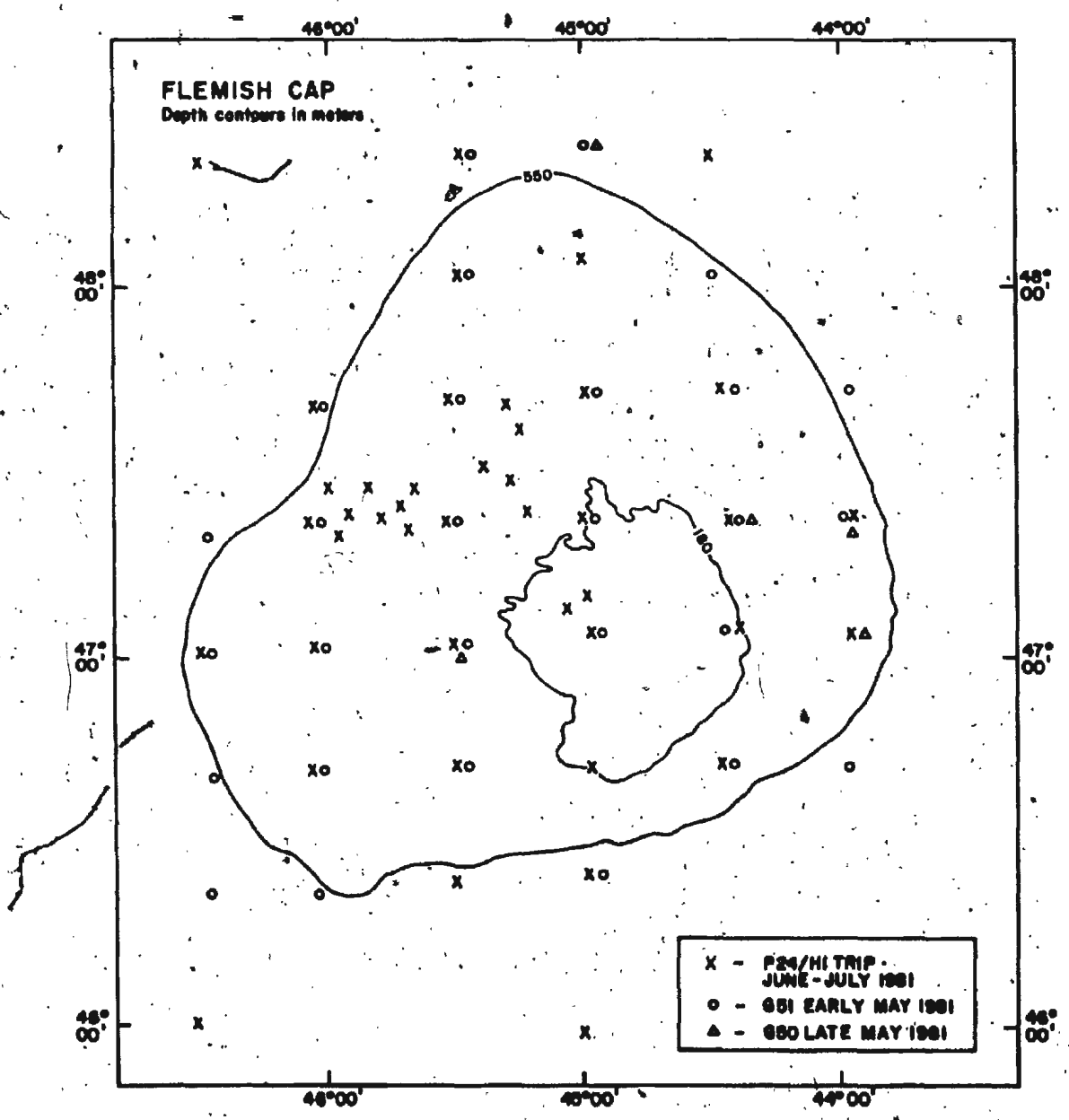


Figure 3. Sample locations at which larval redfish were captured during 1981.


FLEMISH CAP
Depth contours in meters
550
180
46°00'
45°00'
44°00'
48° 00'
47° 00'
46° 00'
X - F24/HI TRIP - JUNE - JULY 1981
o - 651 EARLY MAY 1981
▲ - 650 LATE MAY 1981

Specimens for otolith analysis were selected at random and preserved in 100% anhydrous ethanol as quickly as possible to minimize postmortem shrinkage. Sample to preservative ratios were always kept in excess of 1:10 and after 1-3 weeks the preservative was drawn off and replaced to retain the otoliths in optimum condition for increment counting. Pre-extrusion larvae, which had been stripped from adult females caught by bottom trawling, were similarly preserved.

In the laboratory, larvae were placed on glass slides, their total length measured to the nearest 0.1 mm with an ocular micrometer mounted on a stereomicroscope, and their state of flexion recorded. The head was removed and placed in a drop of glycerin. Sagittae from both sides of the head were dissected out at 20-40X maghification and allowed to remain in glycerin for 1-2 days. The length of time in glycerin was not found to affect the clarity of the otoliths but dissection under glycerin greatly facilitated otolith manipulation. The glycerin was removed by flooding the slide with 100% anhydrous ethanol and the dry sagittae were transferred with a dissecting needle to a drop of Epon resin (Taab Industries, Reading, England) on a clean, glass slide. The resin containing the sagittae was polymerized overnight by heating in a drying oven at 60 degrees

Celsius. Coverslips were not used because they interfered with the optical properties of the preparation.

Otolith growth increments consisting of an inner light band and a narrower, adjacent, dark band were counted using a Zeiss Model II compound microscope at magnifications of 125-800X with bright-field illumination and the condensor lowered to increase contrast between light and dark bands. At first, counts were made on both sagittae from each fish. No difference between the two sagittae from the same fish was found so most later counts were made on only one sagitta per fish. All counts were made at least three times and the greatest of the three counts was taken as final, provided that the successive counts were within 5% of each other. Otherwise, the otoliths were discarded. If the second sagitta gave the same result, the specimen was removed from further analysis. All counts and subsequent verification counts were made by the author to ensure consistency in counting procedures.

Additionally, on sagittae from sea-caught larvae, sagittal radius measurements were made from the center of the focal area along the posterior radius of the sagitta. The posterior radius was found to be consistently the best for increment counting. Measurements taken on each sagitta were: total radius (the distance from the center of the focal area to the edge of the sagitta), focal radius (the

distance from the center of the focal area to the start of the first increment), and successive measurements from the center of the focal area to the end of each fifth increment. Table 1 summarizes data on the number of sagittae from which counts were obtained and their readibility.

II.D. SAMPLE PREPARATION FOR MORPHOLOGY

Larvae for morphological analysis were preserved, along with the other plankton, in 5% formalin buffered with sodium borate. Larvae in good condition were subsequently selected at random to obtain a representative size range of larvae from each trip. In the laboratory, a variety of morphometric variables were measured externally, using a stereomicroscope at 20X magnification, and pigmentation patterns were noted. Larvae were classified as pre-flexion, in-flexion, or post-flexion larvae based on the condition of the notochord as described by Moser et al. (1977). Larvae were then cleared and stained for meristics and observation of head spination by the methodology of Dingerkus and Uhler (1977). All meristic members were counted and categorized into numbers of elements ossified (staining with Alizarin red) or cartilaginous (staining with Alcian blue). Terminology of head spines follows Richardson and Laroche (1979) and Phillips (1957). A composite drawing showing

Table 1. Summary of numbers of redfish larvae examined, and numbers of sagittae found to be suitable for ageing and measurement from 1980 and 1981.

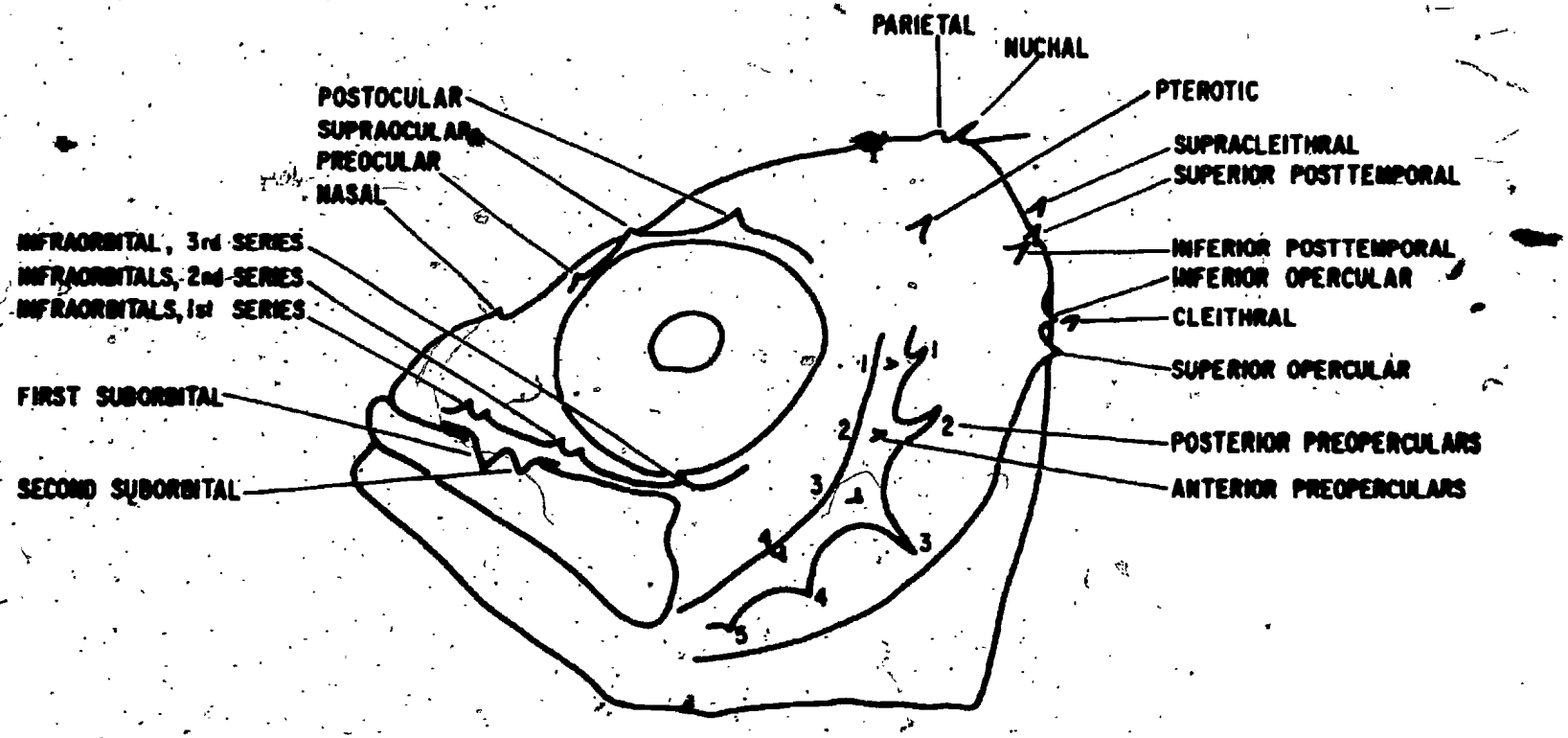
Type of larvae	Trip	# Examined	# Countable	% Countable	# Measurable	% Measurable
Pre-extrude	6-13 April 1980	74	74	100	-	-
Sea-caught	6-13 April 1980	147	147	100	147	100
Sea-caught	20-26 May 1980	462	445	96.3	443	95.9
Lab-reared	20-26 May 1980	25	25	100	-	-
Sea-caught	22-28 July 1980	210	168	80.0	145	69.0
Sea-caught	27 Apr-10 May 1981	23	22	95.7	21	91.3
Sea-caught	22-27 May 1981	243	234	96.3	234	96.3
Sea-caught	26 June-7 July 1981	163	161	98.8	154	94.5
Sea-caught	26 June-5 July 1981	118	116	98.3	116	98.3
Totals		1465	1389	94.8	1260	86.0

the position and terminology of head spines is shown in Figure 4. All head spines were recorded as present or absent and, if present, as ossified or cartilaginous. Terminology used for fin rays and spines is similar to Moser et al. (1977). For a complete listing of morphometric, meristic, and pigmentation variables measured, see Appendix A.

II.E. LARVAL REARING

During the cruises 27 April-10 May 1981 and 22-27 May 1981, ripe, adult female redfish with hatched larvae in the body cavity were collected by bottom trawl to provide pre-extrusion larvae for use in rearing studies to determine the time of first increment formation and the periodicity of subsequent increment formation. Well-developed larvae were extruded by hand into 25-liter, plastic containers with seawater at the ambient sea surface temperature. These were returned to the laboratory onshore and held under controlled temperature regimes in a recirculating seawater system. Newly-hatched Artemia nauplii and locally captured wild plankton were added to the containers to provide a food source. The larvae survived for 12 days but sampling on alternate days revealed they were neither feeding nor growing and were experiencing very high mortality. As it was felt that conditions of active growth were necessary for

Figure 4. Composite diagram of head spines and their location in larval redfish including terminology used in this manuscript.


PARIETAL
NUCHAL
POSTOCULAR
SUPRAOCULAR
PREOCULAR
NASAL
PTEROTIC
SUPRACLEITHRAL
SUPERIOR POSTTEMPORAL
INFRAORBITAL, 3rd SERIES
INFRAORBITALS, 2nd SERIES
INFRAORBITALS, 1st SERIES
INFERIOR POSTTEMPORAL
INFERIOR OPERCULAR
CLEITHRAL
SUPERIOR OPERCULAR
FIRST SUBORBITAL
SECOND SUBORBITAL
POSTERIOR PREOPERCULARS
ANTERIOR PREOPERCULARS

correct determination of otolith increment patterns, the experiment was discontinued.

RESULTS

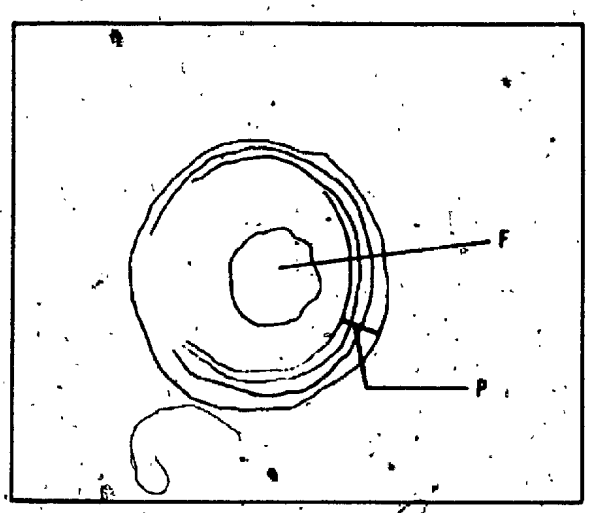
III.A. GROWTH ANALYSIS

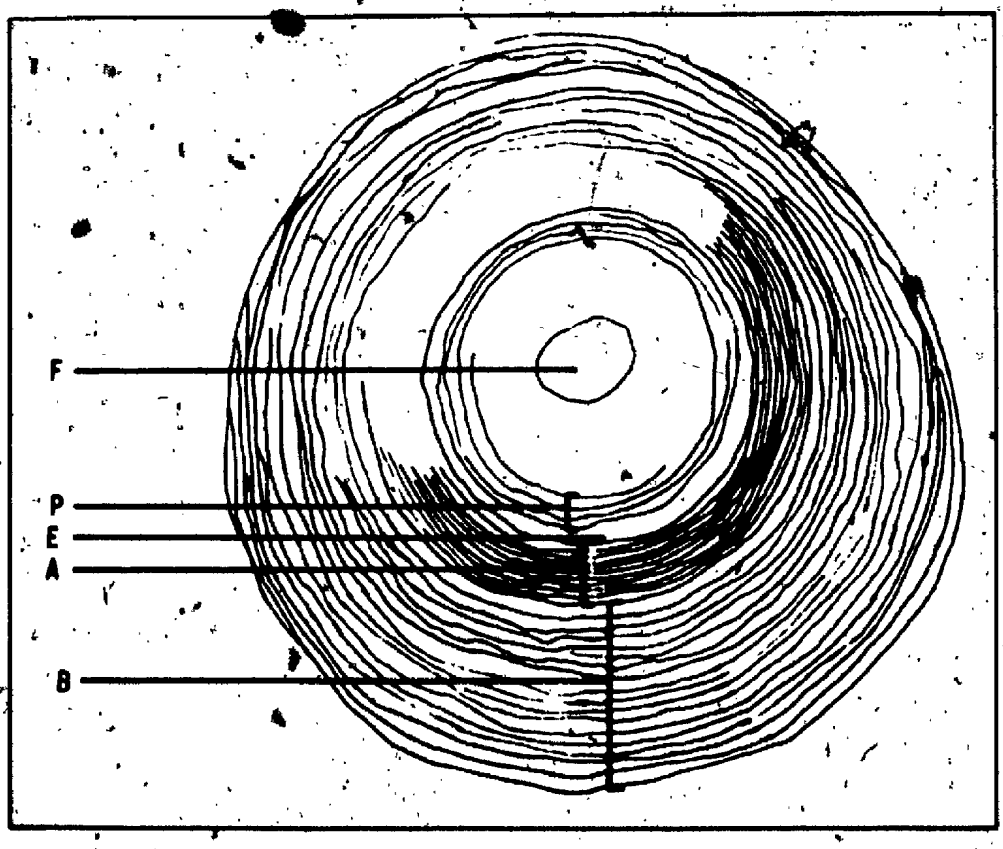
III.A.1. Otolith increment description

Redfish sagittae, from newly extruded larvae, are virtually disk-shaped in the lateral view and measure from 0.014–0.025 mm in radius. Both the distal and proximal surfaces are flat in the frontal view. As the sagittae grow, the anterior edge becomes increasingly elongated, both the dorsal and ventral edges become compressed, and the medial surface becomes concave while the lateral surface becomes convex due to thickening in the focal area.

Three types of rings were observed in larval redfish sagittae (see Figure 5): (1) sagittae of well-developed pre-extrusion larvae with the yolk sac nearly resorbed displayed a pattern of 2-5 weak rings (Mean = 3.39, N = 49). These were still visible in sagittae of most plankton-caught larvae (Range 2-6, Mean = 3.40, N = 49) but tended to become obscured in sagittae larger than 0.15 mm in radius. Typically, these rings (termed pre-extrusion rings) failed to completely encircle the sagittae and so were not regarded as " true " increments and hence were not included in subsequent increment counts. These were the only

Figure 5. Camera lucida drawings of typical increment patterns on sagittae of larval redfish. (A) pre-extrusion larva (B) post-extrusion larva. F is the focal area, P is the pre-extrusion zone, E is the extrusion or heavy increment, A is a zone of closely-spaced increments typical of young larvae, and B is a zone of widely-spaced increments typical of older larvae. (Presented in medial view).


F
P


F
P
E
A
B

rings observed in any pre-extrusion redfish larvae. (2) in plankton-caught larvae, the zone of pre-extrusion rings was followed by a heavy ring composed of a wide, translucent band followed by a prominent dark band. This ring or increment was a conspicuous feature of nearly all sagittae from plankton-caught larvae and was regarded as the first increment for age determination. (3) normal increments, deposited in regular, concentric fashion immediately following the first heavy increment.

III.A.2. Periodicity verification

Laboratory rearing attempts to directly determine the onset and periodicity of increment formation were unsuccessful. Sagittae of laboratory-reared larvae, which were not feeding, only had the 2-5 weak, pre-extrusion rings even up to day 12 post-extrusion. None developed the heavy ring or the regular increments demonstrated by plankton-caught larvae.

Indirectly, a case can be made supporting the idea that onset of increment formation (the first heavy ring) commences at extrusion. It is known that pre-extrusion larvae never have the heavy increment whereas the increment is present in virtually all small, post-extrusion larvae.

Because most of a redfish larva's yolk is used up before extrusion, a newly extruded larval redfish must begin exogenous feeding very quickly. As increment formation is widely regarded as a direct result of feeding and growth, I feel justified in assuming the first heavy increment occurs at extrusion. This belief was also held by Radtke (MS1980).

After increment formation is initiated, subsequent increments are assumed to form daily. This assumption can be indirectly supported. The main redfish extrusion time on Flemish Cap is the April to May period (Bainbridge and Cooper 1971, Templeman 1976). Peak extrusion was estimated from length frequency data to be the last week of April in 1980 (Anderson 1981) and 1981 (Anderson MS1982).

Because extrusion is virtually complete by late June to July (Barsukov and Zakharov 1972, Templeman 1976), the predicted dates of extrusion of larvae captured in this period should match published accounts of redfish extrusion activity. Figure 6 indicates relative extrusion activity throughout the Spring and early Summer of 1980 and 1981 from back-calculation to age 0, assuming one increment equals one day, of the otolith increment counts from larvae captured in late June to early July in 1980 and 1981. Corrected for average instantaneous mortality of Z = 0.05 (Anderson 1981), these counts indicate redfish extrusion was initiated in mid-March, intensified through early April to peak during

Figure 6. Intensity of larval extrusion activity on Flemish Cap during the 1980 and 1981 seasons. Numbers on the vertical axis are relative, not absolute abundances.

the last two weeks of April. Extrusion activity declined rapidly through May and was virtually complete by the first of June.

III.A.3. Age and sagittal radius at length data

Age at length and total sagittal radius at length data are summarized in Tables 2 and 3 respectively for 1980 and in Tables 4 and 5 respectively for 1981. Larvae aged in 1980 ranged from 5.6 mm to 29.6 mm in length and ranged in age from the newly extruded (age 0) to 140 days. Newly extruded larvae ranged from 5.6-8.9 mm in length, a rather large range in initial lengths compared to oviparous, marine species. While it was not unexpected to find a large range of ages within a single millimeter length interval in larger, older larvae, it was quite interesting that smaller larvae, under 10 mm in length, within the same millimeter size interval differed in age by as much as 3 weeks. Total sagittal radii ranged from 14.87 micrometers in one larva of 6.0 mm in length to 358.98 micrometers in an early juvenile of 28.7 mm. The high intra-group variability observed in the age at length data is also evident in the total sagittal radius at length measurements.

During 1981, no larvae smaller than 7.0 mm in length were captured for otolith analysis. Larvae aged in 1981

Table 2. Summary of age in days from otolith increment counts and total length in one millimeter intervals for larval redfish in 1980.

Total length	N	Mean age (days)	Range (days)	St. error of mean
5.0-5.9	3	1.00	0-3	1.00
6.0-6.9	49	1.37	0-8	0.25
7.0-7.9	105	2.28	0-18	0.33
8.0-8.9	73	10.26	0-24	0.72
9.0-9.9	99	12.61	2-26	0.57
10.0-10.9	154	16.23	5-33	0.41
11.0-11.9	79	21.35	7-35	0.58
12.0-12.9	23	28.26	20-46	1.29
13.0-13.9	11	34.73	25-40	1.27
14.0-14.9	9	41.77	31-72	4.02
15.0-15.9	4	53.00	41-78	8.55
16.0-16.9	2	69.00	56-82	13.00
17.0-17.9	11	72.45	59-82	2.55
18.0-18.9	10	75.70	68-89	2.39
19.0-19.9	14	77.29	64-86	1.70
20.0-20.9	18	87.11	65-105	2.60
21.0-21.9	27	86.41	73-102	1.40
22.0-22.9	21	89.62	71-115	2.58
23.0-23.9	17	94.65	80-135	3.21
24.0-24.9	15	99.33	80-140	3.60
25.0-25.9	4	112.00	99-120	4.74
26.0-26.9	3	104.66	96-109	4.33
27.0-27.9	2	113.00	112-114	1.00
28.0-28.9	2	110.50	103-118	7.50
29.0-29.9	1	122.00	-	-

Table 3. Summary of total sagittal radius measurements in micrometers and total length in one millimeter intervals for larval redfish in 1980.

Total length	N	Mean radius (μm)	Range (μm)	St. Error of mean
5.0-5.9	3	16.52	15.63-17.16	0.46
6.0-6.9	49	18.23	14.87-28.59	0.37
7.0-7.9	105	19.37	15.25-40.41	0.40
8.0-8.9	73	30.52	15.25-57.19	1.00
9.0-9.9	99	34.48	21.35-59.48	0.86
10.0-10.9	154	39.11	25.16-64.05	0.65
11.0-11.9	79	48.33	28.21-65.19	0.89
12.0-12.9	23	62.56	51.09-93.03	1.84
13.0-13.9	11	86.84	57.19-112.87	5.64
14.0-14.9	9	102.73	81.59-177.66	9.89
15.0-15.9	4	126.20	94.17-187.09	20.83
16.0-16.9	2	164.84	148.69-180.98	16.15
17.0-17.9	11	184.22	160.80-205.77	4.21
18.0-18.9	10	185.98	171.14-208.74	4.52
19.0-19.9	14	199.79	175.26-217.38	3.52
20.0-20.9	18	207.16	168.89-226.70	3.75
21.0-21.9	27	219.75	182.88-265.18	3.65
22.0-22.9	21	231.85	203.36-262.08	3.24
23.0-23.9	17	237.42	207.02-274.15	4.90
24.0-24.9	15	261.63	226.22-317.83	6.33
25.0-25.9	4	262.45	215.79-310.84	19.62
26.0-26.9	3	280.18	264.92-297.79	9.56
27.0-27.9	1	276.30	-	-
28.0-28.9	2	331.07	303.16-358.98	27.91

Table 4. Summary of age in days from otolith increment counts and total length in one millimeter intervals for larval redfish in 1981.

Total length	N	Mean age (days)	Range (days)	St. Error of mean
7.0–7.9	9	5.56	0–11	1.28
8.0–8.9	29	7.45	0–30	1.26
9.0–9.9	63	13.52	2–41	1.12
10.0–10.9	74	22.53	5–57	1.30
11.0–11.9	81	32.77	12–63	1.32
12.0–12.9	83	40.81	19–74	1.26
13.0–13.9	66	49.20	30–74	1.25
14.0–14.9	52	55.37	35–79	1.37
15.0–15.9	28	58.82	42–75	1.46
16.0–16.9	18	67.72	42–81	2.24
17.0–17.9	11	69.82	52–84	3.34
18.0–18.9	9	76.78	59–87	3.81
19.0–19.9	5	78.40	65–94	5.18
20.0–20.9	2	100.00	90–110	10.00
21.0–21.9	4	94.25	79–114	8.14
22.0–22.9	2	117.00	112–122	5.00
23.0–23.9	2	115.50	110–121	5.50
24.0–24.9	1	127.00	-	-

Table 5. Summary of total sagittal radius measurements in micrometers and total length in one millimeter intervals for larval redfish in 1981.

Total length	N	Mean radius (μm)	Range (μm)	St. Error of mean
7.0-7.9	9	23.72	16.78-29.36	1.56
8.0-8.9	29	25.85	16.01-52.99	1.41
9.0-9.9	63	33.79	18.68-74.73	1.57
10.0-10.9	74	45.60	22.11-84.64	1.76
11.0-11.9	81	64.88	28.98-136.89	2.52
12.0-12.9	83	82.08	37.36-126.19	2.40
13.0-13.9	66	100.49	59.86-140.53	2.16
14.0-14.9	52	116.60	77.39-154.41	2.28
15.0-15.9	28	129.02	103.32-157.85	2.37
16.0-16.9	18	145.55	118.19-166.51	3.41
17.0-17.9	11	148.49	125.05-162.88	3.84
18.0-18.9	9	158.06	150.98-172.71	2.47
19.0-19.9	5	161.46	131.86-178.12	7.91
20.0-20.9	2	216.45	171.94-260.95	44.51
21.0-21.9	4	207.37	190.50-239.46	11.12
22.0-22.9	2	248.29	215.67-280.91	32.62
23.0-23.9	2	267.86	265.56-270.16	2.30
24.0-24.9	1	295.49	-	-

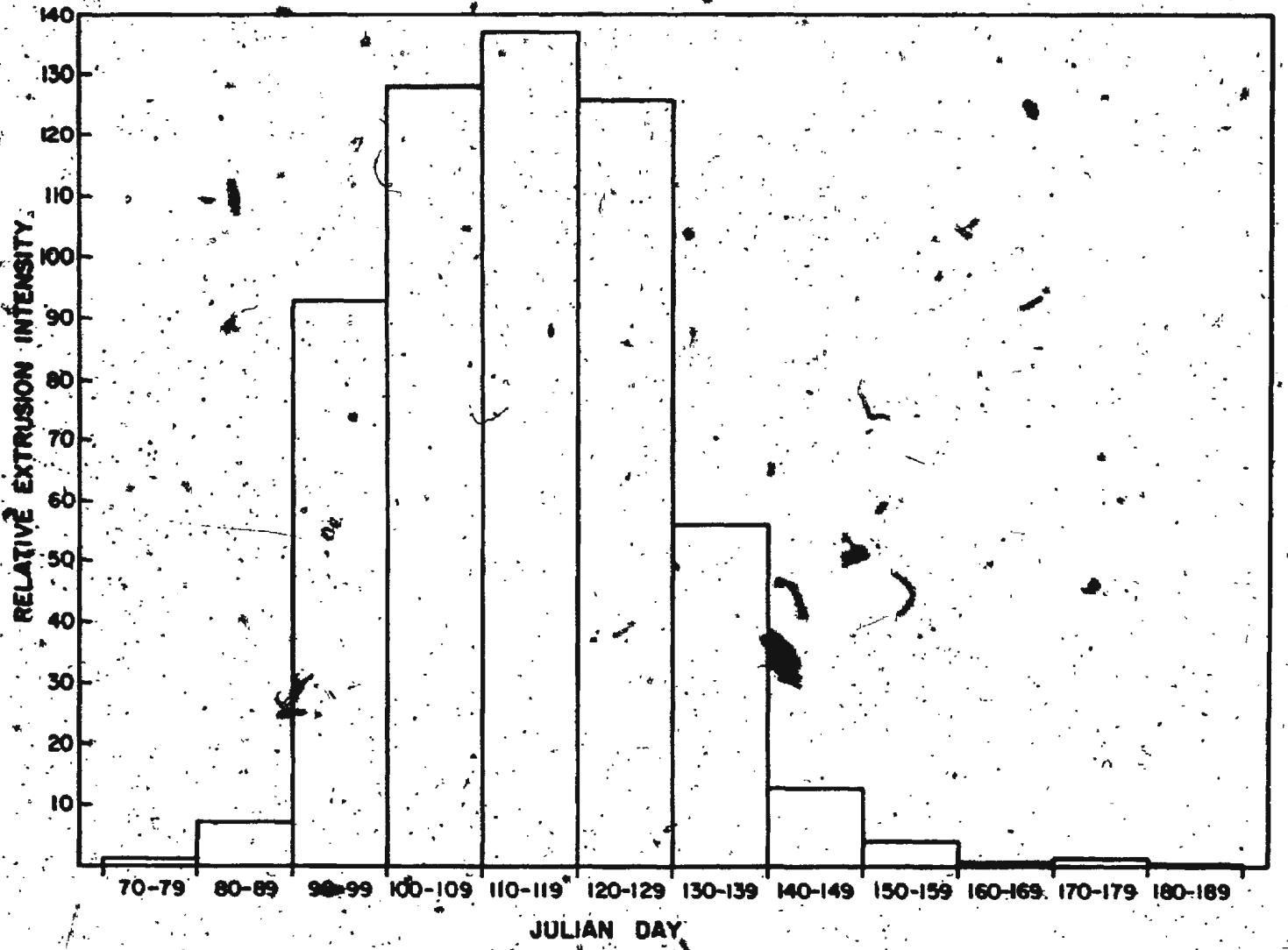
ranged from 7.0 mm to 24.8 mm total length and their ages ranged from the newly extruded (age 0) to 122 days old. The unexpectedly high intra-group age variability observed in small larvae in 1980 was even higher in 1981. Larvae 8.0-8.9 mm in length had an age range of 30 days while larvae 9.0-9.9 mm in length differed in age by as much as 39 days. These high intra-group ranges continued into the larger size intervals. Total sagittal radii ranged from a low of 16.01 micrometers in a larva 8.0 mm in length to 295.49 micrometers in an early juvenile at 24.3 mm.

III.A.4. Length at age regressions

The length at age data for both 1980 and 1981 (Figs. 7 and 8) do not indicate any apparent exponential growth phase or inflection point so the use of growth models such as the Gompertz or Von Bertalanffy equations is inappropriate. One obvious characteristic of both years is the large amount of scatter, probably indicative of large variation in growth between individuals.

From least squares regression procedures (Table 6), the fitted equations for 1980 and 1981 are, respectively:

$$TL = 0.160\ Age + 7.422$$


RELATIVE EXTRUSION INTENSITY
140
130
120
110
100
90
80
70
60
50
40
30
20
10
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
JULIAN DAY

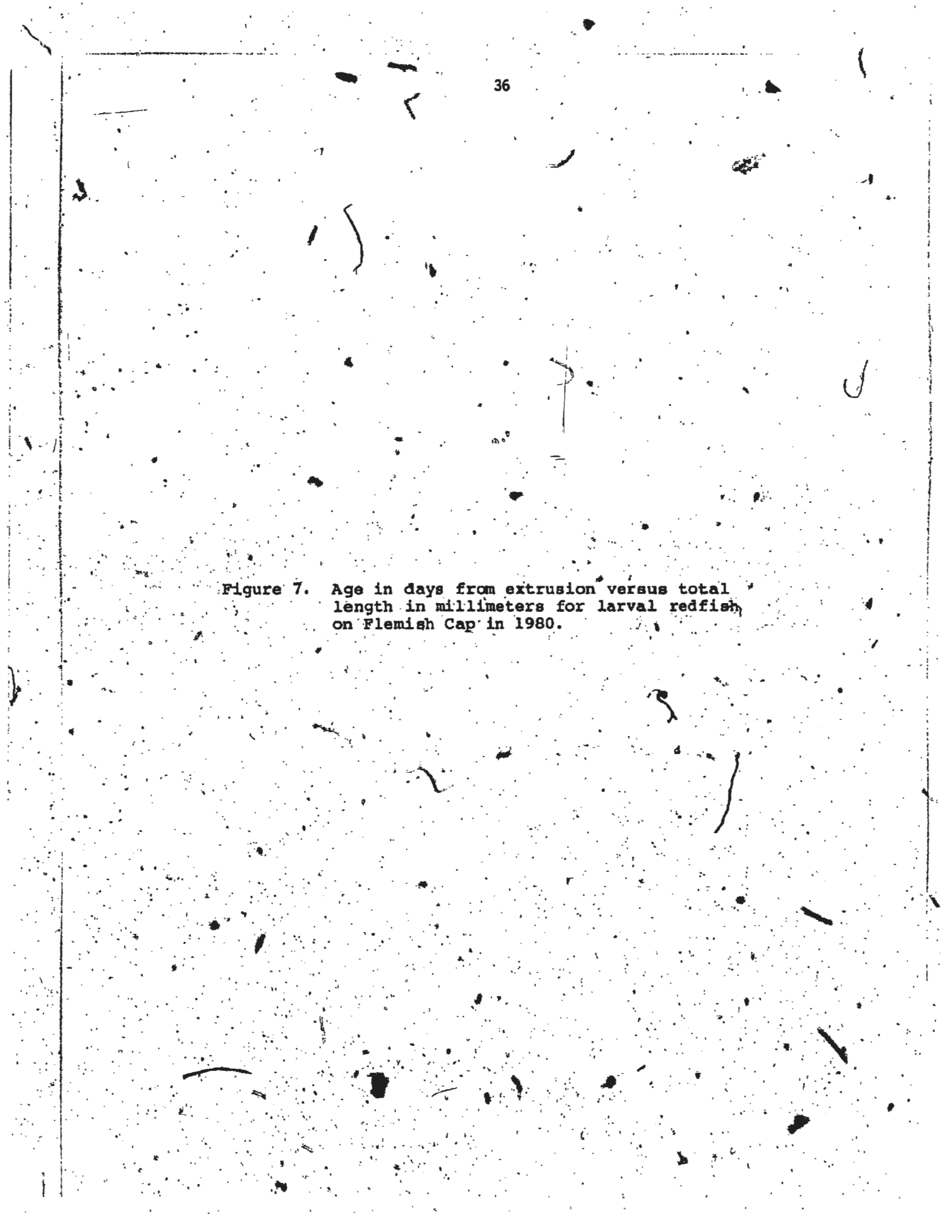
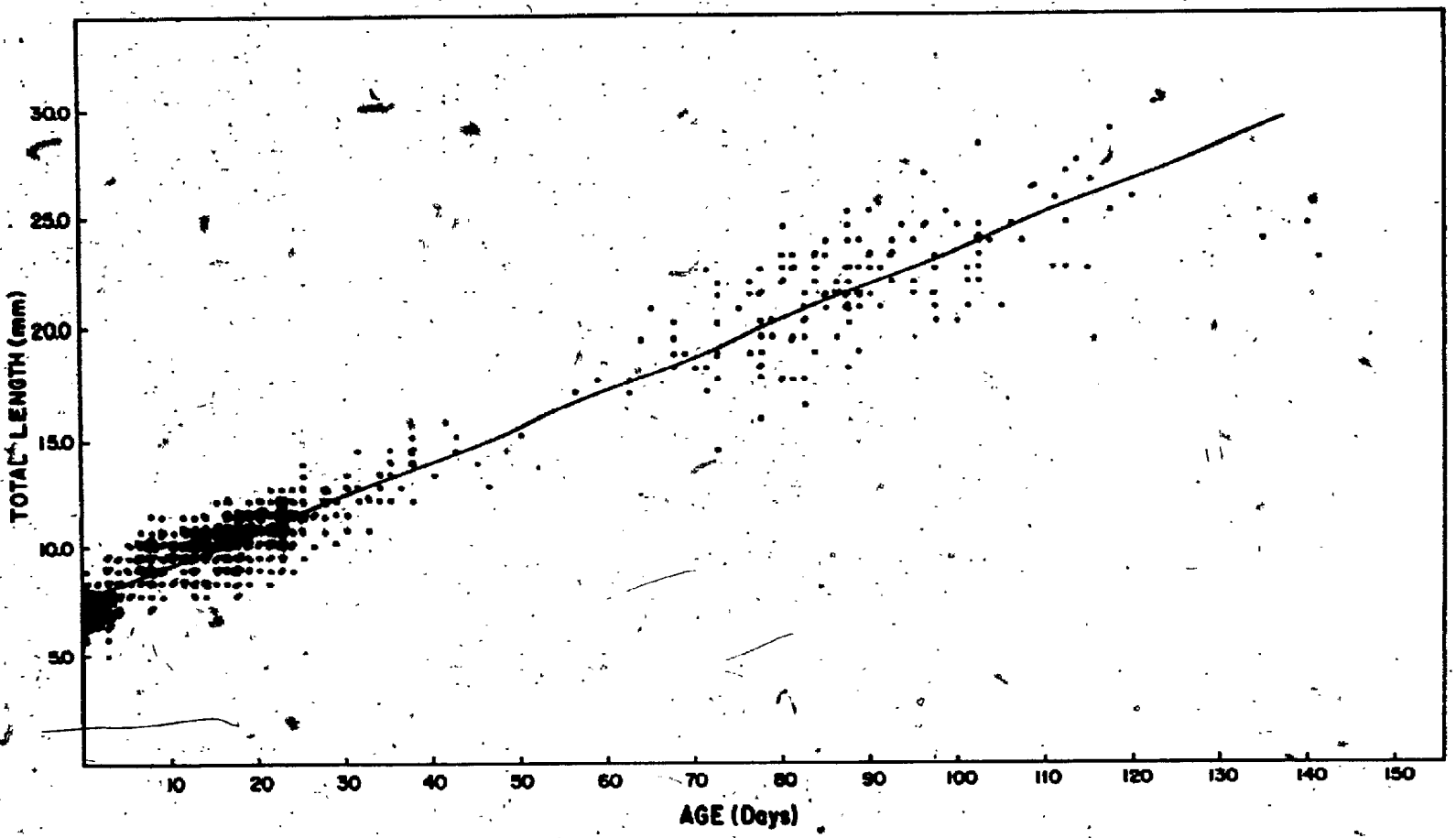


Figure 7. Age in days from extrusion versus total length in millimeters for larval redfish on Flemish Cap in 1980.


TOTAL LENGTH (mm)
30.0
25.0
20.0
15.0
10.0
5.0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
AGE (Days)

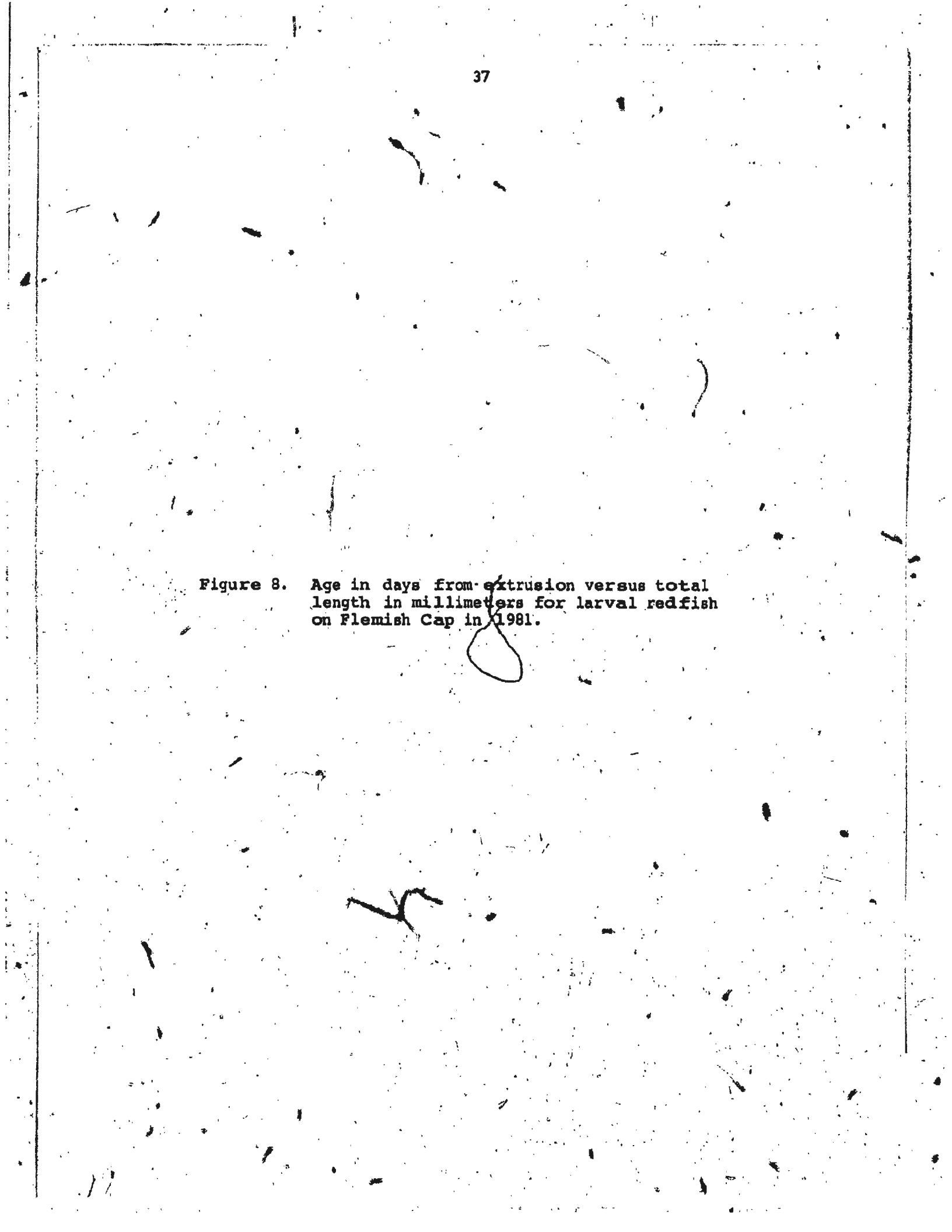


Figure 8. Age in days from extrusion versus total length in millimeters for larval redfish on Flemish Cap in 1981.

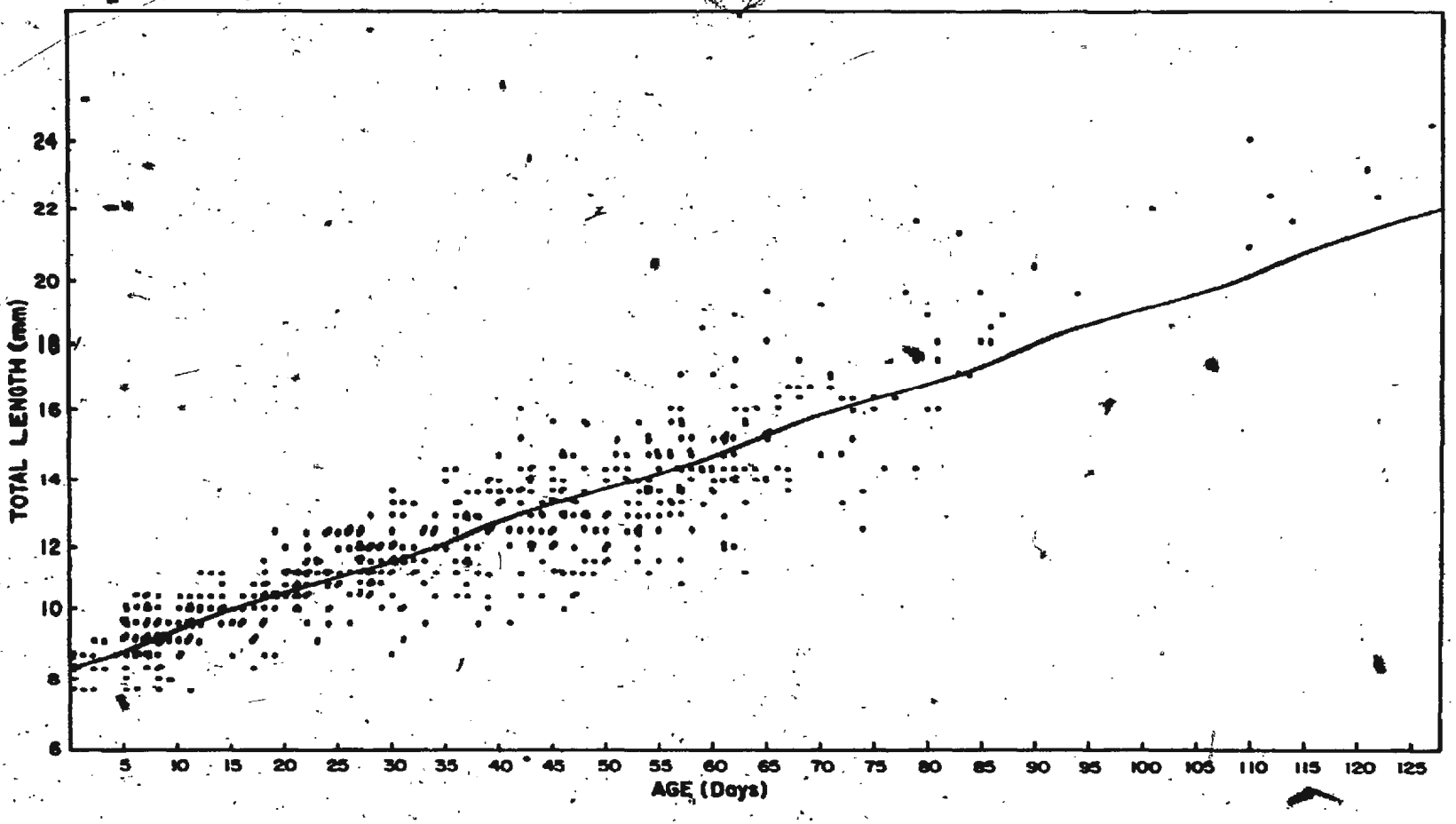

TOTAL LENGTH (mm)
6
8
10
12
14
16
18
20
22
24
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
AGE (Days)

Table 6. Parameter estimation and analysis of variance of least squares regression on length at age data for 1980 and 1981.

A. 1980 Regression

Source	DF	R^2	F Value	Prob > F
Model	1	0.947	13571.95	0.0001
Error	754			
Total	755			

Variable	DF	Parameter estimate	Standard error	T for HO: parameter = 0	Prob > |T|
Intercept	1	7.422	0.058	127.78	0.0001
age	1	0.160	0.00137	116.50	0.0001

B. 1981 Regression

Source	DF	R^2	F Value	Prob > F
Model	1	0.796	2092.37	0.0001
Error	537			
Total	538			

Variable	DF	Parameter estimate	Standard error	T for HO: parameter = 0	Prob > |T|
Intercept	1	8.208	0.107	76.39	0.0001
age	1	0.109	0.00238	45.74	0.0001

$$TL = 0.109\ Age + 8.208$$

where TL is total length in millimeters

and age is number of days post-extrusion

Analysis of variance F statistics for both regressions are highly significant ($P < 0.0001$) and the R^2, particularly for 1980 is high indicating a good fit of the data to the linear model. The slopes of the regression equations are estimates of the mean daily growth rate while the intercepts are estimates of length at extrusion.

Analysis of variance F tests for equality of slopes indicate the slope of the 1980 regression is significantly greater than the slope of the 1981 regression ($F = 355.44$, Prob. $< F = 0.0001$) and the confidence intervals about the intercepts do not overlap at the 99% confidence level. This means that, although redfish larvae at extrusion were larger in 1981, they subsequently grew more slowly. The two regression lines intersect at 15.6 days indicating that, in 1980, larvae older than 15 days were usually larger than larvae in 1981 at the same age.

III.A.5. Length at sagittal radius regressions

The fish length at sagittal radius data for 1980 and 1981 (Figs. 9 and 10) also have no apparent exponential

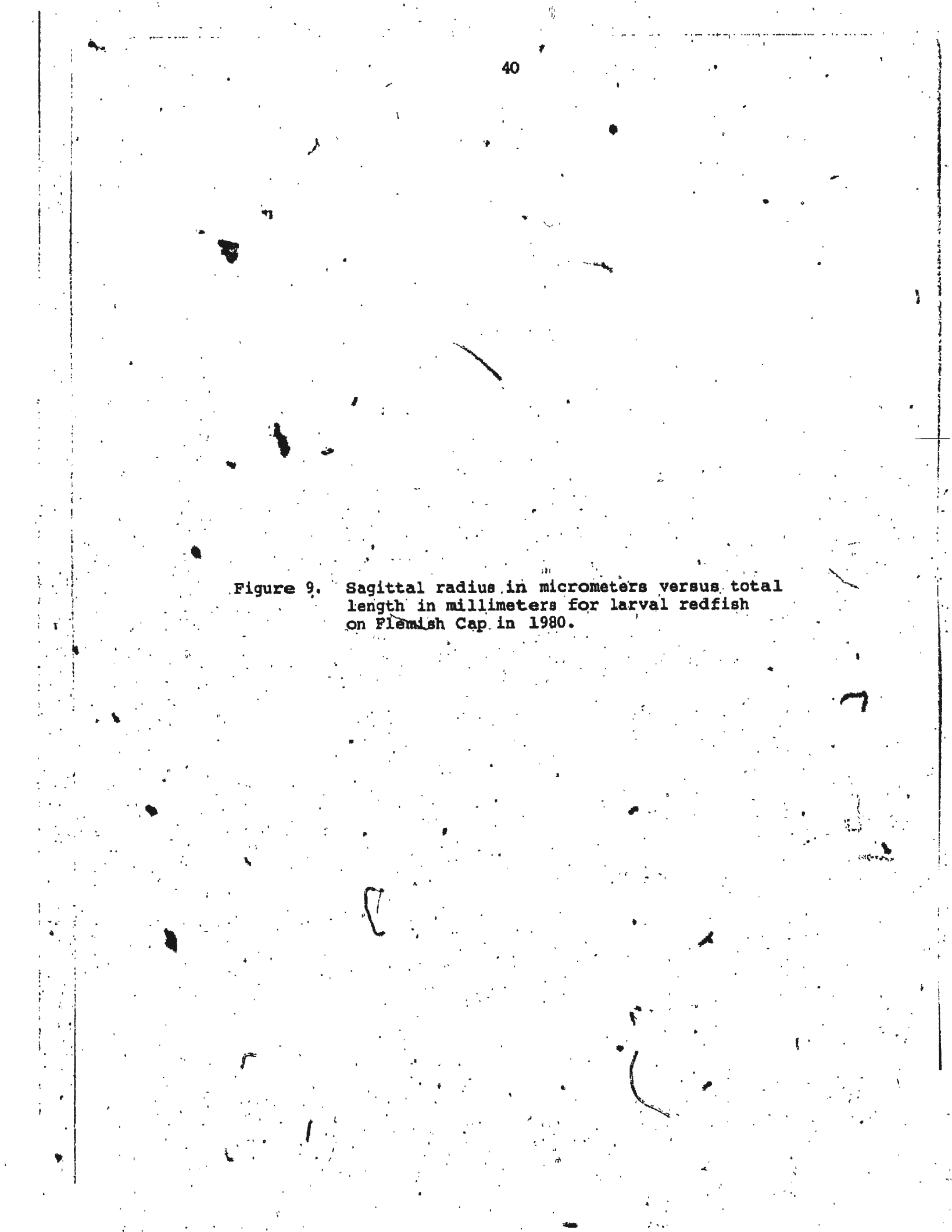


Figure 9. Sagittal radius in micrometers versus total length in millimeters for larval redfish on Flemish Cap in 1980.

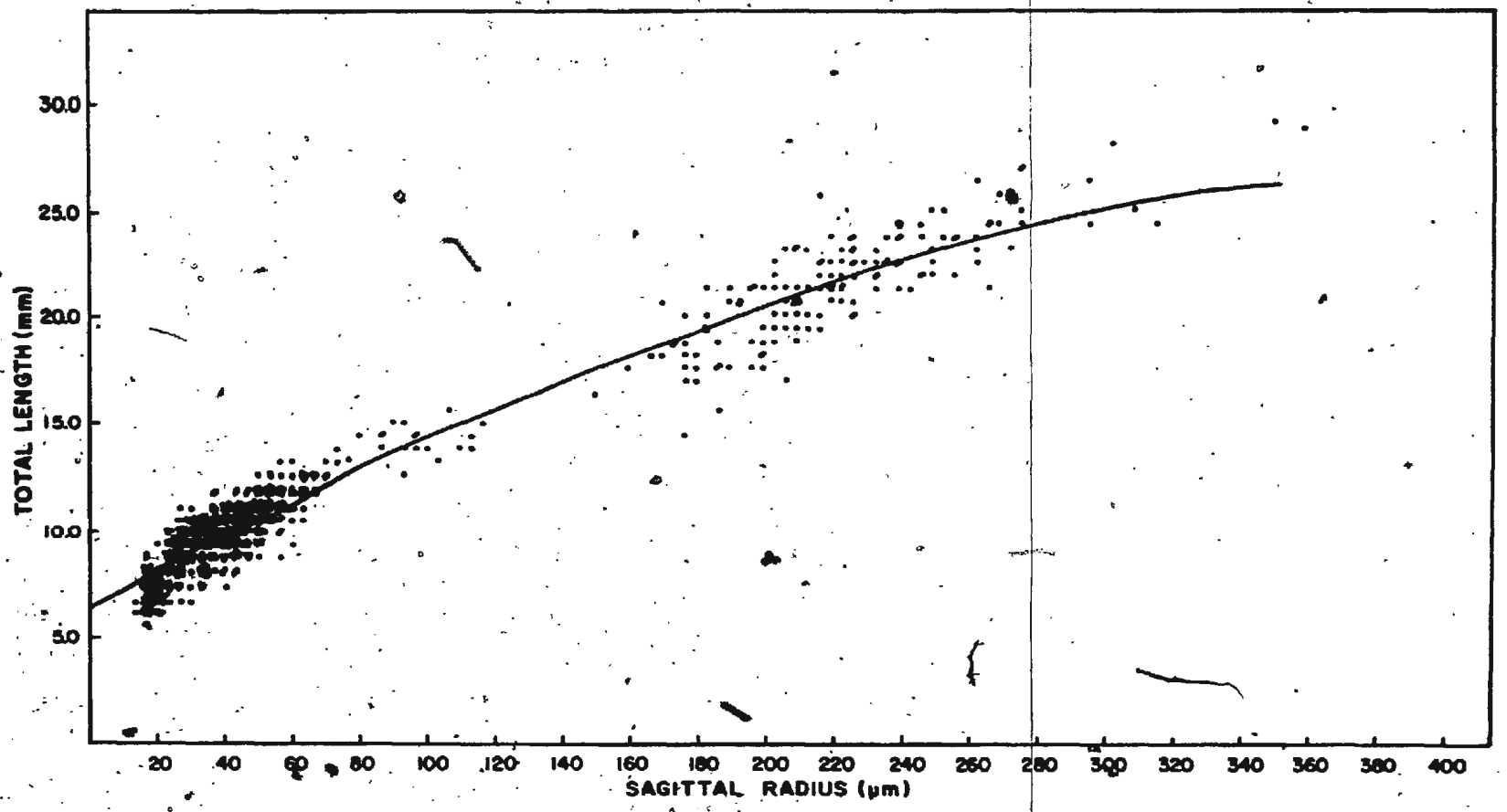
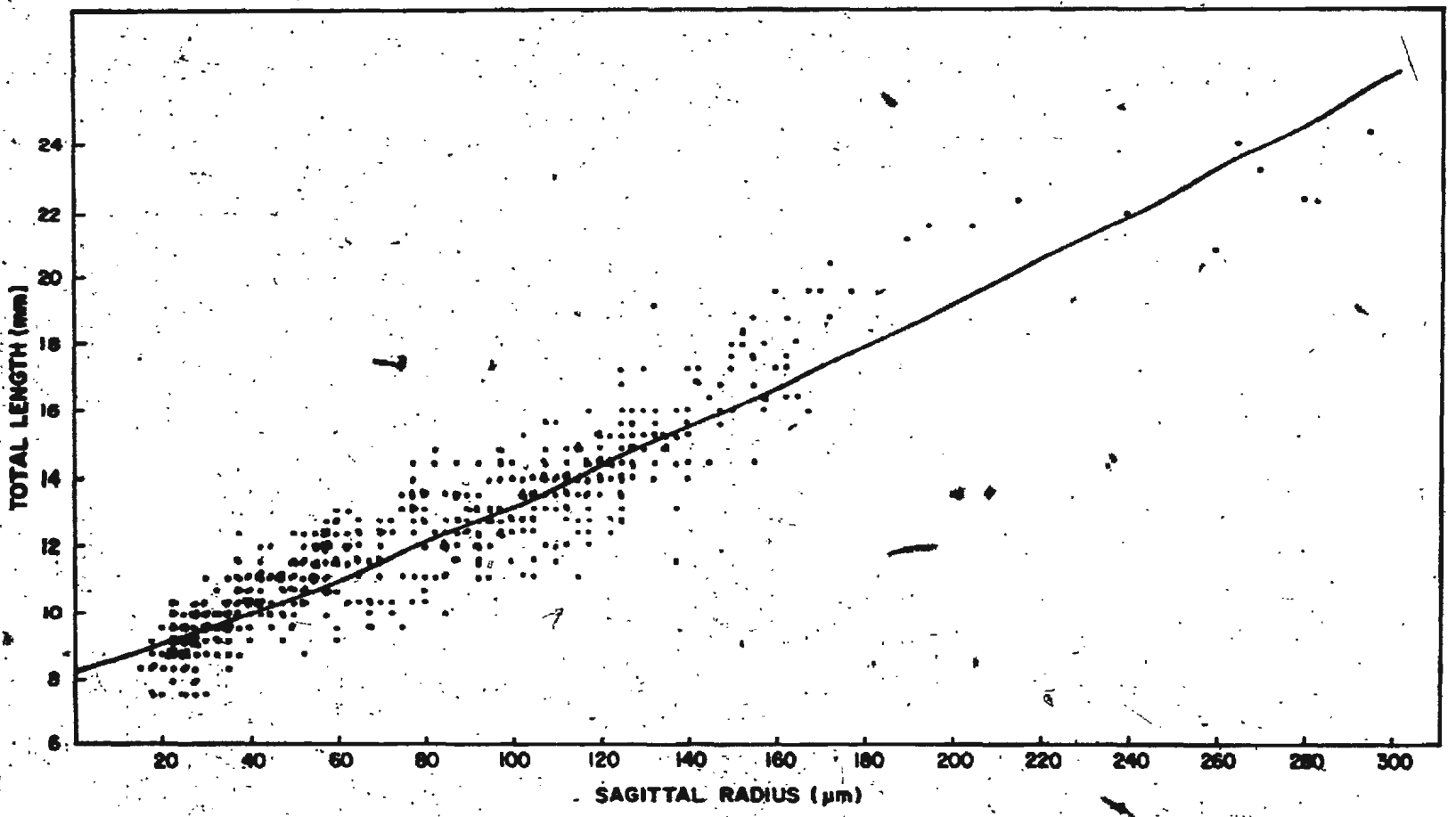

30.0
25.0
20.0
15.0
10.0
5.0
TOTAL LENGTH (mm)
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
360
380
400
SAGITTAL RADIUS (μm)

Figure 10. Sagittal radius in micrometers versus total length in millimeters for larval redfish on Flemish Cap in 1981.


TOTAL LENGTH (mm)
6
8
10
12
14
16
18
20
22
24
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
SAGITTAL RADIUS (μm)

phase or inflection point. However, there is some non-linearity in the data. Non-linear parameter estimation procedures indicated the data were better fit by a polynomial of the form:

$$Y = a_1X^2 + a_2X + b$$

where Y is total length at capture in millimeters and X is the sagittal radius in micrometers

rather than a linear equation or an exponential with an asymptote like the Von Bertalanffy or Gompertz equations. From least squares regression procedures, summarized in Table 7, the fitted equations for 1980 and 1981 were, respectively:

$$TL = -0.000088\ Radius^2 + 0.0885\ Radius + 6.406$$

$$TL = 0.000033\ Radius^2 + 0.0494\ Radius + 8.112$$

Use of the polynomial to describe the length at sagittal radius relationship does not imply any particular biological meaningfulness to its usage. The sign of the squared term is negative in 1980 but positive in 1981. If there is any biological meaning to this it is not apparent. Use of the signs of the squared terms as they are gives the

Table 7. Parameter estimation and analysis of variance of least squares regression on length at sagittal radius data for 1980 and 1981.

A. 1980 Regression

Source	DF	R^2	F Value	Prob > F
Model	2	0.955	8004.25	0.0001
Error	751			
Total	753			

Variable	DF	Parameter estimate	Standard error	T for HO: parameter = 0	Prob > |T|
Intercept	1	6.406	0.0942	68.005	0.0001
$Radius^2$	1	-0.000088	0.000009	-9.113	0.0001
Radius	1	0.0885	0.00259	34.171	0.0001

B. 1981 Regression

Source	DF	R^2	F Value	Prob > F
Model	2	0.860	1647.99	0.0001
Error	536			
Total	538			

Variable	DF	Parameter estimate	Standard error	T for HO: parameter = 0	Prob > |T|
Intercept	1	8.112	0.1386	58.463	0.0001
$Radius^2$	1	0.000033	0.000013	2.570	0.0104
Radius	1	0.0494	0.00284	17.344	0.0001

best fit to the existing data, keeping in mind that any procedure which fits an equation to data will seek a compromise in determination of the best fit over the entire data range.

In both years (Figs. 9 and 10), there is an obvious non-linearity to the data, particularly at the very smallest fish lengths. This results in a downward curve of the data points. The non-linearity seems to be confined to the lower end of the graph with the remaining data apparently linear. The coefficients of the polynomial, as used, represent the best compromise between the linear and non-linear tendencies in the data.

Although the radius squared coefficients appear rather small, the T test for H_0: Parameter = 0 indicates the coefficients are significantly different from zero for both years. Analysis of variance F statistics for both regressions are also highly significant ($P < 0.0001$). Fitting a linear equation to this data would also probably be highly significant. However, with the non-linearity in the sagittal radius to length relationship in smaller fish, the polynomial gives a more satisfactory fit at the lower end of the data set.

The coefficients of the quadratic (a_1) and linear (a_2) terms were evaluated by analysis of variance F tests (H_0 : a_1, 80 = a_1, 81 a_2, 80 = a_2, 81). The overall F

statistic was significant ($F = 75.91$, Prob. $< F = 0.0001$). Evaluation of the standard errors of the estimates of a_1 and a_2 and the intercepts indicate the 99% confidence intervals about the estimates do not overlap.

III.A.6. Length at extrusion

Because of observed wide variation in length of age 0 larvae, the length extrusion was estimated for each larvae individually before its growth history was calculated. Two estimators of length at extrusion were obtained from the regressions of total length versus age. These may be written as:

1. $L_{01} = b$

2. $L_{02} = TL - (a \cdot age)$

where a is the slope and b the intercept of the length at age regression equations and age and TL are the observed age and total length of each individual.

L_{01} is a constant but L_{02} is an estimator based on the slope of the regression equation. As such, L_{02} fluctuates

with deviations of individual growth from the mean predicted from the regression slope.

The variances of L_{01} and L_{02} were the parameter estimates of the linear regression of (1) the squares of the deviations of observed total length from the regression line of total length versus age and (2) the squares of observed age. These regressions, for 1980 and 1981, are summarized in Table 8. The parameter estimates for intercept and age^2 are the variances of L_{01} and L_{02} respectively. These second-order variances were used because the heteroscedasticity in the length at age data with its coincident reduction in the number of older larvae gave a first-order variance for each point which was considered to be unrealistically low for older larvae. Use of the second order variances better reflects the increasing variability in total length with increasing age.

Determination of a single best, or optimal, estimator of L_0, the true length at extrusion, was determined from L_{01} and L_{02}. The optimal estimation equation used was that of Gelb (1974):

$$L_o = \frac{\sigma^2_{02}}{\sigma^2_{01} + \sigma^2_{02}} L_{01} + \frac{\sigma^2_{01}}{\sigma^2_{01} + \sigma^2_{02}} L_{02}$$

Table 8. Parameter estimation (calculation of second-order variances) and analysis of variance of least squares regression on squared deviations of observed total length from the expected versus the square of age for 1980 and 1981.

A. 1980 Regression

Source	DF	R^2	F Value	Prob > F
Model	1	0.219	211.66	0.0001
Error	754			
Total	755			

Variable	DF	Parameter estimate	Standard error	T for HO: parameter = 0	Prob > |T|
Intercept	1	0.7118	0.1046	6.80	0.0001
age	1	0.000405	0.000028	14.55	0.0001

B. 1981 Regression

Source	DF	R^2	F Value	Prob > F
Model	1	0.105	62.86	0.0001
Error	537			
Total	538			

Variable	DF	Parameter estimate	Standard error	T for HO: parameter = 0	Prob > |T|
Intercept	1	0.8269	0.1510	5.48	0.0001
age	1	0.000398	0.00005	7.93	0.0001

where L_0 is the optimal estimator of L_{01} and L_{02} and σ^2_{01} and σ^2_{02} are the variances of the respective estimators

The variance of the optimal estimator itself is given by the equation:

$$\sigma^2_{L_0} = \left(\frac{1}{\sigma^2_{01}} + \frac{1}{\sigma^2_{02}} \right)^{-1}$$

The optimal estimation technique has the desireable quality of emphasizing the individual estimate with the lowest variance. This is accomplished by weighting the estimates in relation to the size of their respective variances.

Because of the nature of the scatter about the regression lines, with the most scatter observed in older, larger larvae, estimates of length at extrusion based on the regression intercepts may be better than estimates based on the slope. Because this optimization procedure is weighted by the variance of the individual estimators, and the variance of L_{02} is highest in older fish, then the procedure weights the resulting optimal estimator for older fish more heavily in favor of L_{01}.

The frequency distributions and means of the various intermediate estimators and the final optimal estimator for 1980 and 1981 are summarized in Tables 9 and 10 respectively. The mean predicted length at extrusion for both 1980 and 1981 are not significantly different from the observed mean length of age 0 larvae captured in 1980, 7.46 mm, and 1981, 8.38 mm (Prob. > 0.05).

Table 9. Frequency of occurrence distribution and summary of final and intermediate estimators of total length at extrusion for 1980.

Estimator	Frequency of occurrence									
	Total length group									
	2	3	4	5	6	7	8	9	10	11
L_{01}						756				
L_{02}	5 (0.7)	3 (0.3)	11 (1.5)	56 (7.4)	185 (24.5)	271 (35.8)	168 (22.2)	44 (5.8)	11 (1.5)	3 (0.4)
L_0				27 (3.6)	179 (23.7)	398 (52.6)	135 (17.9)	16 (2.1)	1 (0.1)	

	L_{01}	L_{02}	L_0
Mean	7.422	7.421	7.418
N	756	756	756

50a

Table 10. Frequency of occurrence distribution and summary of final and intermediate estimators of total length at extrusion for 1981.

Estimator	Frequency of occurrence								
	Total length group								
	4	5	6	7	8	9	10	11	12
L_{01}					539				
L_{02}	4 (0.7)	23 (4.3)	63 (11.7)	113 (21.0)	211 (39.1)	94 (17.4)	20 (3.7)	8 (1.5)	3 (0.6)
L_0			27 (5.0)	155 (28.8)	290 (53.8)	66 (12.2)	1 (0.2)		

	L_{01}	L_{02}	L_0
Mean	8.208	8.212	8.228
N	539	539	539

III.A.7. Temporal variation in length at extrusion

Length at extrusion varies with date of extrusion. For the main extrusion period in 1980 (Fig. 11), the mean length at extrusion steadily increased from 6.86 mm for larvae extruded in the Julian day period 90-99, to a peak of 7.96 mm for larvae extruded in late May from Julian day 140-149. The analysis of variance F statistic comparing differences in length at extrusion with extrusion time is statistically significant ($F = 10.27$, Prob. $> F = 0.0001$). The 95% confidence intervals about the cell means are largely non-overlapping, indicating a trend towards increasing length at extrusion with increasing date of extrusion.

In 1981 (Fig. 11), the trend observed was nearly opposite to 1980. Larvae extruded from Julian day 90-99 had a mean total length of 8.49 mm. This steadily decreased through to the Julian day period 130-139 to a low of 8.11 mm and then increased to 8.56 mm for Julian days 150-159. The analysis of variance F statistic comparing length at extrusion with extrusion date is significant ($F = 2.15$,

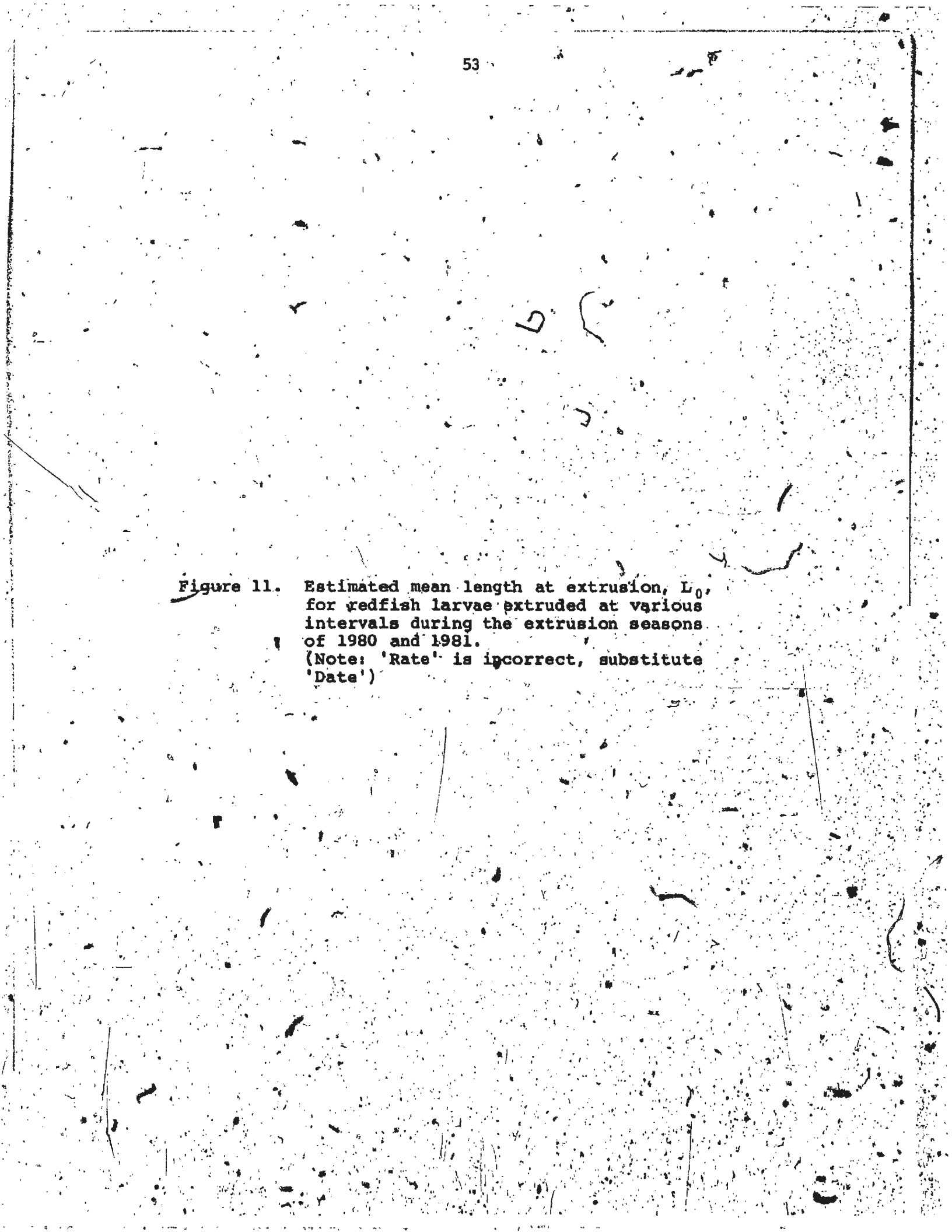
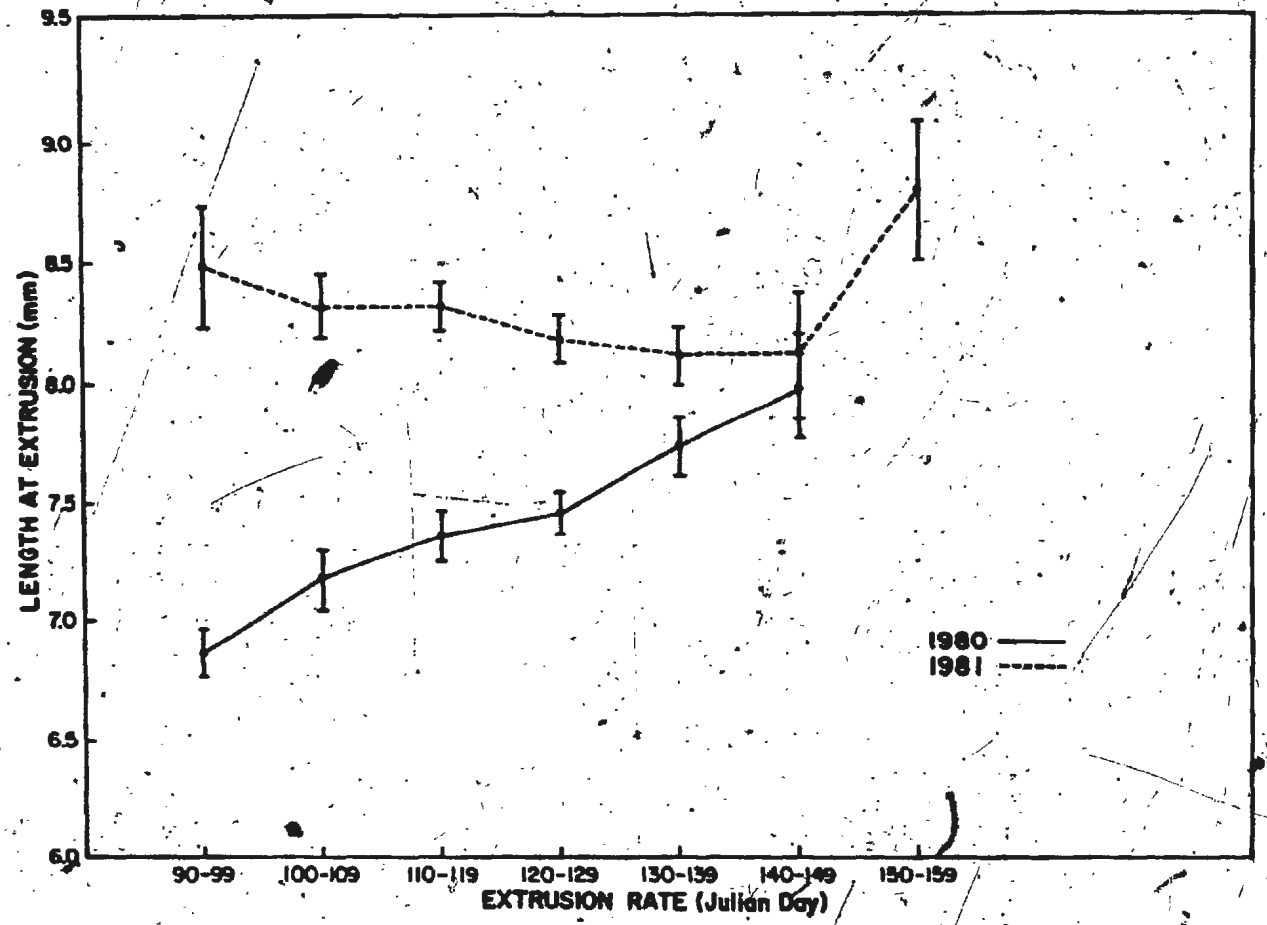


Figure 11. Estimated mean length at extrusion, L_0, for redfish larvae extruded at various intervals during the extrusion seasons of 1980 and 1981.
(Note: 'Rate' is incorrect, substitute 'Date')


LENGTH AT EXTRUSION (mm)
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
90-99
100-109
110-119
120-129
130-139
140-149
150-159
EXTRUSION RATE (Julian Day)
1980
1981

Prob. > F = 0.02) but the 95% confidence intervals about the cell means all overlap indicating that, although length at extrusion does significantly vary with extrusion date, there is no systematic trend towards either increasing or decreasing length at extrusion with date of extrusion.

III.A.8. Back-calculated growth history

The growth history of each larva was determined by a back-calculation procedure based on the predicted length at extrusion and the measurements of sagittal radii at each 5 increment interval. The mean daily growth rate in each interval was calculated both in millimeters per day and as a per cent of body length at the start of the interval.

The back-calculated length at age data for both 1980 and 1981 (Fig. 12) are very similar to the observed length at age data (Figs. 9 and 10), supporting the effectiveness of the back-calculation procedure as an accurate predictor of past larval growth history. Until age 15-20, larvae extruded in 1981 are greater in length than 1980 larvae due to the greater mean length at extrusion in 1981. However, after this time, 1980 larvae are consistently larger than 1981 larvae at all ages through to age 100 as a result of the greater mean daily growth rate in 1980. The mean daily growth rate for each 5 day interval back-calculated over

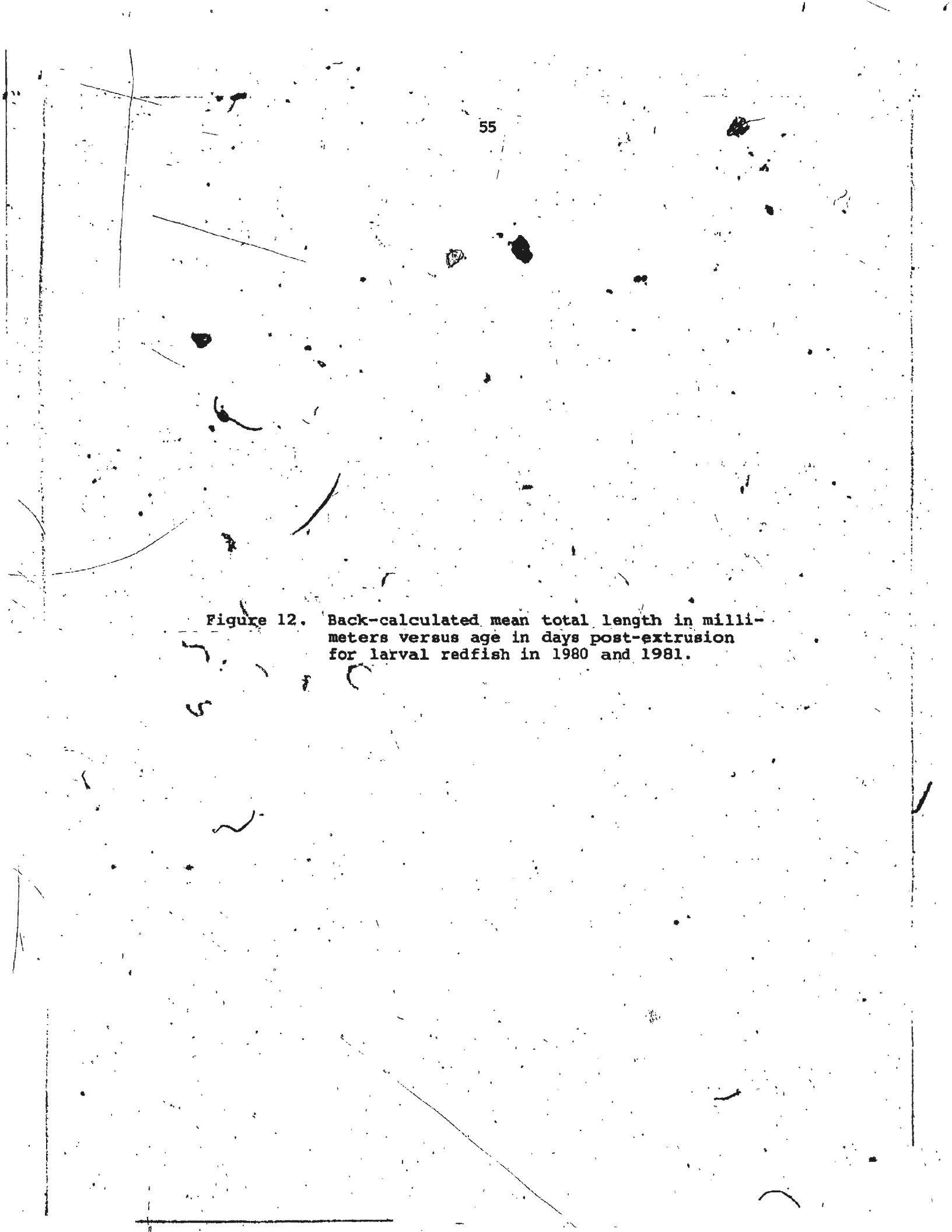
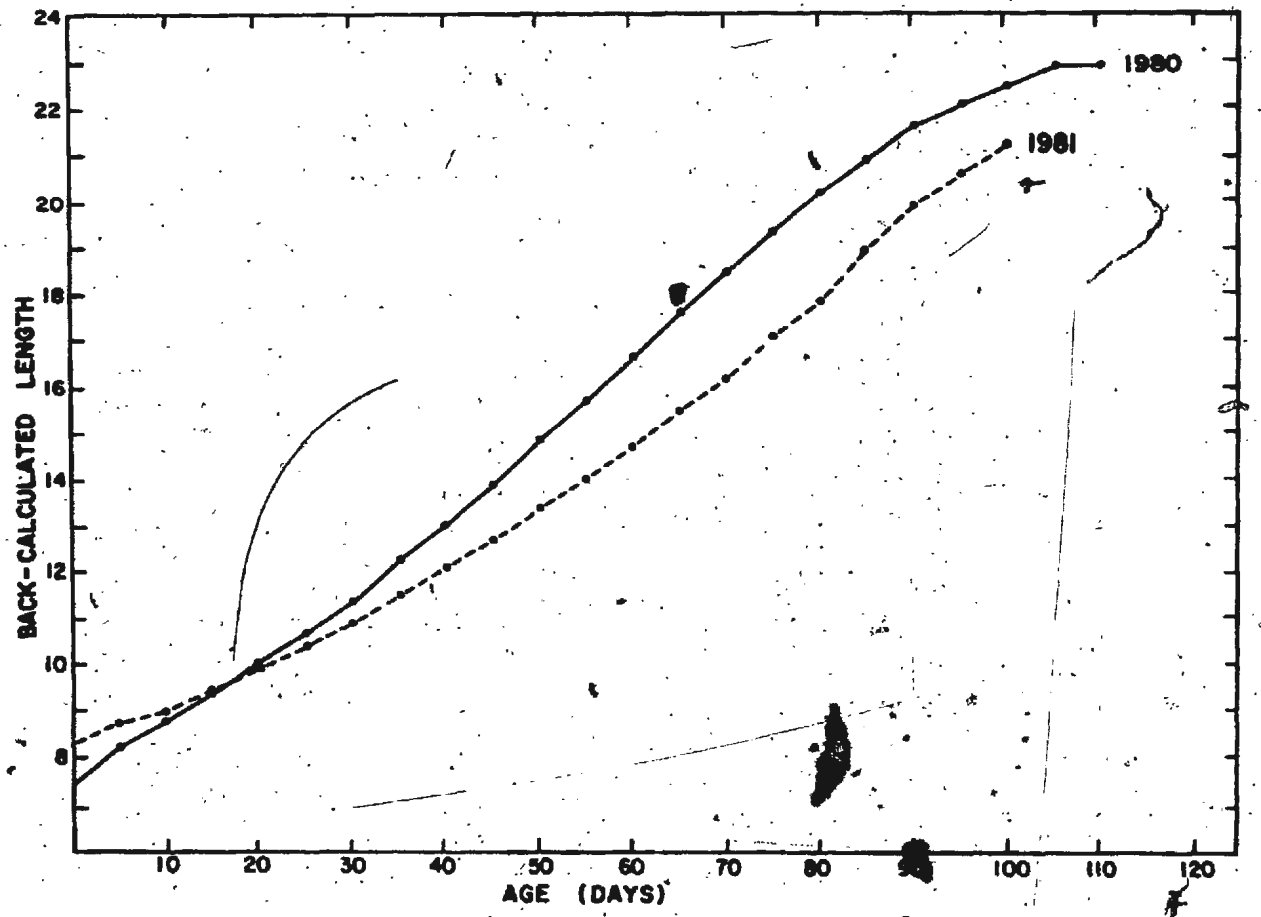


Figure 12. Back-calculated mean total length in millimeters versus age in days post-extrusion for larval redfish in 1980 and 1981.


BACK-CALCULATED LENGTH
AGE (DAYS)
1980
1981
24
22
20
18
16
14
12
10
8
10
20
30
40
50
60
70
80
100
110
120

each larva's lifespan is shown in Figure 13.

In 1980, the mean daily growth rate for the first 5 days after extrusion was 0.143 mm per day. Daily growth rates declined through to age 10 and then increased steadily to peak around age 65 at 0.188 mm per day. Larvae older than 65 days experienced a period of declining growth rates through to age 110 by which time the daily growth rate had fallen to 0.108 mm per day. Expressed as a per cent of total length (Fig. 14), larval growth was greatest initially to age 5 (1.9% per day) and declined steadily with advancing age to 0.49% per day by age 110.

The overall pattern of daily growth rates for 1981 (Fig. 13) was similar to 1980 except that the magnitude of growth was consistently lower in all but the very oldest larvae measured. Initially to age 5, larvae grew at a mean daily growth rate of 0.089 mm per day which declined further by age 10 to 0.086 mm per day before steadily increasing rapidly to 0.131 mm per day by age 45. These higher growth rates were not sustained through to age 65 as in 1980 but, instead, began to decline until age 80 to 0.115 mm per day. A period of recovery then followed which saw daily growth rates peaking at 0.137 mm per day at age 90 but then falling again to 0.112 mm per day at age 110. By age 100, growth rates of larvae in both years were comparable.

Expressed as a per cent of total length (Fig. 14),

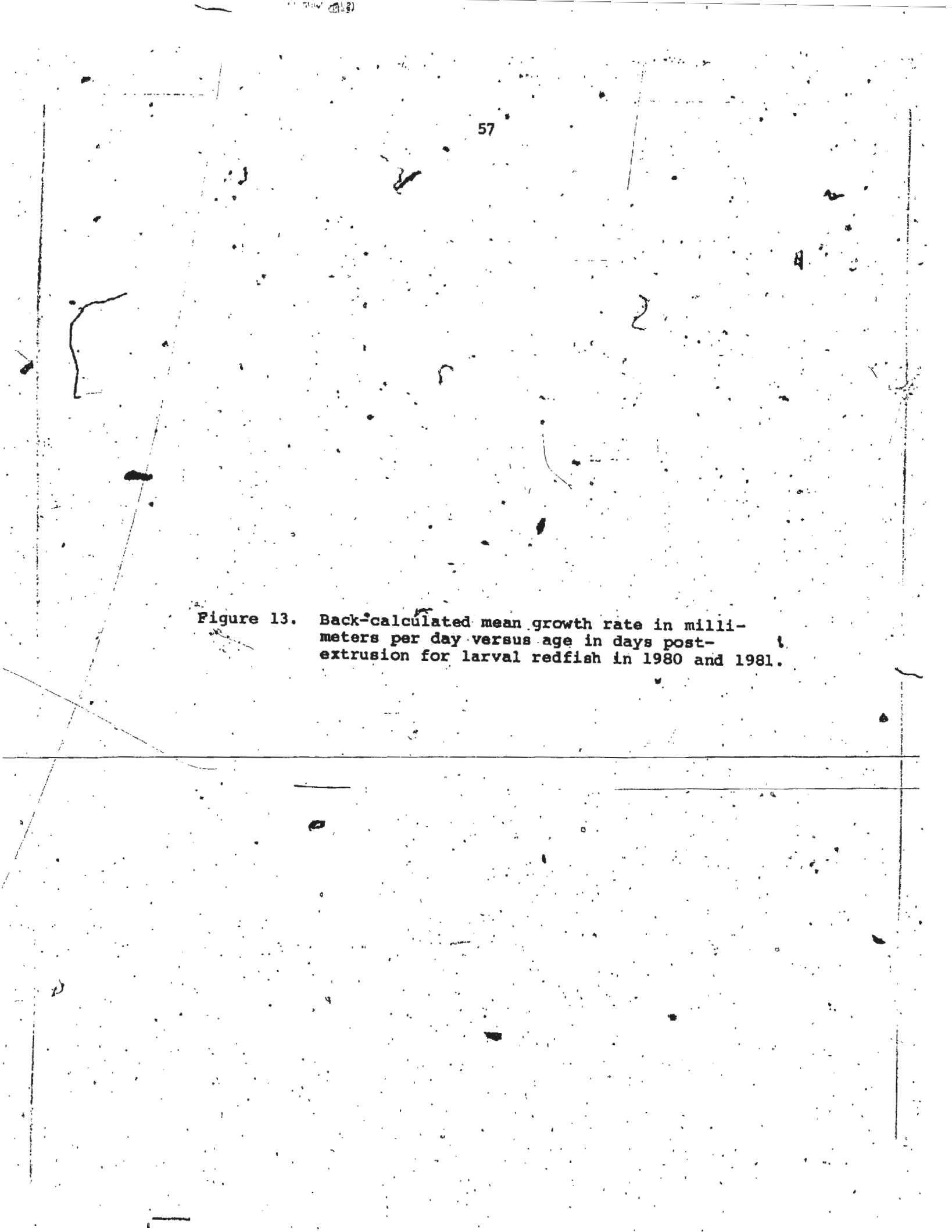


Figure 13. Back-calculated mean growth rate in millimeters per day versus age in days post-extrusion for larval redfish in 1980 and 1981.

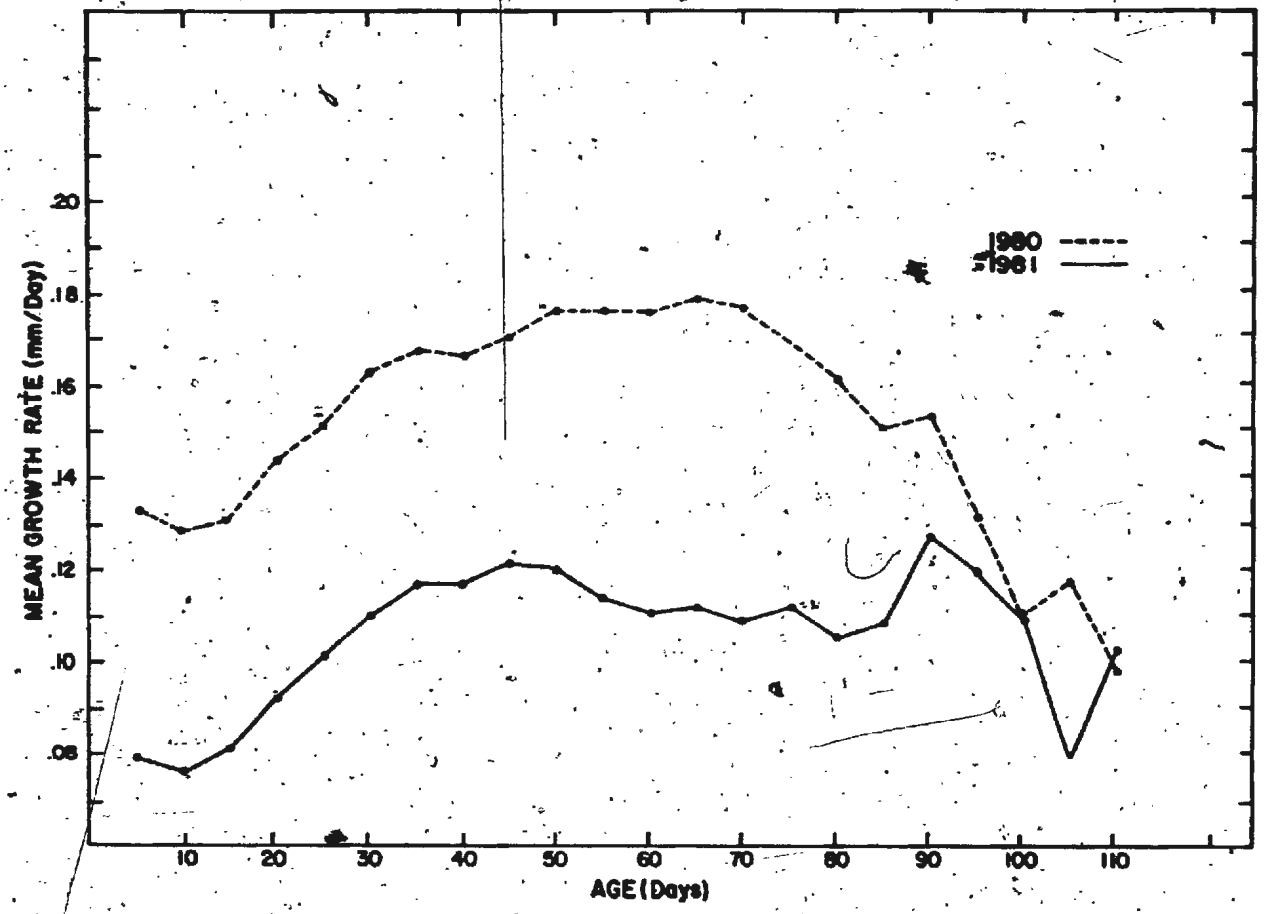
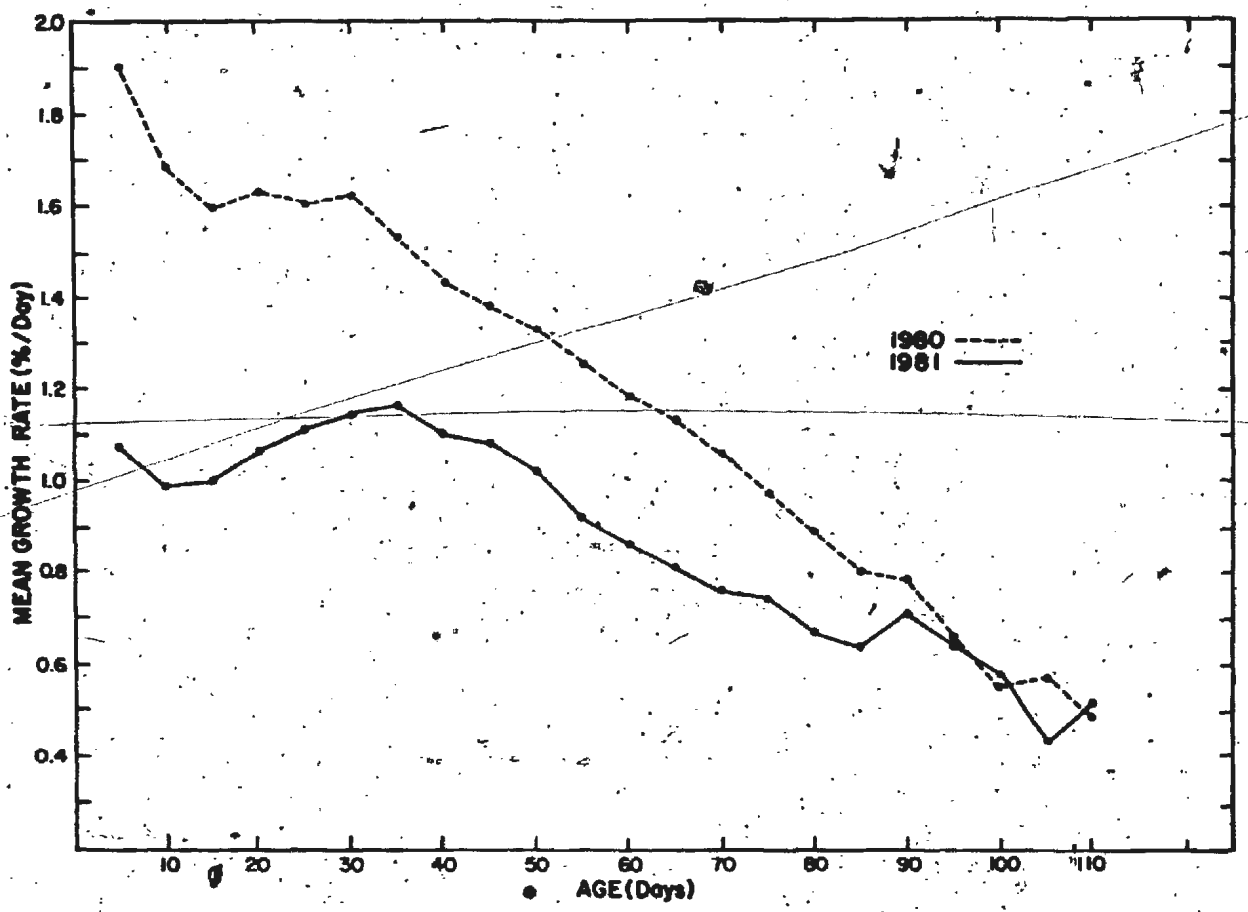

MEAN GROWTH RATE (mm/Day)
.20
.18
.16
.14
.12
.10
.08
1980
1981
10
20
30
40
50
60
70
80
90
100
110
AGE (Days)

Figure 14. Back-calculated mean growth rate in per cent of total length versus age in days post-extrusion for larval redfish in 1980 and 1981.

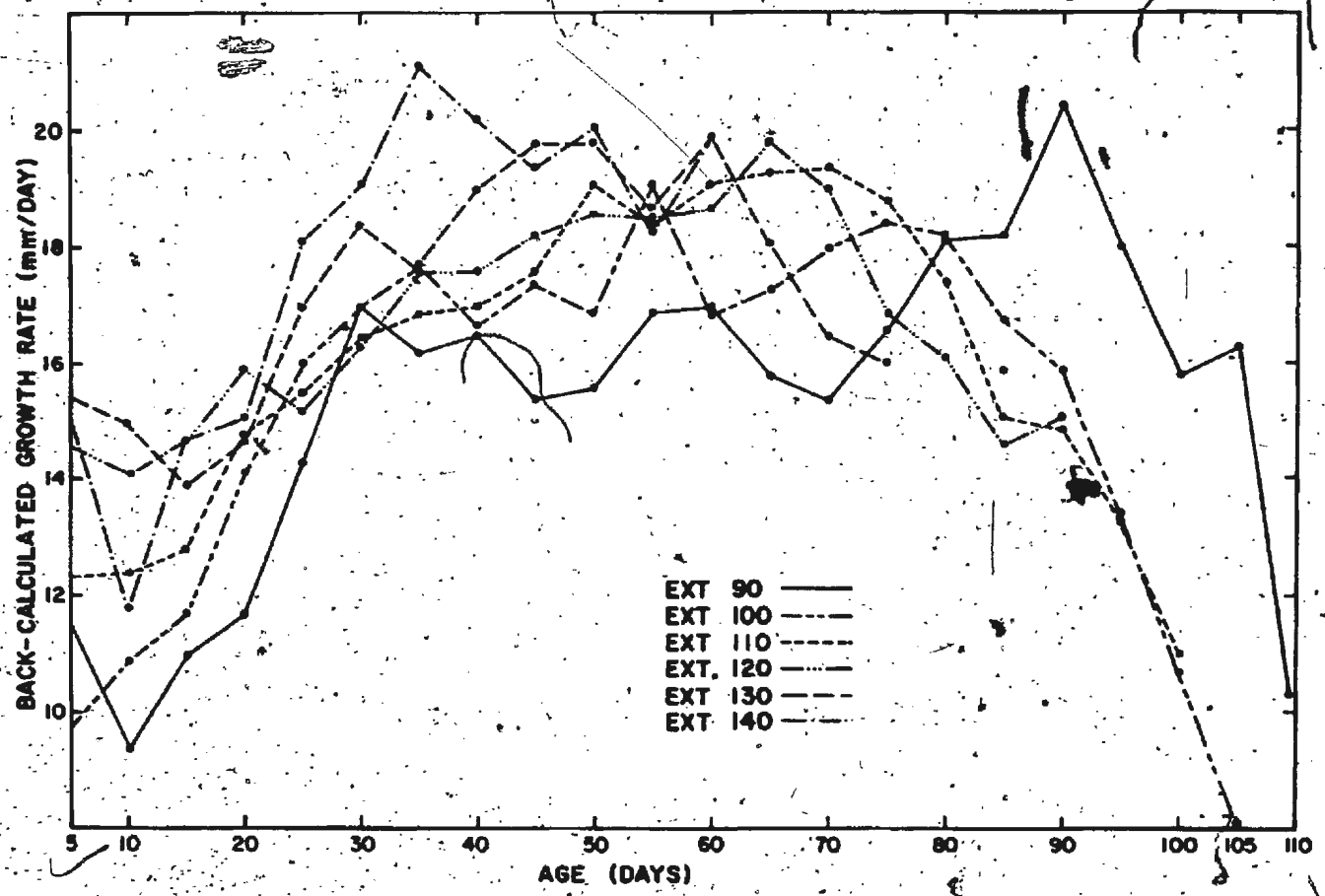

MEAN GROWTH RATE (%/Day)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
1980
1981
10
20
30
40
50
60
70
80
90
100
110
AGE (Days)

initially to age 5, larvae grew at 1.08% per day declining to 0.99% per day at age 10 before recovering to peak at 1.16% per day at age 35. Daily growth as a per cent of total length then declined steadily, as in 1980, to 0.52% per day by age 110. Comparing 1980 to 1981, larvae in 1981 grew much more slowly, on average, at all ages through to age 110 than did larvae in 1980 and, as a result, were consistently smaller, at corresponding ages, than 1980 larvae as well.

III.A.9. Temporal variation in growth history

The growth history of larvae extruded at different times within the same year varied considerably. Figure 15 shows these results for 1980. In this figure and Figs. 16-18, Ext90 means larvae extruded on Julian days 90-99 and Ext100 means larvae extruded on days 100-109, etc. In 1980, larvae extruded prior to day 120 initially grew more slowly than those extruded on day 120 or later. Only Ext100 and Ext110 larvae did not experience a temporary decline in growth rate by age 10. Growth rates in all larvae, irrespective of date of extrusion, fluctuated considerably over the larval period. The lower initial growth rates in larvae extruded prior to day 120 continued, on average, through the larval period with mean growth rates of 0.153 mm per day, 0.151 mm per day, and 0.154 mm per day for Ext90,

Figure 15. Back-calculated mean growth rate in millimeters per day versus age in days post-extrusion for redfish larvae extruded in 10-day intervals during 1980.


BACK-CALCULATED GROWTH RATE (mm/DAY)
AGE (DAYS)
EXT 90
EXT 100
EXT 110
EXT. 120
EXT 130
EXT 140

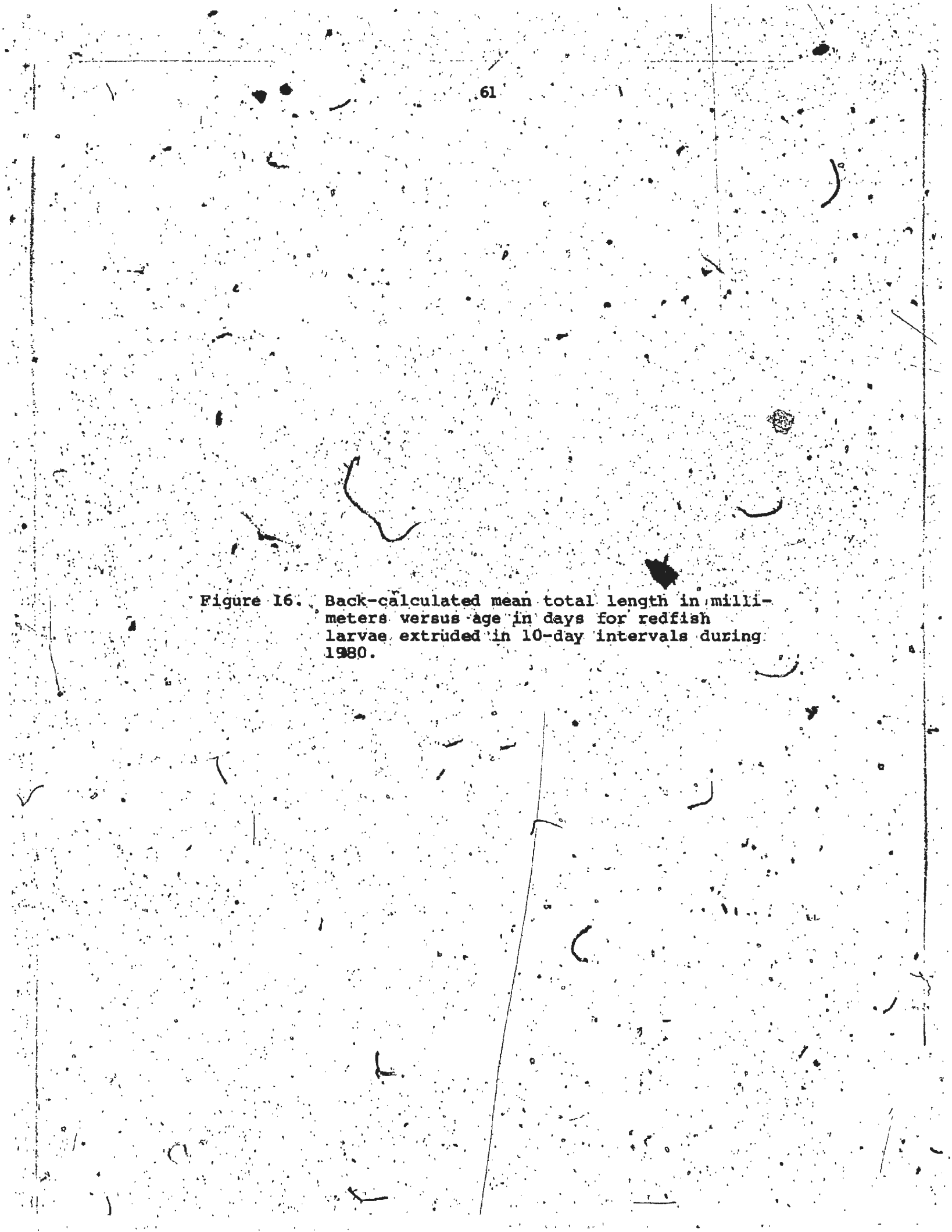


Figure 16. Back-calculated mean total length in millimeters versus age in days for redfish larvae extruded in 10-day intervals during 1980.

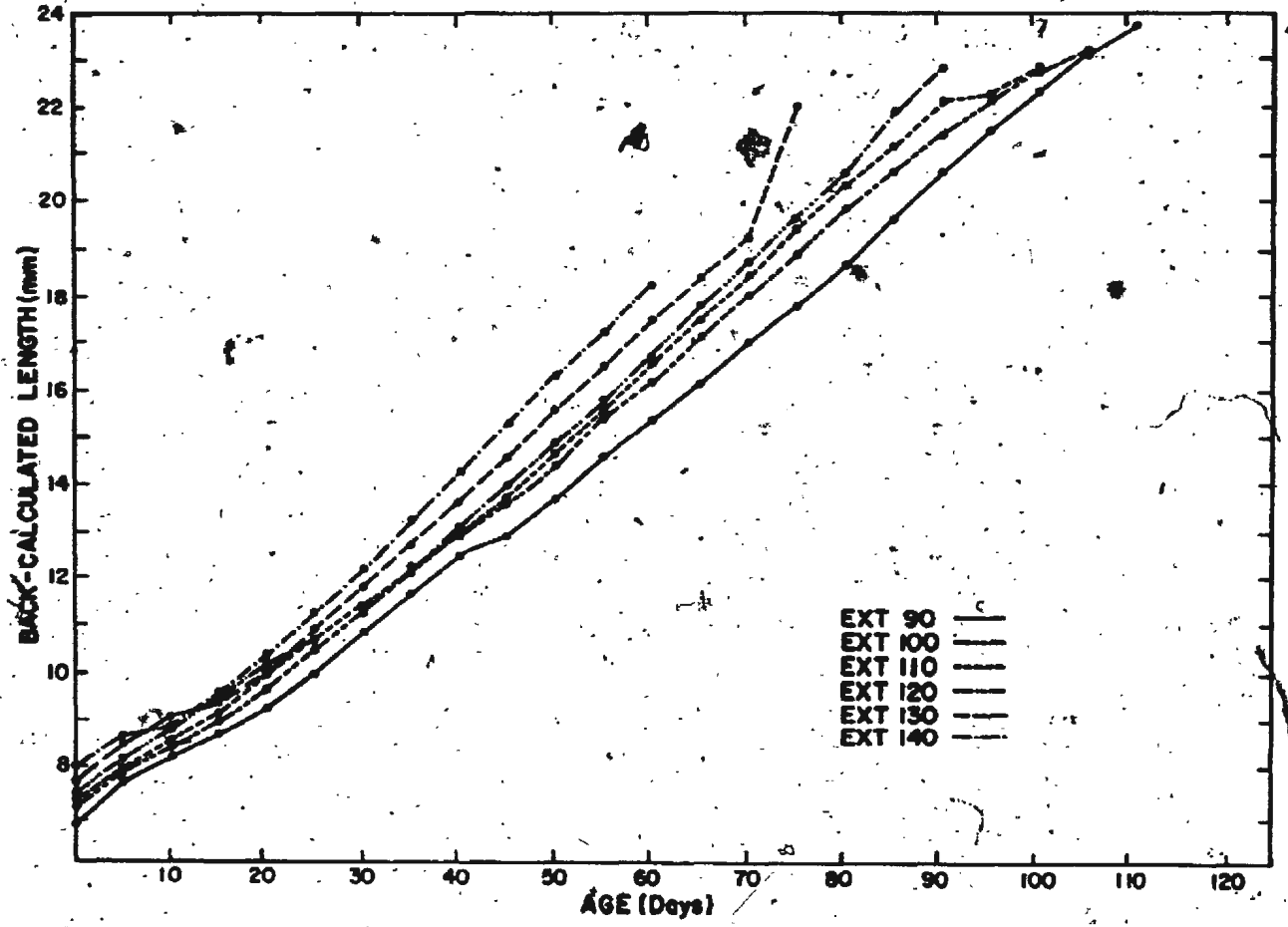

BACK-CALCULATED LENGTH (mm)
AGE (Days)
EXT 90
EXT 100
EXT 110
EXT 120
EXT 130
EXT 140

Figure 17. Back-calculated mean growth rate in millimeters per day versus age in days post-extrusion for redfish larvae extruded in 10-day intervals during 1981.

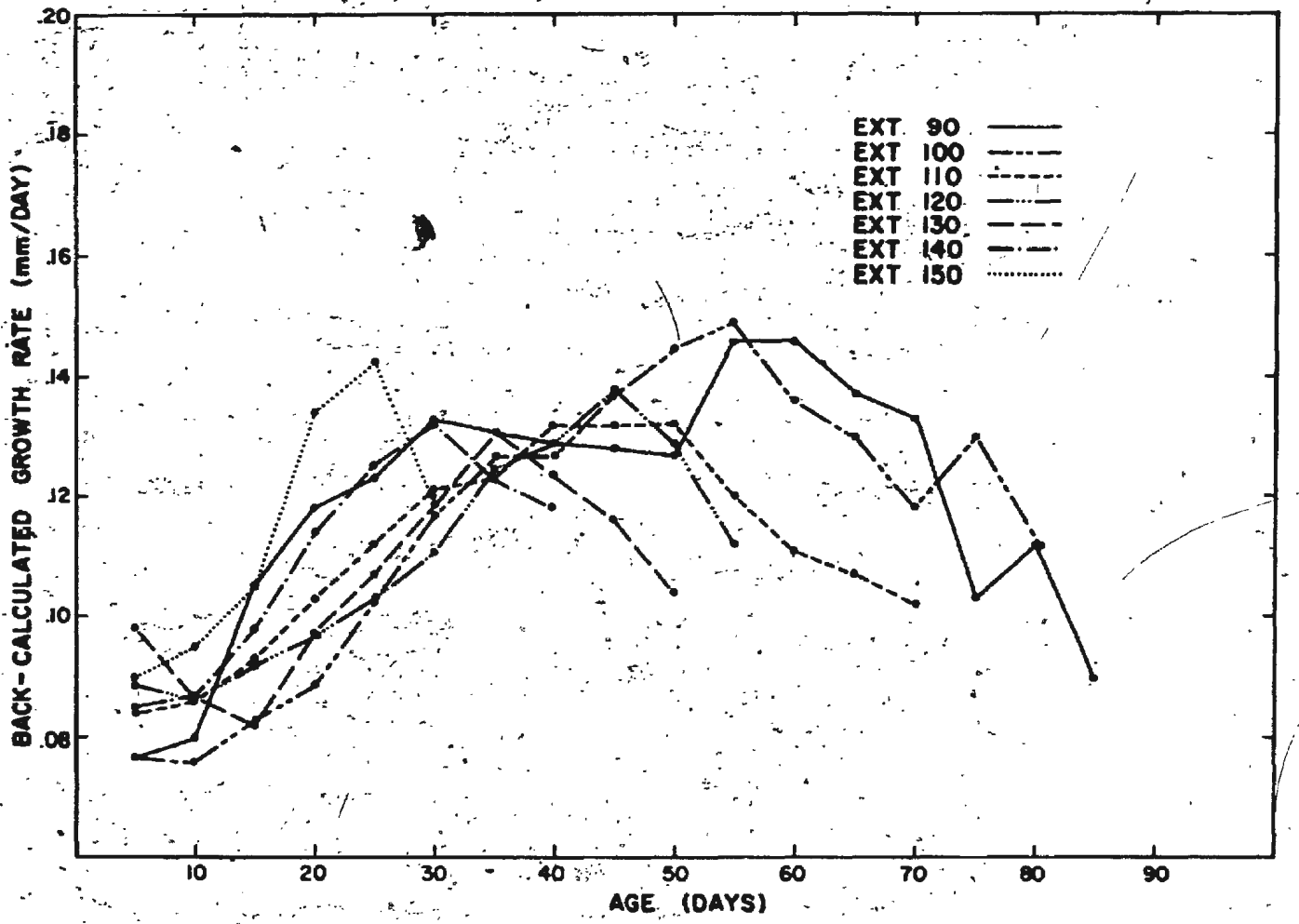
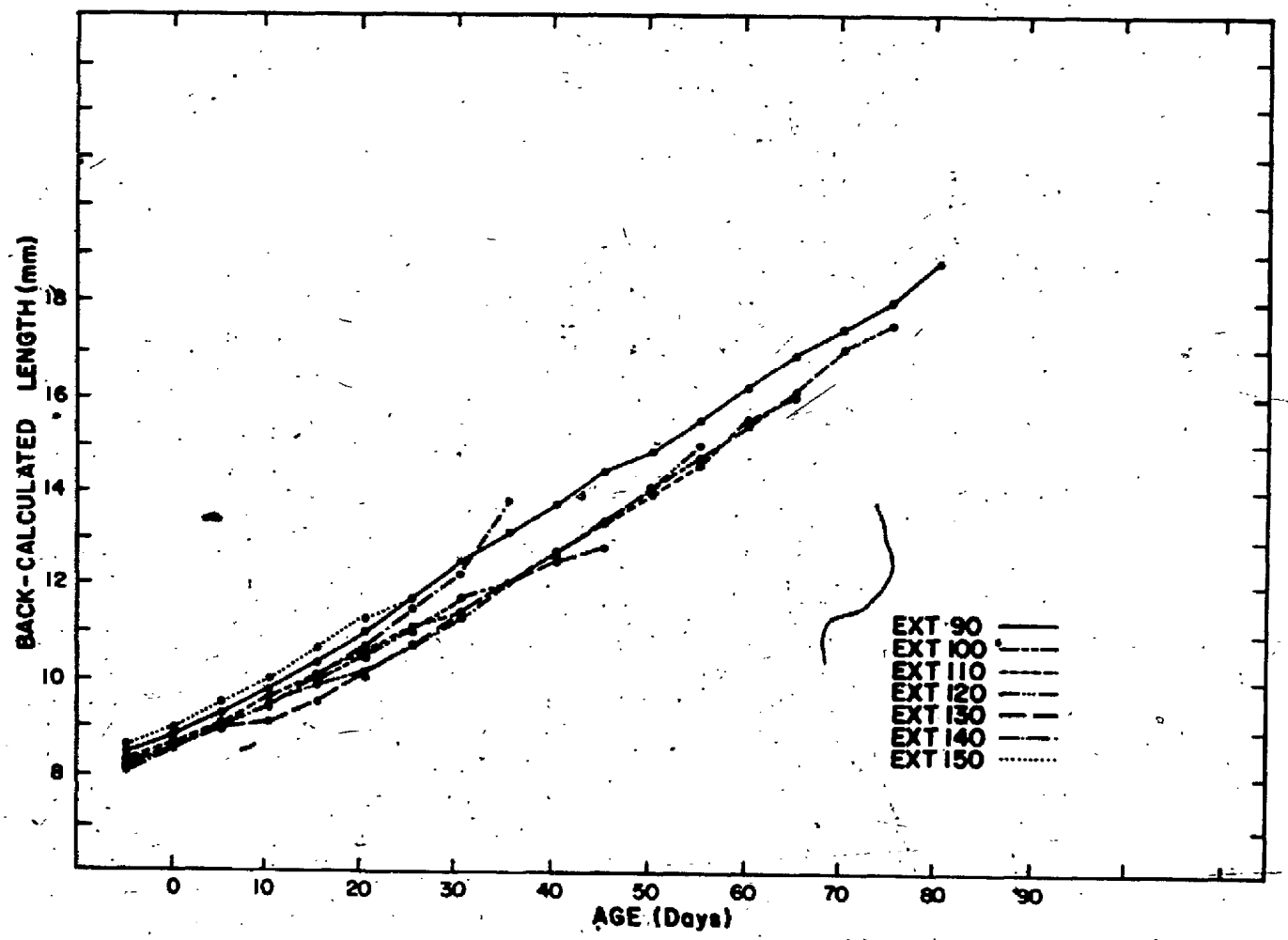

BACK-CALCULATED GROWTH RATE (mm/DAY)
.20
.18
.16
.14
.12
.10
.08
10
20
30
40
50
60
70
80
90
AGE (DAYS)
EXT 90
EXT 100
EXT 110
EXT 120
EXT 130
EXT 140
EXT 150

Figure 18. Back-calculated total length in millimeters versus age in days for redfish larvae extruded in 10-day intervals during 1981.


BACK-CALCULATED LENGTH (mm)
8
10
12
14
16
18
0
10
20
30
40
50
60
70
80
90
AGE (Days)
EXT 90
EXT 100
EXT 110
EXT 120
EXT 130
EXT 140
EXT 150

Ext100, and Ext110 larvae respectively. Ext120, Ext130, and Ext140 larvae had mean growth rates of 0.171 mm per day, 0.190 mm per day, and 0.172 mm per day respectively.

The highest mean growth rate for any 5 day interval, 0.211 mm per day, was attained by Ext140 larvae at age 35. Despite the considerable variation with age, larvae extruded later than day 119 enjoyed higher mean daily growth rates compared to larvae extruded earlier. These higher growth rates over the entire age range measured, coupled with the increasing initial length at extrusion for those larvae extruded later in the season, result in the later extruded larvae being consistently larger at all ages than earlier extruded larvae (Fig. 16).

In 1981 (Fig. 17), there was no strong tendency towards increasing growth rates for later extruded larvae. Ext140 larvae attained the highest mean growth rate at 0.142 mm per day but Ext130 and Ext150 larvae grew much more slowly at 0.095 mm per day and 0.100 mm per day respectively. Indeed, except for Ext140 larvae, there seemed to be a tendency for decreased growth rates in later extruded larvae in 1981. Mean daily growth rates for Ext90, Ext100, Ext110, and Ext120 larvae were 0.121 mm per day, 0.115 mm per day, 0.109 mm per day, and 0.113 mm per day respectively. The highest growth rate for any 5 day interval in 1981, 0.149 mm per day, was attained by Ext100 larvae at

age 55, although Ext90 larvae at age 55-60 grew only slightly slower at 0.146 mm per day.

Considering the different growth rates for larvae extruded at various times together with the differences in their mean length at extrusion, the resulting back-calculated lengths at age for Ext100, Ext110, Ext120, and Ext130 larvae are remarkably similar (Fig. 18). Ext90, Ext140, and Ext150 larvae are noticeably larger at corresponding ages than larvae extruded at other times.

III.B. MORPHOLOGY ANALYSIS

I used two approaches to differentiate the three putative redfish species. These were: (1) evaluation of morphological variables identified in the literature on adult or larval redfish with examination of others not previously investigated and (2) multivariate Principal Component Analysis.

III.B.1. Published identification criteria

The best morphological discriminators between the putative species, identified by Barsukov and Zakharov (1972), Templeman (1980), and Ni (1981b) are as follows:

(1) body coloration
(2) eye diameter
(3) projection of the lower jaw tubercle
(4) number of vertebrae
(5) number of anal fin rays
(6) number of dorsal fin rays
(7) number of gill rakers
(8) angle of the third posterior preopercular spine
(9) fusion of the occipital-nuchal ridge
(10) tip of the pectoral fin in relation to the anus
(11) gas bladder musculature
(12) sub-caudal melanophores

All these characters, with the exception of the sub-caudal melanophores, were derived from studies on adult fish. Due to ontogenetic changes, body coloration, eye diameter, angle of the third posterior preopercular spine, and relation of the tip of the pectoral fin to the anus cannot be applied to larvae. Projection of the jaw tubercle, total number of dorsal fin rays, number of gill rakers, fusion of the occipital-nuchal ridge, and gas bladder musculature are characters which develop after the larval period and hence are inapplicable to larvae.

Larvae with two or more sub-caudal melanophores have been identified by Templeman (1980) as probably S.

fasciatus while S. mentella and S. marinus are more likely to have none or one. Sub-caudal melanophores can only be reliably counted in larvae less than approximately 14 mm due to increasing pigmentation in the caudal area. Development of the hypural elements also alters the orientation of the melanophores. Larvae with two or more sub-caudal melanophores were compared to larvae with none or one by T tests on all applicable morphometric means and by chi-square tests on meristic frequencies. Because time of extrusion introduced unwanted variability into the procedure, only larvae extruded in the same period were compared. The reasons for this restriction will be addressed later in this paper. All T tests and chi-square statistics were not significant.

Larvae 15 mm or larger with fully ossified adult complements of vertebrae and anal fin rays were similarly compared. The utility of these tests was hampered by the necessity of pooling several millimeter size intervals due to low sample sizes of older larvae. First, larvae with 29 vertebrae were compared to larvae with 30 or more vertebrae. All T tests and chi-square statistics were not significant. Secondly, larvae with 7 anal fin rays were compared with larvae having 8 or more anal fin rays. Only 5.6% of all larvae with the adult complement of anal fin rays had a frequency of 7. Again, all T tests and chi-square statistics were not significant. Lastly, larvae with 29 vertebrae and 7

anal fin rays together were compared with larvae having 30 or more vertebrae and 8 or more anal fin rays. Only 3.5% of all larvae with the adult complements of vertebrae and anal fin rays had meristic frequencies of 29 and 7 vertebrae and anal fin rays respectively. Again, T tests on morphometric means were not significant. Due to low sample sizes with both 29 vertebrae and 7 anal fin rays, chi-square statistics could not be performed due to low expected cell frequencies in the test procedure.

III.B.2. Morphometry

Measurements of 25 morphometric variables were used in a Principal Component Analysis (PCA) procedure (SAS, Proc PRINCOMP) to detect the presence of morphometrically distinct groups. Because some variables can only be measured in larvae undergoing flexion or having completed flexion, to facilitate optimum usage of the variables measured, the data were sub-divided into two subsets: subset 1 in which larvae had not initiated or had not completed notochord flexion, and subset 2 in which all larvae had completed notochord flexion.

Table 11 summarizes the results of PCA on subset 1. Two components had eigenvalues greater than 1.0. An eigenvalue less than 1.0 indicates random data noise, no

Table 11. Summary of eigenvector and eigenvalue scores from principal component analysis on morphometric variables of larval redfish in subset 1, 1980 and 1981 combined.

	Eigenvalue	Proportion	Cummulative
Principal Component 1.	9.37	0.669	0.669
Principal Component 2.	1.40	0.100	0.769

	Eigenvectors	
Variable[1]	Prin. 1	Prin. 2
TL	0.295	0.111
SNANLEN	0.303	-0.071
HDLEN	0.299	0.004
SNTLEN	0.242	-0.127
CAUPED	0.291	-0.169
BODPEC	0.308	-0.117
BODAN	0.275	0.173
EYED	0.279	0.046
INTORB	0.236	0.283
HDDEP	0.294	-0.102
PECTLEN	0.191	0.455
PECTDEP	0.223	0.445
PRO2	0.239	-0.467
PRO3	0.232	-0.437

[1]See Appendix A for variable descriptions and definition of abbreviations.

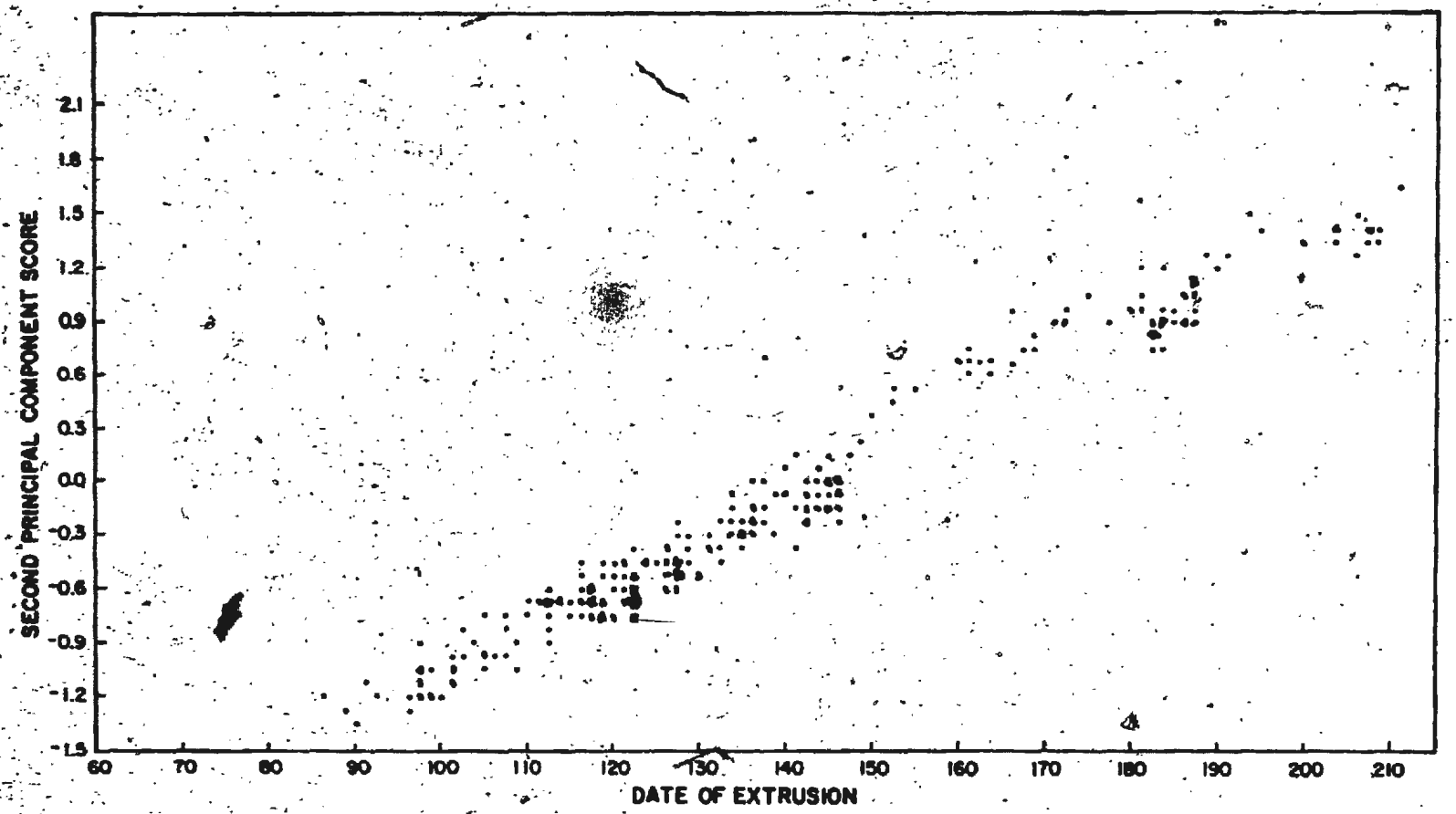
component exists and the variables are generally uncorrelated. Only the first two components are statistically significant (Bartlett's sphericity test, Prob. < 0.01).

Because the individual variable loading on the first component are of approximately equal magnitude for all variables, the first component is interpreted as an indicator of the general relationship of these variables to the variation in fish length in the dataset. The first component explains 67% of the total common variation. The second component is a comparison or differentiation component describing aspects of pectoral fin morphology in relation to preopercular spine formation and secondarily, interorbital width and body depth at the anus with caudal peduncle width, snout length, and head depth. The second component explains a further 10% of the total common data variation.

Using the length at age regression derived from the otolith data for 1980 and 1981, the estimated date of extrusion for each larva was calculated from total length and date of capture. As Figure 19 shows, the second component is highly correlated with the estimated date of extrusion ($R^2 = 0.969$). The second component, therefore, may be interpreted as an extrusion date component.

PCA on subset 2, containing large larvae only and which included the additional variables CAULEN, CANLEN, PDORLEN, PANLEN, PELLEN, PELSLEN, PRO1, PRO4, PRO5, DORLEN,

Figure 19. Second principal component scores (PCA: subset 1) and estimated day of extrusion of redfish larvae during 1980 and 1981.


SECOND PRINCIPAL COMPONENT SCORE
2.1
1.8
1.5
1.2
0.9
0.6
0.3
0.0
-0.3
-0.6
-0.9
-1.2
-1.5
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
DATE OF EXTRUSION

and ANLEN, gave similar results for component 1. Although 2 components had eigenvalues greater than 1.0, only the first was significantly different from 1.0 (Bartlett's sphericity test, Prob. < 0.05). Table 12 summarizes the PCA results. The eigenvector loadings for component 1 are similar for all variables indicating this component may be termed a general length relationship component as in the analysis on subset 1. Although the second component is not statistically significant, it is highly correlated with estimated date of extrusion (R^2 = 0.721). This indicates that, after variation due to larval length is removed, the next most important influence on variation is strongly related to extrusion time.

The relationship of each morphometric variable with the estimated time of extrusion was evaluated by analysis of variance F tests on the interaction of extrusion time with fish length. To facilitate the analysis, larvae were placed into two groups: Group 1 contains larvae whose estimated extrusion time is before Julian day 123 and Group 2 larvae whose extrusion time was on or after Julian day 123. This date was chosen because it approximates the time of completion of peak extrusion in the seasonal extrusion cycle on Flemish Cap.

Analysis of variance F tests, performed on each

Table 12. Summary of eigenvector and eigenvalue scores from principal component analysis on morphometric variables of larval redfish in subset 2, 1980 and 1981 combined.

	Eigenvalue	Proportion	Cumulative
Principal Component 1.	18.51	0.740	0.740
Principal Component 2.	1.09	0.043	0.783

Variable.	Eigenvectors Prin. 1
TL	0.228
SNANLEN	0.225
HDLEN	0.203
SNTLEN	0.142
CAUPED	0.222
BODPEC	0.223
BODAN	0.209
EYED	0.207
INTORB	0.124
HDDEP	0.210
PECTLEN	0.206
PECTDEP	0.174
PELLEN	0.211
PELSLEN	0.217
PRO1	0.179
PRO2	0.179
PRO3	0.174
PRO4	0.170
PRO5	0.185
CAULEN	0.208
CANLEN	0.208
PDORLEN	0.200
PANLEN	0.224
DORLEN	0.221
ANLEN	0.209

variable used in the PCA procedure, found significant interaction effects of estimated extrusion time and larval length (Table 13). Of the 25 morphometric variables included, only 10 (SNTLEN, PELLEN, PELSLEN, PRO1, PRO5, CAULEN, PDORLEN, PANLEN, DORLEN, and ANLEN) did not have significant F values. All but the first of these ten were not measurable in subset 1 larvae.

Plots of individual variable means for one millimeter length groups and their associated 95% confidence intervals for both extrusion groups indicate the length range over which the two extrusion groups differed the most.

Snout to anus length (Fig. 20) was most different between the two extrusion groups in the 8, 11, 13, and 15 mm length intervals. Snout to anus length tended to be greater in Group 2 rather than Group 1 larvae at all sizes up to 16 mm.

Caudal peduncle width (Fig. 21) also had non-overlapping confidence intervals over a wide size range from the 8-13 mm and 15-17 mm length intervals. Caudal peduncle width tended to be greater in all larval length intervals in Group 2 rather than Group 1 larvae.

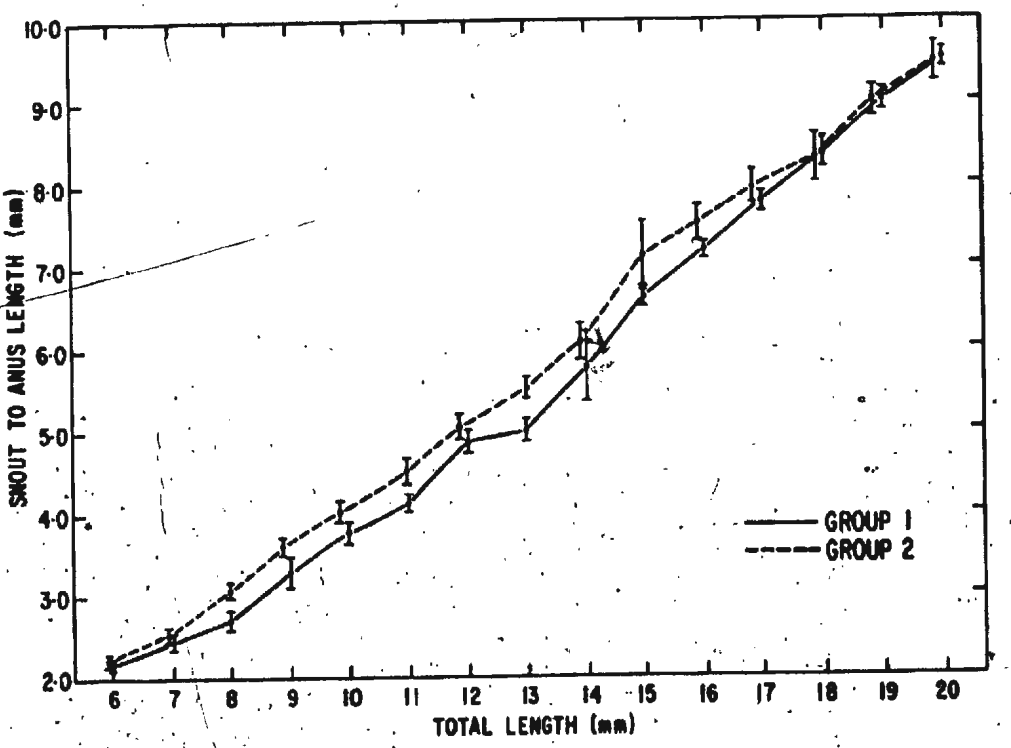
Body depth measured at both the insertion of the pectoral fin and at the anus (Figs. 22 and 23) had non-overlapping confidence intervals in the 8-9 mm, 11 mm, and 15-16 mm length intervals with BODPEC group confidence

Table 13. Summary of analysis of variance F statistics for the interaction effects of extrusion date with total length for larval redfish, 1980 and 1981 combined.

Variable	N	F value	DF	Prob > F
SNANLEN	614	2.40	14	0.0029
HDLEN	614	1.87	14	0.0265
SNTLEN	614	1.42	14	N.S.
CAUPED	614	3.61	14	0.0001
BODPEC	614	3.15	14	0.0001
BODAN	614	3.07	14	0.0001
MAXLEN	526	1.90	12	0.0326
EYED	614	2.60	14	0.0012
INTORB	614	3.45	14	0.0001
HDDEP	610	1.89	14	0.0250
PECTLEN	614	2.53	14	0.0016
PECTDEP	616	2.27	14	0.0052
PELLEN	249	1.69	6	N.S.
PELSLEN	249	1.76	6	N.S.
PRO1	223	1.59	7	N.S.
PRO2	445	3.12	11	0.0005
PRO3	510	2.61	11	0.0032
PRO4	410	3.70	11	0.0001
PRO5	197	0.43	5	N.S.
CANLEN	215	2.14	6	N.S.
CAULEN	225	2.33	6	0.0340
PDORLEN	18	0.97	6	N.S.
PANLEN	230	1.75	6	N.S.
DORLEN	223	1.97	6	N.S.
ANLEN	228	1.52	6	N.S.

Figure 20. Mean snout to anus length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 21. Mean caudal peduncle width in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


SNOUT TO ANUS LENGTH (mm)
10·0
9·0
8·0
7·0
6·0
5·0
4·0
3·0
2·0
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

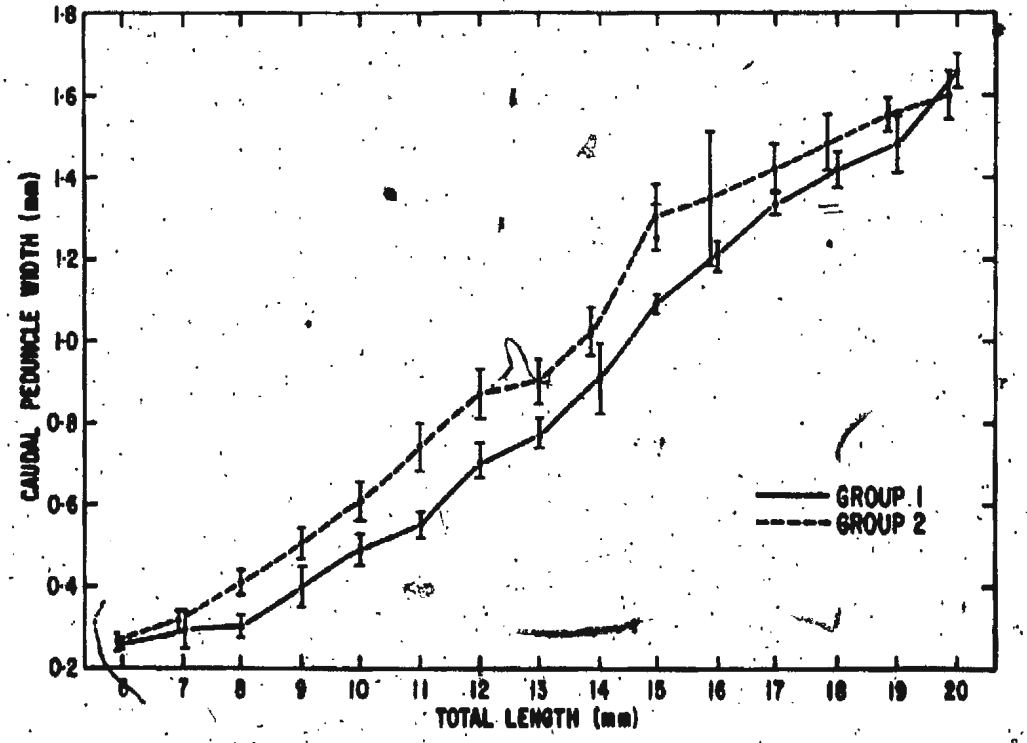
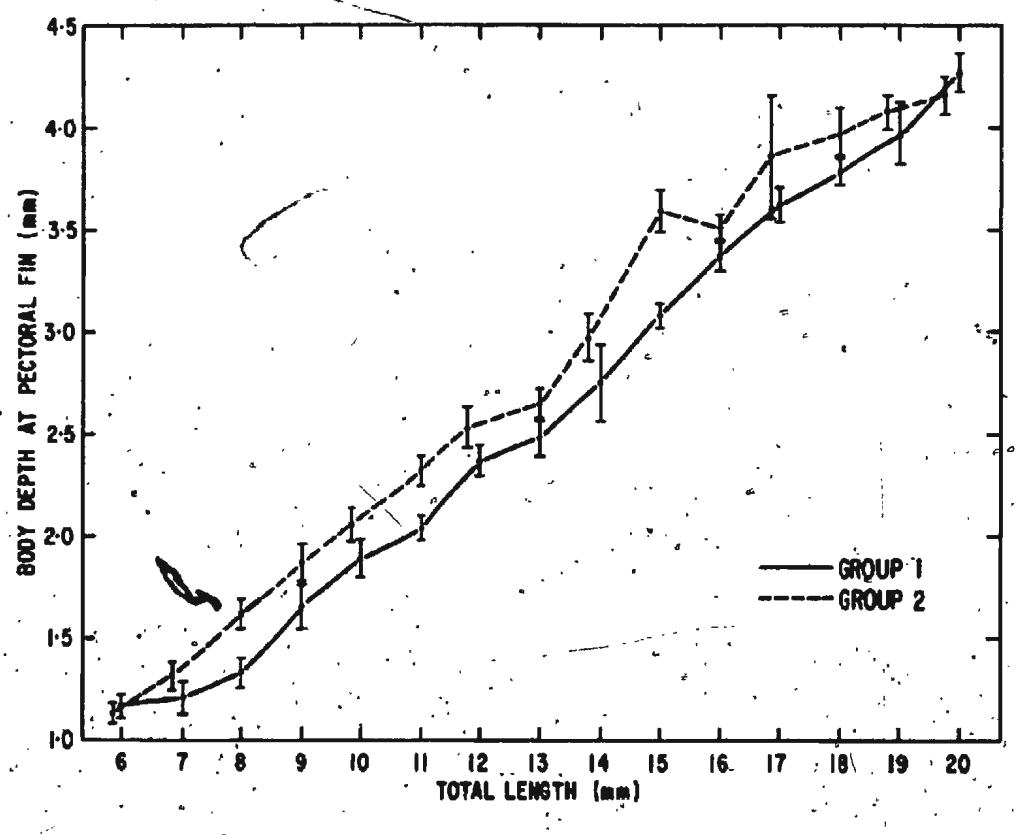
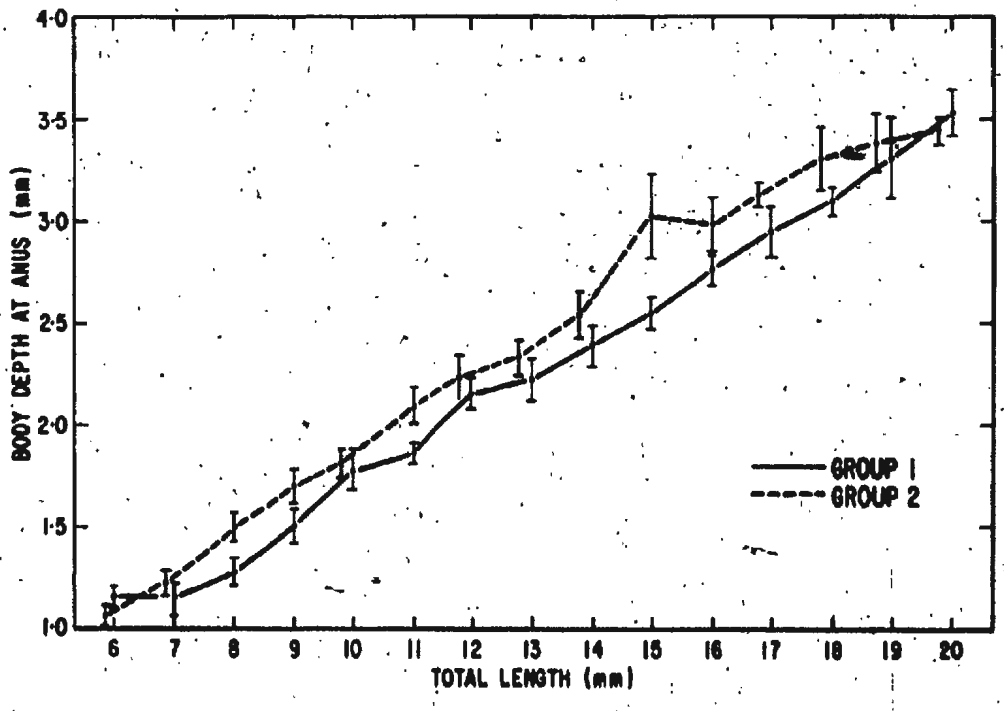

CAUDAL PEDUNCLE WIDTH (mm)
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 22. Mean body depth at the pectoral fin in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 23. Mean body depth at the anus in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


BODY DEPTH AT PECTORAL FIN (mm)
4·5
4·0
3·5
3·0
2·5
2·0
1·5
1·0
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


BODY DEPTH AT ANUS (mm)
4·0
3·5
3·0
2·5
2·0
1·5
1·0
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

intervals not overlapping in the 13 mm and 18 mm length intervals as well. Body depth measurements tended to be greater in Group 2 rather than Group 1 larvae at corresponding length intervals.

Head depth (Fig. 24) was most different between the two extrusion groups in the 8-11 mm, 13 mm, and 15-16 mm length intervals. Head depth tended to be larger in all length intervals in Group 2 larvae.

Head length (Fig. 25) was significantly different over nearly the entire length range with non-overlapping 95% confidence intervals in the 8-13 mm, 15-17 mm, and 19 mm length intervals. Head length tended to be larger in Group 2 larvae in all but the 6 and 7 mm length intervals.

Eye diameter group means (Fig. 26) had non-overlapping confidence intervals in the 8-11 mm, and 13 mm length intervals. Eye diameter was larger in Group 2 rather than Group 1 larvae over all larval length intervals.

Interorbital width means (Fig. 27) had overlapping 95% confidence intervals at all length intervals. Interorbital width had no noticeable tendency towards either larger or smaller values in either of the two extrusion groups.

Pectoral fin length means (Fig. 28) had non-overlapping 95% confidence intervals in the 8 mm, and 14-15 mm length intervals while pectoral fin depth means (Fig.

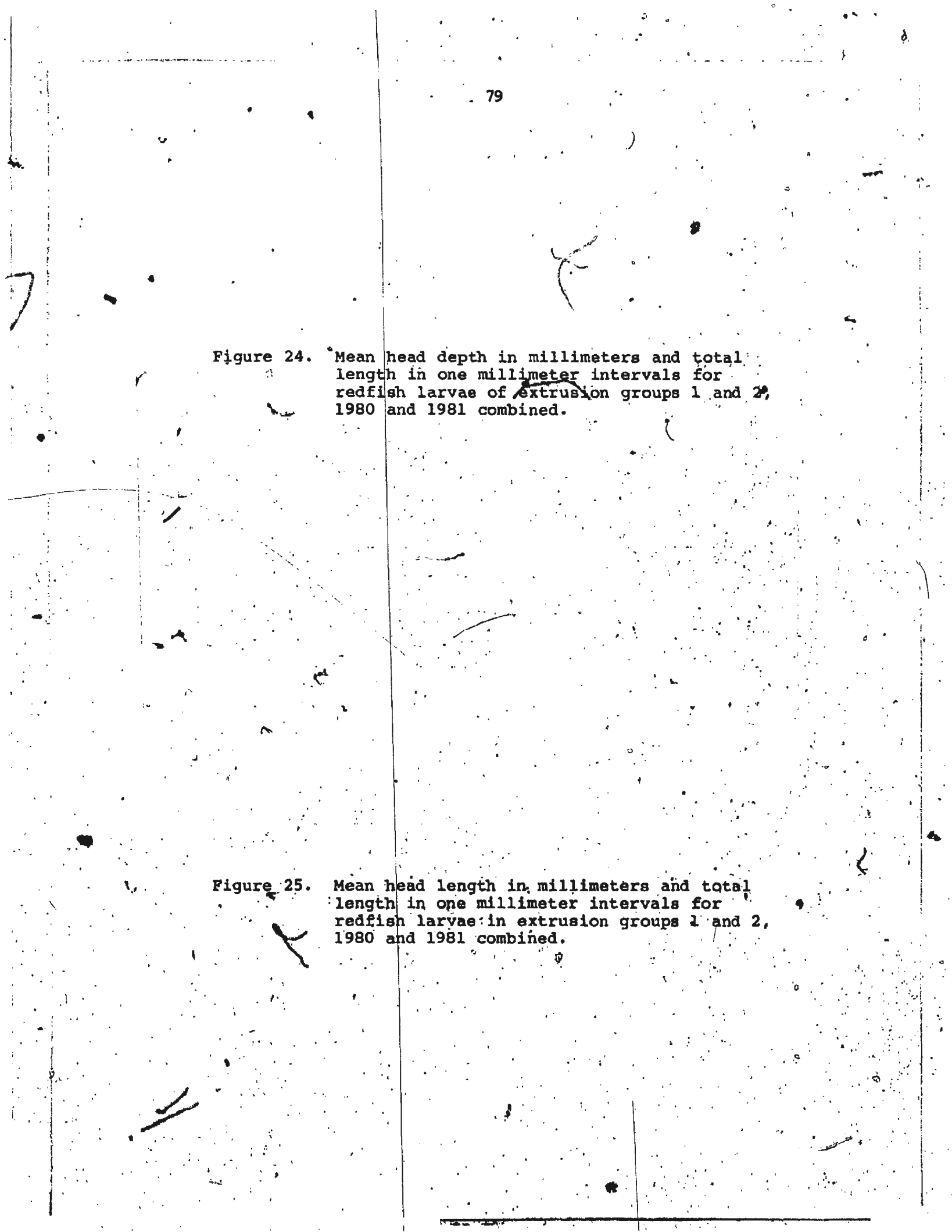
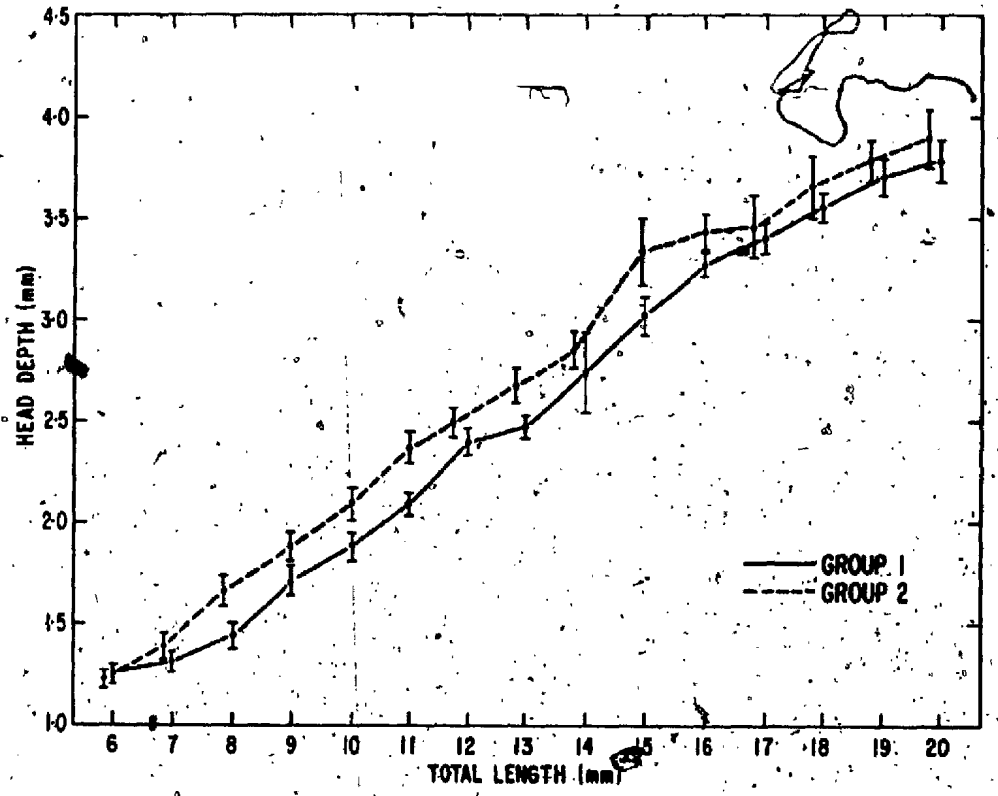
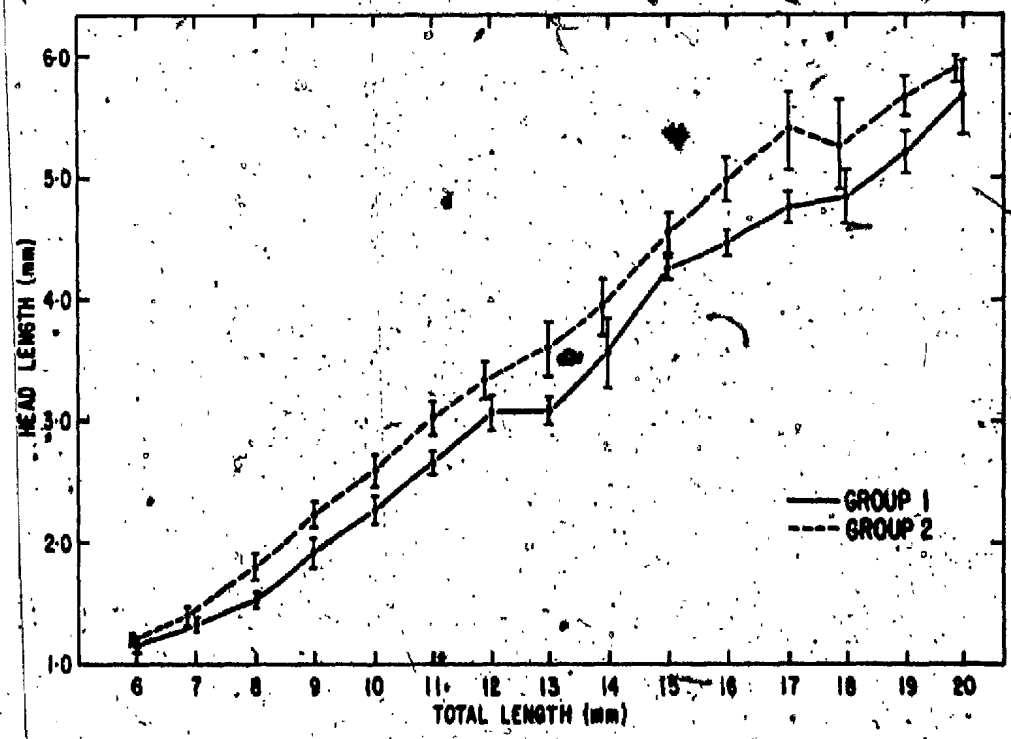


Figure 24. Mean head depth in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 25. Mean head length in millimeters and total length in one millimeter intervals for redfish larvae in extrusion groups 1 and 2, 1980 and 1981 combined.


HEAD DEPTH (mm)
4·5
4·0
3·5
3·0
2·5
2·0
1·5
1·0
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


HEAD LENGTH (mm)
6·0
5·0
4·0
3·0
2·0
1·0
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

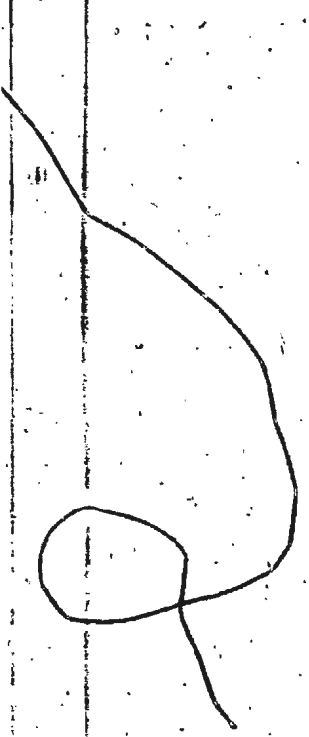


Figure 26. Mean eye diameter in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

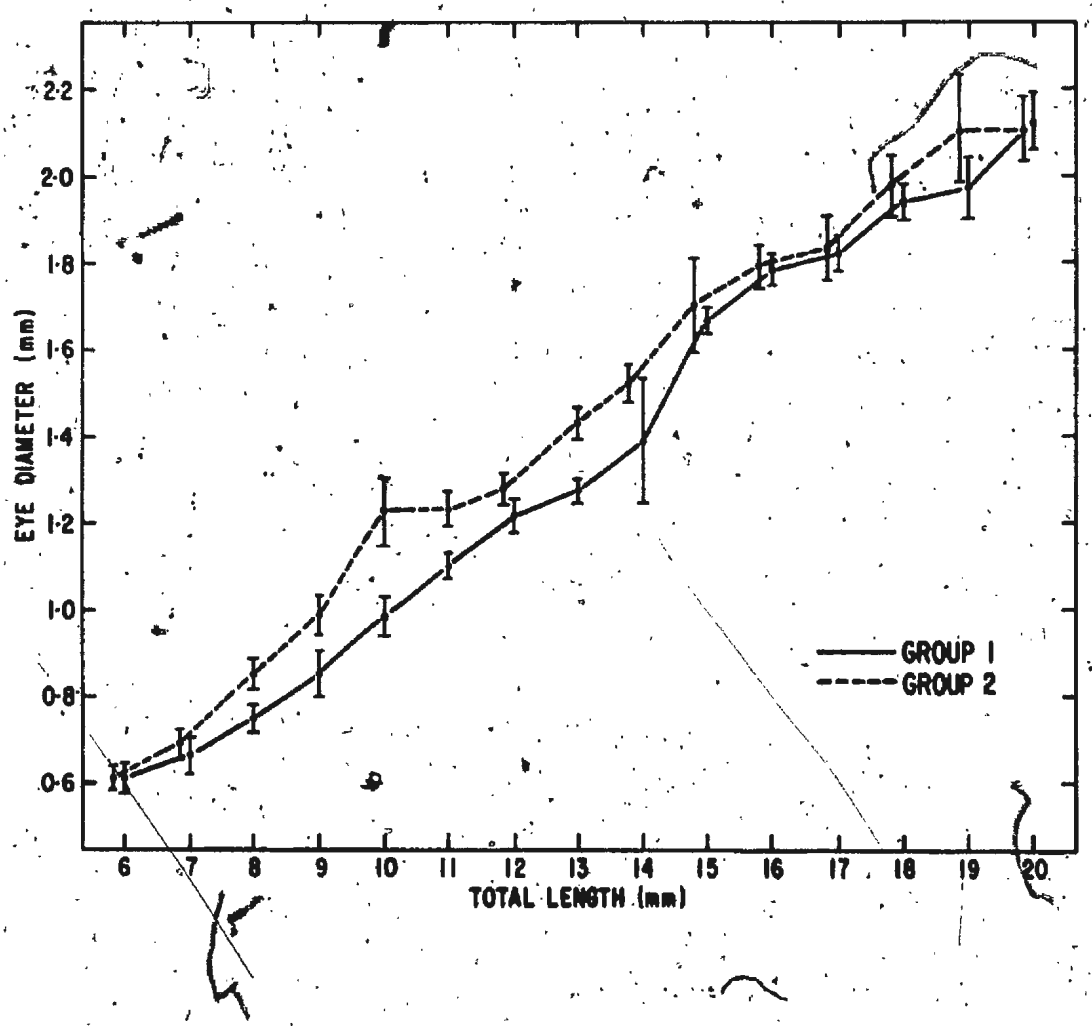
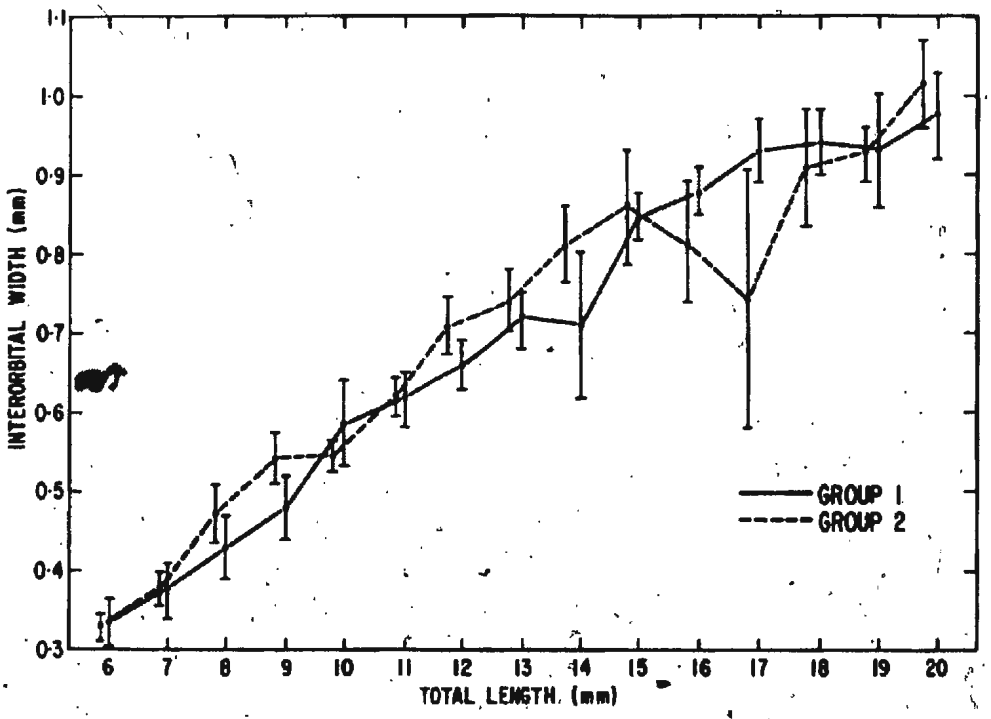
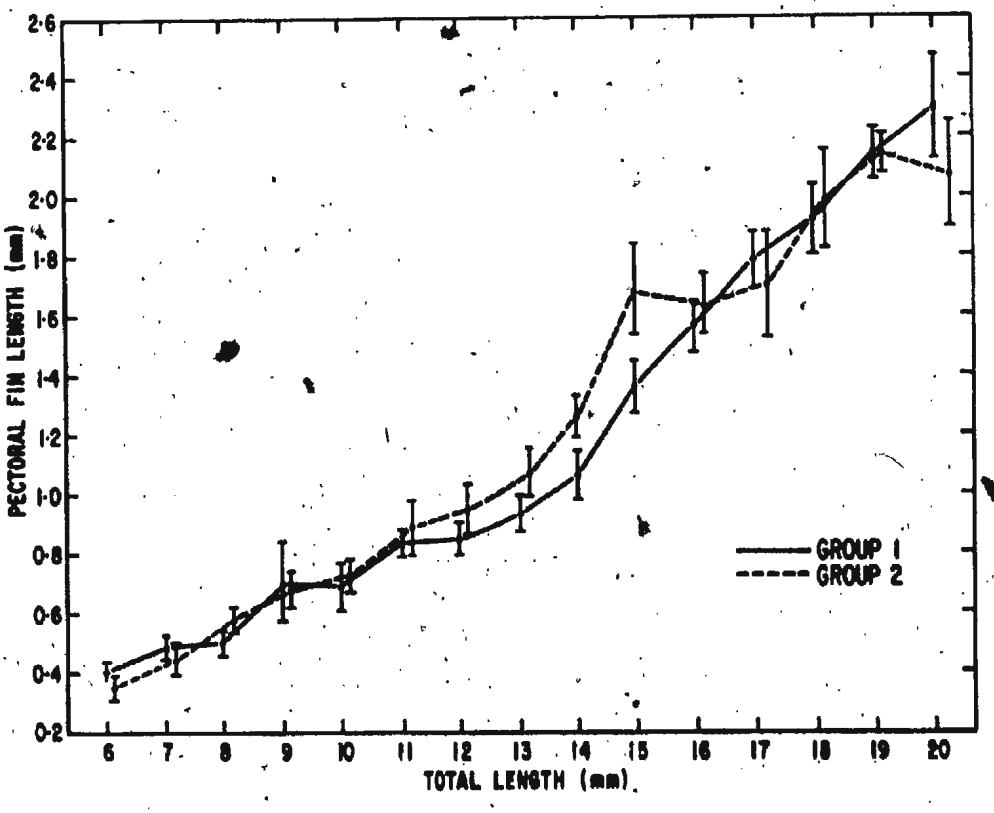

EYE DIAMETER (mm)
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 27. Mean interorbital width in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 28. Mean pectoral fin length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


INTERORBITAL WIDTH (mm)
1·1
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


PECTORAL FIN LENGTH (mm)
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

29) had non-overlapping 95% confidence intervals for only the 7 and 8 mm length intervals. Pectoral fin length was larger in Group 2 rather than Group 1 larvae for all but the 6 mm length interval. Pectoral fin depth tended to be larger in Group 2 larvae at corresponding lengths up to 16 mm.

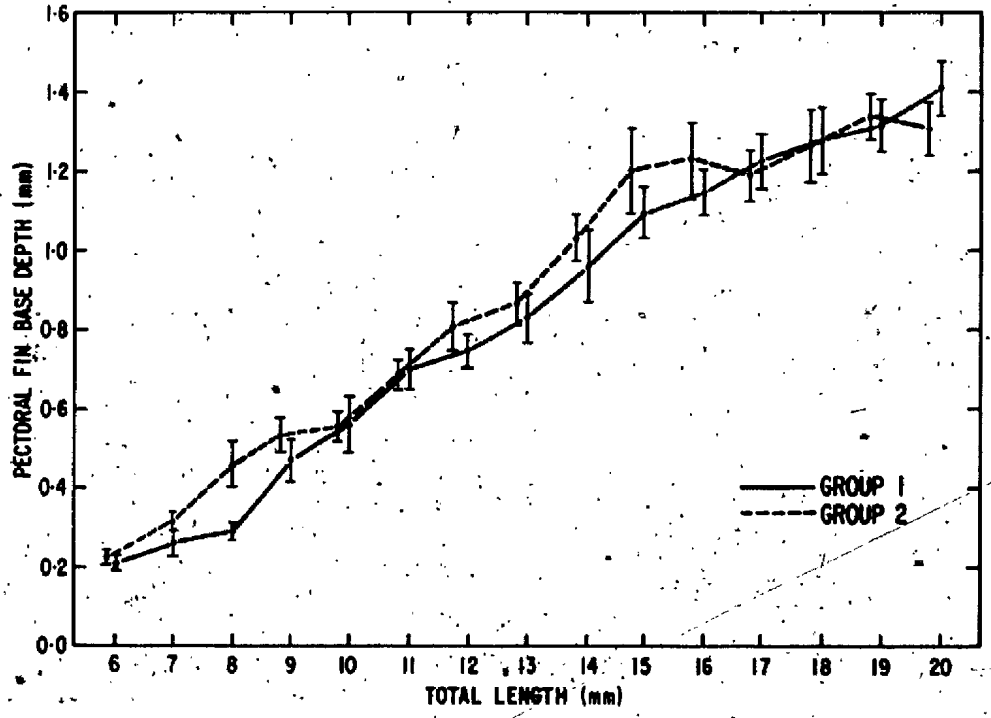
Measurements of CANLEN, the distance from the last ray of the anal fin to the hypural elements, was only possible in fish 14 mm or larger due to the incomplete formation of anal fin rays in smaller larvae. The 95% confidence intervals about the length interval means did not overlap in the 15 and 16 mm length intervals (Fig. 30). CANLEN was the only morphometric variable which tended towards smaller values in Group 2 rather than Group 1 larvae at corresponding larval lengths.

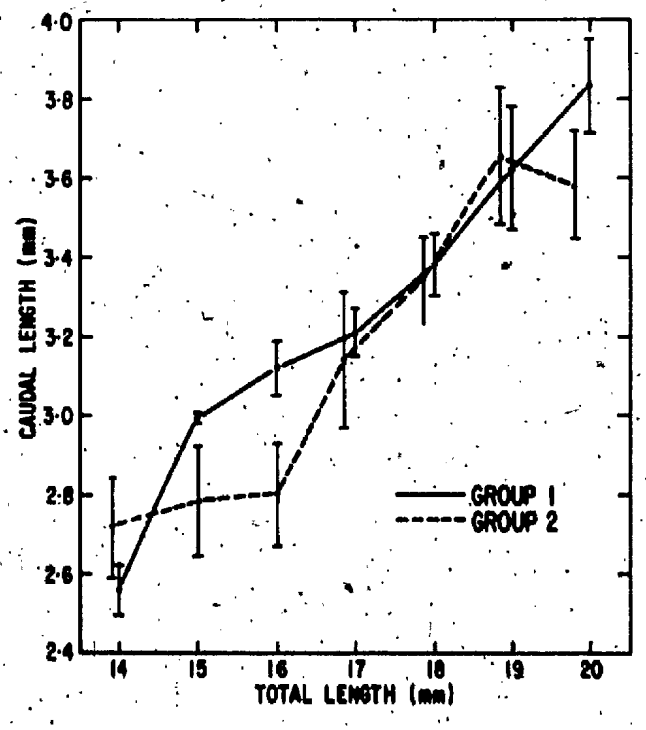
The remaining four morphometric measurements, MAXLEN, PRO2, PRO3, and PRO4, are not obtainable on newly extruded larvae due to the absence of a cartilaginous maxilla and posterior preopercular head spines. These structures develop after extrusion. Differences in the frequency of occurrence of the three head spines between the two extrusion groups will be discussed later in the section on meristics.

The maxilla was not present as an identifiable cartilaginous structure in all larvae of both extrusion groups until 9 mm. In larvae smaller than 9 mm, a greater percentage of Group 2 rather than Group 1 larvae had developed a

Figure 29. Mean pectoral fin base depth in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 30. Mean caudal length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


PECTORAL FIN BASE DEPTH (mm)
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


CAUDAL LENGTH (mm)
4·0
3·8
3·6
3·4
3·2
3·0
2·8
2·6
2·4
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

cartilaginous maxilla (Fig. 31). The differences between extrusion groups in frequency of occurrence of the maxilla was statistically significant ($\chi^2 = 55.53$; Prob. $> \chi^2 = 0.0001$). Subsequent differences between extrusion groups in the length of the maxilla are greatly influenced by the later development of this structure in Group 1 larvae. The 95% confidence intervals around the length interval means for both extrusion groups are not overlapping in the 9-14 mm length intervals (Fig. 32).

Length measurements of posterior preopercular spines 1 and 5 are not significantly different between extrusion groups but measurements of the second, third, and fourth posterior preopercular spines are significantly different. The 95% confidence intervals do not overlap for PRO2 in the 10-15 mm, and 17 mm length intervals with Group 2 larvae having the consistently longer spines (Fig. 33). The third posterior preopercular spine, which is the longest spine of the posterior preopercular series for all larvae in both extrusion groups, is longer in Group 2 rather than Group 1 larvae of corresponding lengths (Fig. 34). The 95% confidence intervals do not overlap in the 10-12 mm and 14-15 mm length intervals. The fourth posterior preopercular spine also tends to be longer in Group 2 larvae. The 95% confidence intervals about the length interval means do not overlap between extrusion groups in the 10-15 mm length

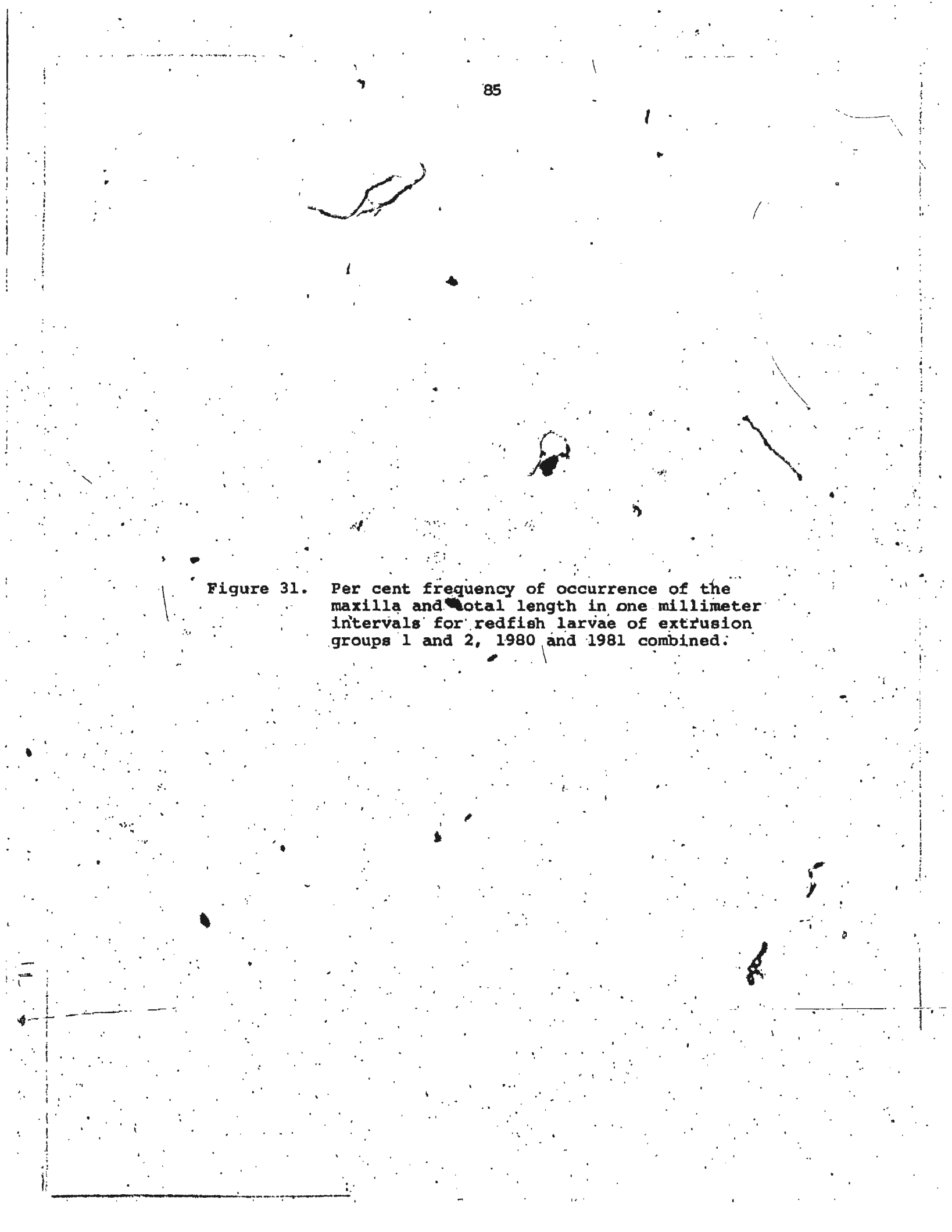


Figure 31. Per cent frequency of occurrence of the maxilla and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

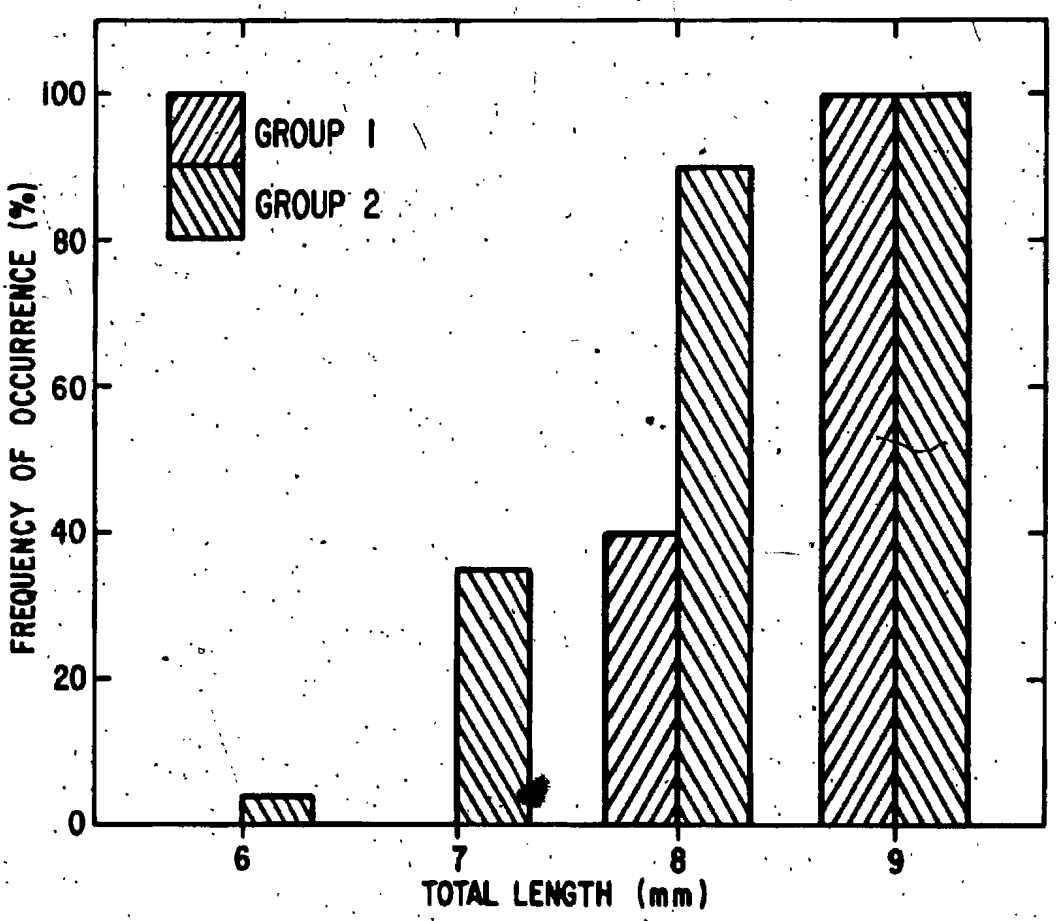
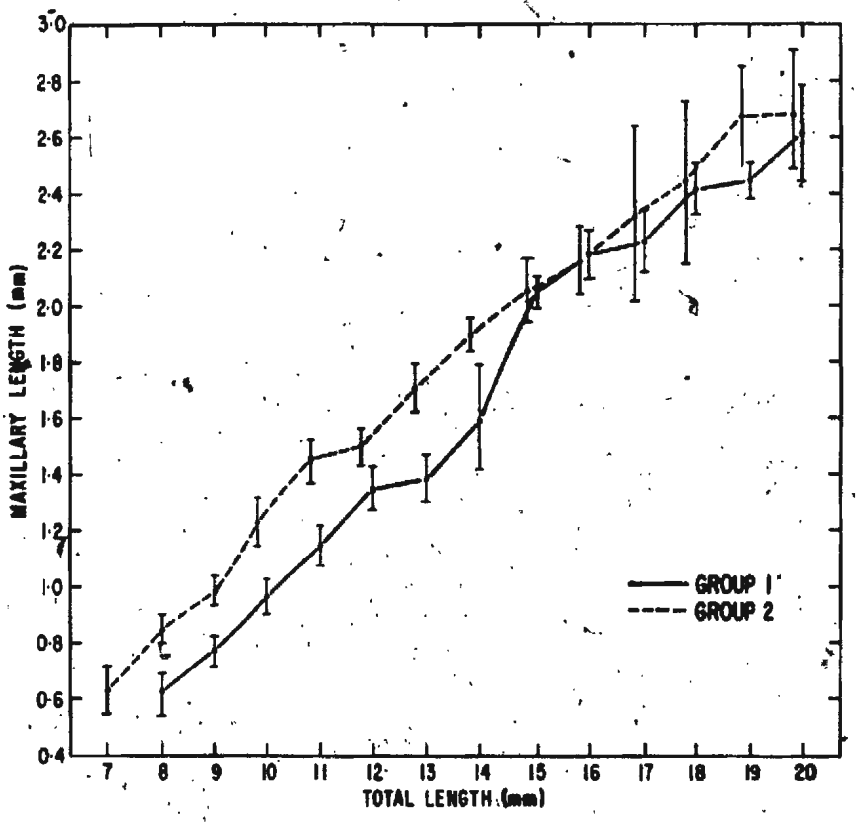

GROUP 1
GROUP 2
FREQUENCY OF OCCURRENCE (%)
100
80
60
40
20
0
6
7
8
9
TOTAL LENGTH (mm)

Figure 32. Mean maxillary length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 33. Mean second posterior preopercular spine length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


MAXILLARY LENGTH (mm)
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

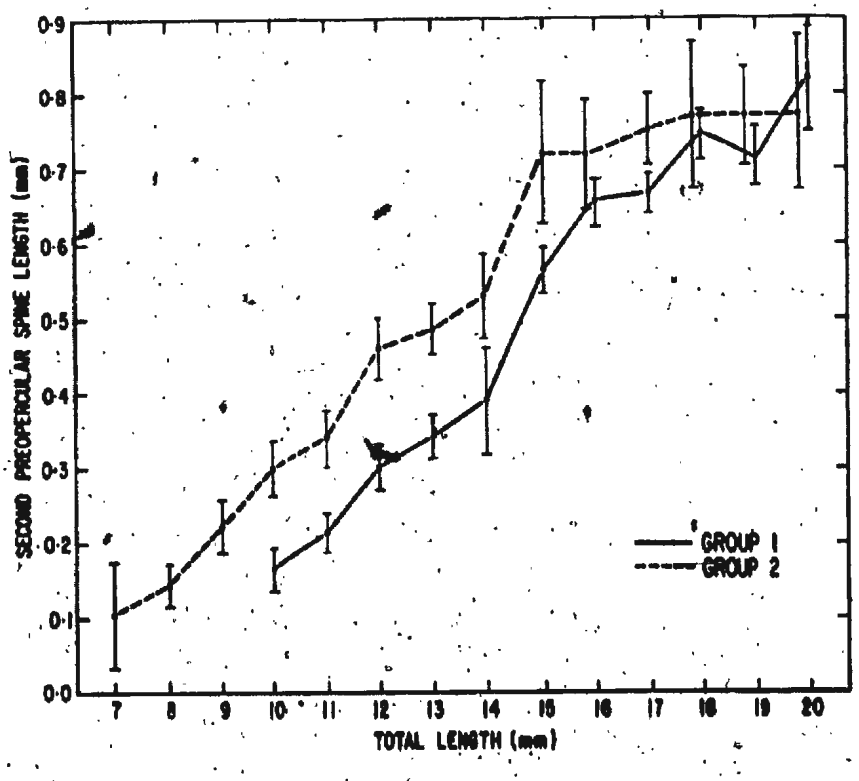
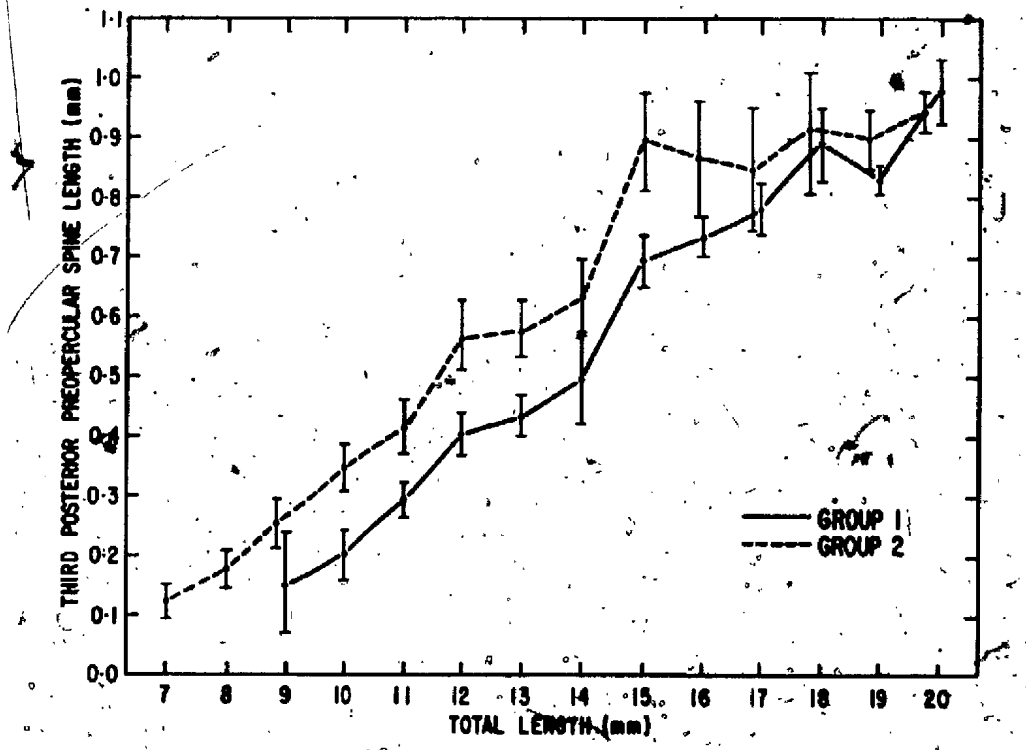
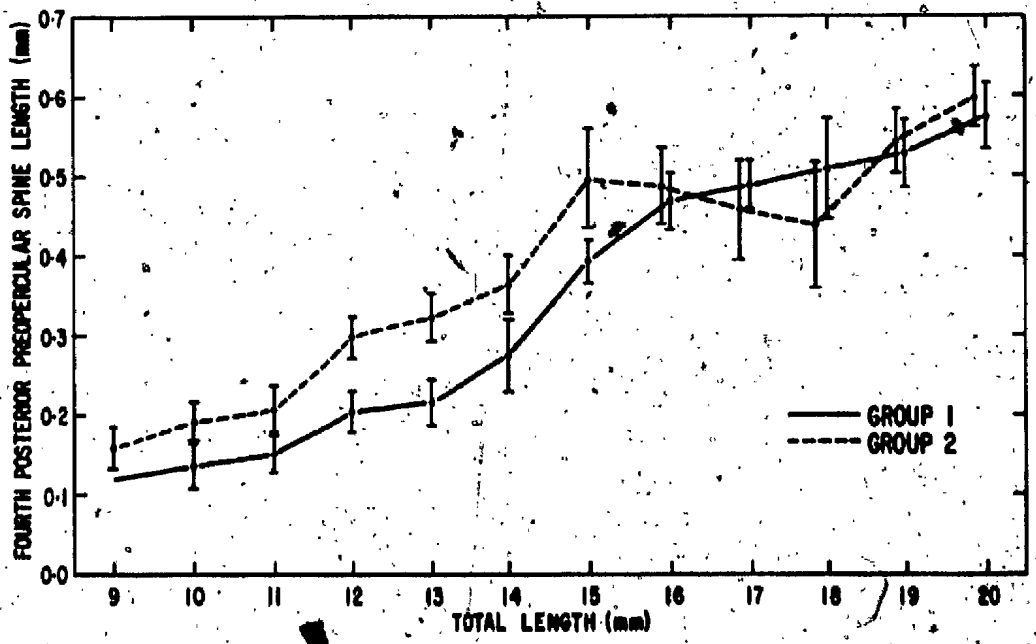

SECOND PREOPERCULAR SPINE LENGTH (mm)
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0·0
7 8 9 10 11 12 13 14 15 16 17 18 19 20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 34. Mean third posterior preopercular spine length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 35. Mean fourth posterior preopercular spine length in millimeters and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


THIRD POSTERIOR PREOPERCULAR SPINE LENGTH (mm)
0·0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
1·1
7
8
9
10
11
12
13
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


FOURTH POSTERIOR PREOPERCULAR SPINE LENGTH (mm)
0·0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
9
10
11
12
13
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

range (Fig. 35).

III.B.3. Meristics

The development of cartilaginous and ossified meristic structures was analysed by comparison of the same extrusion groups as those used in the morphometric analysis. Comparison of Groups 1 and 2 indicated the first occurrence of bony structures such as fin supports and rays, head spines, vertebrae, and gill rakers all usually took place in comparatively smaller Group 2 rather than Group 1 larvae. Comparing larvae of the same total length, Group 2 larvae were usually more advanced in ossification of all bony structures than Group 1 larvae.

Larval meristics were compared between extrusion groups by performing serial Kruskal-Wallis tests on each one millimeter length interval for each meristic variable. The overall significance of the serial Kruskal-Wallis tests for each variable was obtained by pooling the probabilities for each Kruskal-Wallis test into a single chi-square approximation statistic:

$$\chi^2 = -2 \sum_{i=1}^{N} \ln Pi$$

where Pi is the probability of a greater Kruskal-Wallis score for each test i
and N is the number of individual Kruskal-Wallis tests performed on each variable

The chi-square approximation results for differences in the frequency of occurrence and size at ossification of the meristic variables between extrusion groups are summarized in Table 14. The significance of the individual Kruskal-Wallis tests for each variable is indicated graphically in Figs. 36-69. Plotting of the length interval means of meristic variables is done for ease of graphical presentation eliminating the need for extensive and cumbersome histograms or bar charts. Their usage does not imply any statistical meaning or validity. Neither the chi-square nor Kruskal-Wallis tests used are parametric statistics.

The elements of the dorsal fin (DOR = spines + rays) first appeared in Group 2 larvae at 12 mm (Fig. 36) but did not appear in Group 1 until 14 mm. The number of dorsal fin elements had stabilized at 29-30 elements in both extrusion groups by 17 mm. When they first appear, elements of the dorsal fin are undifferentiated into spines and rays. Also, with increasing size, the number of dorsal spines increases with the additional formation of spines anteriorly

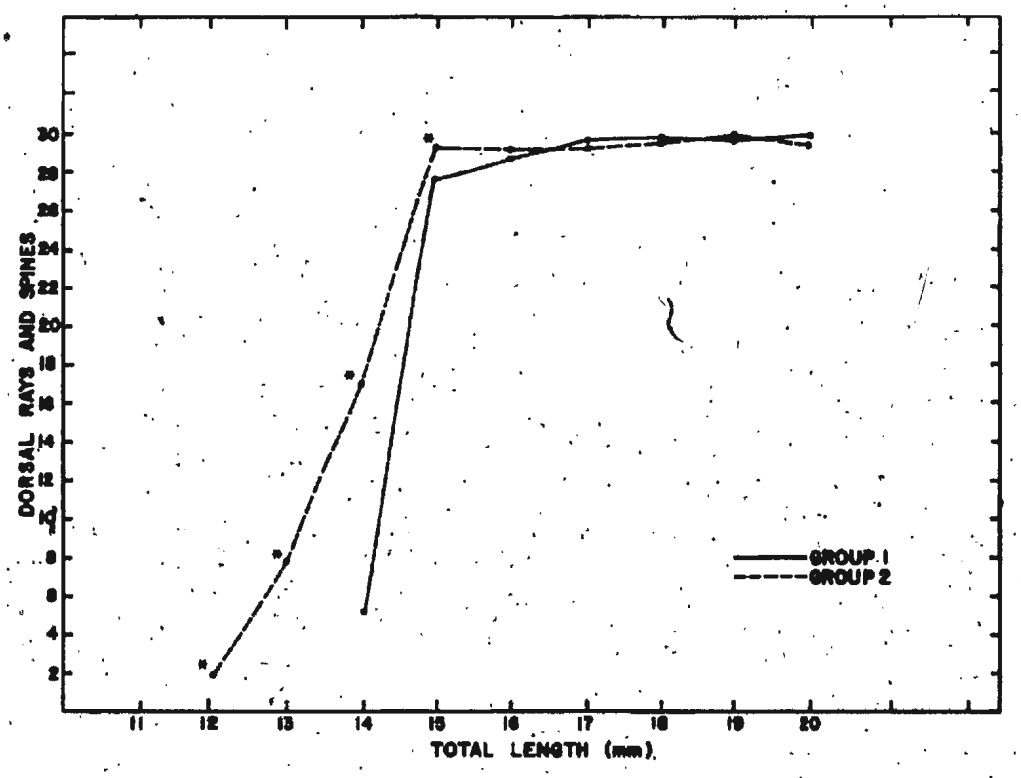
Table 14. Summary of Chi-square approximation statistics for serial Kruskal-Wallis tests on meristic variables comparing redfish in extrusion groups 1 and 2, 1980 and 1981 combined.

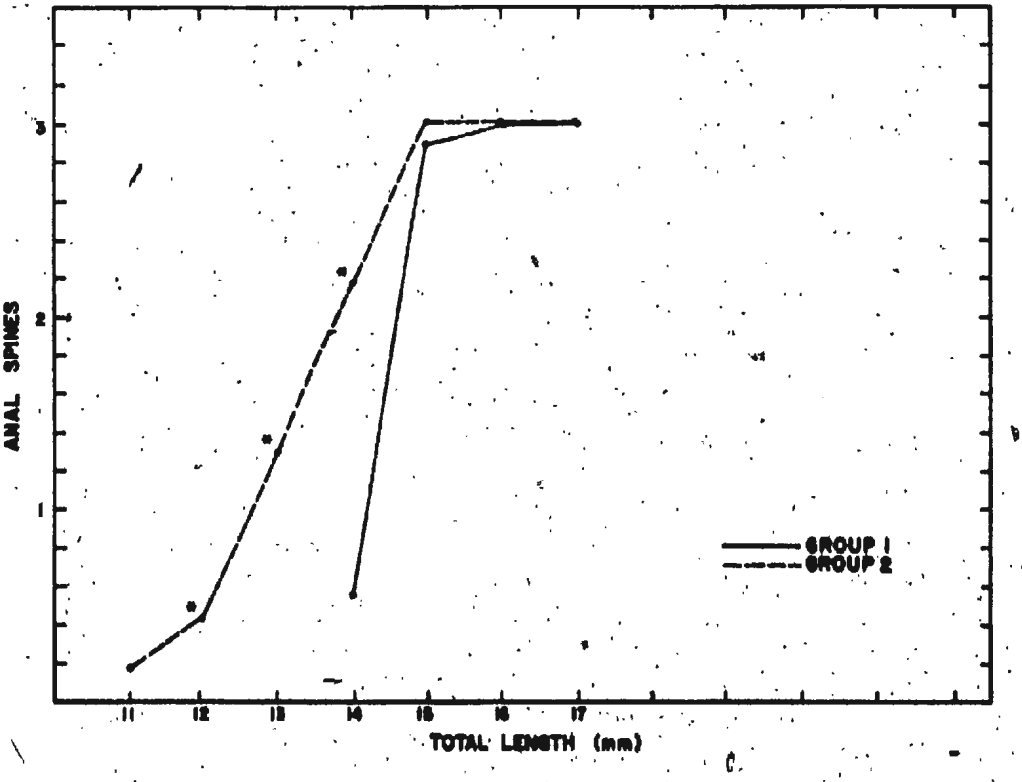
Variable	DF	χ^2	Prob > χ^2
Fin rays and spines			
DOR	18	55.68	0.001
ANSP	12	46.13	0.001
ARAY	20	67.01	0.001
PEC	26	103.95	0.001
PELS	8	43.67	0.001
PELR	10	46.22	0.001
SPRIN	16	115.19	0.001
SPROC	22	81.74	0.001
IPRIN	14	68.31	0.001
IPROC	24	105.57	0.001
Head Spines:			
NU	14	54.66	0.001
PR	10	29.59	0.005
PP1	8	9.80	N.S.
PP2	14	54.53	0.001
PP3	14	72.30	0.001
PP4	14	60.03	0.001
PP5	10	14.56	N.S.
AP1	12	15.31	N.S.
AP2	14	66.52	0.001

Variable	DF	χ^2	Prob > χ^2
AP3	18	45.22	0.001
AP4	14	58.37	0.001
SP	16	71.44	0.001
IP	12	40.62	0.001
PT	16	67.32	0.001
SCL	14	42.15	0.001
PTS	10	58.33	0.001
IN11	12	31.01	0.005
IN12	6	10.23	N.S.
IN3	10	8.94	N.S.
SUB1	12	42.44	0.001
SUB2	14	29.26	0.010
POC	12	45.19	0.001
NA	12	33.58	0.001
PTI	4	6.06	N.S.
Other variables:			
FLEX	14	94.11	0.001
BR	26	131.56	0.001
GRAKL	28	121.36	0.001
GRAKU	22	93.11	0.001
MYOM	18	27.35	N.S.
ANMYOM	18	59.42	0.001
VERT	22	87.28	0.001

Figure 36. Mean number of dorsal rays and spines combined, and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 37. Mean number of anal spines and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


DORSAL RAYS AND SPINES
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


ANAL SPINES
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

to about 18-20 mm. The most posterior of the dorsal fin ray elements are also late to form and the last ray is divided at its base. Where spines and rays abut each other, the posteriormost spines form from differentiation of rays at 18-20 mm in both extrusion groups.

Anal spines (Fig. 37) and rays (Fig. 38) first appeared in Group 2 larvae at 11 mm compared to 14 mm in Group 1. At first, spines and rays are undifferentiated but, as development proceeds, the first two spines can be distinguished. The rays nearest the spines form first with the posteriormost ray, which is divided at its base, forming last. Differentiation of the third element of the anal fin into a spine occurs around 16 mm in Group 1 and 15 mm in Group 2. Most larvae in both extrusion groups had also reached the adult complement of 7-10 anal fin rays at this size as well. The adult complement of rays ranged from 8-10 in Group 1 larvae and 7-10 in Group 2 larvae. A chi-square test to compare differences in the adult complement of anal fin rays between the two extrusion groups was not significant (Prob. > 0.05). However, larvae with complete anal fin ray counts of 7 were found only in Group 2.

Pectoral fin rays were present in some Group 2 larvae at 8 mm but did not appear until 10 mm in Group 1 (Fig. 39). The first occurrence of pectoral rays as cartilaginous structures and their subsequent ossification proceeds from

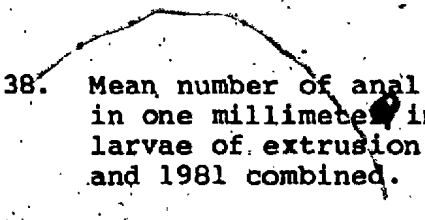
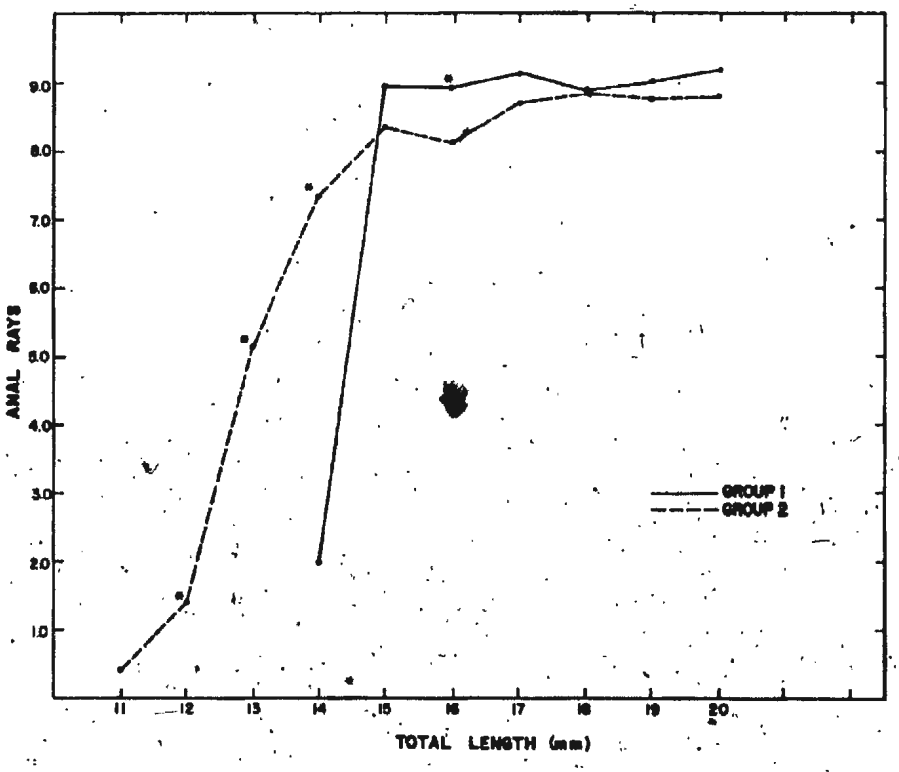
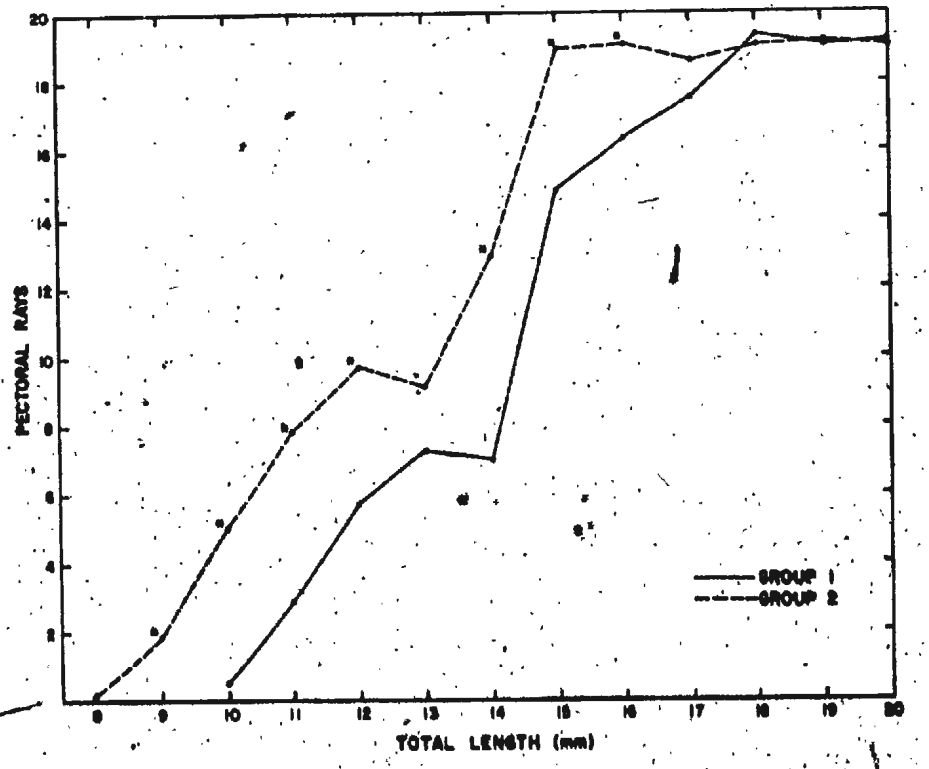


Figure 38. Mean number of anal rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 39. Mean number of pectoral rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


ANAL RAYS
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
11
12
13
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


PECTORAL RAYS
20
18
16
14
12
10
8
6
4
2
8
9
10
11
12
13
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

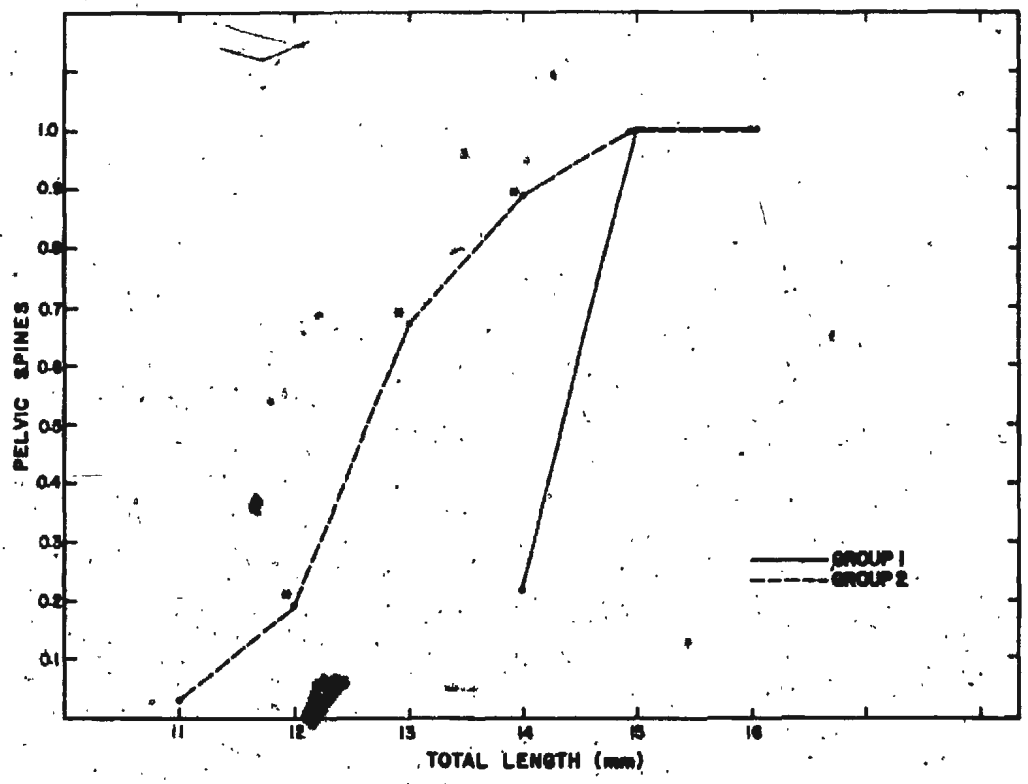
the uppermost rays ventrally to the ventral fin margin. The adult complement of 19-20 pectoral fin rays was reached in all Group 2 larvae by 15 mm and Group 1 larvae by 18 mm. A chi-square test comparing the adult complement of pectoral rays between extrusion groups was not significant (Prob. > 0.05).

Development of elements of the pelvic fin (Figs. 40 and 41) also began earlier in Group 2 larvae. Both pelvic spines and rays first occurred at 11 mm in Group 2 larvae but were delayed until 14 mm in Group 1. All larvae of both extrusion groups had the adult complement of one pelvic spine by 15 mm. All Group 2 larvae had the adult complement of 5 pelvic rays at 15 mm but this was delayed in Group 1 until 16 mm.

Both superior and inferior principal elements of the caudal fin appeared at 7 mm in Group 2 larvae but did not appear until 9 mm in Group 1 (Figs. 42 and 43). The adult complement of 8 superior principal caudal rays was reached in all Group 2 larvae by 14 mm and all Group 1 larvae by 15 mm. The adult complement of 7 inferior principal caudal rays was reached in Group 2 at 13 mm and in all Group 1 larvae at 14 mm. In both extrusion groups, development and ossification of the inferior elements seemed to precede the superior elements. First occurrence as cartilaginous structures and subsequent ossification of the superior

Figure 40. Mean number of pelvic spines and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 41. Mean number of pelvic rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


PELVIC SPINES
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
11
12
13
14
15
16
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

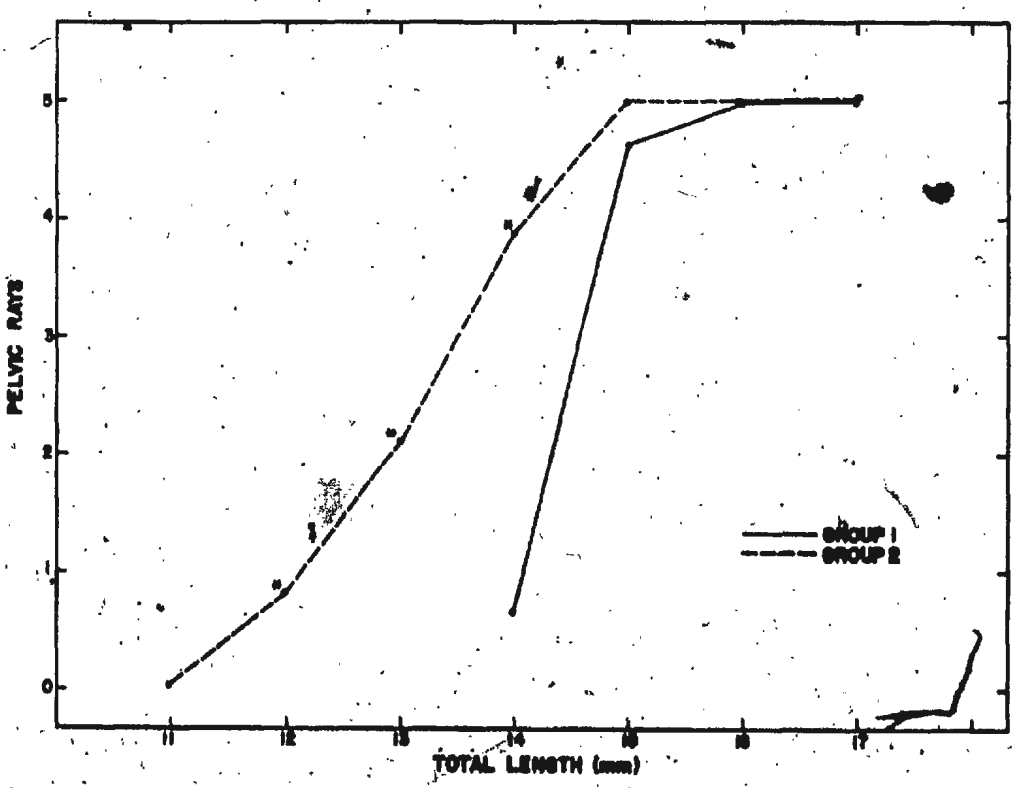
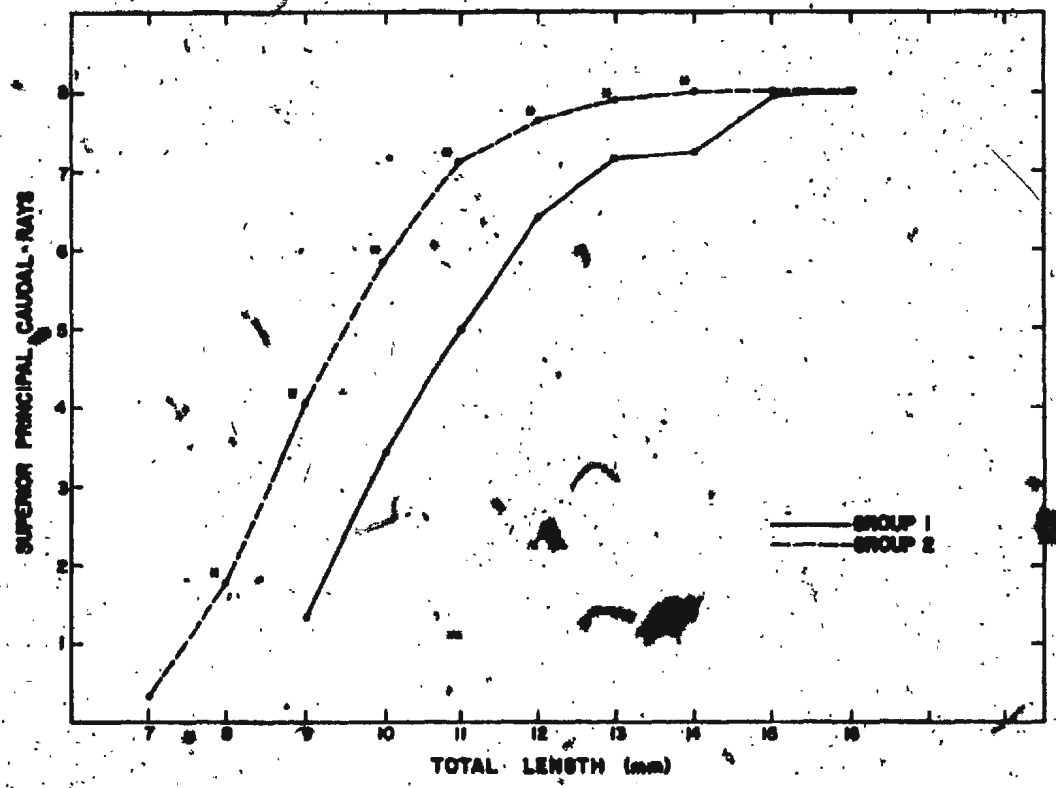
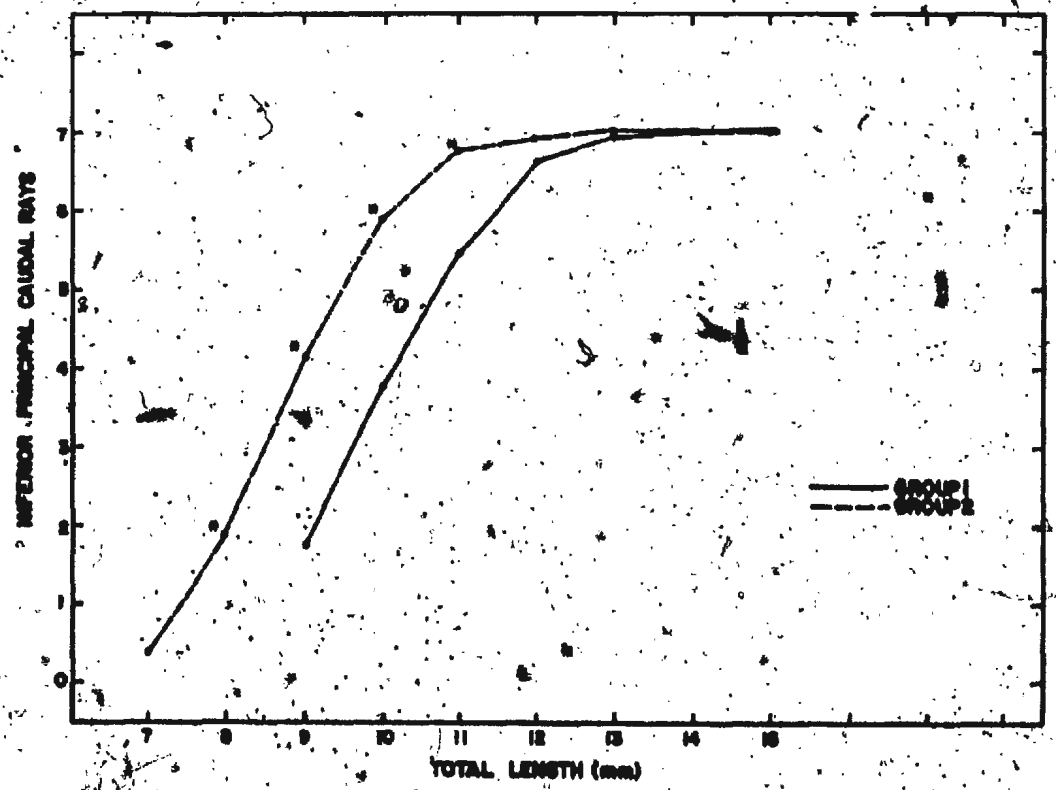

PELVIC RAYS
5
4
3
2
1
0
11
12
13
14
15
16
17
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 42. Mean superior principal caudal rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 43. Mean inferior principal caudal rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


SUPERIOR PRINCIPAL CAUDAL RAYS
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


INFERIOR PRINCIPAL CAUDAL RAYS
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

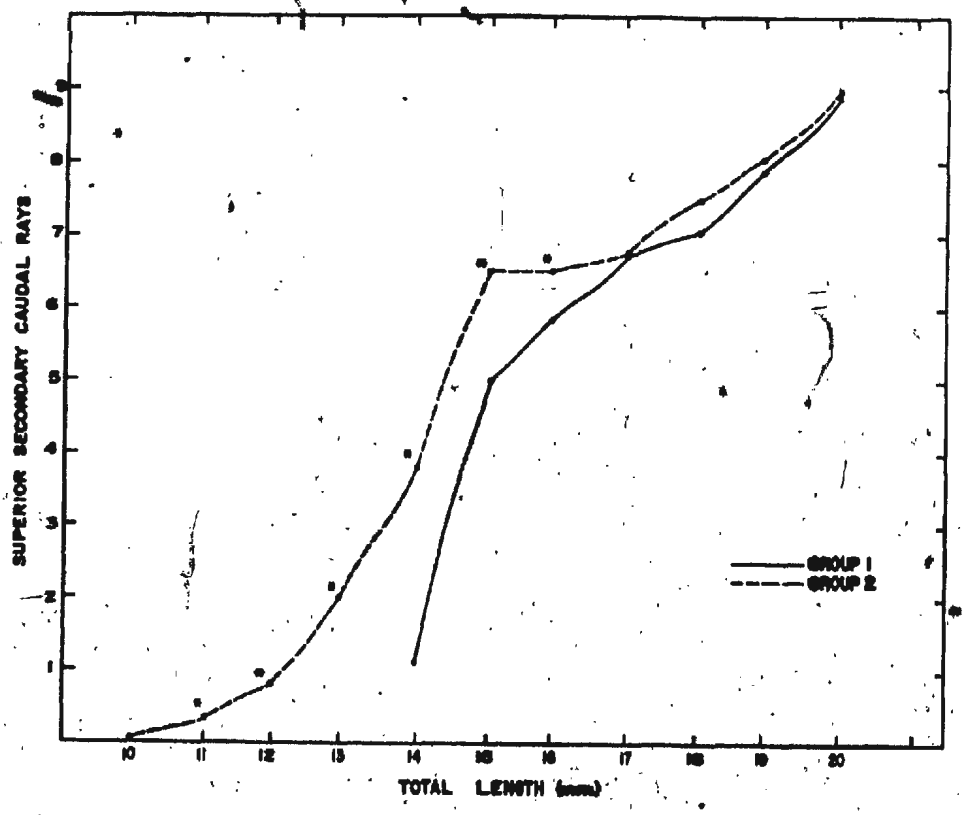
principal caudal rays started with the most ventral rays and proceeded dorsally while the inferior principal caudal rays started with the most dorsal and proceeded ventrally.

Inferior secondary elements of the caudal fin appeared before the superior secondary elements in both extrusion groups. Inferior secondary caudal rays appeared at 9 mm in Group 2 larvae but were delayed until 11 mm in Group 1. The adult complement was not attained in either extrusion group by 20 mm. Superior secondary caudal rays appeared at 10 mm in Group 2 larvae but did not appear until 14 mm in Group 1. The adult complement of superior secondary caudal rays was also not reached in both extrusion groups by 20 mm (Figs. 44 and 45). The first occurrence as cartilag- inous structures and subsequent ossification of the secondary rays was from dorsal to ventral for the inferior rays and from ventral to dorsal for the superior rays.

Notochord flexion, which is associated with development of the hypural elements of the caudal fin, first occurred at 8 mm in Group 2 larvae but was delayed until 10 mm in Group 1 (Fig. 46). Larvae in various intermediate stages of completion of notochord flexion were found in all length intervals from 8-13 mm in Group 2 and 10-14 mm in Group 1. All Group 2 larvae had completed notochord flexion by 14 mm in Group 2 and 15 mm in Group 1.

Figure 44. Mean superior secondary caudal rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 45. Mean inferior secondary caudal rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


SUPERIOR SECONDARY CAUDAL RAYS
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

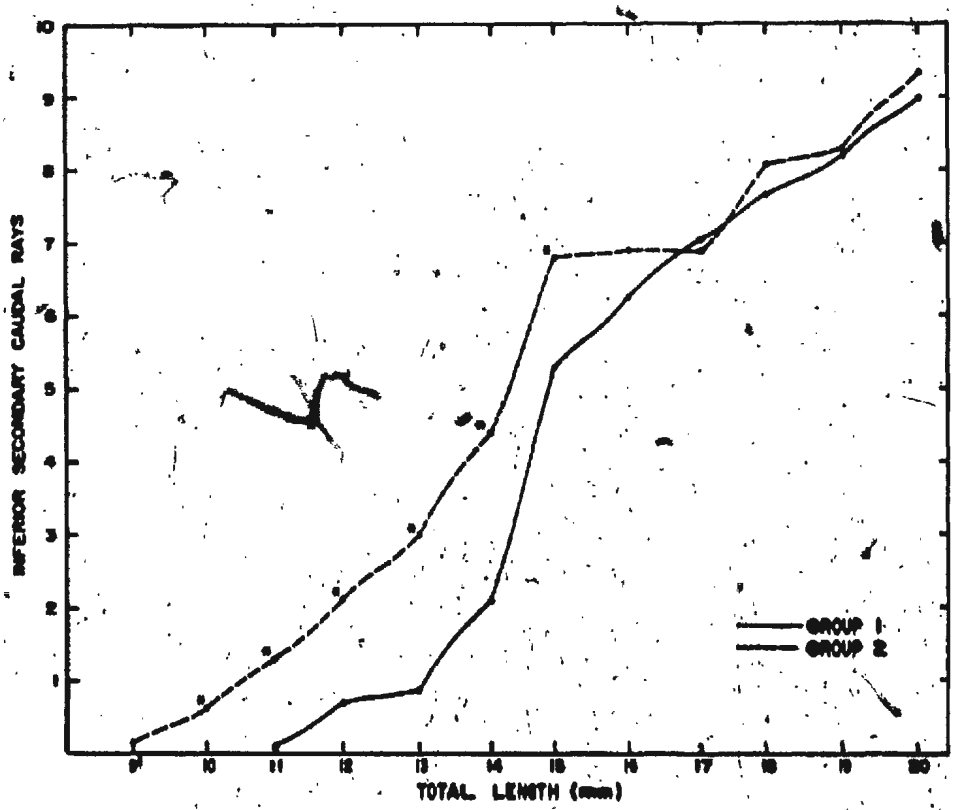
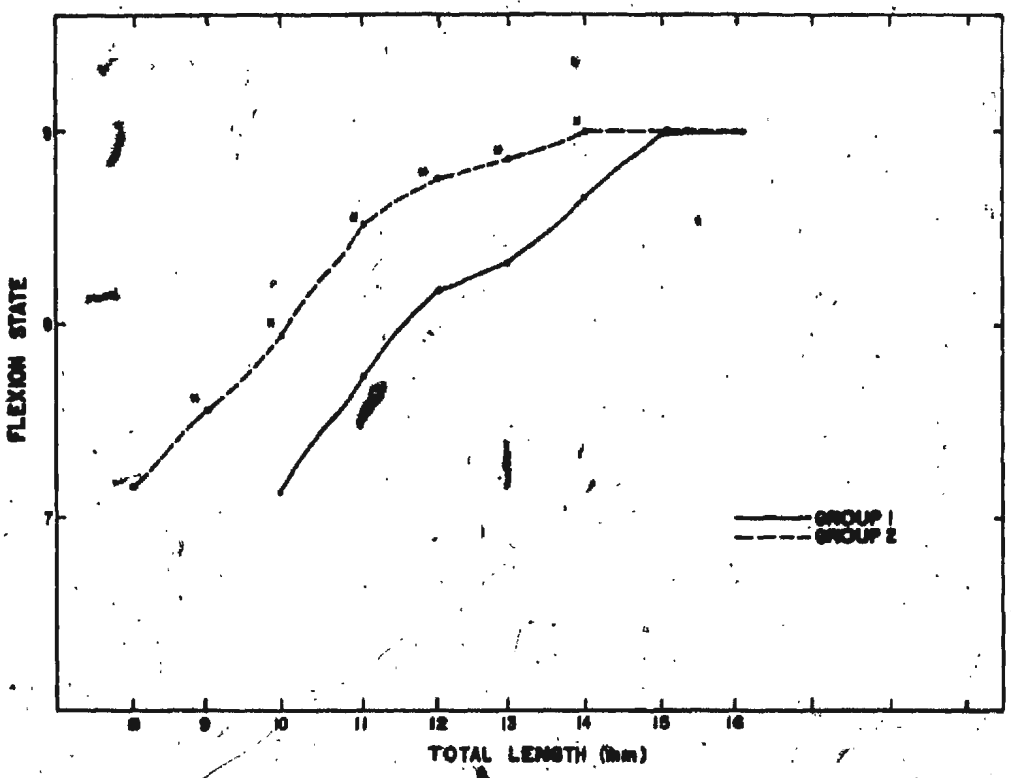
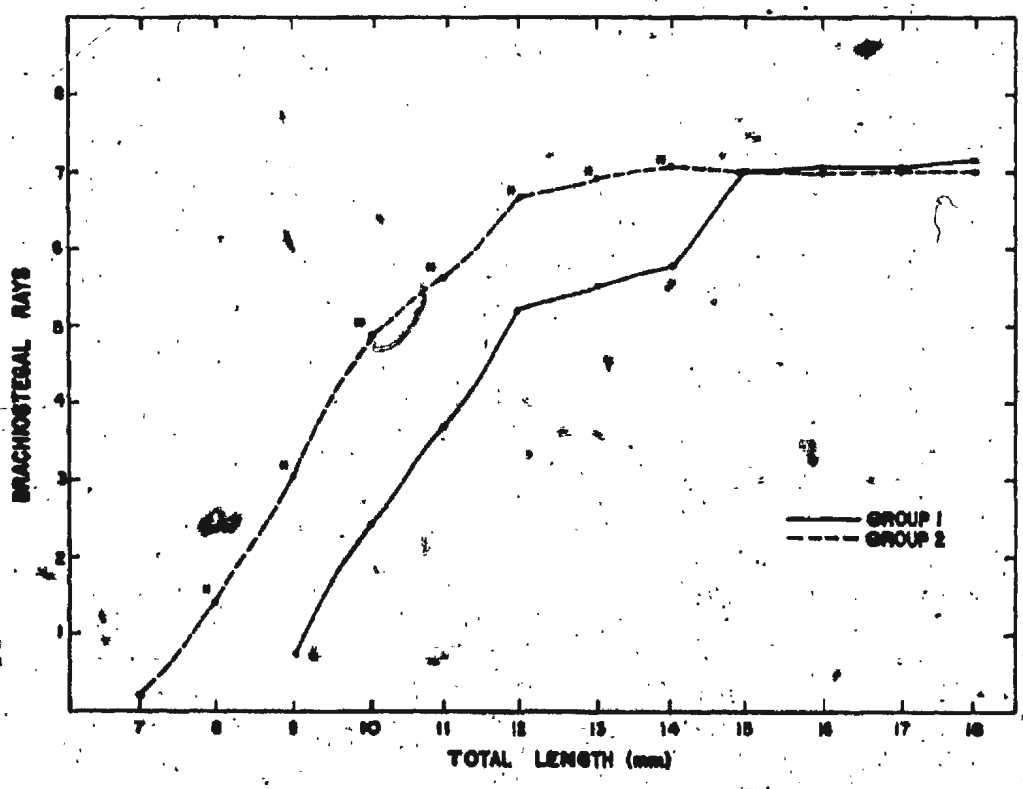

INFERIOR SECONDARY CAUDAL RAYS
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 46. Mean state of flexion of the notochord and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. (flexion state 7 is pre-flexion, 8 is in-flexion and 9 is post-flexion)

Figure 47. Mean number of brachiostegal rays and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


FLEXION STATE
9
8
7
8
9
10
11
12
13
14
15
16
TOTAL LENGTH (mm)
GROUP I
GROUP 2


BRACHIOSTEGAL RAYS
8
7
6
5
4
3
2
1
7
8
9
10
11
12
13
14
15
16
17
18
TOTAL LENGTH (mm)
GROUP I
GROUP 2

Brachiostegal rays first occurred at 7 mm in Group 2 larvae and at 9 mm in Group 1 (Fig. 47). The adult complement of 7-8 brachiostegal rays was reached in all Group 2 larvae at 14 mm and all Group 1 larvae at 15 mm. Fewer than 2% of all larvae from both extrusion groups had 8 brachiostegal rays as the adult complement.

Gill rakers of the lower arm of the first gill arch (Fig. 48) first appeared in 7 mm larvae from Group 2 and 9 mm larvae from Group 1. The number of gill rakers on the lower arm of the gill arch had still not stabilized by 20 mm. Gill rakers did not appear on the upper arm of the first gill arch until 10 mm in Group 2 larvae and 12 mm in Group 1 larvae (Fig. 49). By 20 mm, larvae in both extrusion groups had 21-24 lower gill rakers and 6-9 upper gill rakers.

Vertebrae first began forming at 10 mm in Group 2 larvae and 12 mm in Group 1 (Fig. 50). All larvae in Group 2 had reached the adult complement of 29-31 vertebrae by 15 mm but Group 1 larvae did not all reach the adult complement until 17 mm. Larvae with adult complements of 29, 30, and 31 vertebrae were found in both extrusion groups. A chi-square test comparing differences in frequency of occurrence of adult vertebral counts between extrusion groups was not significant (Prob. $>$ 0,05).

Body myomeres in both extrusion groups ranged from 29-

Figure 48. Mean number of lower gill rakers on the first gill arch and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

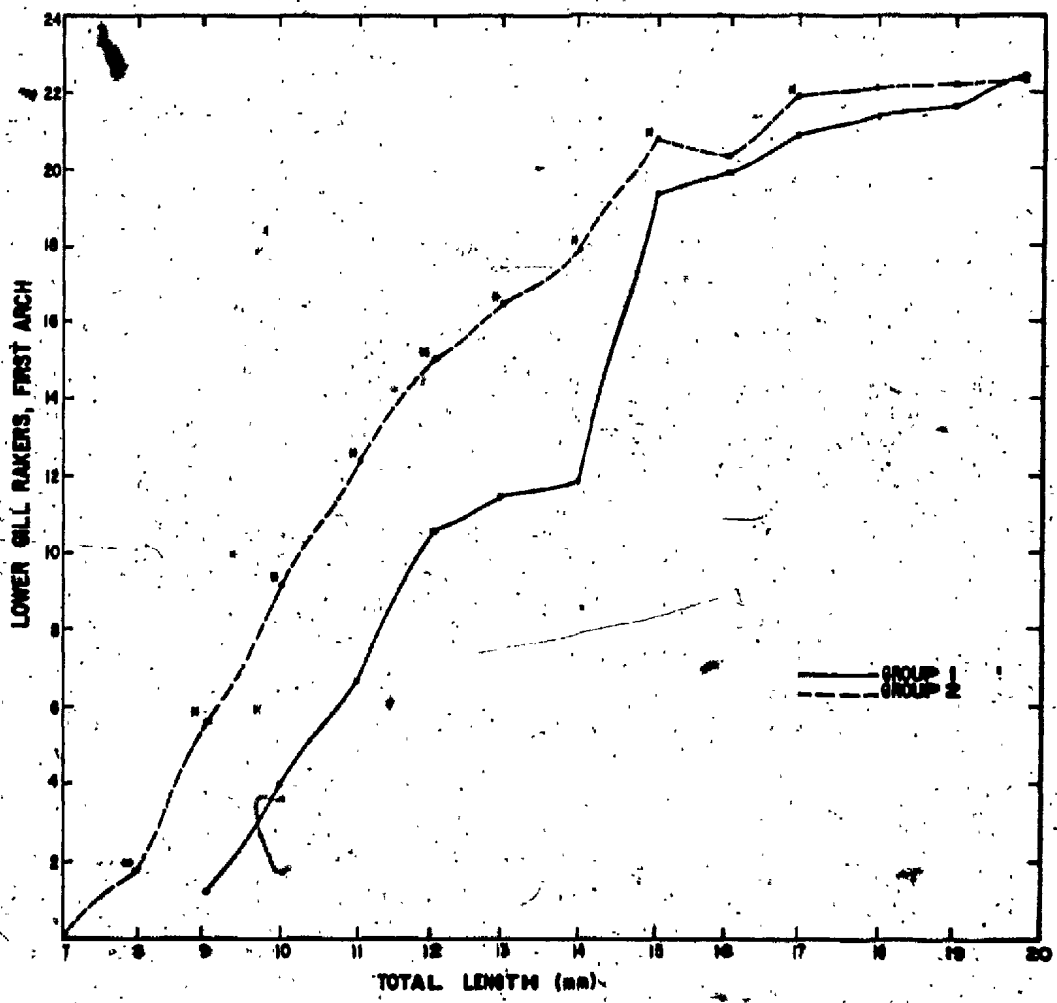
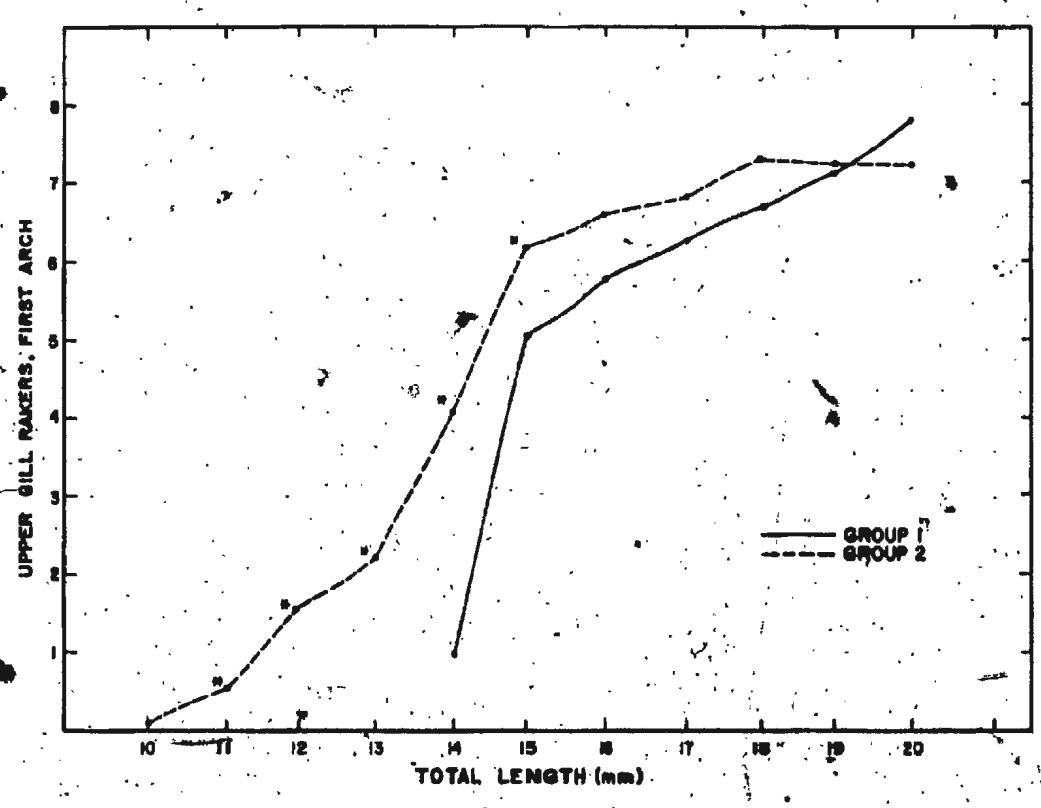
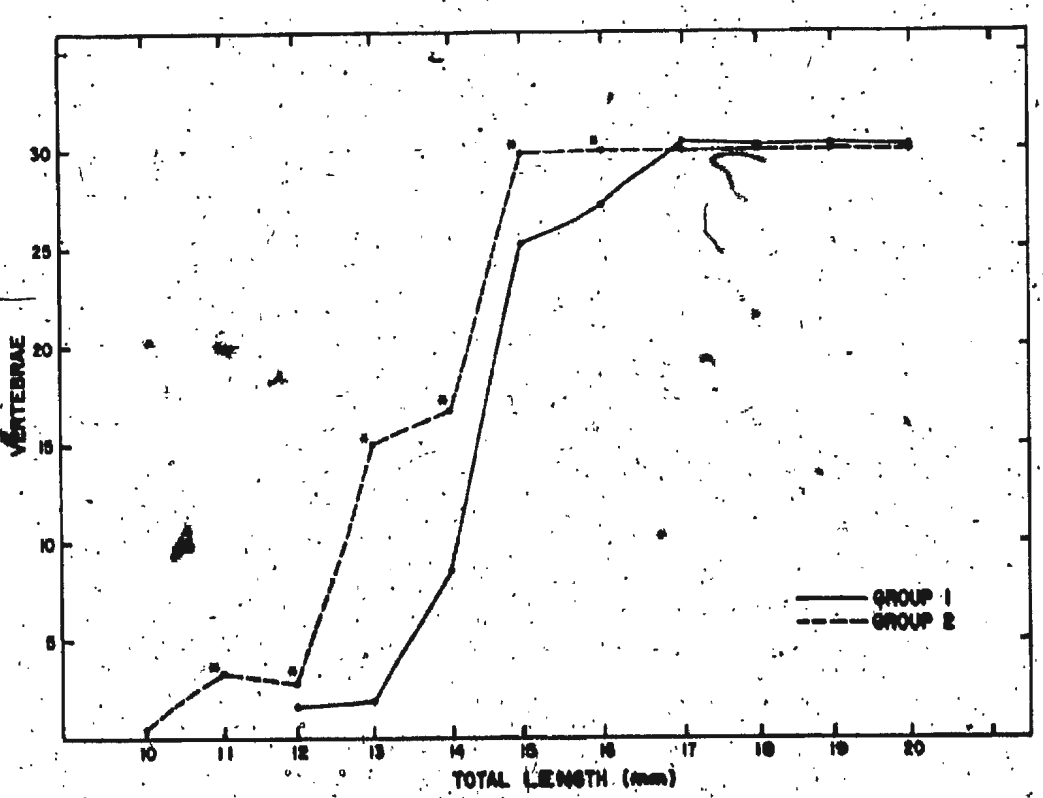

LOWER GILL RAKERS, FIRST ARCH
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 49. Mean number of upper gill rakers on the first gill arch and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 50. Mean number of vertebrae and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


UPPER GILL RAKERS, FIRST ARCH
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

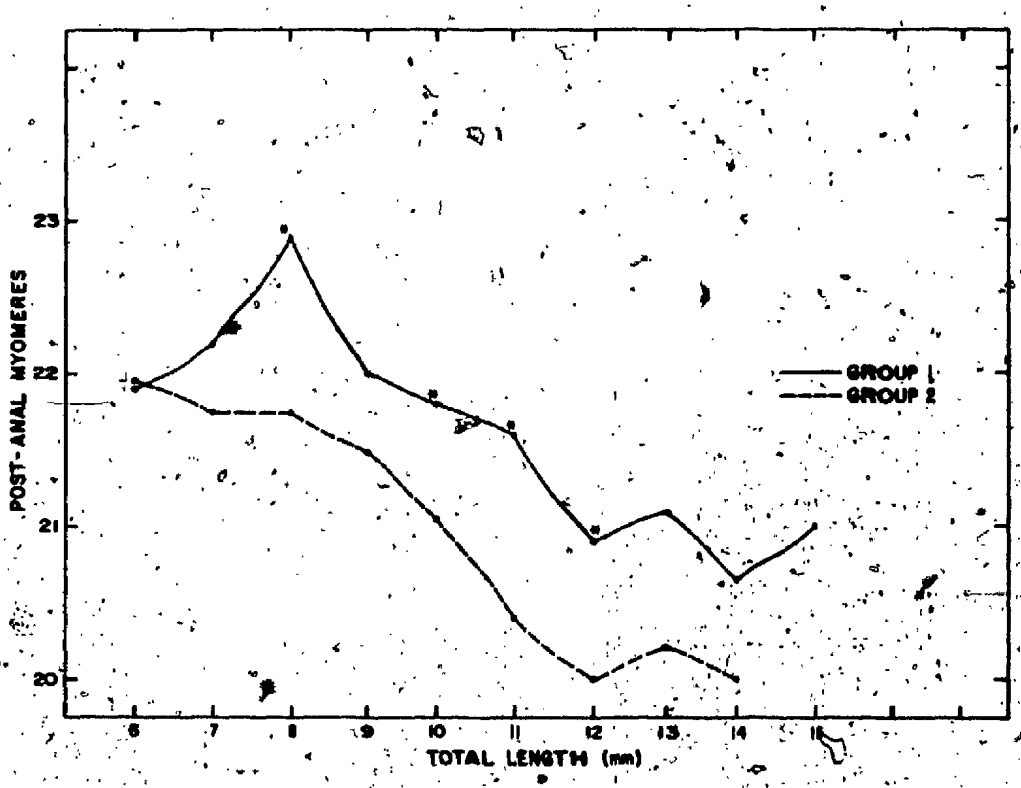

VERTEBRAE
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

32. A chi-square test comparing differences in frequency between the two extrusion groups was not significant (Prob. > 0.05). However, the extrusion groups did differ in number of post-anal myomeres. Group 1 larvae consistently had more post-anal myomeres at corresponding lengths than did Group 2 larvae (Fig. 51). Counts of post-anal myomeres were only done for larvae less than 15 mm in length. The statistically fewer post-anal myomeres in Group 2 larvae appears to be a consequence of their greater snout to anus length rather than to any differences in total body myomeres because there is no significant difference between the total myomere counts of both extrusion groups.

Head spine development and ossification was significantly different for all but 6 spines: the first and fifth posterior preoperculars, the first anterior preopercular, the second infraorbital of the first series, the single infraorbital of the third series, and the inferior posttemporal. Generally spines in Group 2 larvae appeared earlier and subsequently ossified earlier than in Group 1. As the results summarized in Table 13 show, the earlier ossification and development of the spines in Group 2 larvae is statistically significant for most spines. The relative sequence of first occurrence of various spines found in redfish larvae is summarized for both extrusion groups in Table 15.

Figure 51. Mean number of post-anal myomeres and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 52. Mean state of ossification development of the nuchal spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous, and 3 is spine ossified.


POST-ANAL MYOMERES
23
22
21
20
GROUP 1
GROUP 2
6
7
8
9
10
11
12
13
14
15
TOTAL LENGTH (mm)

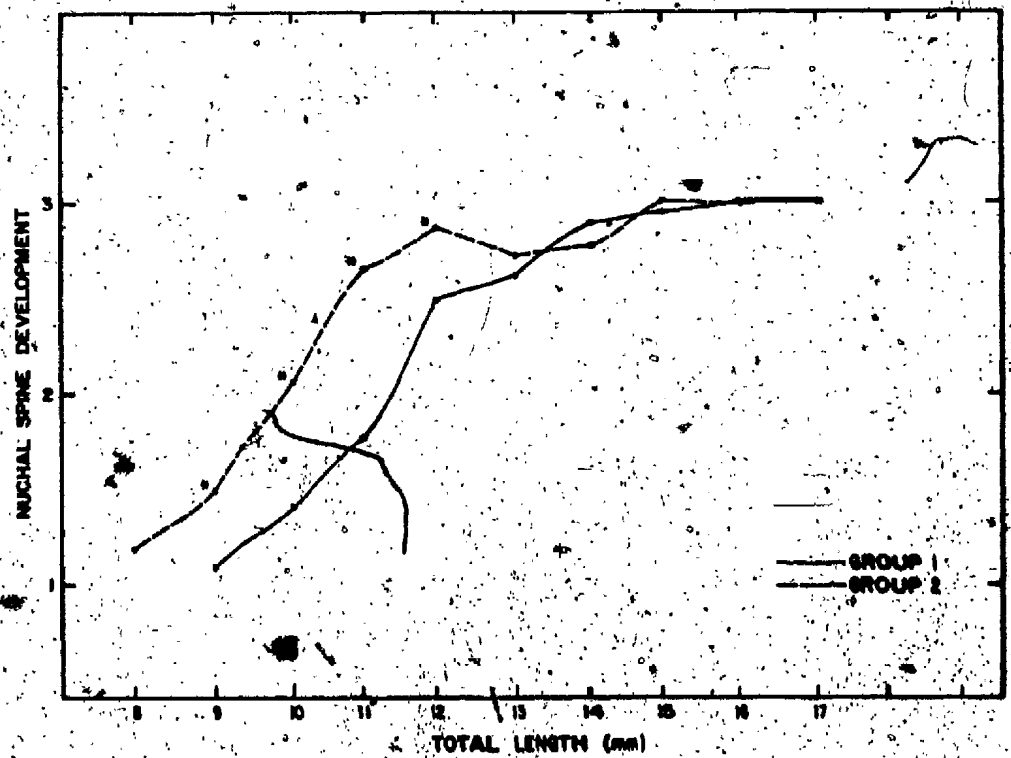

NUCHAL SPINE DEVELOPMENT
3
2
1
GROUP 1
GROUP 2
8
9
10
11
12
13
14
15
16
17
TOTAL LENGTH (mm)

Table 15. Development of spines in the head region of redfish larvae. + denotes spine present in some but not all individuals and * denotes spine present in all individuals per millimeter length interval.
[1] occurs in both extrusion groups at 21 mm

Total Length	Nuchal	Parietal	Posterior preopercularis					Anterior preopercularis			
			1	2	3	4	5	1	2	3	4
6	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
7	- -	- -	- -	- +	- +	- -	- -	- -	- +	- -	- -
8											
9	+ +	- -	- -	+ +	+ +	+ +	- -	- -	+ +	- +	+ +
10	+ +	- -	- -	+ +	+ +	+ +	- -	- -	+ +	- +	+ +
11	+ +	- -	- -	+ +	+ +	+ +	- -	- -	+ +	+ +	+ +
12	+ +	- +	- -	+ +	* +	+ +	- -	- -	+ +	+ +	+ +
13	+ +	- +	+ +	* +	* +	+ +	+ +	- -	+ +	+ +	+ +
14	+ +	+ +	+ +	* *	* *	+ *	+ +	- -	* *	+ +	+ *
15	+ *	+ +	+ *	* *	* *	* *	+ +	- +	* *	+ +	* *
16	* *	* *	* *	* *	* *	* *	+ +	+ +	* *	* *	* *
17	* *	* *	* *	* *	* *	* *	* *	+ +	* *	* *	* *
18	* *	* *	* *	* *	* *	* *	* *	+ +	* *	* *	* *
19	* *	* *	* *	* *	* *	* *	* *	+ +	* *	* *	* *
20	* *	* *	* *	* *	* *	* *	* *	+ +	* *	* *	* *

Total length	Cleithral		Supra-cleithral		Posttemporals Superior		Posttemporals Inferior		Infraorbitals 1st 1		Infraorbitals 1st 2		Infraorbitals 2nd[1] 1		Infraorbitals 2nd[1] 2		Infraorbitals 3rd	
6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	–	–	–	–	+	+	–	–	–	+	–	–	–	–	–	–	–	–
12	–	–	–	–	+	+	–	–	+	+	–	–	–	–	–	–	–	–
13	–	–	–	–	+	+	–	–	+	+	–	–	–	–	–	–	–	–
14	–	–	–	–	+	+	–	–	+	+	–	–	–	–	–	–	–	–
15	–	–	+		+	+	+	+	+	*	–	–	–	–	–	–	–	–
16	–	–	–	+	*	*	–	–	+	*	–	–	–	–	–	–	–	+
17	–	–	+	+	*	*	+	+	*	*	–	+	–	–	–	–	+	+
18	–	–	+	+	*	*	–	–	*	*	+	+	–	–	–	–	+	+
19	–	–	+	+	*	*	–	–	*	*	+	+	–	–	–	–	+	+
20	+	+	*	*	*	*	–	–	*	*	+	+	–	–	–	–	+	+

Total Length	Opercular Superior	Opercular Inferior	Nasal	Pterotic
6	- -	- -	- -	- -
7	- -	- -	- -	- +
8	- -	- -	- -	- +
9	- -	- -	- -	+ +
10	- +	- -	- -	+ +
11	- +	- -	- -	+ +
12	+ +	- +	- -	+ +
13	+ +	- +	- -	+ +
14	+ +	+ +	- -	* +
15	+ *	+ *	- +	* *
16	+ *	+ *	- +	* *
17	+ *	+ *	- +	* *
18	* *	* *	+ +	* *
19	* *	* *	+ +	* *
20	* *	* *	+ +	* *

Total length	Suborbitals 1	Suborbitals 2	Preocular[1]	Supraocular[1]	Postocular	
6	–	–	–	–	–	–
7	–	–	–	–	–	–
8	–	–	–	–	–	+
9	–	–	–	–	+	+
10	–	–	–	–	+	+
11	–	+	–	–	+	+
12	+	+	–	–	+	+
13	+	+	–	–	+	+
14	+	+	–	–	+	+
15	+	+	+	–	–	+	+
16	+	+	+	–	–	+	+
17	+	+	+	–	–	+	+
18	+	+	+	–	–	+	+
19	+	+	+	–	–	+	+
20	+	+	+	–	–	+	+

The nuchal spine (Fig. 52) first appears as a cartilaginous spine at 8 mm in Group 2 larvae and 9 mm in Group 1. All Group 2 larvae have completely ossified nuchal spines by 15 mm and all Group 1 larvae have ossified nuchal spines by 16 mm.

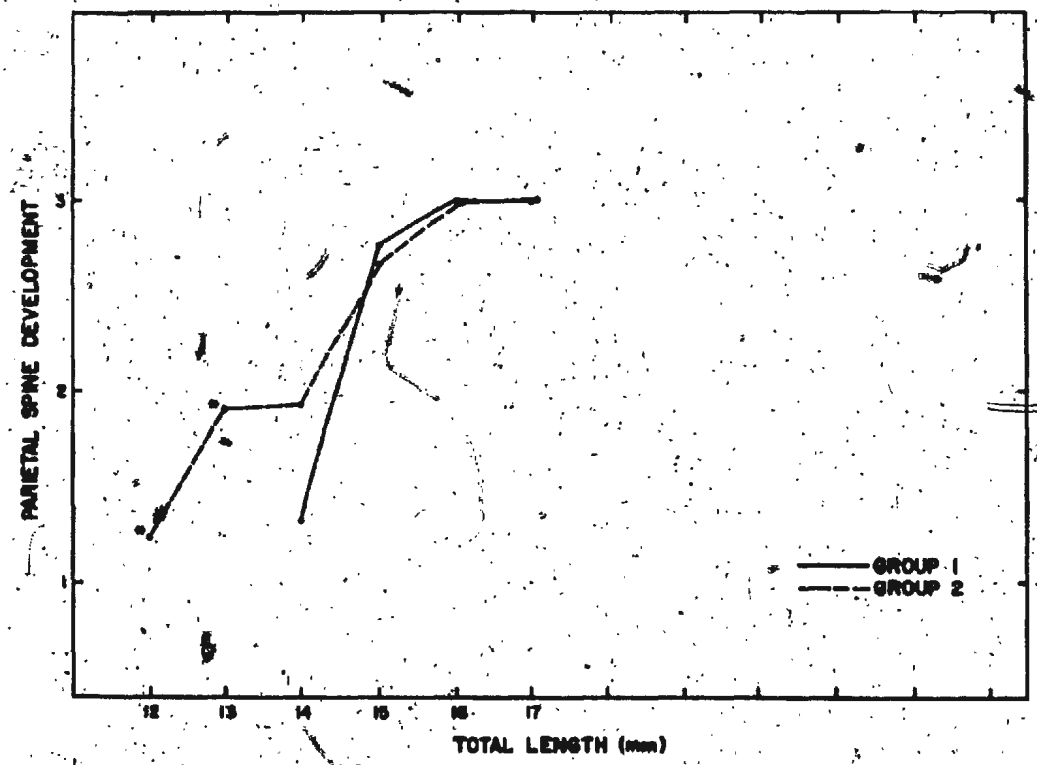
The parietal spine (Fig. 53) which is located immediately adjacent to the nuchal is relatively later developing. It first occurs in Group 2 larvae at 12 mm and in Group 1 larvae at 14 mm. Of the two spines, the nuchal is the larger and most prominent. All larvae from both extrusion groups have ossified parietal spines by 16 mm.

Spines of the posterior preopercular series are among the first head spines to appear. The second and third posterior preopercular spines first appear in Group 2 larvae at 7 mm (Figs. 54 and 55) while the fourth posterior preopercular spine forms shortly thereafter at 8 mm (Fig. 56). In Group 1, all three of these spines first appear at 9 mm. The first and fifth posterior preopercular spines are comparatively much later forming. The first posterior preopercular spine first occurs at 13 mm and 14 mm for Groups 2 and 1 respectively. The fifth posterior preopercular spine first appears at 13 mm and 15 mm for Groups 2 and 1 respectively.

The second, third, and fourth posterior preopercular spines are ossified in all Group 2 larvae by 14 mm with the

Figure 53. Mean state of ossification development of the parietal spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous, and 3 is spine ossified.

Figure 54. Mean state of ossification development of the second posterior preopercular spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous, and 3 is spine ossified.


PARIETAL SPINE DEVELOPMENT
12
13
14
15
16
17
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

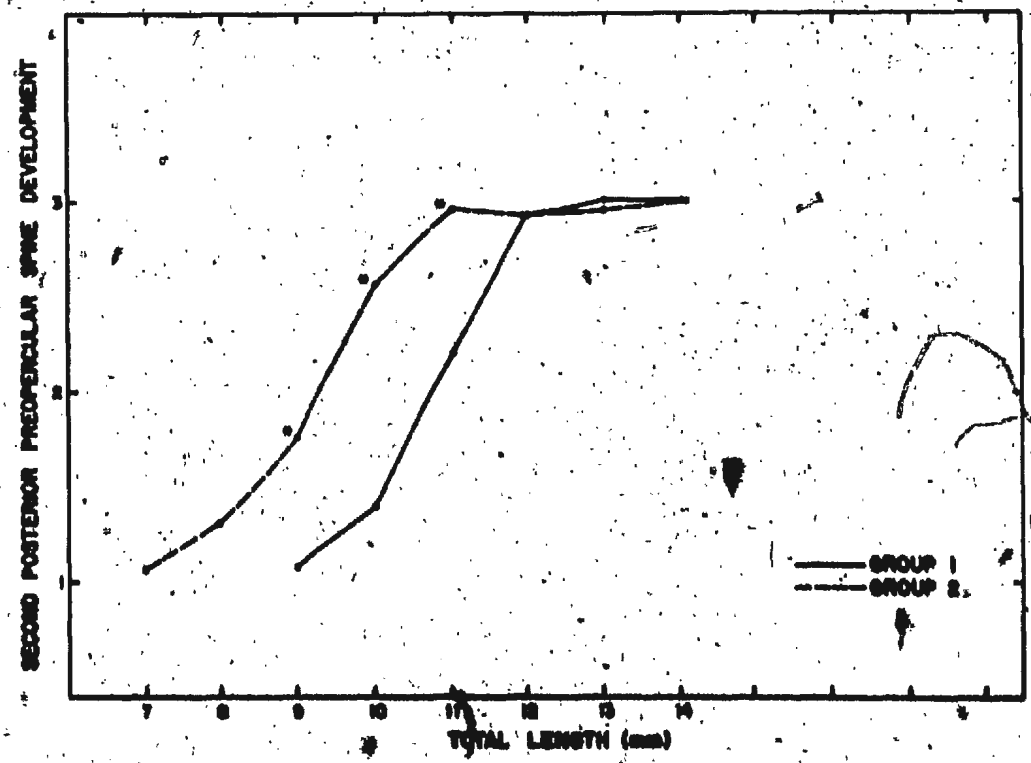
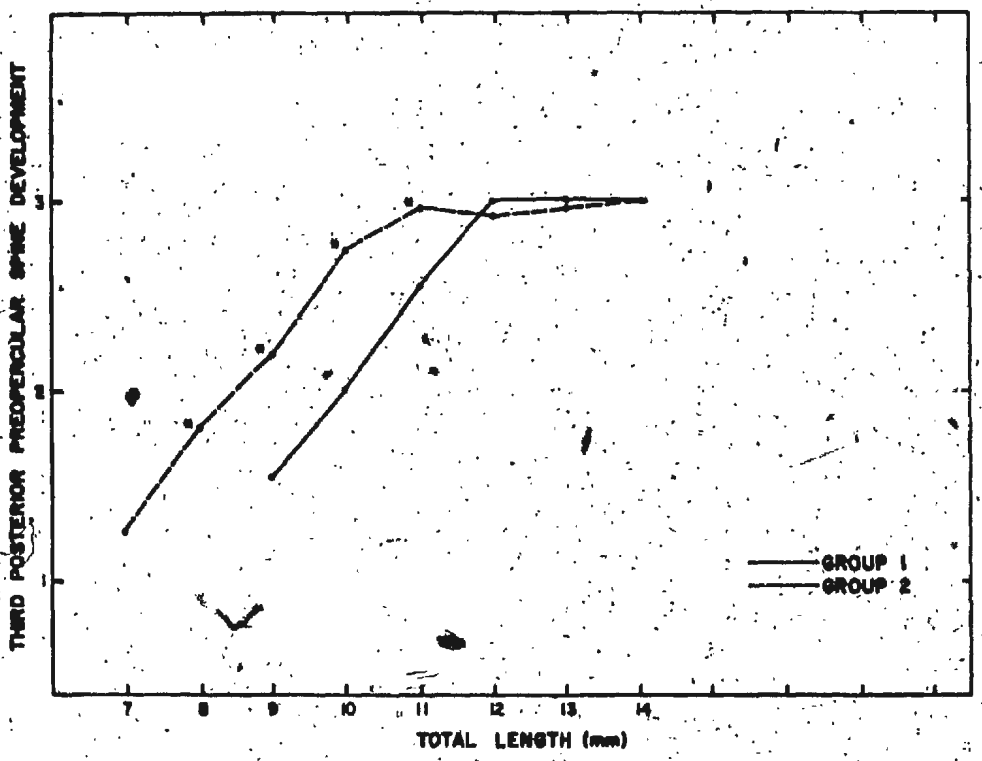
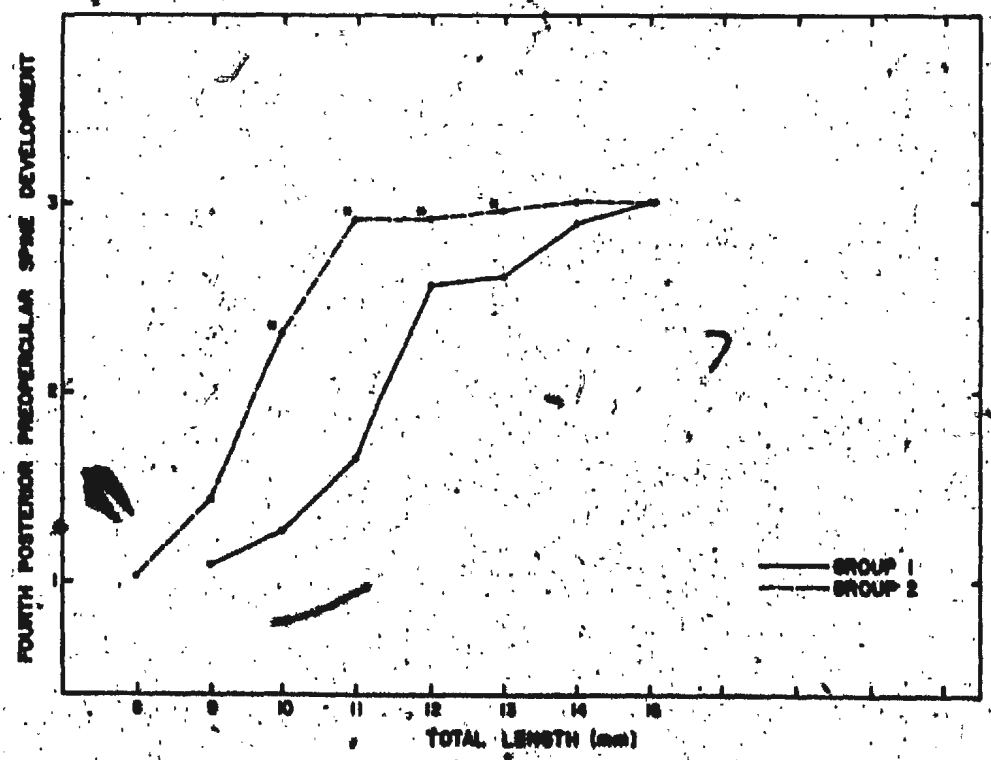

SECOND POSTERIOR PREOPERCULAR SPINE DEVELOPMENT
7
8
9
10
11
12
13
14
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 55. Mean state of ossification development of the third posterior preopercular spine and total length for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous, and 3 is spine ossified.

Figure 56. Mean state of ossification development of the fourth posterior preopercular spine and total length for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous, and 3 is spine ossified.


THIRD POSTERIOR PREOPERCULAR SPINE DEVELOPMENT
GROUP 1
GROUP 2
7
8
9
10
11
12
13
14
TOTAL LENGTH (mm)


FOURTH POSTERIOR PREOPERCULAR SPINE DEVELOPMENT
GROUP 1
GROUP 2
8
9
10
11
12
13
14
15
TOTAL LENGTH (mm)

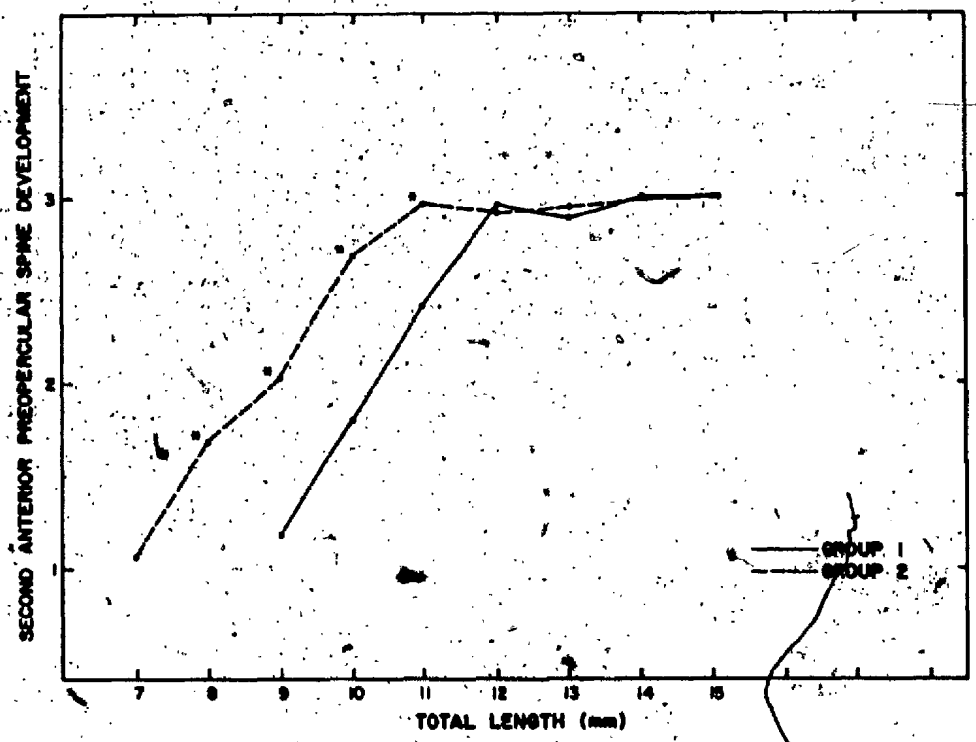
first and fifth posterior preoperculars ossified at 15 mm and 17 mm respectively. In Group 1, the third posterior preopercular spine is ossified in all larvae at 12 mm, the second posterior preopercular by 13 mm, the fourth posterior preopercular by 15 mm, the first posterior preopercular by 16 mm, and the fifth trailing at 17 mm. The sequence of ossification of spines of the posterior preopercular series is 3-2-4-1-5. Differences in frequency of occurrence and size at ossification of the first and fifth posterior preopercular spines are not significant between extrusion groups.

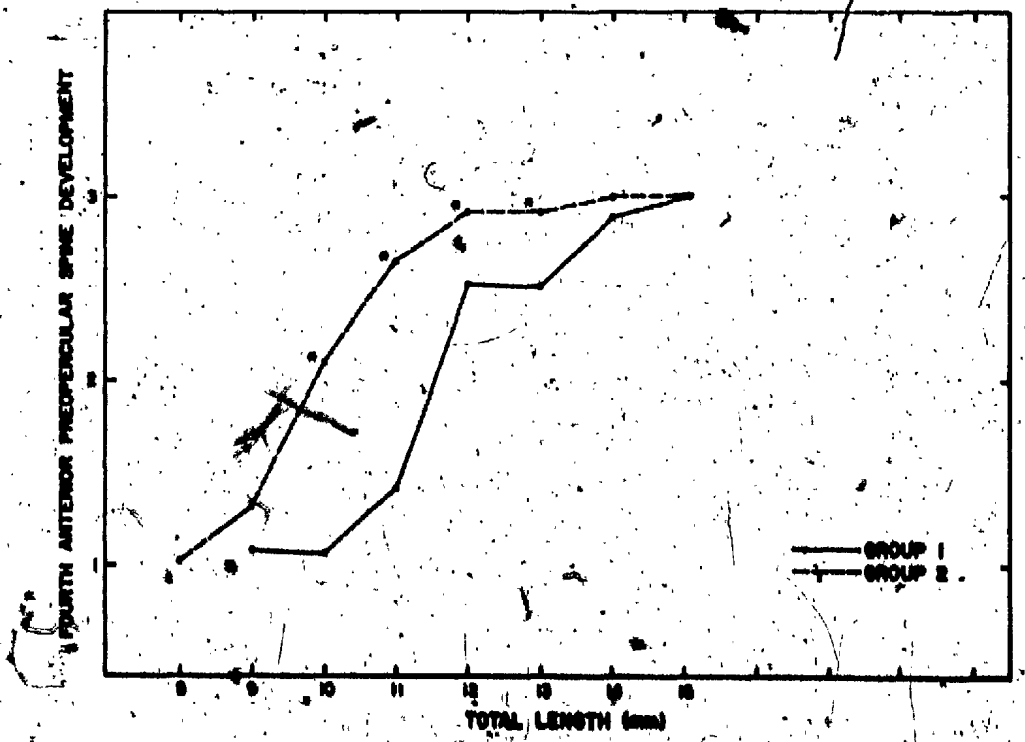
Spines of the anterior preopercular series also form early. The second anterior preopercular spine is the first of the series to form in either extrusion group (Fig. 57). It appears in Group 2 larvae at 7 mm and Group 1 larvae at 9 mm. The fourth anterior preopercular spine appears shortly thereafter at 8 mm and 9 mm in Groups 2 and 1 respectively (Fig. 58). The third anterior preopercular spine forms next at 9 mm and 11 mm in Groups 2 and 1 respectively (Fig. 59). The first anterior preopercular spine first appears much later at 16 mm and 17 mm for Groups 2 and 1 respectively.

The second and fourth anterior preoperculars are ossified in all Group 2 larvae by 14 mm, the third at 16 mm, and the first is not ossified in all larvae by 20 mm. In

Figure 57. Mean state of ossification development of the second anterior preopercular spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous, and 3 is spine ossified.

Figure 58. Mean state of ossification development of the fourth anterior preopercular spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous and 3 is spine ossified.


SECOND ANTERIOR PREOPERCULAR SPINE DEVELOPMENT
1
2
3
7
8
9
10
11
12
13
14
15
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


FOURTH ANTERIOR PREOPERCULAR SPINE DEVELOPMENT
1
2
3
8
9
10
11
12
13
14
15
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

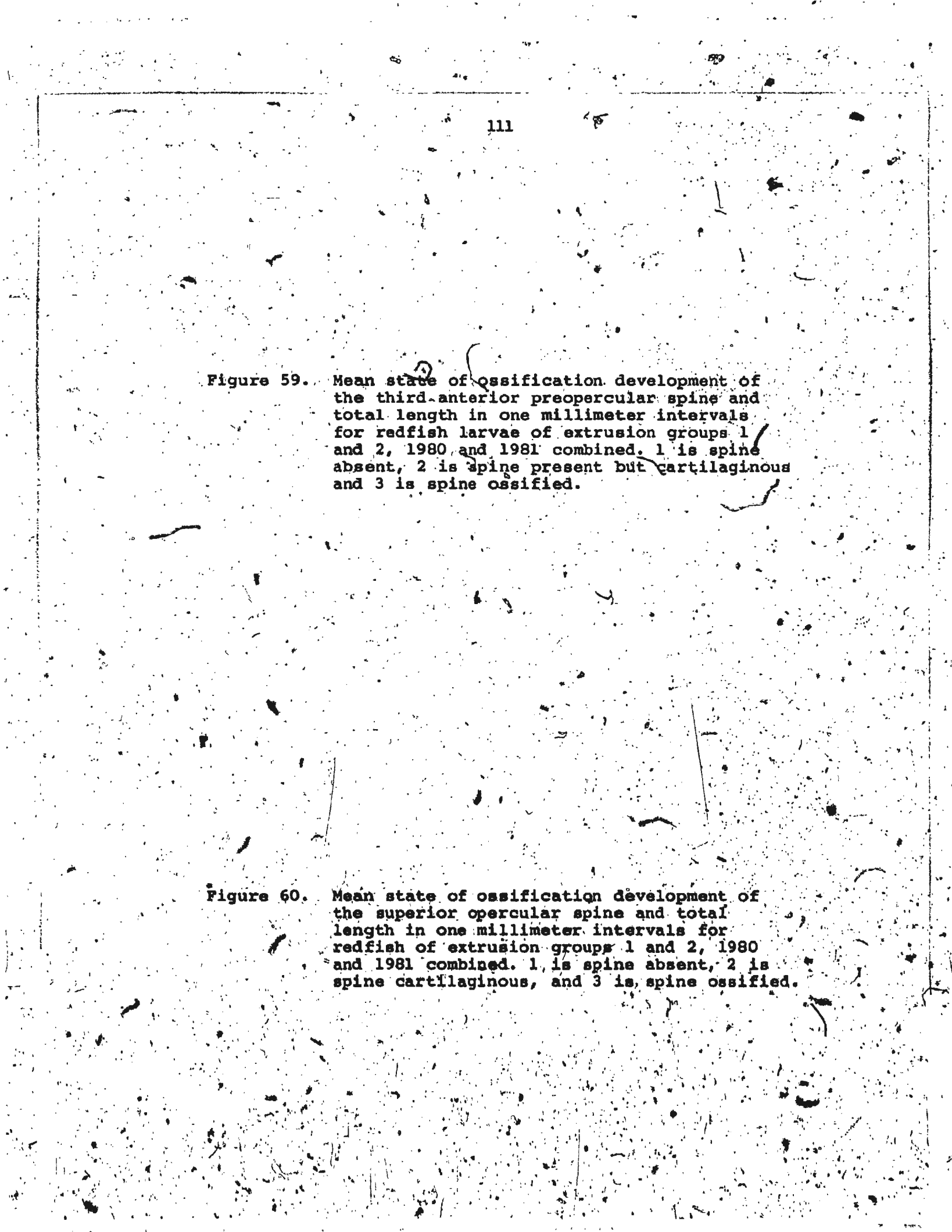
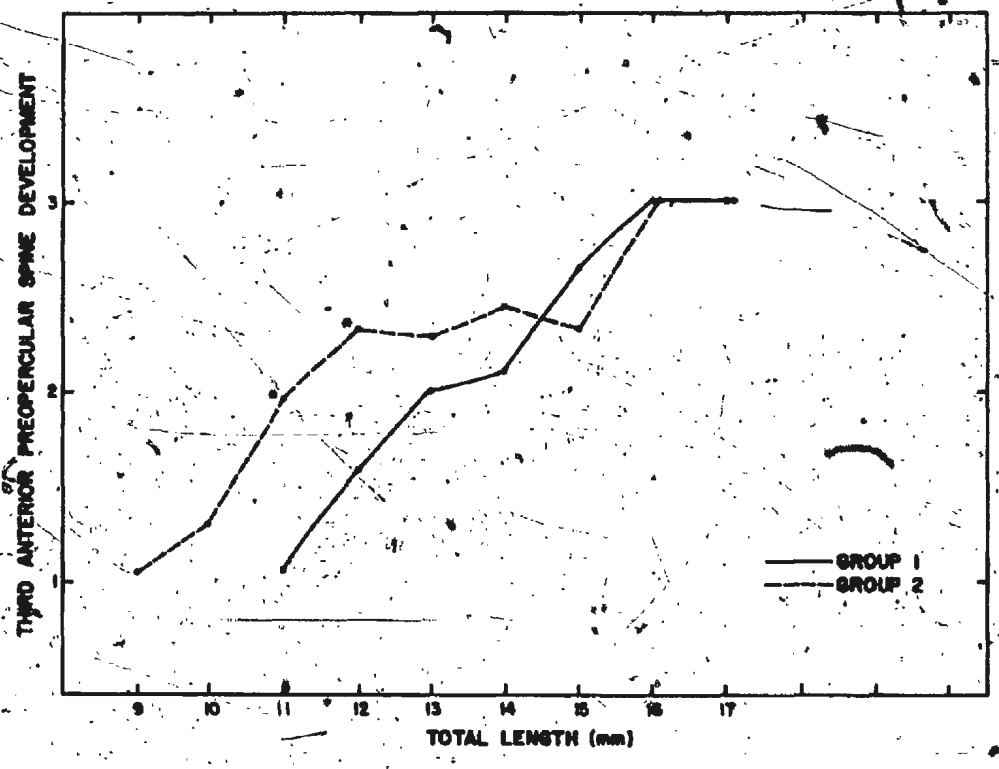
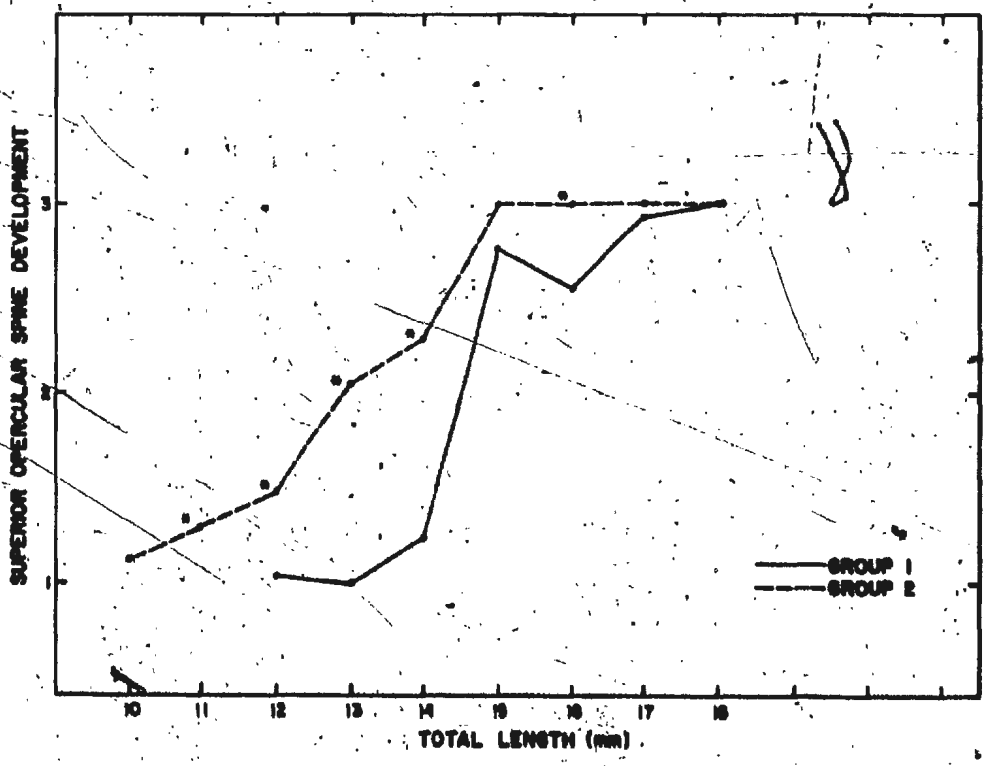


Figure 59. Mean state of ossification development of the third anterior preopercular spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine present but cartilaginous and 3 is spine ossified.

Figure 60. Mean state of ossification development of the superior opercular spine and total length in one millimeter intervals for redfish of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.


THIRD ANTERIOR PREOPERCULAR SPINE DEVELOPMENT
9
10
11
12
13
14
15
16
17
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


SUPERIOR OPERCULAR SPINE DEVELOPMENT
10
11
12
13
14
15
16
17
18
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

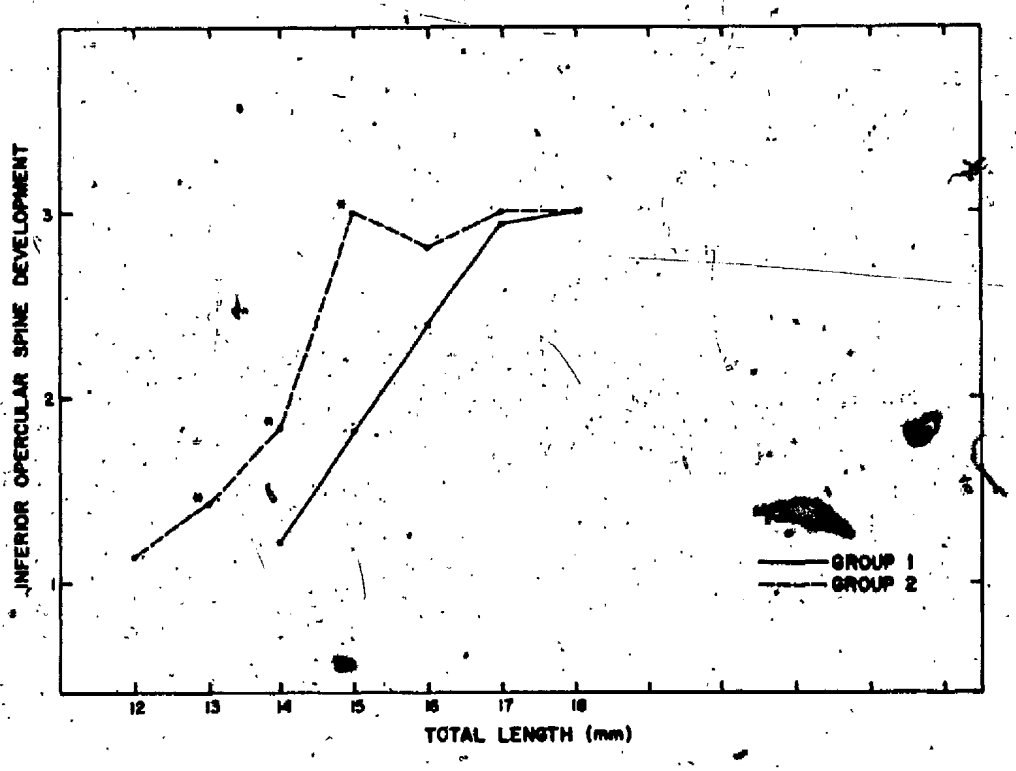
Group 1, ossification of the second anterior preopercular spine is complete for all larvae by 14 mm. The third is complete by 16 mm and ossification of the fourth is complete by 15 mm. Ossification of the first anterior preopercular spine is still not complete in all Group 1 larvae by 20 mm. The frequency of occurrence and size at ossification of the first anterior preopercular spine is not significantly different between extrusion groups. The sequence of ossification of the anterior preopercular spines is 2-4-3-1. In comparison to the posterior preopercular series, the anterior series spines are much less prominent.

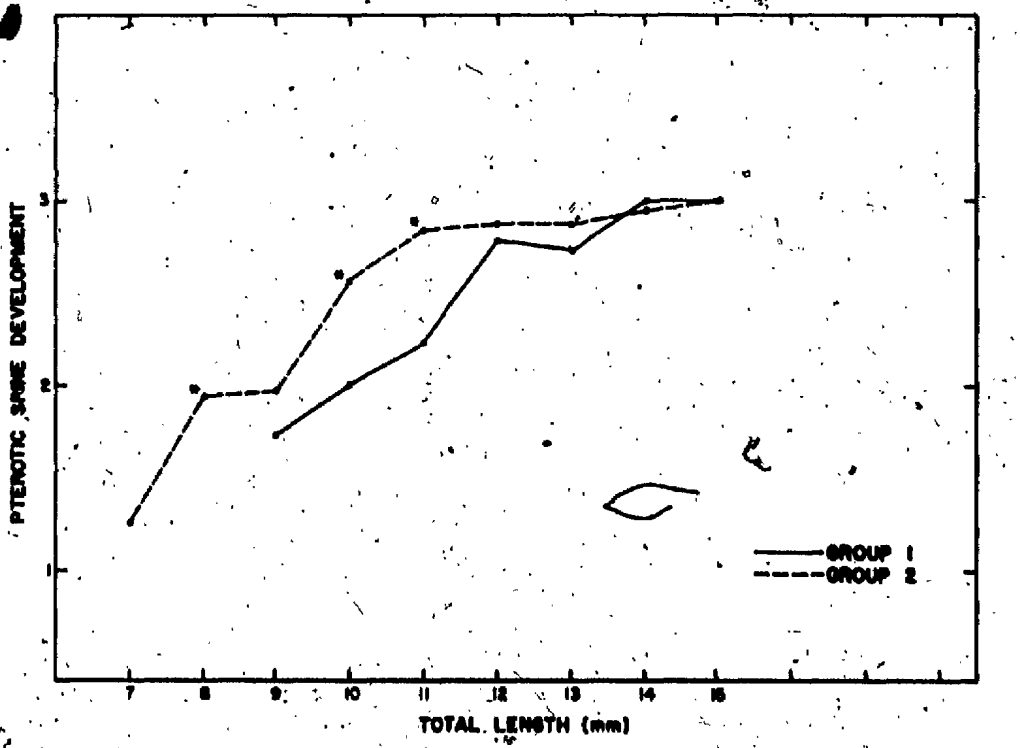
The two spines in the opercular series, the superior and inferior operculars, begin formation later than the spines of the preopercular series (Figs. 60 and 61). The first to appear, the superior opercular, is found in some Group 2 larvae at 10 mm but does not occur in Group 1 until 12 mm. All Group 2 larvae have ossified superior operculars by 15 mm but all Group 1 larvae do not have ossified superior operculars until 18 mm. The inferior opercular does not first occur in Group 2 larvae until 12 mm and in Group 1 larvae at 14 mm. All Group 2 larvae have ossified inferior operculars by 17 mm and all Group 1 larvae by 18 mm.

The pterotic (Fig. 62), also one of the first spines to form, first occurs in Group 2 larvae at 7 mm and Group 1 larvae at 9 mm. All larvae have ossified pterotic spines by

Figure 61. Mean state of ossification development of the inferior opercular spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.

Figure 62. Mean state of ossification development of the pterotic spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.


INFERIOR OPERCULAR SPINE DEVELOPMENT
1
2
3
12
13
14
15
16
17
18
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


PTEROTIC SPINE DEVELOPMENT
1
2
3
7
8
9
10
11
12
13
14
15
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

14 mm in Group 1 and 15 mm in Group 2, one of the few instances of ossification of a head spine occurring earlier in Group 1 rather than Group 2 larvae.

The supracleithral spine (Fig. 63) forms relatively late in redfish larvae. In both extrusion groups, the supracleithral spine does not occur until 14 mm and all larvae of both extrusion groups have not completed ossification of the supracleithral spine by 20 mm.

The posttemporal series includes two spines, the superior and inferior posttemporal. In both extrusion groups, the superior posttemporal occurs at 11 mm (Fig. 64). All Group 2 larvae have ossified superior posttemporal spines by 15 mm and Group 1 larvae by 16 mm. The status of the inferior posttemporal spine in larval redfish is unclear. It first occurs in isolated individuals in Group 1 at 15 mm and Group 2 at 17 mm. It is not found in larger individuals in either of the two extrusion groups.

Comparison of the frequency of occurrence and size at ossification of the spines of the infraorbital series indicates only the first infraorbital spine of the first series differs significantly between extrusion groups (Table 14). In Group 2 larvae, this spine first appears at 12 mm. All Group 2 larvae have completed ossification of the first infraorbital, first series by 16 mm and all larvae of Group 1 by 17 mm (Fig. 65).

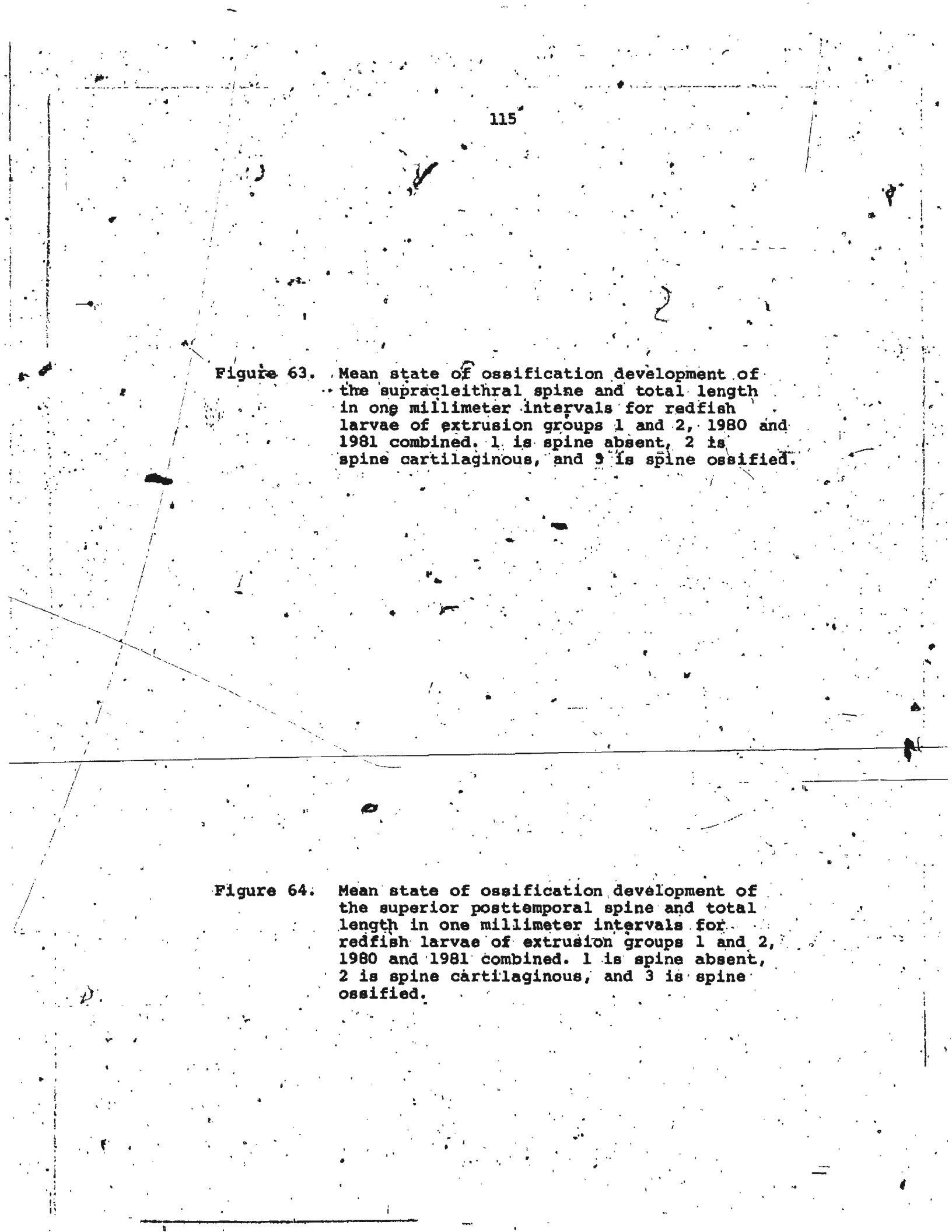
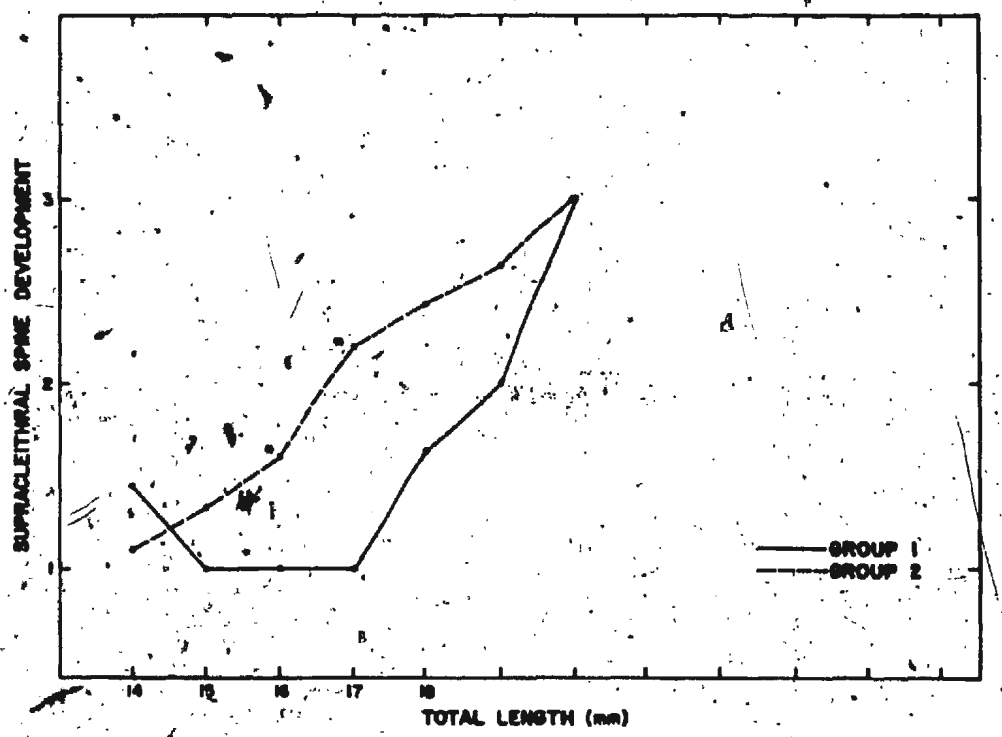


Figure 63. Mean state of ossification development of the supracleithral spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.

Figure 64. Mean state of ossification development of the superior posttemporal spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.


SUPRACLEITHRAL SPINE DEVELOPMENT
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

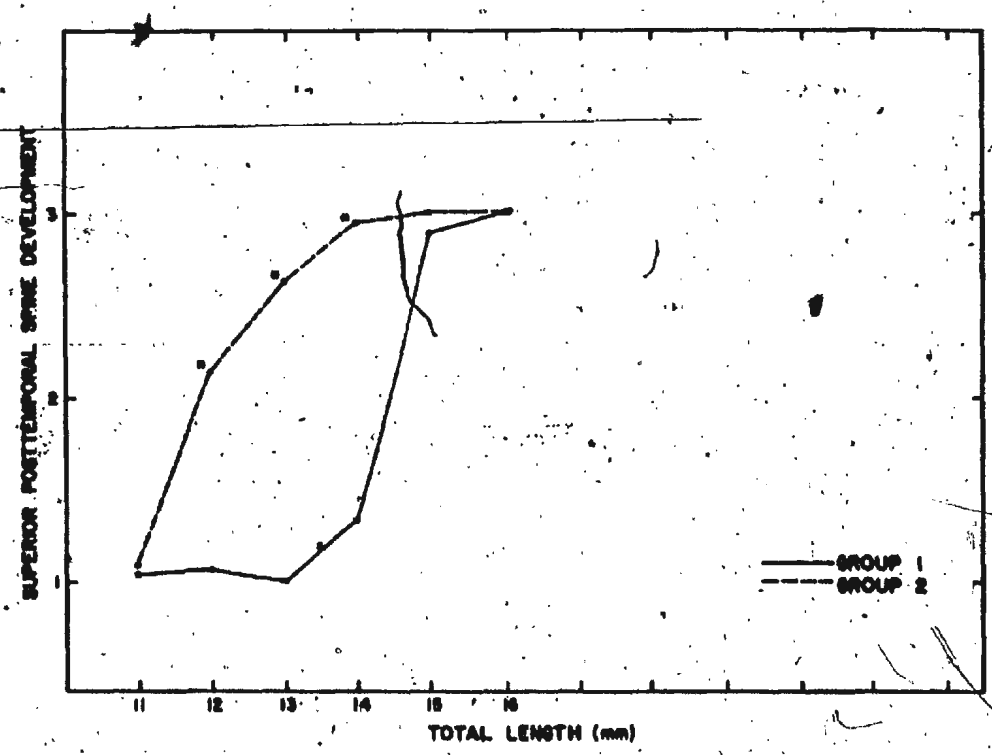
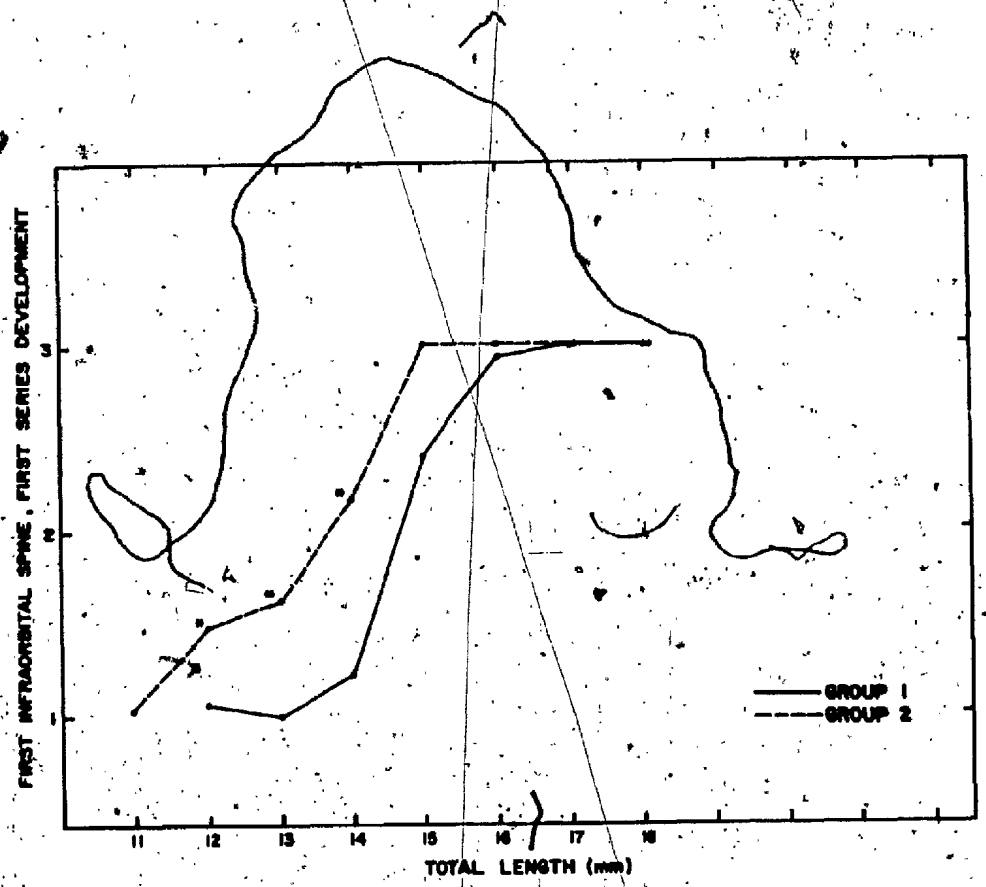
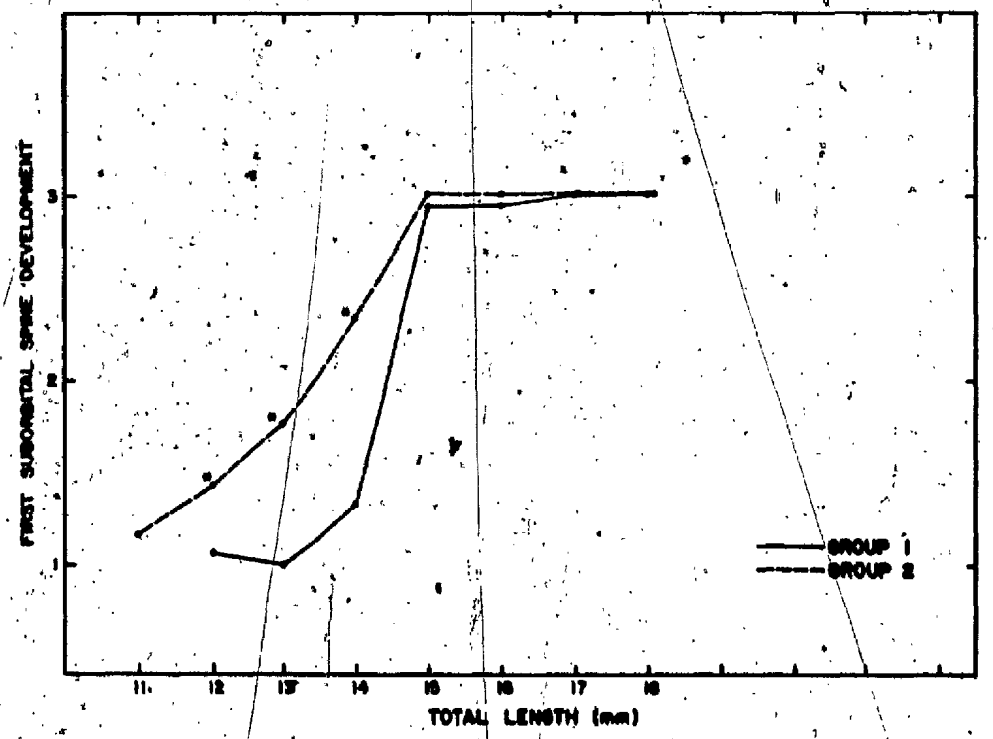

SUPERIOR POSTTEMPORAL SPINE DEVELOPMENT
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

Figure 65. Mean state of ossification development of the first infraorbital spine, first series and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.

Figure 66. Mean state of ossification development of the first suborbital spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.


FIRST INFRAORBITAL SPINE, FIRST SERIES DEVELOPMENT
GROUP 1
GROUP 2
11
12
13
14
15
16
17
18
TOTAL LENGTH (mm)


FIRST SUBORBITAL SPINE DEVELOPMENT
GROUP 1
GROUP 2
11
12
13
14
15
16
17
18
TOTAL LENGTH (mm)

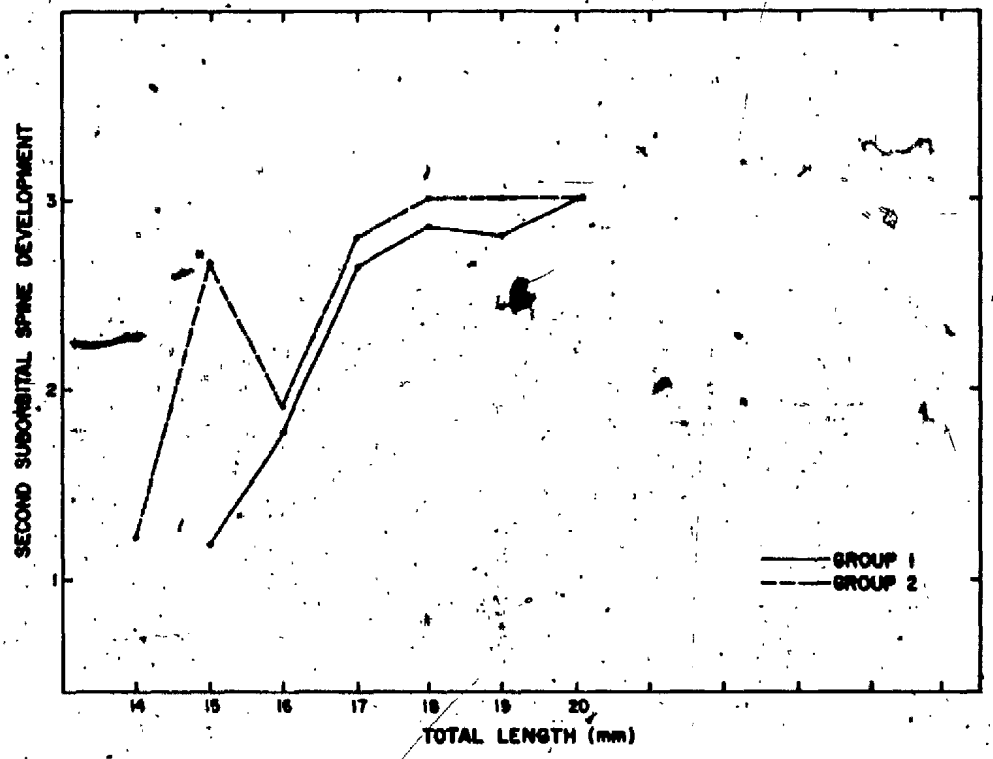
The status of the two spines of the second infraorbital series is uncertain. These spines only occurred in a single individual at 21 mm. The single spine of the third infraorbital series first occurred in Group 2 larvae at 17 mm. Neither extrusion group had completed ossification of this spine by 20 mm. The frequency of occurrence and size at ossification of the spine of the third infraorbital series and not significantly different between extrusion groups.

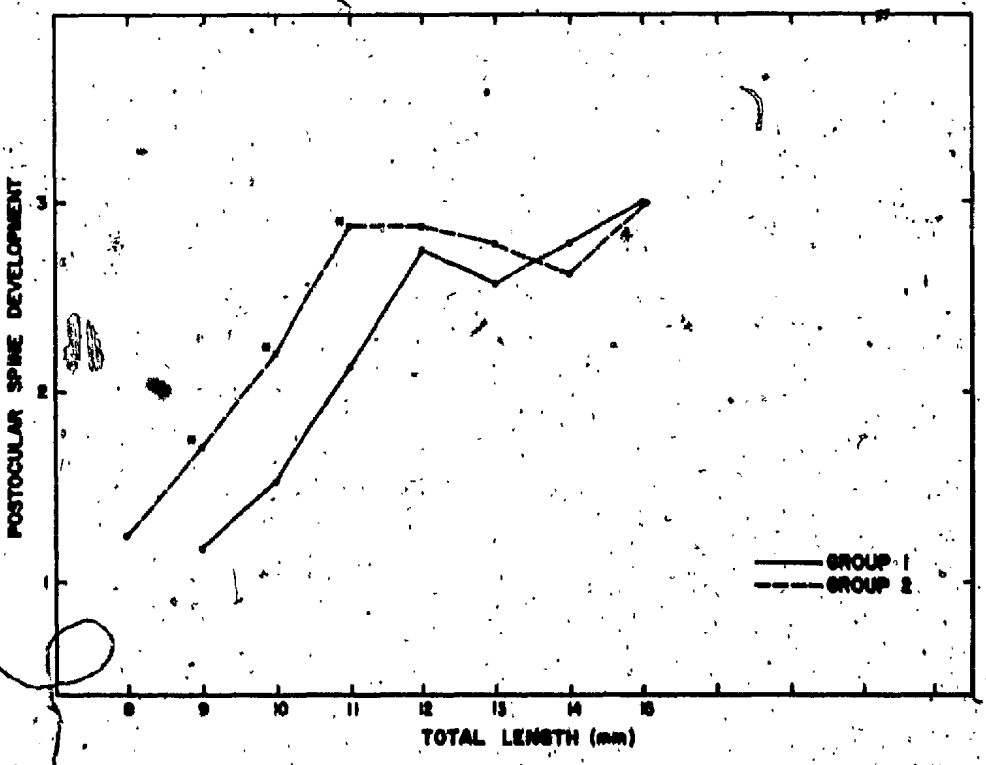
There are two spines found on the suborbital in redfish larvae. The first suborbital, the more prominent of the two, first appears at 11 mm in Group 2 and 12 mm in Group 1 (Fig. 66). All Group 2 larvae have ossified first suborbital spines at 15 mm while all Group 1 larvae do not have ossified first suborbital spines until 17 mm. The second suborbital spine first appears later than the first suborbital spine in both extrusion groups. In Group 2, it first appears at 14 mm and in Group 1 at 15 mm (Fig. 67). All Group 2 larvae have ossified second suborbital spines by 18 mm and all Group 1 larvae by 20 mm.

Preocular and supraocular spines also occur in redfish larvae but are relatively late forming. Neither spine occurs until after 21 mm. Due to lack of sufficient specimens in both extrusion groups at this large size, no comparisons of their frequency of occurrence and size at

Figure 67. Mean state of ossification development of the second suborbital spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.

Figure 68. Mean state of ossification development of the postocular spine and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined. 1 is spine absent, 2 is spine cartilaginous, and 3 is spine ossified.


SECOND SUBORBITAL SPINE DEVELOPMENT
3
2
1
14
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


POSTOCULAR SPINE DEVELOPMENT
4
3
2
1
8
9
10
11
12
13
14
15
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

ossification were possible.

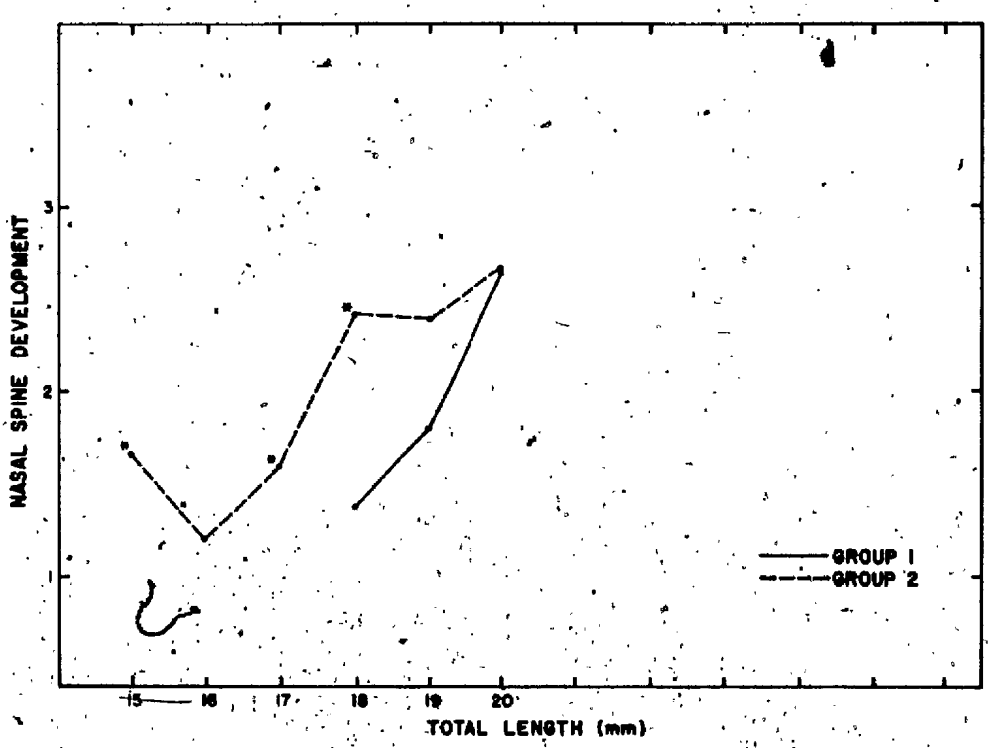
In contrast, the postocular spine (Fig. 68) occurs quite early. In Group 2, the postocular spine first appears at 8 mm and in Group 1 at 9 mm. In both extrusion groups, all specimens had ossified postocular spines by 15 mm.

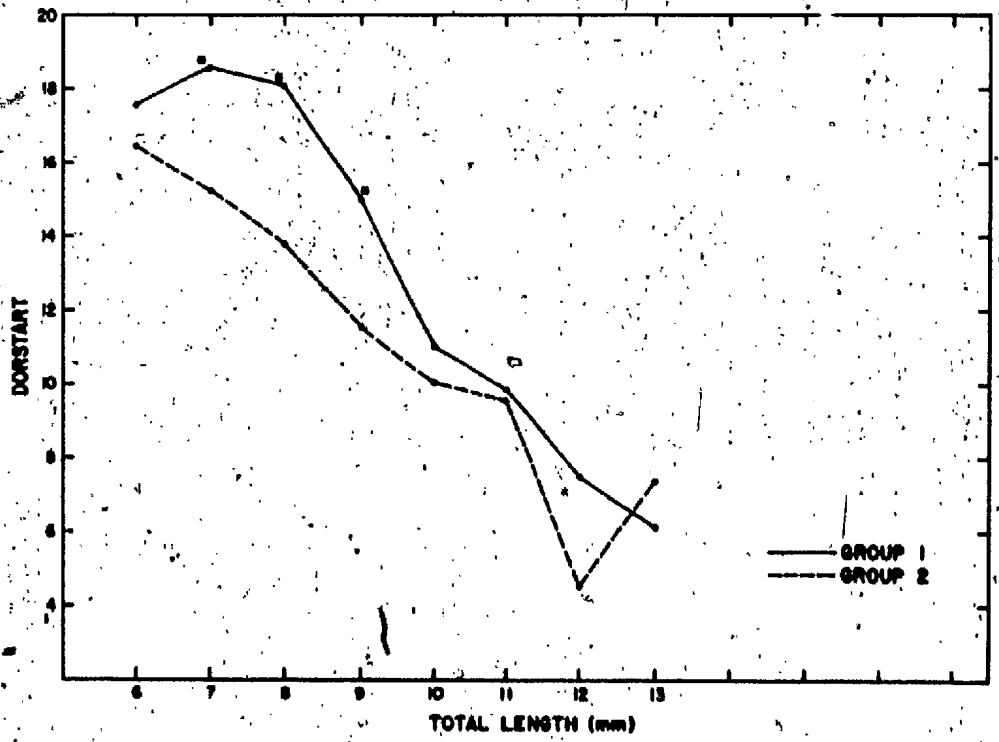
The single nasal spine (Fig. 69) first occurs in Group 2 larvae at 15 mm and in Group 1 larvae at 18 mm. Neither extrusion group had all individuals with ossified nasal spines by 20 mm. The nasal spine is small and inconspicuous in even the largest larvae examined.

III.B.4. Pigmentation

Pigmentation patterns were also evaluated as possible species identification criteria. The extent of dorsal and ventral body pigment lines, the shape and pattern of melanophores on the body and several areas of the head were noted. Melanophore patterns on the body and head could be grouped into a few categories in small larvae but, in larvae approximately 9 mm or larger, the increasing tendency towards heavier pigmentation over the entire body surface tended to obscure the original patterns.

As with the morphometrics and meristics, pigmentation differences were associated with extrusion time. The observed differences were compared similarly to the


NASAL SPINE DEVELOPMENT
1
2
3
15
16
17
18
19
20
TOTAL LENGTH (mm)
GROUP 1
GROUP 2


DORSTART
4
6
8
10
12
14
16
18
20
6
7
8
9
10
11
12
13
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

meristics. Table 16 summarizes the chi-square statistics for serial Kruskal-Wallis tests on dorsal and ventral body melanophore patterns. Serial tests on each one millimeter length interval per variable were necessitated by the extent of changes in amount and shape of the melanophores with increasing length within each extrusion group.

Pigmentation on the dorsum consists of a line of melanophores sometimes separate and distinct from each other but often substantially merged to form a long band. The number of melanophores combined into the band consequently cannot be determined. In newly extruded larvae from 6-8 mm, the dorsal body pigment starts on body myomeres 10-14 but most frequently on myomeres 15-18 in Group 1. In Group 2, the dorsal line starts on myomeres 5-28 but most commonly on myomeres 12-15. Within the same length interval, the dorsal body pigment extends further anteriorly in Group 2 larvae compared to Group 1 larvae (Fig. 70). There was no significant difference between extrusion groups on which myomere the dorsal pigment ended posteriorly. Consequently, the total length of the pigment band was longer, at comparable larval lengths, in Group 2 than Group 1 larvae (Fig. 71).

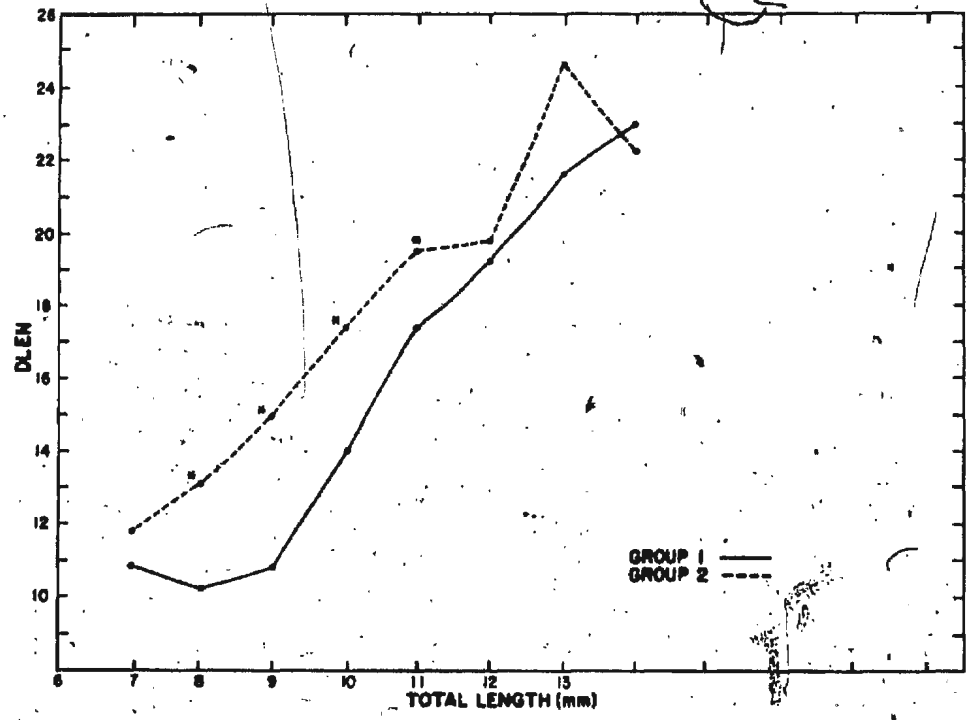
Larvae 6-8 mm in length from the two extrusion groups also differed in the tendency for the melanophores to merge into a band. In group 1, 97% of all larvae had more than

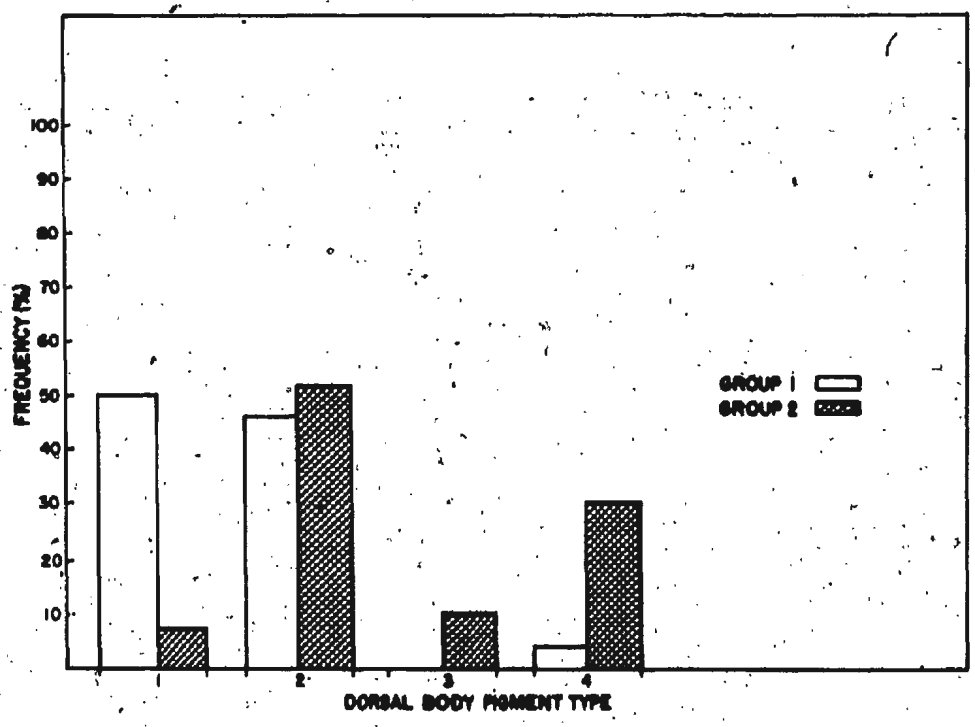
Table 16. Summary of Chi-square approximation statistics for serial Kruskal-Wallis tests on dorsal and ventral body pigmentation for redfish larvae in both extrusion groups, 1980 and 1981 combined.

Variable	DF	χ^2	Prob > χ^2
DORSTART	16	43.90	0.001
DOREND	18	23.04	N.S.
VENSTART	18	31.42	0.050
VENEND	18	35.14	0.010
DLEN	18	48.01	0.001
VLEN	18	24.11	N.S.

Figure 71. Mean length of the melanophore band on the dorsum in numbers of body myomeres and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 72. Per cent frequency of occurrence of pigmentation types on the dorsum in redfish larvae under 9 mm total length of extrusion groups 1 and 2, 1980 and 1981 combined. (see Appendix A for description of pigment types)


DLEN
TOTAL LENGTH (mm)
GROUP 1
GROUP 2

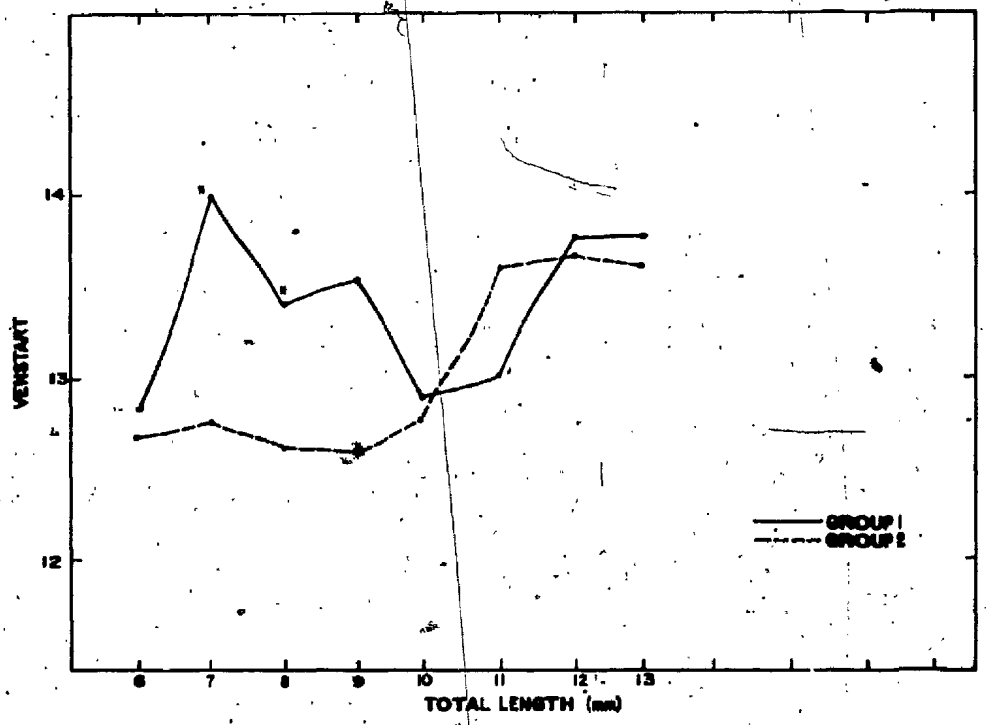

FREQUENCY (%)
DORSAL BODY PIGMENT TYPE
GROUP 1
GROUP 2

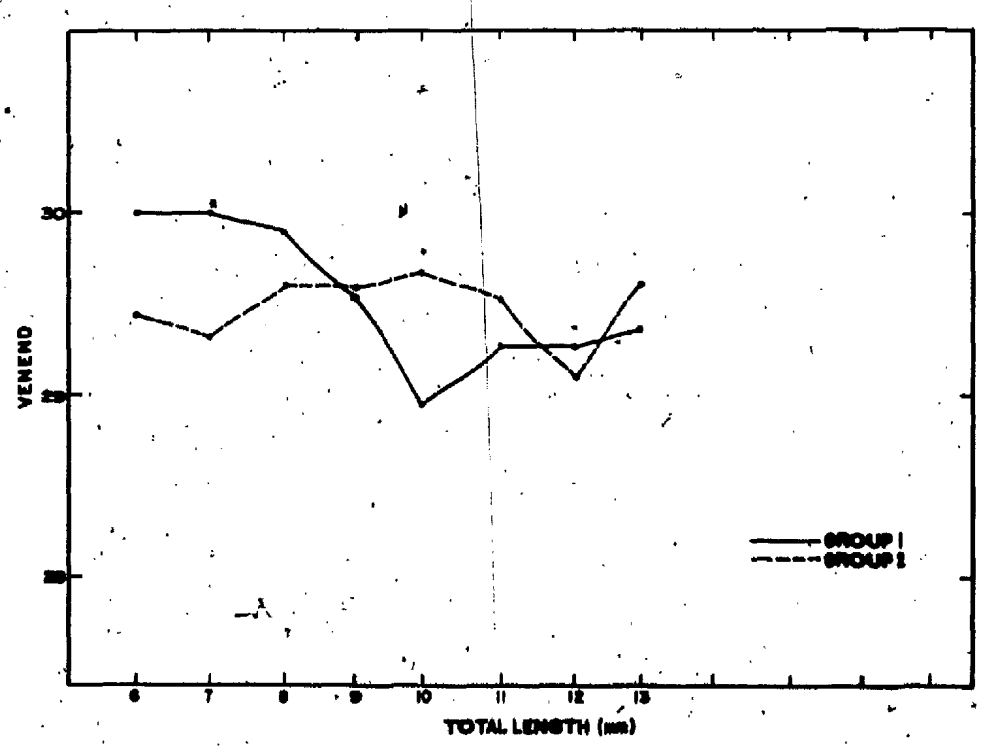
half of the length of the dorsal melanophore pattern composed of merged melanophores (Fig. 72). Only 3% had a melanophore pattern of all or nearly all distinct, spatially separate melanophores. In Group 2, only 60% of 6-8 mm larvae had more than half the melanophores merged into a band. A further 30% of Group 2 larvae had a pattern of all separate melanophores. Additionally, the number of melanophores in these individuals with all spatially separate melanophores seemed to be very much reduced. This difference in frequency of occurrence of the different melanophore patterns, tested by chi-square, is statistically significant ($\chi^2 = 36.44$, Prob. $> \chi^2 = 0.001$). As larvae grow, the dorsal melanophores spread anteriorly and laterally over the dorsum in both extrusion groups and differences in their pigment patterns tend to become obscured.

In newly extruded larvae of 6-8 mm, the ventral body pigmentation also usually consists of a group of melanophores joined into a band. The ventral body pigment band tends to start slightly more anteriorly in Group 2 rather than Group 1 larvae (Fig. 73). This is also true of the posterior end of the ventral band (Fig. 74). However, the length of the pigment band is not significantly different between extrusion groups. As larvae grow, the anteriormost melanophores of the ventral band tend to become

Figure 73. Mean anterior starting body myomere for the melanophore band on the ventrum and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.

Figure 74. Mean posterior ending body myomere for the melanophore band on the ventrum and total length in one millimeter intervals for redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


VENSTART
14
13
12
6
7
8
9
10
11
12
13
TOTAL LENGTH (mm)
GROUP I
GROUP II


VENEND
30
6
7
8
9
10
11
12
13
TOTAL LENGTH (mm)
GROUP I
GROUP II

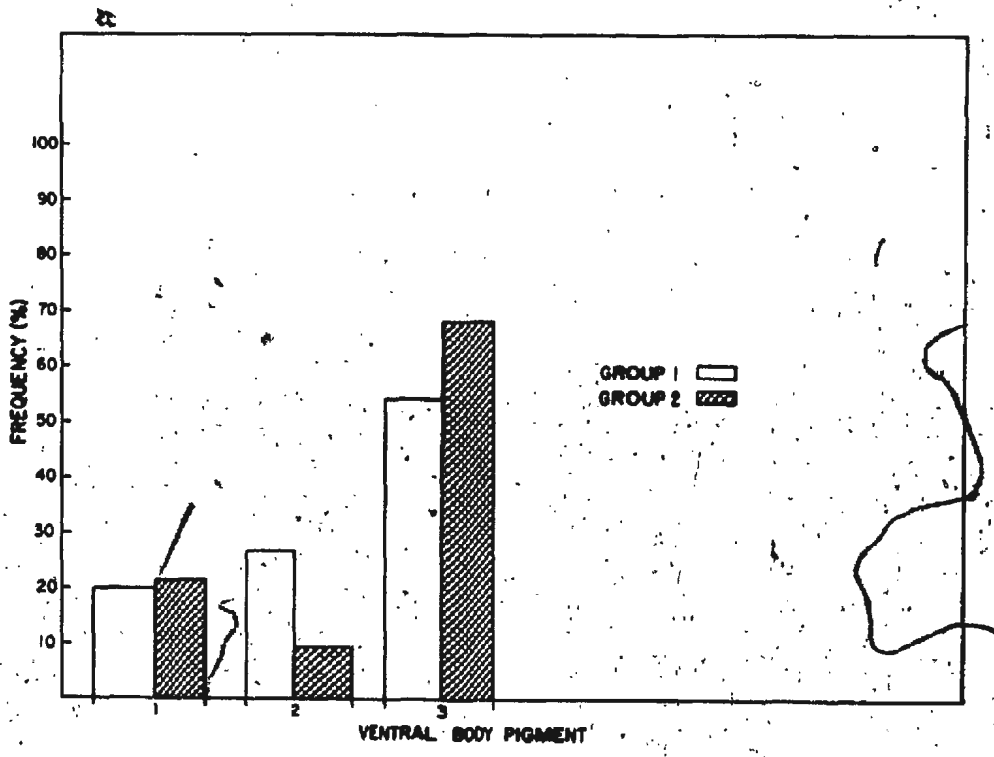
embedded.

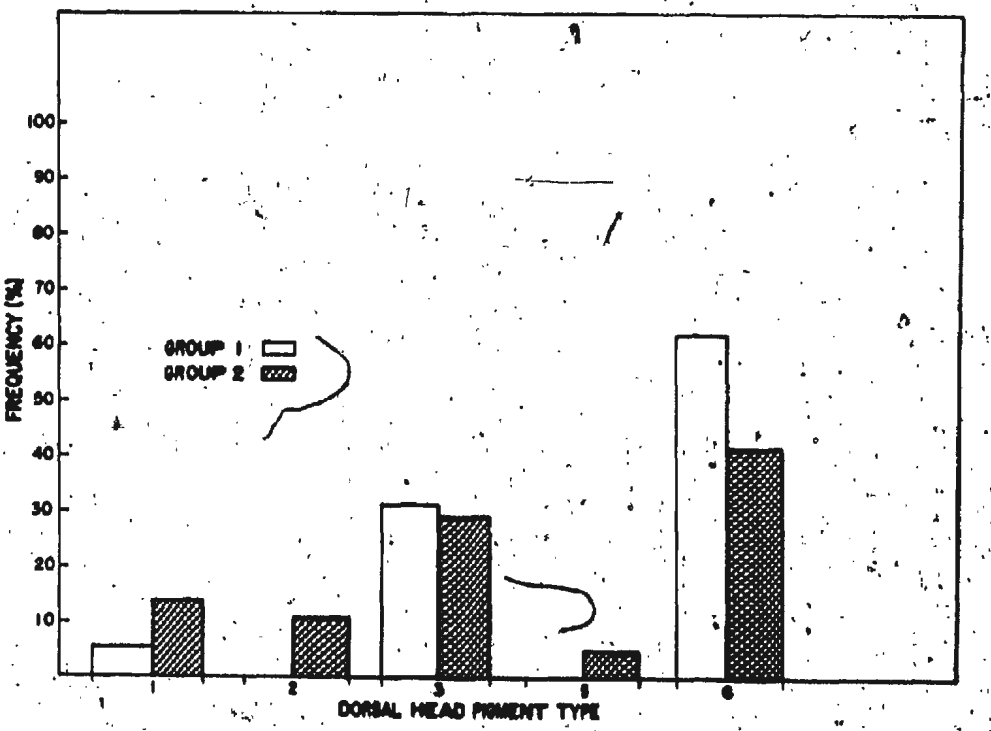
The form of the ventral body melanophores differs between 6-8 mm larvae of both extrusion groups (Fig. 75). Both extrusion groups had approximately the same frequency of occurrence of larvae with contracted and spatially distinct melanophores on the ventrum (20% for Group 1, 22% for Group 2) and both extrusion groups had approximately the same frequency of occurrence of expanded melanophores on the ventrum (80% for Group 1, 78% for Group 2). However, in Group 1 there was a higher frequency of larvae with expanded but still spatially distinct melanophores (27%) than in Group 2 (9%). In the remainder of both extrusion groups, the expanded melanophores were merged into a continuous band. The differences in the shape of the melanophore pattern on the ventrum are statistically significant ($\chi^2 = 31.70$, Prob. $> \chi^2 = 0.001$). Like the dorsal body pigment, the differences in pattern of ventral body pigmentation between extrusion groups tends to be obscured in larger larvae by the increasing overall pigmentation laterally over the body.

Melanophore patterns on the dorsal surface over the brain differed between 6-8 mm larvae in the two extrusion groups (Fig. 76). In Group 1, 50% of all larvae had a pattern of diffuse pigment, with no distinct, separate

Figure 75. Per cent frequency of occurrence of pigmentation types on the ventrum in redfish larvae under 9 mm total length of extrusion groups 1 and 2, 1980 and 1981 combined. (see Appendix A for description of pigment types)

Figure 76. Per cent frequency of occurrence of pigmentation types on the dorsal surface over the brain in redfish larvae under 9 mm total length of extrusion groups 1 and 2, 1980 and 1981 combined. (see Appendix A for description of pigment types)


FREQUENCY (%)
100
90
80
70
60
50
40
30
20
10
GROUP 1
GROUP 2
1
2
3
VENTRAL BODY PIGMENT

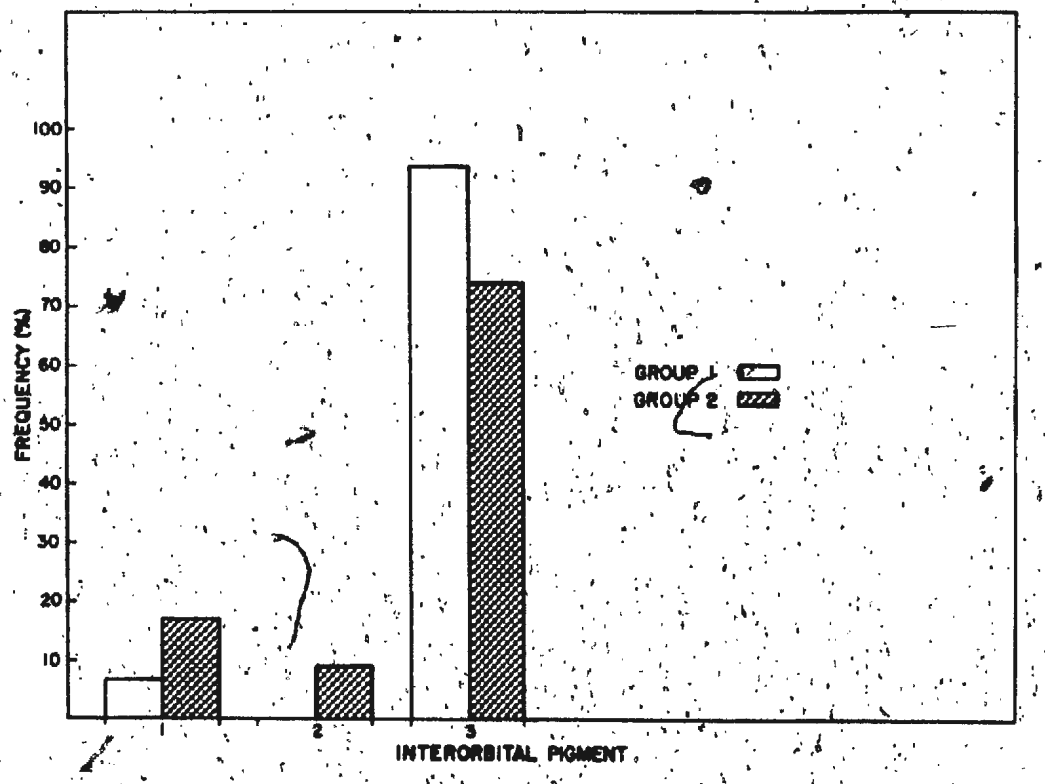

FREQUENCY (%)
100
90
80
70
60
50
40
30
20
10
GROUP 1
GROUP 2
1
1
2
3
5
6
DORSAL HEAD PIGMENT TYPE

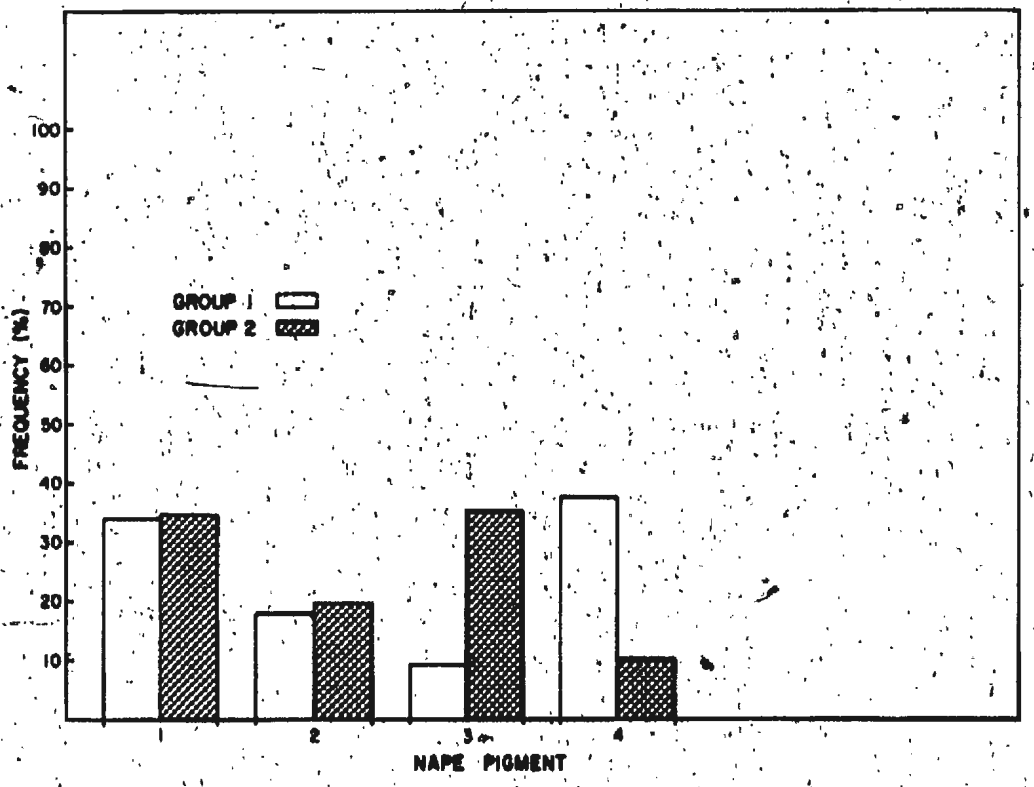
melanophores identifiable. A further 46% had mostly diffuse pigment but with a few separate melanophores as well. The remaining 4% had a pattern of distinct melanophores partly merged into a cap and partly separate. In Group 2, only 6% had all diffuse pigment while 53% had mostly diffuse pigment with some distinct melanophores included. A further 10% had all distinct melanophores joined to form a solid cap and the remaining 30% had mostly distinct melanophores merged into a cap but accompanied by diffuse pigment as well. Tested by chi-square, these differences are statistically significant. ($\chi^2 = 11.36$; Prob. > $\chi^2 = 0.02$). Only larvae 6-8 mm were included in this analysis because of changes in pigmentation within extrusion groups due to development.

Pigment patterns on the dorsal surface of the interorbital space were also found to differ in 6-8 mm larvae between extrusion groups (Fig. 77). The dominant pattern in both extrusion groups was a complete absence of pigment in the interorbital space. In Group 1, 94% of all larvae had no interorbital pigment while 74% of Group 2 larvae had none. In Group 1, the remaining 6% had spatially distinct melanophores resembling those found on the dorsal surface over the brain. In Group 2, however, the remaining larvae either had spatially distinct melanophores similar to Group 1 (17%) or had diffuse, amorphous pigment (9%). These differences in frequency of occurrence of various

Figure 77. Per cent frequency of occurrence of pigmentation types on the dorsal surface of the interorbital space in redfish larvae under 9 mm total length of extrusion groups 1 and 2, 1980 and 1981 combined. (see Appendix A for description of pigment types)

Figure 78. Per cent frequency of occurrence of pigmentation types on the nape in redfish larvae under 9 mm total length of extrusion groups 1 and 2, 1980 and 1981 combined. (see Appendix A for description of pigment types)


FREQUENCY (%)
100
90
80
70
60
50
40
30
20
10
GROUP 1
GROUP 2
1
2
3
INTERORBITAL PIGMENT

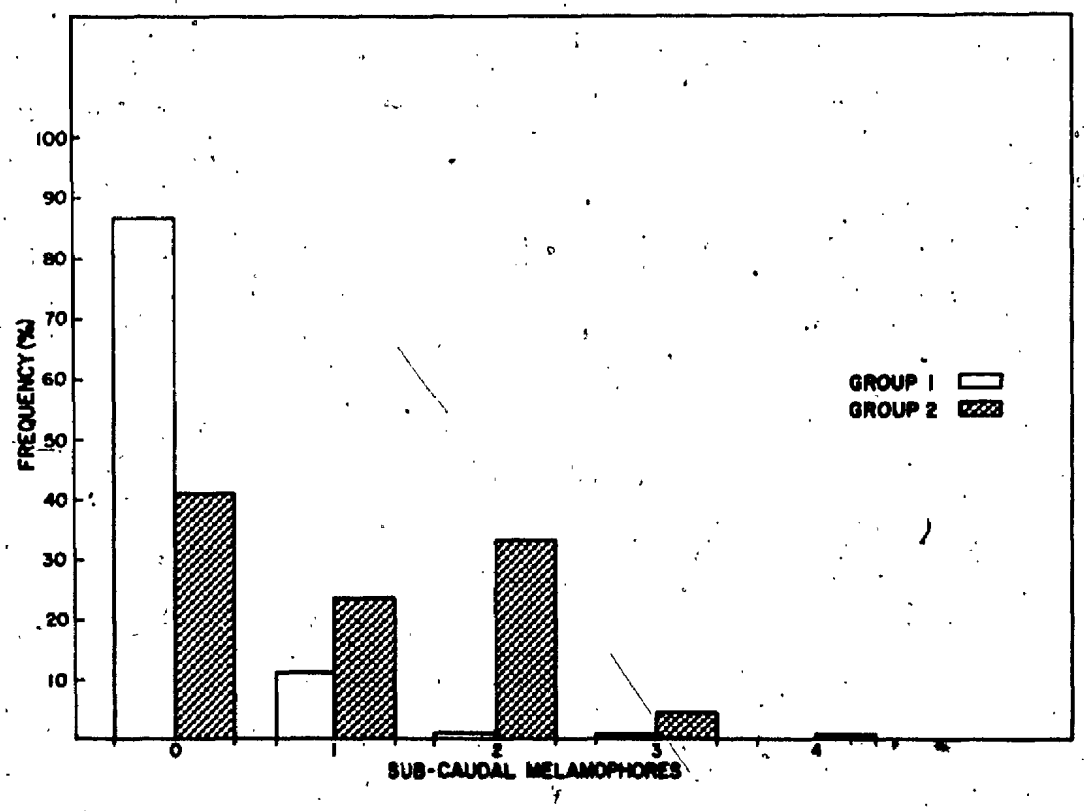

FREQUENCY (%)
100
90
80
70
60
50
40
30
20
10
GROUP 1
GROUP 2
1
2
3
4
NAPE PIGMENT

melanophore patterns were statistically significant (χ^2 = 8.84, Prob. > χ^2 = 0.01).

Pigmentation on the dorsal surface of the nape was also examined in 6-8 mm larvae of both extrusion groups (Fig. 78). Usually, the pigment at the nape consisted of a single melanophore but two or three sometimes occurred. Both extrusion groups had similar frequencies of occurrence of the expanded melanophores (34% for Group 1, 35% for Group 2) and the contracted melanophores (19% for Group 1, 20% for Group 2). However, the remaining Group 1 larvae usually had no pigment (38%) while 9% had diffuse, amorphous pigment. In Group 2, these latter two frequencies were nearly reversed. Only 10% of Group 2 larvae had no pigment while 35% had diffuse, amorphous pigment. These differences between extrusion groups were statistically significant (χ^2 = 16.04, Prob. > χ^2 = 0.001). In both extrusion groups, the pigment at the nape tends to become embedded with increasing size. No larvae with embedded pigment were included in this analysis.

Prior to the completion of notochord flexion, one or more melanophores were often found below the caudal portion of the notochord. The number of these sub-caudal melanophores also varied between extrusion groups (Fig. 79). In Group 1, 87% had no sub-caudal melanophores with most of the remainder having only a single sub-caudal melanophore. In

Figure 79. Per cent frequency of occurrence of various numbers of sub-caudal melanophores in pre-flexion and in-flexion redfish larvae of extrusion groups 1 and 2, 1980 and 1981 combined.


100
90
80
70
60
50
40
30
20
10
FREQUENCY (%)
GROUP 1
GROUP 2
0
1
2
3
4
SUB-CAUDAL MELANOPHORES

contrast, Group 2 larvae had a tendency towards more of these melanophores. Only 41% of Group 2 larvae had no sub-caudal melanophores, 24% had a single melanophore and 35% had two or more sub-caudal melanophores. No larvae in either extrusion group had more than four sub-caudal melanophores. These frequency differences between extrusion groups are statistically significant ($\chi^2 = 95.65$, Prob. > $\chi^2 =$ 0.0001). Because of increasing pigmentation in the caudal area with increasing size and the change in position of the melanophores with notochord flexion, only pre-flexion and in-flexion larvae were included in this analysis.

DISCUSSION

A. GROWTH

Larval redfish sagittae are relatively small in relation to body size compared to some other commercially important species, notably the gadoids, in the Newfoundland area. This size aspect, coupled with their flattened shapes, makes larval redfish sagittae ideal for ageing purposes. No laborious grinding, polishing, or sectioning is required in virtually all sagittae from fish under 20 mm in length. At larger sizes, redfish sagittae become markedly asymmetrical and the lateral surface thickens, particularly in the focal area. Sagittae from such larvae would require extra preparation before all growth increments would become discernible.

Pre-extrusion larvae develop 2-6 rings on their sagittae prior to extrusion. These are not regarded as true growth increments because they typically do not completely encircle the sagitta. The zones of pre-extrusion rings and later post-extrusion increments are separated by a heavy check-like ring easily identifiable by its unusually dark, thick slow-growth band preceeded by a light, fast-growth band typically wider than any of the adjacent increments. This heavy ring is believed to be the first daily increment

and probably is laid down at extrusion. Subsequent increments are believed to occur daily, provided the larvae are actively growing.

The exact time of onset of formation of pre-extrusion rings in redfish larvae is unknown. The duration of larval residence time in the adult body cavity from hatching to extrusion has been estimated to exceed 4 weeks (Templeman and Sandeman 1959). Because larvae normally have 2-6 rings at extrusion, the periodicity of ring formation may range on the order of one every 4-14 days or longer, assuming no rings are present at hatching. No pre-extrusion larvae were found with the heavy, check-like ring but even the smallest post-extrusion larvae had this ring. Check-like marks on larval fish otoliths associated with an abrupt change in environment have been found in other species (Victor 1982) and the sudden change from maternal incubation to extrusion into the water would certainly be a likely cause for check formation.

The period of extended parental care in the adult body cavity in redfish is analagous to the post-hatch mouth-brooding of larval Tilapia mossambica in which the first daily increment forms when the larvae leave the adult female's mouth (Taubert and Coble 1977). Indeed, the only marine species known to have first increment formation delayed after they have been released into the water as

larvae are species such as English sole (Laroche et al. 1982) and anchovy (Brothers et al. 1976) which hatch from pelagic eggs as small larvae in a relatively early stage of development (Brothers and McFarland 1981). In those species, first increment formation is delayed until yolk sac absorption is complete. By comparison, larval redfish at extrusion are large, active swimmers with only a vestige of yolk sac remaining. Additionally, other species, such as grunion (Brothers et al. 1976) and tilapia (Tanaka et al. 1981), known to begin formation of growth marks on their otoliths prior to release into the water, continued to form daily growth increments without delay after hatching into the water.

Due to the failure of the laboratory rearing experiments, evidence supporting the daily periodicity of increments after the heavy, check-like increment at extrusion is also indirect. The time of most intense extrusion on Flemish Cap is April and May (Templeman 1976, Bainbridge and Cooper 1971) with residual extrusion activity still occurring into July (Barsukov and Zakharov 1972). The period of peak extrusion in 1980 and 1981 was estimated from length frequency data to be the last week of April (Anderson 1981, MS1982). Back-calculation to age zero of the increment counts in larvae collected during late June to July is in agreement with the published data.

The procedure estimates April to early May as the period of maximum extrusion activity with a peak during the last two weeks in April and a decline through May with some residual extrusion still occurring into July.

Regression-style linear and non-linear parameter estimation procedures, used to find the equations best fitting the observed length at age and length at sagittal radius data, indicated an excellent linear fit to the length at age data while the length at sagittal radius data was best fit by a polynomial. Although the coefficients of the sagittal radius squared terms are rather small and introduce only slight curvature to the line of best fit, Student's T tests indicate the parameters are significantly different from zero.

The mean growth rate of larvae in 1981, estimated from the length at age regression equation, was 0.109 mm per day, only 68% of the rate observed in 1980, 0.160 mm per day. Larvae in 1981 were, on average, 0.8 mm larger at extrusion than 1980 larvae. The estimated growth rate in 1980 compares well with the estimate of 0.146 mm per day by Anderson (MS1982) based on length frequency data from late May to July. However, Anderson's estimate for 1981, 0.152 mm per day, is much higher than my estimate. This may be partially due to the inclusion in my estimate of growth in April and early May, a period of much reduced growth rates.

The observed length at age data indicated considerable variation in ages among larvae in the same size groups. Even in small larvae, a difference in length of just one millimeter could mean a difference of up to three weeks in age in 1980 and five weeks in 1981. Newly extruded larvae, captured on day of extrusion, ranged from 5.6-8.9 mm. This wide size range at extrusion is probably largely due to the ovoviviparous nature of redfish reproduction and coincident long residence time, after hatching, which the larvae spend in the adult female's body. Because of the magnitude of this variation, calculations of growth rate, particularly for small larvae, based on the intercept of the length at age regression alone, could be very misleading and prone to error. Incorporating an estimator based on the growth of each individual larva helps alleviate this problem and allows back-calculation of individual growth histories as well. The resulting optimal estimate approximates the true length at extrusion for each larva on an individual basis.

The observed mean lengths at extrusion in 1980 and 1981, 7.46 mm and 8.38 mm respectively, are not significantly different from the predicted mean length at extrusion based on the optimal estimation procedure, namely 7.418 mm and 8.228 mm for 1980 and 1981 respectively. In 1980, mean length at extrusion increased steadily with date

of extrusion from a low of 6.86 mm for larvae extruded during early April to a high of 7.96 mm for larvae extruded during the latter part of May. In contrast, mean length at extrusion in 1981 seemed to decline slightly from early April to late May but larvae extruded during the first week of June were larger than those extruded at any other time. Apparently, size at extrusion can be quite variable in redfish, not only from year to year but within a single extrusion season as well.

Back-calculated length at age data, based on the length at sagittal radius data and estimated lengths at extrusion, closely agreed with the observed length at age data. In 1981, redfish larvae were, on average, larger than 1980 larvae of the same age until about 15 days of age. Due to the higher growth rate of larvae in 1980, at all ages greater than 15 days, larvae in 1980 were larger than 1981 larvae, at least for the first 110 days of life.

Redfish larvae do not grow at a uniform rate over the entire larval period. In both 1980 and 1981, growth tended to be relatively slow for the first 10-15 days post-extrusion, relatively high from age 30-90, then slowing as larvae entered the post-larval, pelagic juvenile stage. Mean daily growth rates in 1980 ranged from 0.143 mm per day at extrusion to 0.188 mm per day by age 65, falling to 0.108 mm per day by age 110. Mean daily growth rate in 1981 was much

slower than 1980 over the entire larval period although greater growth rates in the oldest post-larvae entering the pelagic juvenile stage appeared to be comparable. Mean daily growth in 1981 ranged from 0.089 mm per day at extrusion to 0.139 mm per day at age 90 before declining to 0.112 mm per day by age 110.

Expressed as a per cent of total length, larval redfish growth in 1980 was highest at 1.9% per day at extrusion, fluctuating from 1.59-1.63% per day until age 30, then declining steadily to 0.49% per day by age 110. In 1981, the pattern was somewhat different in that, although growth slowed immediately following extrusion, growth actually increased as a per cent of body length to peak at 1.16% per day at age 35. Thereafter, growth steadily declined as in 1980 to a low of 0.52% per day by age 110.

Within a single extrusion season, larvae extruded from early April to late May experienced variable growth conditions as indicated by fluctuations in their growth rates. In 1980, larvae extruded during most of April (Julian days 100-119) did not experience any early post-extrusion decline in growth rate while larvae extruded in early April and all of May underwent declines in growth rate ranging from 0.005 mm per day to 0.032 mm per day for the first 10-15 days post-extrusion. In contrast, in 1981 only larvae extruded in early to mid May experienced early post-

extrusion declines in growth and these declines were much less substantial (0.001 mm per day to 0.012 mm per day) than in 1980.

It has long been postulated that a critical period exists in the early life history of fish larvae during which high mortality occurs (May 1974). The term "critical period" was first applied to fish by two early French fish culturists, Fabre-Domergue and Bietrix (1897, cited from May 1974), who used it to describe the time of completion of yolk sac absorption. At this time they observed high mortality among marine fish larvae in laboratory rearing attempts. Hjort (1914) further advanced the concept by linking its severity in a given year to fluctuations in the year class strengths of commercial fish populations. The existence of a critical period soon after hatching has been substantiated in laboratory rearing experiments (Blaxter and Hempel 1963, Lasker et al. 1970, Wyatt 1972) but demonstration of its occurrence in the sea has remained elusive (Marr 1956, May 1974).

Periods of poor growth may also be periods of high mortality, and lack of suitable prey or the inability to capture it at the time of switchover from yolk sac to exogenous feeding was originally cited by Hjort (1914) as the most likely cause of mortality in the critical period. Theilacker and Dorsey (1980) regarded larval survival as

being dependent upon the larva's ability to find and capture sufficient prey at the time of completion of yolk sac absorption. Lack of demonstration of a critical period at sea may in part be due to poor growth determination techniques, particularly reliance on length frequency data (May 1974). Accurate growth determinations from otolith analyses will eliminate this restriction and improve the accuracy of survivorship curves and, in turn, increase the likelihood of critical period detection.

The present analysis of larval redfish growth exhibits the potential of otolith analysis in this regard. Redfish larvae, in both 1980 and 1981, exhibited initial declines in growth rate in the early post-extrusion period. I contend that this period of relatively poor growth over the first 10-15 days post-extrusion may also be a period of high mortality and represents a critical period of adjustment to environmental conditions and a switchover to exogenous feeding.

Redfish larvae have virtually no yolk remaining at extrusion. Failure to quickly become a proficient predator and adjust to prevailing environmental circumstances results in declining growth rates, poor condition, and consequent high mortality. Survivors of this 10-15 day period have successfully accomplished the required adjustments and their success is indicated by the subsequent period of rapid

increase in growth rate and a long period of relatively high, stable growth through the larval phase. Without suitable abundance data to construct a survivorship curve, this contention may only be regarded as speculatory. The present data demonstrate that larval otolith analyses have the capability of establishing the existence of critical periods in the early life histories of fish species.

In 1980, irrespective of time of extrusion or age of larvae, growth of most larvae peaked in late June to early July (Julian days 170-190). In 1981, except for larvae extruded about the first week of April, growth of most larvae in the other extrusion groups peaked in early to late June (Julian days 150-170). While the causative factor of this apparent synchrony of good growth within extrusion groups in a year is unresolved, it is assumed that some environmental event, either biotic, abiotic, or a combination of both, provided conditions conducive to accelerated growth during these time periods.

In 1980, larvae extruded after Julian day 120 (last day of April) grew faster over the entire larval period than did larvae extruded in April. This pattern did not appear in 1981. In 1981, larvae extruded in early April (Julian days 90-99) and late May (Julian days 140-149) grew fastest of all extrusion groups but larvae extruded between these times and in June grew more slowly. In 1980,

the combination of increasing length at extrusion and increasing growth rate together result in later extruded larvae continuing to be larger than early extruded larvae of the same age throughout the larval period. In 1981, larvae extruded in early April and from late May to early June were larger at the same age than larvae extruded at other times. These size at age differences with date of extrusion have important consequences for growth and mortality computations based on a progression of length frequency modes.

IV.B. MORPHOLOGY

Evaluation of the possible usage of morphological variables published from work on adult redfish as species discriminators in larvae was disappointing. The only criterion by which the three putative species may be differentiated with certainty is the morphology of the gas bladder musculature and its passage between the ventral ribs (Power and Ni 1982) although Hallacher (1974) considered differences in gas bladder musculature in scorpaenids in general to be useful only in separation of sub-genera, not species. Gas bladder musculature was not investigated in this study but its applicability to larvae is doubtful in any case. Differentiation of the gas bladder musculature occurs coincidently with the first stages of gas bladder

inflation in anchovy around 10 mm in length (O'Connell 1982), but its timing in redfish is unknown. However, although the musculature may appear fairly early, the ventral ribs do not ossify in redfish until 18-20 mm, near the end of the larval period. Therefore, this identification criterion cannot be applied to all but the very largest larvae immediately prior to entering the pelagic juvenile stage.

Total gill rakers on the first left gill arch, fusion of the occipital-nuchal ridge, relation of the pectoral fin to the anus, and downward angle of the third posterior preopercular spine, all reported by Ni (1981b) to be useful in discrimination of S. fasciatus from S. mentella, are not applicable to larvae either by reason of incompleteness of their development in the larval stage or by continuing changes in larval body form.

Barsukov and Zakharov (1972) and Ni (1982b) reported S. fasciatus typically have 29 vertebrae, 7 anal fin rays, and 14 dorsal fin rays while S. mentella and S. marinus typically have 30-31, 8-10, and 15 respectively. Other criteria, such as body coloration, eye diameter, and projection of the bony tubercle on the lower jaw have been used to differentiate S. marinus from S. fasciatus and S. mentella but these characters are not considered fully reliable (Barsukov and Zakharov 1972) and, except for eye

diameter, are not applicable to larvae.

Thus, at present, no single morphological character or combination of morphological characters have been identified which may be used to differentiate larval S. mentella and S. marinus. A similar situation exists with respect to differentiation of S. fasciatus. S. fasciatus typically has 29 vertebrae but Barsukov and Zakharov (1972) report 13.2% of S. fasciatus from Flemish Cap and adjacent banks have 30 vertebrae and 1.1% of S. marinus and 4.1% of S. mentella have 29 vertebrae. Ni (1981b) reported over 30% of S. fasciatus on the adjacent Northeast Grand Bank have 30 vertebrae and 1-2% of S. mentella have 29 vertebrae. Ni (1982b) reports some S. marinus on Flemish Cap have 29 vertebrae as well. In this study, of all larvae with the adult complement of vertebrae, only 7% had a frequency of 29. No statistically significant differences were found between larvae with 29 vertebrae and those with 30-31 vertebrae on any of the morphometric or meristic variables measured.

Ni (1981b) reports 98% of S. fasciatus on the adjacent Northeast Grand Bank have 7 anal fin rays, but Barsukov and Zakharov (1972) report 30.1% of S. fasciatus from Flemish Cap and adjacent banks have 8 or more anal fin rays. In this study, of all larvae with the adult complement of anal fin rays, only 5.6% had a frequency of 7 and no significant differences were found between larvae with 7

anal fin rays and those with 8 or more on any of the morphometric means or meristic frequencies measured. Only 3.5% of all larvae had both 29 vertebrae and 7 anal fin rays together. No significant differences were found between larvae with 29 vertebrae and 7 anal fin rays and those with 30 or more vertebrae and 8 or more anal fin rays together.

Barsukov and Zakharov (1972) also noted differences in dorsal fin ray frequencies as well but this character cannot be applied to larvae because, even by 20 mm, most larvae still have not differentiated dorsal spines and rays. In Sebastes, the posteriormost dorsal spine first forms as a soft ray and then transforms later into a spine, beginning at the base and continuing distally (Moser et al. 1977, Richardson and Laroche 1979). If one assumes, on the basis of these data, that the proportion of S. fasciatus with vertebral counts other than 29 and fin ray counts other than 7 is small on Flemish Cap, then these data suggest that less than 10% of the redfish on Flemish Cap belong to S. fasciatus yet species identification of the adult stock assemblage in the February to March period indicates that 32% of all redfish on the Cap at that time are S. fasciatus (see Appendix B), 57% are S. mentella and 11% are S. marinus. Because the extent of seasonal variation in species abundance on Flemish Cap is unknown, these proportions may not be representative of the April to July extrusion

period.

Magnusson (1981) contended that, in juvenile S. marinus, the upper of the two longest preopercular spines is shorter than the lower while in S. mentella the condition is reversed. The upper spine is assumed to be the second preopercular spine and the lower one the third preopercular spine. All the specimens reported in this study fit the pattern reported by Magnusson to be S. marinus. As Appendix B indicates, this is not likely on Flemish Cap.

Templeman (1980) found pre-extrusion larvae of the three putative species differed in sub-caudal melanophore pigmentation. While 90% of S. marinus adult females , 76% of adult S. mentella females, and 100% of S. fasciatus females had at least some larvae with sub-caudal melanophores, the actual frequencies of larvae with sub-caudal melanophores were 21% for S. marinus, 11% for S. mentella and 99% for S. fasciatus. Additionally, S. fasciatus larvae usually had two sub-caudal melanophores while in S. marinus and S. mentella with sub-caudal melanophores, the typical number was one. While interesting, this is not a good species identification tool. A larva lacking sub-caudal melanophores or with a single melanophore could reliably be ruled out as S. fasciatus, but one would not be able to differentiate between S. marinus and S. mentella. While

Templeman (1980) does not report the actual frequency of larvae with two or more sub-caudal melanophores, his data indicate that 19% of S. marinus adult females and 25% of S. mentella adult females contain at least some larvae with two or more sub- caudal melanophores. Presumably, the actual frequency in the larvae is small. In this study, the number of larvae with two or more sub-caudal melanophores is less than 2% of all larvae extruded in April, the period of maximum extrusion activity. However, 35% of larvae extruded in May or later had two or more sub-caudal melanophores. It seems probable that those larvae extruded before May are S. mentella or S. marinus or, more probably, a mixture of unknown proportions of both and that larvae extruded in May or later contain an increased proportion of S. fasciatus. This distinction in extrusion times is supported by Barsukov and Zakharov (1972) who reported that S. mentella and S. marinus extrusion is mainly in April and May, and S. fasciatus extrusion is delayed until May through July.

Comparison of meristic frequencies and morphometric means of larvae with two or more sub-caudal melanophores and those with fewer than two melanophores did not show any differences between these groups. Larvae with two or more sub-caudal melanophores were otherwise indistinguishable, from larvae with fewer than two sub-caudal melanophores extruded during the same period. Because of the increasing

pigmentation in the caudal area with age, larvae with ossified vertebrae and anal fin rays could not be counted for sub-caudal melanophores. Thus, unfortunately, no direct comparison of numbers of sub-caudal melanophores with numbers of vertebrae and anal fin rays was possible.

Principal Component Analysis has been previously used in attempts to distinguish between redfish species. Jones (1969), in a study of adult redfish morphometrics in the Irminger Sea, found no grouping of component scores and concluded that redfish had a wide but continuous variation in body proportions.

Technically, only continuous variables with a discrete, normal distribution may be included in a multivariate clustering procedure such as PCA (Thorndike 1978). In this dataset, this restriction limited PCA to morphometric variables only because, due to the manner in which ossification of meristic structures occur in larval redfish, and probably fish larvae in general, the frequency distributions of the meristics invariably were strongly skewed and often discontinuous.

The PCA procedure showed that, after variation associated with fish length was removed, a statistically significant pattern with respect to time of extrusion was evident. The PCA scores were positively correlated with increasing lateness of extrusion. This was most evident in

pre-flexion and in-flexion larvae. This pattern correlated with extrusion time was further investigated by comparison of larvae extruded in April from the onset of seasonal extrusion to its peak around the end of April, and larvae extruded in May or later after peak extrusion had passed.

Examination of morphometric means and meristic frequencies for these two extrusion groups by one millimeter length intervals showed that the differences between extrusion groups are similar for most of the variables measured. In general, the later extruded larvae had larger values for most morphometric means throughout the larval period from 6-20 mm. Meristic development was characterized by earlier onset of ossification of fin elements and supports, head spination, vertebrae, and all skeletal elements generally, followed usually by earlier completion of the ossification process. Not only do the observed differences have a bearing on the species identification problem, but they also have important ecological consequences.

All body morphometrics which were measureable on newly extruded larvae, including snout to anus length, head length, snout length, caudal peduncle width, body depth at the pectoral fin and anus, eye diameter, interorbital width, head depth, and pectoral fin length and base depth, showed that larvae in the two extrusion groups were indistinguish-

able at 6 mm. No ossification of meristic structures is present at 6 mm nor are any meristic structures present as cartilaginous elements, irrespective of extrusion time.

However, as the larvae grow, differences become more pronounced. At 7 mm, larvae extruded in May or later had larger pectoral fin base depths than larvae extruded in April and ossification of the gill rakers on the lower arm of the first gill arch had begun, a process which was delayed to 9 mm in the April-extruded larvae. Principal rays of the caudal fin, both superior and inferior, and brachiostegal rays also appear at 7 mm in the later extruded larvae.

At 8 mm, the later extruded larvae had longer and deeper heads, a larger snout to anus length, and were much deeper-bodied, as evidenced by larger body depth at both the pectoral fin and anus. Also by 8 mm, 90% of the later extruded larvae had ossified maxillae, the maxillae of the later extruded larvae also being longer than those of the early extruded larvae. The longer maxillae and larger heads of the later extruded larvae result in a broader gape and hence the ability to ingest larger food particles. Gill rakers, which function in food handling, are also more numerous and better developed in the later extruded larvae. The development of gill rakers retains and improves their ability to feed on small food particles (Bainbridge and

McKay 1968). The utility of prey, in terms of energy gain, increases greatly with increases in prey size (Werner 1974) even though the larger prey may be less abundant (Kerr 1971). Small prey have the advantage of usually greater abundance and hence lower search and capture energy costs to the predator if the prey are at high densities.

The ability to feed on both large and small prey results in a wide feeding niche. This allows the later extruded larvae to eat large, high energy content prey, when such prey are available. This promotes fast growth and enhances survival. Later extruded larvae can still eat small, low-cost prey, if necessary. The earlier extruded larvae, on the other hand, are dependent on small prey. Thus, they may be vulnerable to starvation in areas of low prey density of the smaller size prey even though larger prey are in abundance (McCullough and Stanley 1981). Whether later extruded redfish larvae do actually selectively ingest larger food particles is unknown.

The coincident development of a larger, more advanced gut area, as evidenced by the larger snout to anus length and greater body depth at both the pectoral fin and anus, indicate a greater ability to more efficiently digest and assimilate food items.

Also at 8 mm, later extruded larvae have larger eyes and thicker caudal peduncles than those larvae extruded in

April. The larger eyes may indicate a better developed visual sense and hence increased ability to perceive prey at relatively greater distances while the larger caudal peduncle width, and coincident development of the caudal and pectoral fin elements, make the later extruded larvae faster and more maneuverable predators.

The greater comparative speed and maneuverability of the later extruded larvae probably continues through to completion of notochord flexion around 15 mm. Principal caudal fin ray and pectoral fin ray numbers in the later extruded larvae continue to exceed those in the early extruded larvae, although ultimately the numbers of rays are the same in each group. Anal spines and rays, the pelvic spine and rays, dorsal spines and rays, and secondary caudal rays all appear in the later extruded larvae before they appear in the early extruded larvae but, by 15 mm, both extrusion groups have developed the adult complement of fin ray elements, except those of the secondary caudal series which continue to develop into the pelagic juvenile stage and pectoral fin rays which are complete around 18 mm.

This pattern towards robustness, thicker bodies, and generally advanced development in the later extruded larvae continues throughout the larval period. Some of the morphometrics, such as snout to anus length, head length and depth, caudal peduncle width, body depth at the pectoral fin and anus, eye diameter, maxillary length, and lengths of the

second, third, and fourth posterior preopercular spines, remain consistently greater in the later extruded larvae. Others, such as pectoral fin length and base depth, are significantly different between extrusion groups only over more restricted size ranges. The two extrusion groups are most different morphometrically in the pre-flexion and in-flexion stages, but the differences between extrusion groups become progressively less pronounced. By completion of notochord flexion, around 15 mm in both extrusion groups, eye diameter and maxillary length means are overlapping and, from 16-20 mm, the confidence intervals about all morphometric means for the two extrusion groups overlap. By 20 mm, most meristic frequencies were also not significantly different between extrusion groups, making the larvae virtually indistinguishable again.

Thus, larvae of the two extrusion groups do not ultimately differ from each other in morphology. The only difference between them is the rate and timing of occurrence of developmental events during the larval stage. There are two possible explanations for these differences. The first is that larvae extruded in April are entirely or mostly of one or two of the putative redfish species whose extrusion activity peaks in April and becomes much less common in May. Larvae extruded in May and later are the result of extrusion activity of a different redfish species. Because there seems

to be only a single extrusion peak in each year, then either the extrusion activity of the different species must be overlapping or the respective species abundances must be such that one species overwhelmingly dominates on Flemish Cap and the extrusion activity of the other two species is negligible by comparison. The latter seems unlikely given the reported species proportions (see Appendix B). As to the timing of their respective extrusions, S. mentella and S. marinus are believed to have peak extrusion in April, declining into May, while S. fasciatus is believed to extrude larvae from May to July (Barsukov and Zakharov 1972).

The second equally possible explanation is that changing environmental parameters in the progression of Spring into Summer induce growth-related developmental changes in the later extruded larvae such that development in general is greatly accelerated.

Processes determining the formation of meristic and morphometric characters are generally sensitive to environmental changes (Chen 1971). Jean (1945) found that herring, Clupea harengus, taken from colder waters of the Gulf of St. Lawrence were characterized by a slower growth rate and smaller heads than those from warmer waters. Templeman and Pitt (1961) found a negative correlation between vertebral number and surface temperature in S.

mentella. In Cyprinodon macularius, any departure from 32 degrees Celsius, the temperature of fastest growth, produced increases in the proportion of most measured body parts (Sweet and Kinne 1964). Lindsay (1954), in a study of the meristic characters of Macropodon opercularis, reported some meristic series were still subject to environmental influence 20 days after hatching. Fahy (1981), in a study of embryos of the cyprinodont, Fundulus majalis, found that fewer dorsal fin rays were formed with increasing temperature.

The mean temperature in the surface waters of Flemish Cap in April ranges from 1 degree Celsius in the cold, northwest corner, to 6 degrees Celsius in the central, shallow region. By July, the mean temperature has increased to about 8 degrees Celsius in the northwest corner and 14-15 degrees Celsius in the central area (Hayes et al. MS1977). Because the redfish larvae extruded from April to July are indistinguishable at 6 mm and develop at different rates through to 20 mm, by which time they are indistinguishable again, the differences observed may be the result of seasonal environmental change rather than temporal differences in extrusion activity of different species, although it is conceivable that both are happening at the same time.

The failure to find criteria for species identifica-

tion gives one cause to argue that the three putative species of redfish may not be valid. Given the species proportions of adults in February and March, reported in Appendix B, it seems likely that sufficient numbers of all three species exist on the Cap. The larval samples examined in this study most likely contained representatives of all three species. Comparison of specimens from different locations where the stocks are known to be predominantly one or the other of the three species may be helpful. However, this will introduce the complication of geographic differences in morphology obscuring or inflating potential interspecies differences. The present analysis could have been improved by provision of extra sampling through June and July. Also, an integrated study of temporal variation in specific extrusion activity coupled with morphological studies of newly-extruded larvae would improve the chance of identification of interspecific differences. Another avenue for further study would be to investigate biochemical aspects of larval redfish to determine if any such differences might be correlated with morphological criteria.

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Appendix A. List of morphological variables measured, and their abbreviations with a description of each variable and its coding, where applicable.

APPENDIX A

EXTERNAL MEASUREMENTS

The following were measured from the left side, where applicable. Abbreviations in brackets are those used in the text.

(1) tip of snout to posteriormost edge of the caudal rays (TL)

(2) tip of snout to the anus (SNANLEN)

(3) tip of snout to posteriormost edge of the opercles (HDLEN)

(4) tip of snout posteriad to the intersection of a vertical line from the anteriormost edge of the orbit (SNTLEN)

(5) tip of snout posteriad to the intersection of a vertical line from the first dorsal spine (PDORLEN)

(6) tip of snout posteriad to the intersection of a vertical line from the first anal spine (PANLEN)

(7) width of the caudal peduncle at its narrowest point (CAUPED)

(8) body depth measured at the insertion of the pectoral fin (BODPEC)

(9) body depth measured at the anus (BODAN)

(10) length of the maxilla (MAXLEN)

(11) horizontal width of the eye measured through its center (EYED)

(12) length from the last ray of the dorsal fin to the intersection of a vertical line drawn through the posterior edge of the hypural elements (CAULEN)

(13) length from the last ray of the anal fin to the intersection of a vertical line drawn through the hypural elements (CAULEN)

(14) horizontal distance through the interorbital space (INTORB)

(15) head depth measured along a vertical line through the center of the eye (HDDEP)

(16) length of the longest ray of the pectoral fin (PECT LEN)

(17) length of the base of the pectoral fin (PECTDEP)

(18) state of flexion of the notochord according to Moser et al. (1977)

7. pre-flexion
8. in-flexion
9. post-flexion

(19) number of body myomeres (MYOM)

(20) number of post-anal body myomeres (ANMYOM)

(21) length of the dorsal body melanophore line in myomere units (DLEN).

(22) length of the ventral body melanophore line in myomere units (VLEN)

MEASUREMENTS AFTER CLEARING AND STAINING

Counts of all meristics were categorized into numbers of elements ossified (staining with alizarin red) or cartlaginous (staining with alcian blue).

(23) length of the dorsal fin from the first spine to the last ray (DORLEN)

(24) length of the anal fin from the first spine to the last ray (ANLEN)

(25) length of the longest ray of the pelvic fin (PEL LEN)

(26) length of the pelvic spine (PELSLEN)

(27) lengths of all posterior preopercular spines (PRO1-PRO5)

(28) number of gill rakers in the upper arm of the first gill arch (GRAKU)

(29) number of gill rakers in the lower arm of the first gill arch (GRAKL)

(30) number of brachiostegal rays (BR)

(31) number of vertebrae (VERT)

(32) number of superior principal caudal rays (SPRIN)

(33) number of inferior principal caudal rays (IPRIN)

(34) number of superior secondary caudal rays (SPROC)

(35) number of inferior secondary caudal rays (IPROC)

(36) number of dorsal spines and rays (DOR)

(37) number of anal spines (ANSP)

(38) number of anal rays (ARAY)

(39) number of pectoral rays (PEC)

(40) number of pelvic spines (PELS)

(41) number of pelvic rays (PELR)

PIGMENTATION

Several areas of body pigmentation were observed and the pattern of melanophores was categorized into one of several types coded as below.

(42) melanophores on top of the brain

1. pigment diffuse, no distinct melanophores
2. partly diffuse and partly forming a solid cap of pigment
3. distinct melanophores merging into a solid cap
4. some distinct, some merged into a cap
5. some distinct and separate, and partly diffuse pigment
6. all separate, distinct melanophores

(43) melanophores in the interorbital space

1. all separate, distinct melanophores
2. melanophores arranged into a ring
3. pigment diffuse, no distinct melanophores
4. no pigment

(44) melanophores at the nape

1. single melanophore, expanded in appearance
2. one or more contracted melanophores
3. diffuse pigment
4. no pigment
5. pigment has become embedded

(45) melanophores on the dorsum

1. distinct melanophores forming a complete line or nearly so
2. distinct melanophores forming a line for more than half the total extent of the melanophore pattern
3. distinct melanophores forming a line less than half of the total extent of the melanophore pattern
4. all distinct, separate melanophores
5. line of melanophores has become bisected by dorsal fin development

(46) melanophores on the ventrum

1. contracted, separate melanophores not forming a line

2. expanded but separate melanophores not forming a line
3. melanophores merged into a distinct line

Appendix B. Estimated proportions of all putative species of *Sebastes* present on Flemish Cap during February and March, 1983.

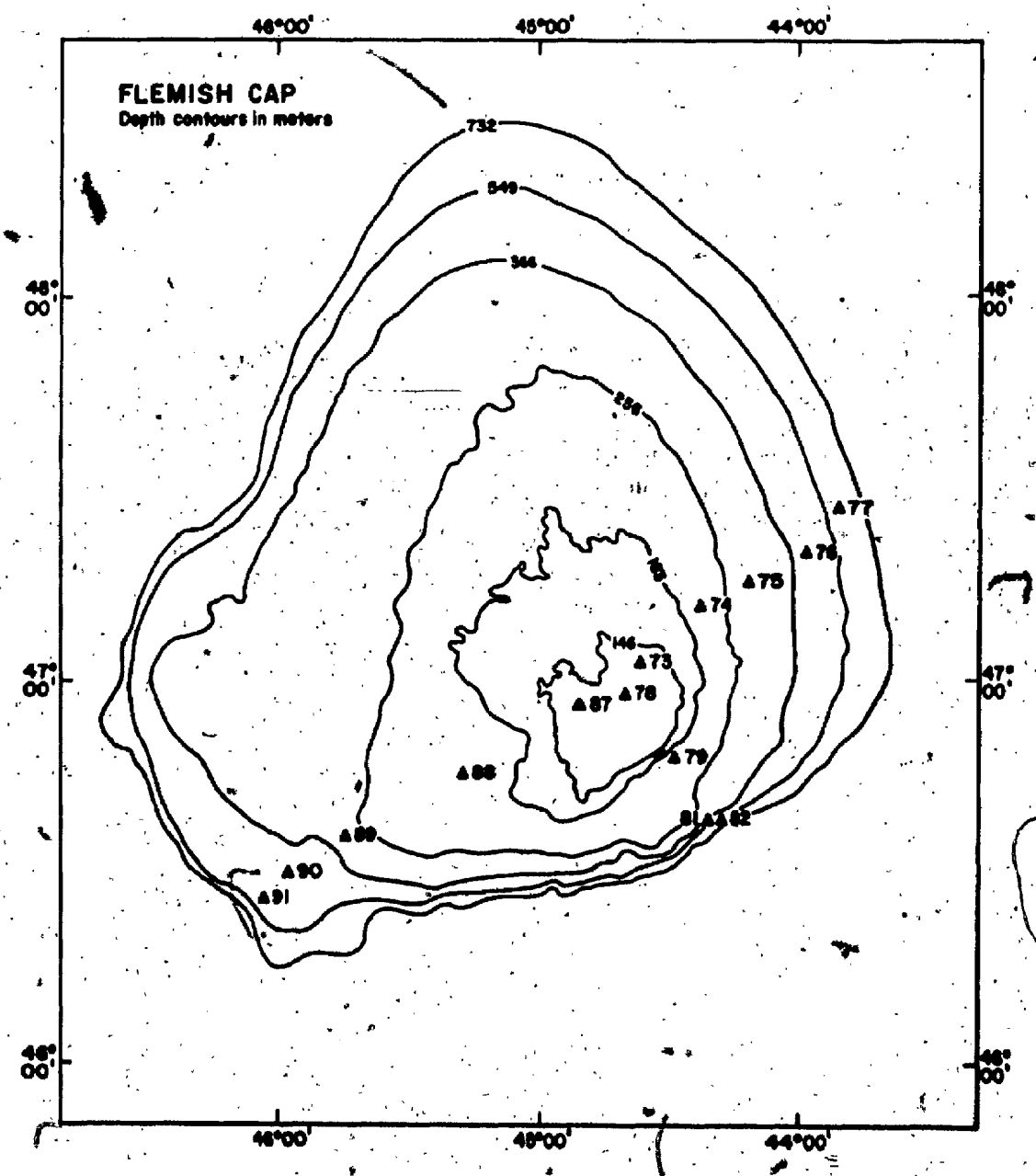
APPENDIX B

During February and March, 1983, two cruises to collect information on adult redfish abundance were made to Flemish Cap. The first was a random stratified trawl survey during which 133 tows were completed and total number of adult redfish in each was recorded. Tows were completed in each of 5 depth zones (1) 0-184 meters (2) 185-258 meters (3) 259-369 meters (4) 370-554 meters (5) 555-739 meters. The total number of adult redfish 25 cm or larger and the area in each depth zone were combined to estimate the total number of such redfish in each depth zone.

On the second cruise, 14 trawl tows were completed in line transects with tows in each of the same depth zones covered in the first cruise. The sample locations are indicated in the accompanying figure. In each tow, the first 160 redfish 25 cm or larger were selected for identification according to gas bladder musculature criteria (Ni 1981a and b, Litvinenko 1980). The proportion of each of the three putative species was then determined separately for each depth zone. This was done because of the reported depth stratification of their respective distributions (Barsukov and Zakharov 1972, Ni 1982).

The results of the two surveys were combined to give estimates of the species proportions on Flemish Cap as a

Figure 80. Fishing trawl locations for collection of adult redfish for species proportion determinations, February-March, 1983.


FLEMISH CAP
Depth contours in meters
732
549
366
256
146
46°00'
45°00'
44°00'
48°00'
47°00'
46°00'
Δ77
Δ76
Δ75
Δ74
Δ73
Δ78
Δ87
Δ79
Δ86
Δ82
Δ80
Δ90
Δ91

whole (see Table 17). Adult redfish are strongly depth stratified. Relatively few redfish of any species are found at depths shallower than 185 meters. Redfish are most abundant from 259-554 meters (zones 3 and 4) with relatively large abundances recorded in zone 5 as well. Because redfish abundance is still high in zone 5, the total abundance figures for the entire Cap are probably underestimated in that some redfish will be found below 739 meters, the maximum depth included in zone 5.

The individual species are also depth stratified. In zone 1 and 2, S. marinus is the most abundant species comprising 57% and 93% of the populations in these zones respectively. S. marinus is rare in zone 3, absent in zone 4, and comprises 12.5% of the population in zone 5. The appearance of S. marinus in the deepest zone is somewhat surprising because published accounts of its distribution from Flemish Cap and other areas indicate it is predominantly found at depths shallower than 400 meters.

S. fasciatus is rare in the shallow zones 1 and 2. However, it comprises 95% of the population in zone 3. It is rare in zones 4 and 5 as well. Again, this is surprising because S. fasciatus has been identified as a shallow water redfish in other areas. S. fasciatus was expected to be a major constituent of the redfish population in the shallow zones, particularly zone 2.

Table 17. Total estimated proportion and abundance, and estimated proportion and abundance by depth zone of adult S. marinus, S. mentella, and S. fasciatus on Flemish Cap in February-March, 1983.

Zone #	Depth (m)	S. marinus p	S. marinus St. Err.	S. marinus Est. # (10^{-4})	S. fasciatus p	S. fasciatus St. Err.	S. fasciatus Est. # (10^{-4})	S. mentella p	S. mentella St. Err.	S. mentella Est. # (10^{-4})	Total # (10^{-4})
1	(0-184)	.568	.053	4.7	.011	.011	0.1	.421	.053	3.5	8.3
2	(185-258)	.934	.021	2649	.022	.013	62	.044	.017	125	2836
3	(259-369)	.042	.015	515	.946	.017	11597	.012	.008	147	12259
4	(370-554)	0	0	0	.052	.008	777	.948	.008	14170	14947
5	(555-739)	.125	.026	1099	.013	.009	114	.862	.027	7581	8794
Total		.110	.022	4268	.323	.016	12550	.567	.015	22027	38844

As expected, S. mentella is the dominant species in the deeper zones 4 and 5 where it comprises 95% and 86% of the respective populations. S. mentella also comprised 42% of the population in the shallow zone 1 and is of negligible importance in zones 2 and 3.

Corrected for the observed depth stratification of specific abundances, the proportion of the three putative species on Flemish Cap are 11%, 32%, and 57% for S. marinus, S. fasciatus, and S. mentella respectively. These proportions are consistent with previously published accounts of the redfish population on Flemish Cap (Templeman 1976).

Because the extent of seasonal changes in distribution and abundance of the three putative species is unknown, these estimates should be used with caution when extended to other times of the year. Also, collection of samples to establish species proportions did not include stations in the northern or northwestern part of Flemish Cap. Because only 14 tows were completed to collect the species identification samples, and because the northern ares were excluded from sampling, the real variation in species proportions within each depth zone may be higher than indicated in these data.