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COMPARATIVE REPRODUCTIVE BIOLOGY OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM* (LESUEUR), AND THE THREADFIN SHAD, *D. PETENENSE* (GUNTHER), IN LAKE TEXOMA, OKLAHOMA

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

by

WILLIAM L. SHELTON

Norman, Oklahoma

1972

COMPARATIVE REPRODUCTIVE BIOLOGY OF THE GIZZARD SHAD,

DOROSOMA CEPEDIANUM (LESUEUR), AND THE THREADFIN

SHAD, *D. PETENENSE* (GUNTHER),

IN LAKE TEXOMA, OKLAHOMA

APPROVED BY

DISSERTATION COMMITTEE

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COMPARATIVE REPRODUCTIVE BIOLOGY OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM* (LESUEUR), AND THE THREADFIN SHAD, *D. PETENENSE* (GUNTHER), IN LAKE TEXOMA, OKLAHOMA

CHAPTER I

INTRODUCTION

Comparative studies have the potential of yielding information that might otherwise be overlooked. Sympatric species are studied for interaction and overlap in their biology while allopatric forms may be studied to predict the potential of such action. If a barrier separating two species is suddenly removed, the two may coexist compatibly or one might eliminate the other.

In Lake Texoma, *Labidesthes sicculus* was rapidly replaced by *Menidia audens*. *L. sicculus* was abundant in Texoma from shortly after impoundment in 1942 until 1952 (Riggs and Bonn, 1959). *Menidia* was first collected in the lake in

1953, and in 1954 it was more abundant than Labidesthes. By 1959 Menidia was the only atherinid in lake collections.

Dorosoma cepedianum has been in Lake Texoma since impoundment and was the most abundant fish there until the late 1950's. In the spring of 1957 the lake flooded, and for the first time water passed over the spillway. That same year young-of-year D. petenense, previously only reported in the river below the dam, were initially collected in Lake Texoma and in greater abundance than young-of-year D. cepedianum (Riggs and Moore, 1958). During the years since its first appearance, D. petenense has superseded but not replaced D. cepedianum. Apparently the two species are able to coexist, neither to the great detriment of the other. They are sympatric over much of the southern portion of the range of D. cepedianum. A relatively high minimum temperature tolerance has been the presumed factor which limited northern extension of the range of D. petenense. It has been introduced in many areas, however, and now exists in several regions outside the range of D. cepedianum (Johnson, 1969).

As larvae the two species probably occupy a similar niche, but are ecologically distinct as adults. D. cepedianum

is predominantly a nonschooling, littoral, sometimes bottom-feeding fish; D. petenense is an actively schooling, limnetic, plankton-filtering fish. However, young of both pass through pelagic, schooling, and planktonivorous larval stages during which they may be competitive if comparable stages exist simultaneously. A period of overlap in larvae is dependent on a common reproductive period. Reproduction of the two species has been studied separately to varying degrees but not comparatively in the same body of water. The purpose of this study was to compare the reproductive biology of D. petenense and D. cepedianum, including development, seasonal and diurnal spawning patterns, spawning habitats, and possible influencing factors.

The earliest portion of a fish's life encompasses many critical periods--vulnerability of the egg to external conditions, transition of newly-hatched larvae from the semi-protection of the egg to the less buffered external environment, and conversion from its self-contained food source. Competition may be intra-specific or inter-specific in ecologically related forms.

This comparative study was conducted primarily in the Buncombe Creek arm of Lake Texoma. The arm represents about 900 acres of the 93,000-acre impoundment. The physico-chemical features of the lake were described by Sublette (1955), and more recently Grinstead (1965) discussed some chemical features of the Buncombe Creek arm. Additional information on the lake is contained in publications by the United States Army Corps of Engineers (1948, 1961).

CHAPTER II

METHODS AND MATERIALS

This study was based primarily on observation of the fishes in the natural environment, supplemented by laboratory experimentation. The study was initiated during the spring of 1967 and continued until the spring of 1971. Residency was established at the University of Oklahoma Biological Station during the summer of 1967 and the period February-August, 1968. Frequent visits to the study area augmented periods of residency.

The area of intensive study was the Buncombe Creek arm of Lake Texoma. The shoreline was examined during periods of low water, primarily to ascertain potential spawning substrate.

Areas 6, 7, and 8 composed the upper region of the arm (Figure 19). Generally, areas 7 and 8 have a very shallow slope, predominantly sandy substrate at the edge with mixed clay in the deeper water. Various terrestrial plants,

especially Bermuda grass, encroached during low water levels. Much of the area adjacent to the creek mouth was thickly covered with willows. Area 6 is transitional from a shallow to moderate slope with predominantly sandy substrate. The upper half had a well established Bermuda grass cover, and the edge usually had an accumulation of much drift material. There are numerous submerged stumps along the shore. The lower portion was lined by inundated willows.

The lower region of the arm was composed of areas 1 through 5. Area 5 abruptly transitions to a moderate slope, and the substrate is rocky interspersed with sandy clay. Area 3 is essentially like area 5 in substrate with a slightly greater clay content and a prevalence of rocks as it is partially underlain by Goodland limestone (Bullard, 1926). Area 4 is mostly steep slope which abruptly descends into deep water. The entire shoreline is composed of Goodland limestone strata with some clay interspersed. Area 2 is at the edge of the limestone ridge extending from area 4, but much of the shoreline has been modified by dredging for the University of Oklahoma Biological Station boat harbor and riprapping most of the contiguous shoreline. The substrate

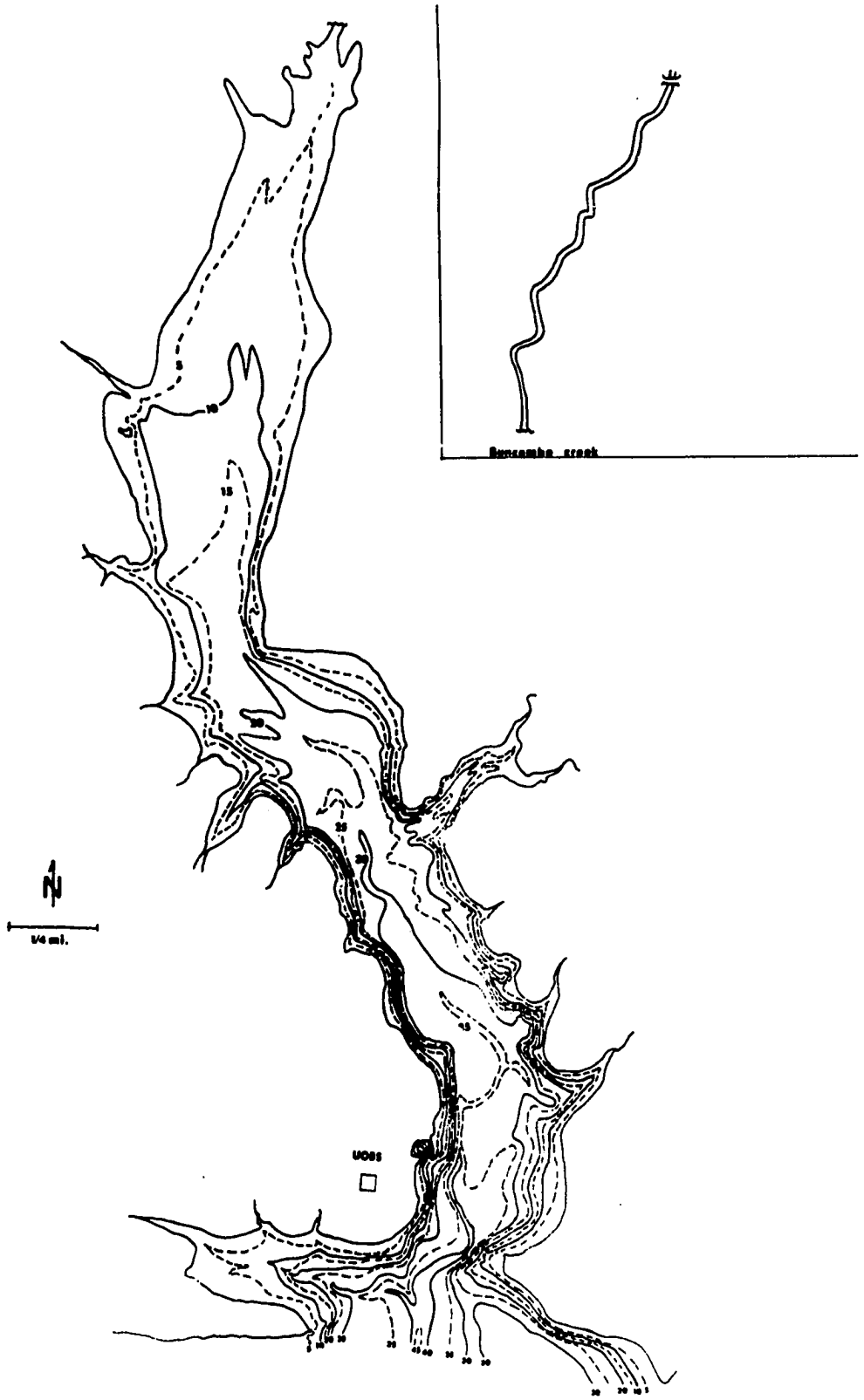
is clay with some sand. Groups of willows scattered along the edge were frequently inundated. Area 1 is much like the upper area in that it is partially protected from wave action and has a fairly shallow slope. The substrate is sand with some clay. Portions which have been exposed to wave action are eroded. The point of land at the mouth is hard-packed clay and is continually exposed to wave action.

Major embayments included area 0 and Beaver Bay. Area 0 is shallow in slope, and the entire shoreline was heavily covered with willows and salt cedar. The bottom of the bay is mud with sand at the margins. The wave-swept point of land at the mouth is hard-packed clay. The bay between areas 3 and 5, designated Beaver Bay, has a range of edge types. The south shore is rocky and moderately steep. The north shore is steep with clay substrate which transitions into a shallow slope and sandy substrate between the two.

A bottom contour distribution (Figure 1) was accomplished with a Bendix depth recorder. Timed, intersecting transects were made between points of identifiable topography and plotted on a pre-existing map (Grinstead, 1965).

Developmental period was studied at various temperatures and an embryological comparison was made. Collection

Figure 1. Depth distribution map of the Buncombe Creek arm of Lake Texoma; taken 14 June 1967 at 614 feet M.S.L.



BUNCOMBE CREEK ARM
14 June 1967
614 m.s.l.

of adults was by a variety of methods--shocking, gill-netting, seining, and dipping. One of the most dependable and convenient methods for capturing D. petenense was a small-mesh gill net (3/8 to 3/4 inch) suspended from the edge of the boathouse. It could be periodically lifted and the required number of fish removed. D. cepedianum were most frequently collected by shocking or conventional gill netting.

A wet method of fertilization was always used since Dorosoma eggs are extremely small and very adhesive. Eggs for embryological study were stripped into disposable petri dishes containing lake water and freshly stripped milt. The eggs were separated by swirling the dish, then allowing them to settle and adhere. This procedure was important as the eggs adhered permanently upon contacting a surface. If not adequately separated, a higher mortality occurred due to oxygen depletion or spreading fungus.

The level of fertilization was extremely variable, and several factors may have been responsible. It was noted that milt of some males coagulated on contacting the water; often these fish had recently died. Chemical changes probably began soon after death or while the fish was under

stress and rendered the milt less useable. Fertilization was regularly low if milt in this condition was used. Another possible cause of low fertility or early death might have been mechanical shock during movement. Fish were collected away from the laboratory and died rapidly, necessitating fertilization shortly after collection and subsequent movement of eggs. Jars of eggs had to be transported to the laboratory, approximately one-quarter of a mile. Transportation was usually accomplished within the second hour after fertilization in order to minimize exposure to uncontrolled temperature.

If eggs were to be used for developmental period experiments, a slightly different technique was used which was better adapted for use in remote areas. Gallon jars were used to receive eggs, and egg separation was accomplished by replacing the lid and slowly rotating the jar on its side. The suspended eggs settled and adhered to the side of the jar. Rate of rotation determined the degree of egg separation. A modified lid was substituted for the original after the jar was returned to the laboratory. It contained two holes; a small funnel was sealed over one hole

and a rubber stopper was inserted into the other. The stopper had a section of stiff plastic tubing inserted so as to reach the bottom of the jar when the lid was replaced. A section of rubber tubing and a clamp were attached to the funnel. This arrangement (Figure 2) permitted a series of jars to be inverted in a rack so they could be drained and refilled with minimal disturbance. Water, drained into a black enamel pan when sampled, was replaced by gravity flow from a reservoir. Lake water was stored in a 25-gallon reservoir, aerated, and allowed to equilibrate to the selected room temperature. Some chambers could be sealed from light and sampled without exposure. Incubation was performed in controlled temperature rooms with a regulated photoperiod.

Records of surface water temperature of the lake on particular dates were used to match the photoperiod with the selected temperature. A constant record of air temperature was maintained during each experiment, and temperature and oxygen readings were taken on water from the chambers. After establishing that oxygen depletion was not excessive, actual oxygen level was not determined; chemical analysis was carried only to the stage of color development. The water was changed at 6- to 12-hour intervals during early incubation

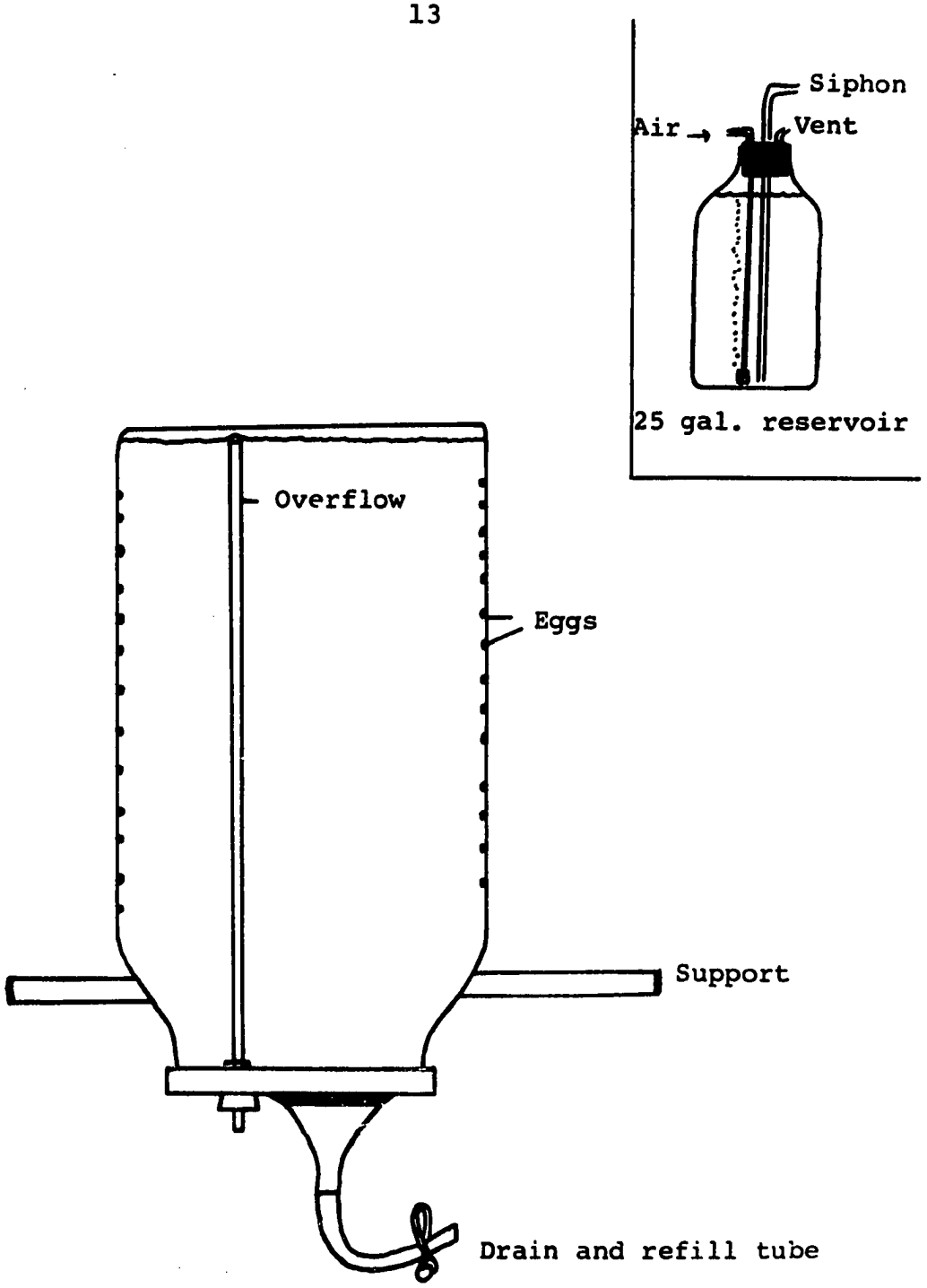


Figure 2. One gallon incubation chamber and water supply.

and at necessary sampling intervals during the hatching period. Sampling began prior to anticipated hatching and continued until no more larvae were collected. Larvae were collected in black enamel pans in which the bottom had been gridded. The nearly transparent larvae were easier to see against a dark background. Each sample was counted as soon as collected unless it was excessively large. In the latter instance, larvae were preserved and counted at a later time. Developmental period was determined for D. cepedianum from 60-75° F and from 65-80° F for D. petenense. These temperature ranges encompass the spawning temperatures for each species.

Embryological material was gathered by fertilizing eggs at intervals, thereby permitting observation of several successive stages simultaneously. This also allowed for re-examination of critical periods in successive series and short intervals of absence from observation. Photographs were taken with a Miranda Sensorex camera mounted on a Bausch and Lomb triocular, compound microscope.

Larvae less than 8-10 mm were described from laboratory-reared fish. Despite numerous and varied rearing attempts, mass mortality occurred from 7 to 10 days after

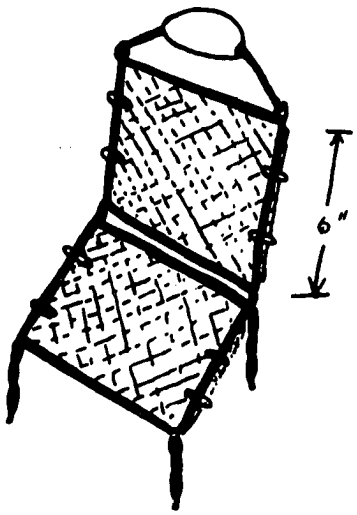
hatching. Larger sizes were described from pond-reared larvae. These larvae were obtained from eggs naturally spawned on burlap bags. Samples were periodically taken from the ponds utilizing a plankton net or small seine with very fine-meshed material attached to the normal webbing. Bone development of larvae and young was studied by clearing and staining in five percent potassium hydroxide and Alizarin Red-S.

The spawning period was delimited by four methods--observation of gonadal development, egg sampling, larvae sampling, and direct observation of spawning. Gonads were collected from the two species at weekly intervals during late winter and throughout the spring. The fish were collected with gill nets at two sites, designated upper Buncombe arm and lower Buncombe arm, and at various locations with an electric shocker. The fish were weighed and the gonads removed and weighed to the nearest 0.1 gm on a triple-beam balance. From this information, a gonadal somatic index (gonadal weight/body weight X 100) was calculated. Some gonads were examined under low power magnification to record gross changes in developing eggs. The annual ovarian cycle was described for D. petenense by Shelton (1964) and for

D. cepedianum by Bodola (1966). The cycle differed mainly in timing, due partially to latitudinal differences. However, differences also exist to a lesser degree at the same locality. Fecundity has been determined by Kilambi and Baglin (1969) and Johnson (1971) for D. petenense and by Baglin (1968) and Bodola (1966) for D. cepedianum.

Another approach employed to delimit spawning season for the two species was a program of egg sampling. Egg samplers were constructed of 6-inch square, welded steel rods fashioned into a chair-like form (Figure 3). Surfaces were made from nylon veiling (tulle) with meshes approximately 0.5 mm in width. These were attached to the vertical and horizontal frames. Each surface was tagged for identification.

Samplers were placed biweekly in groups of three at various locations within Buncombe Creek (Appendix D, Table 1). Temperature, weather, and wind conditions were recorded when samplers were set and retrieved. A shallow bottom sampler (S) was in water approximately one foot deep while an adjacent bottom sampler (B) was in five feet of water. A sampler with floats (F) was attached to a bottom sampler by



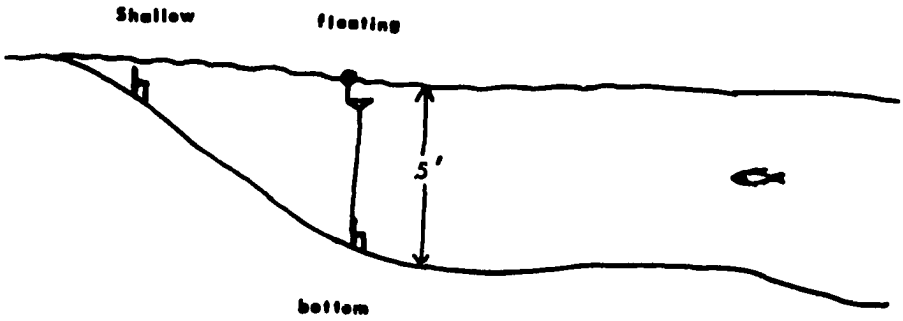


Figure 3. Individual egg sampler and typical combination during sampling.

a line so as to be suspended just under the water surface (Figure 3). One of these sets was located within each of the ten areas depicted in Figure 19. These areas differed as to bottom type, vegetation, and slope.

Samplers were set for 48 hours, then removed and the surfaces examined for eggs. If present, eggs were removed and incubated for identification. In addition, single samplers were set at the creek mouth and in the creek. A series of the two floating samplers at the University of Oklahoma Biological Station boathouse was monitored daily during the 1968 spawning period. A sheltered thermometer was suspended one foot under the water surface at the boathouse. Maximum-minimum surface water temperatures were recorded daily during 1968 and periodically during 1969.

Sampling for yolk-sac larvae was conducted with a modified meter net trawl as described by Taber (1969). Hauls were made as close to shore as depth permitted and only at the surface. Each haul was of 3-minutes duration and covered approximately 150 yards as judged by shoreline distances. Only daytime trawling was done due to visual necessity and collection efficiency. Taber (1969) indicated daytime surface hauls captured the most shad larvae. Hauls were made

within the areas previously described. Extent of each area generally determined the number of hauls. Trawling sites were not pre-selected but were spaced along the margin of each area. However, small areas, such as bays, upper Buncombe Creek, etc., necessitated repeated trawl runs over the same section on consecutive dates. During 1968 and 1969, 302 and 90 samples were taken respectively. When possible, trawling was conducted in conjunction with biweekly egg samples.

Planned spawning observations were frequent in the University of Oklahoma Biological Station area. These began prior to dawn and lasted for varying periods of time, often for as long as 24 hours. Chance observations often occurred in other areas. Observations were initially placed on a tape recorder and transcribed later. Some movie filming was attempted. A few sites offered excellent vantage points for viewing spawning activities. At the University of Oklahoma Biological Station boathouse, a platform 15 feet directly above the water aided observation. North of the boathouse a bluff 15-20 feet above the water permitted better viewing of general spawning patterns. The boathouse area was used extensively for frequency and diurnal periodicity

determination for D. petenense. Certain areas in tributaries were likewise used for observation of D. cepedianum spawning as they had good vantage points on high banks. Light intensity readings were regularly taken during spawning, and the surface water temperature was always taken for comparison with the University of Oklahoma Biological Station maximum-minimum record. Climatological data were entered daily in a field notebook as were many other factors not recorded elsewhere.

CHAPTER III

EMBRYOGENY AND DEVELOPMENT

Embryogeny of Dorosoma petenense

Embryogenetic development of D. petenense was studied from living material (74° F). D. cepedianum was studied in a like manner at the same temperature and will be discussed in a later section. Gross morphological stages in the embryogeny of D. cepedianum were described by Warner (1940) from preserved material. His description will be compared with my observations on both D. petenense and D. cepedianum.

When possible, Oppenheimer's classification (1937) was followed in describing gross changes that were observed in living material. Included in the following description are Oppenheimer's stages, incubation period in hours and minutes post-fertilization, and percentage of incubation completed.

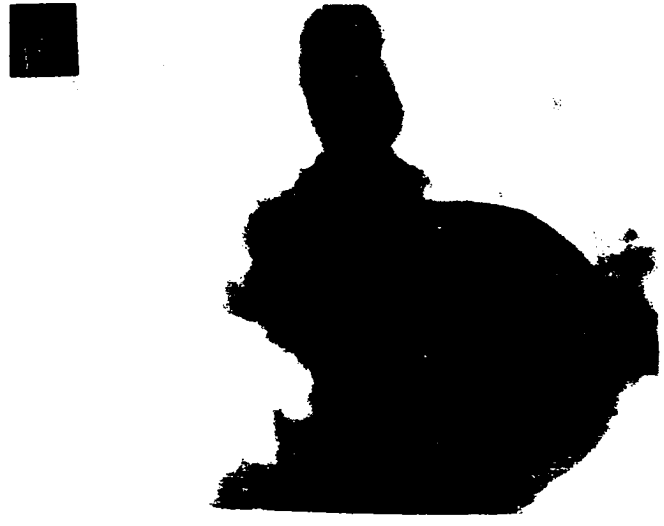
Stage 1. Unfertilized egg. (Figure 4a)--Eggs of both species are small, demersal, and adhesive. The outside

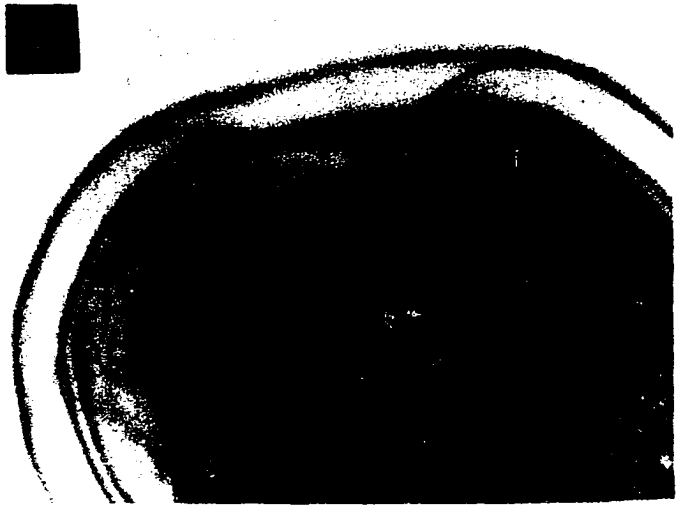
Figure 4. Eggs of D. petenense. A. Fertilized and unfertilized egg. B. Unovulated egg. C. Freshly shed egg with depression from ovarian attachment. D. Micropyle in unfertilized egg.

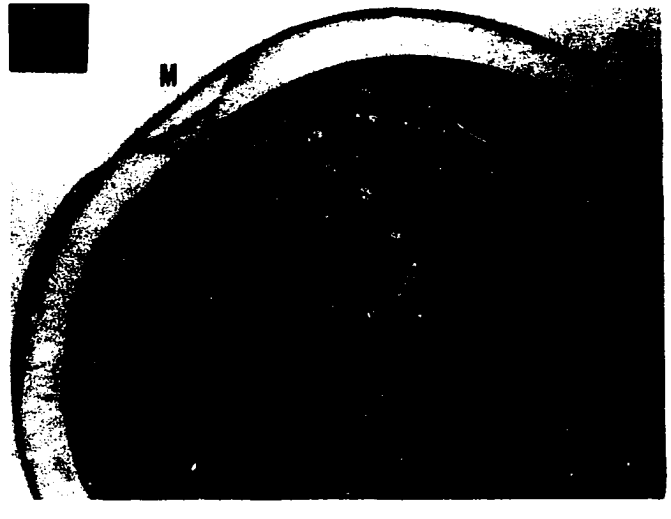
Legend

F - fertilized egg
U - unfertilized egg
M - micropyle
ch- chorion (Follicular epithelium)


U
F



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diameter of living eggs ranges from 0.9-1.1 mm. The color is an opaque creamy yellow in freshly extruded eggs, but later becomes light brown as debris adheres to the surface. Yolk-cytoplasm occupies the entire cavity in unfertilized eggs. One clear oil globule (0.2 mm in diameter) is located within the granular yolk mass, and there may be either several smaller ones or another nearly as large as the first.

Two distinct membranes are present in the eggs of each species. The outer membrane is relatively thick (0.05-0.09 mm), weakly striated, and very adhesive. This membrane adheres tenaciously to any substrate contacted. The adhesive character persists throughout incubation, resulting in collection and retention of debris. This outer membrane has usually been called the chorion regardless of its ontogeny. In D. petenense this membrane was described as the degenerate follicular epithelium by Shelton (1964). This layer is also retained as a part of the egg of D. cepedianum and is not left in the ovary at ovulation as reported by Bodola (1966). The unovulated egg is attached in the ovary by a stalk-like structure (Figure 4b). At ovulation this attachment is probably broken, leaving a slight depression in the surrounding follicular epithelium. The depression can be

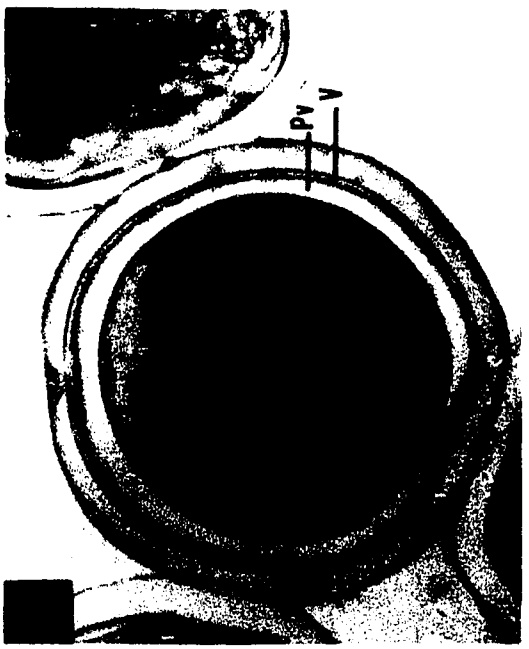
seen in freshly shed, irregularly-shaped eggs (Figure 4c). I believe that this point of attachment is also the site of the funnel-shaped micropyle (Figure 4d). A micropyle has been reported in eggs of a relatively small number of fishes of diverse phylogeny. In Clupeidae a micropyle has been reported for Alosa mediocris (Mansueti, 1962), A. sapidissima (Ryder, 1887), Clupea harengus (Brook, 1885), and Dorosoma cepedianum (Miller, 1960). The inner membrane (Figure 4d) is relatively thin (0.01 mm), nonadhesive, and its surface is covered with numerous minute perforations. In stained material this layer appeared as two distinct membranes (Shelton, 1964) which were termed the vitelline membrane and the zona radiata. In gross structure, however, there appears to be only a single membrane, the vitelline.

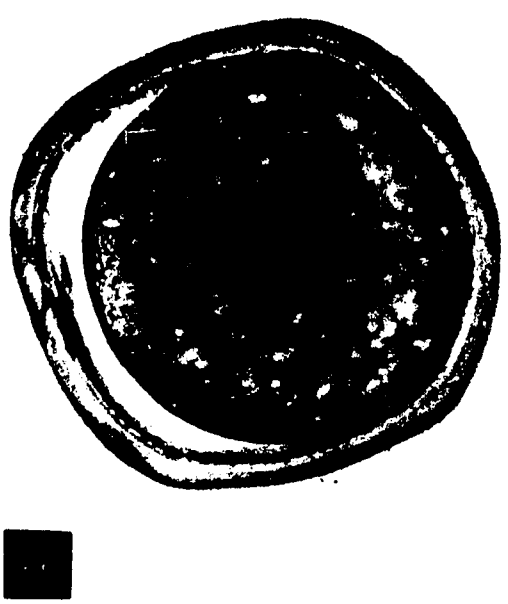
Stage 2. One-celled zygote.--The freshly-released egg is irregular in shape because of crowding in the ovarian lumen. Upon contact with water the egg rounds out, but undergoes no additional changes until fertilization. The micropyle is located at the animal pole, and reorganization begins there following fertilization. Cytoplasm collects beneath the micropyle at the yolk surface; concomitantly, the yolk mass shrinks away from the membranes (Figure 5a).

Figure 5. Fertilization and early division of D. petenense egg at 74° F. A. Cytoplasmic reorganization following fertilization. B. Cytoplasmic cap, 0:10 hours post-fertilization. C. Polar cap at the animal pole, 0:20 hours post-fertilization. D. Two-celled zygote, 0:35 hours post-fertilization.

Legend

Pv - perivitelline space
V - vitelline membrane


Pv
V



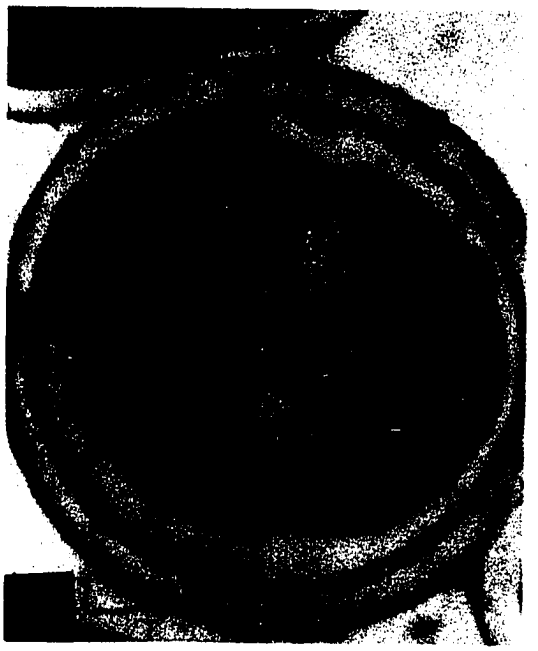
The chorion (degenerate follicular epithelium) and vitelline membrane remain in close contact and change little following initial rounding. Within 10 minutes, the yolk mass separates entirely from the surrounding membranes to form a perivitelline space (0.05-0.1 mm in width) and an early cytoplasmic cap (Figure 5b). The yolk mass does not seem to rotate freely in the space. Warner (1940) reported no perivitelline space in D. cepedianum, but a definite space forms between the cytoplasm and the vitelline membrane following fertilization in both species. The change in the egg is primarily due to shrinkage of the yolk-mass and not to distention of the membrane as reported by Bodola (1966), although this does occur to a minor degree. According to Blaxter (1969), the perivitelline space is formed by breakdown of the alveolar area of the egg cortex beginning at the animal pole. This releases colloids into the space and results in shrinkage of the cytoplasm and inbibition of some water. A well-defined polar cap was formed by approximately 15 minutes post-fertilization and became high and dome-shaped within 30 minutes (Figure 5c). The cytoplasmic movements result in marked clearing of the opacity of unfertilized eggs.

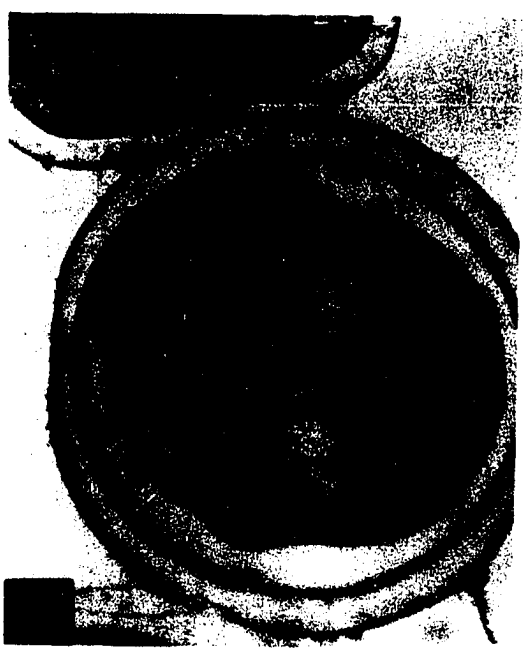
Stage 3. Two-celled zygote. (0:30-0:40, 0.8%)--The polar cap is a high, dome-shaped cell within 30 minutes of fertilization, and the first division is soon initiated. Cleavage is meroblastic as no yolk is included. The first division is complete within five to ten minutes (Figure 5d).

Stage 4. Four-celled zygote. (0:45-1:00, 1.3%) (Figure 6a)--The second division is perpendicular to the first and is normally parallel to the substrate. Eggs that developed with the animal-vegetal pole axis parallel to the substrate permitted continuous lateral viewing until gastrulation. The second division appears to coincide with the presumptive longitudinal axis. Smith (1957) stated this seems to be the general tendency for fishes. Price (1934) also noted this relationship in Coregonus clupeaformis. The second cleavage was first noted 45-50 minutes post-fertilization and was complete by the end of one hour. Four large blastomeres occupy approximately the upper one-fourth of the yolk.

Stage 5. Eight-celled zygote. (1:15-1:30, 2.1%) (Figure 6b)--After one hour and 15 minutes, six to eight cells were present. The large blastomeres occupy the uppermost portion of the yolk beneath the micropyle. The oil

Figure 6. Cleavage of D. petenense eggs at 74° F. A. Four-celled zygote, 0:45 hours post-fertilization. B. Eight-celled zygote, 1:15 hours post-fertilization. C. Sixteen-celled zygote, 1:35 hours post-fertilization. D. Thirty-two-celled zygote, 1:50 hours post-fertilization.





globules may be seen near the vegetal portion of the egg.

Stage 6. Sixteen-celled zygote. (1:35-1:45, 2.3%) (Figure 6c)--Following 1.5 hours of incubation, 16-32 cells were observed. The blastoderm was elongate along the future longitudinal axis.

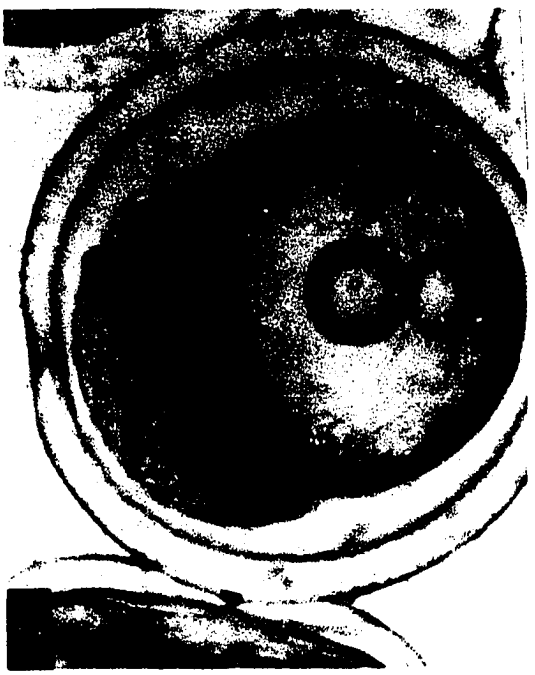
Stage 7. Thirty-two-celled zygote. (1:50-2:00, 2.7%) (Figure 6d)--The dividing cells were smaller and occupied little more of the yolk than in the preceding stage. The blastodisc was now several cells thick.

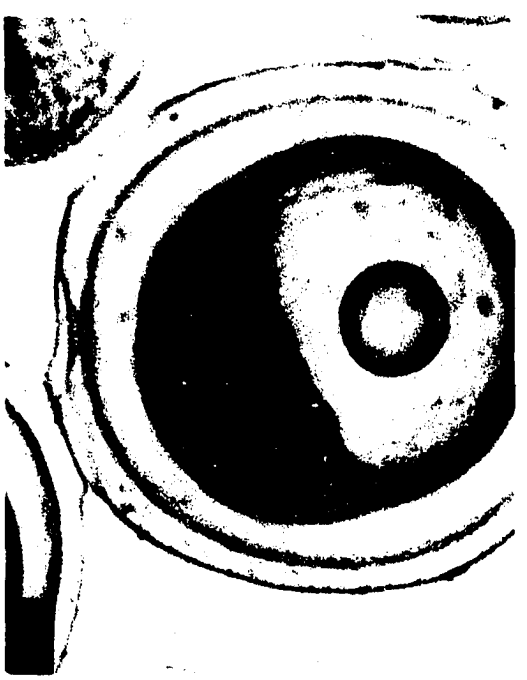
Stage 8. Early high blastula. (2:30-2:45, 3.8%) (Figure 7a)--The blastomeres were still massed on the upper one-third of the yolk but some spreading was apparent. The dome-shaped blastoderm was above the general outline of the yolk mass.

Stage 9. Late high blastula. (3:00-3:30, 4.8%) (Figure 7b)--The blastomeres were smaller than in the previous stage but with little additional spreading. The dome-shaped mass of cells was much elongated over the yolk mass.

Stages 10-11. Flat blastula-expanding blastula. (5:00-5:45, 7.8%) (Figure 7c)--The blastoderm flattens and conforms to the general yolk outline. Early epiboly can be

Figure 7. Blastula and early gastrula formation in D. petenense at 74° F. A. Early high blastula, 2:30 hours post-fertilization. B. Late high blastula, 3:00 hours post-fertilization. C. Flat or expanding blastula, 5:00 hours post-fertilization. D. Early gastrula, 6:00 hours post-fertilization.



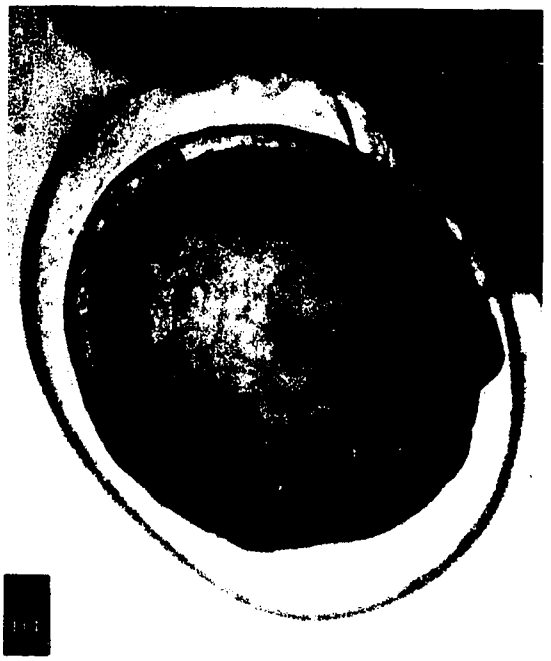


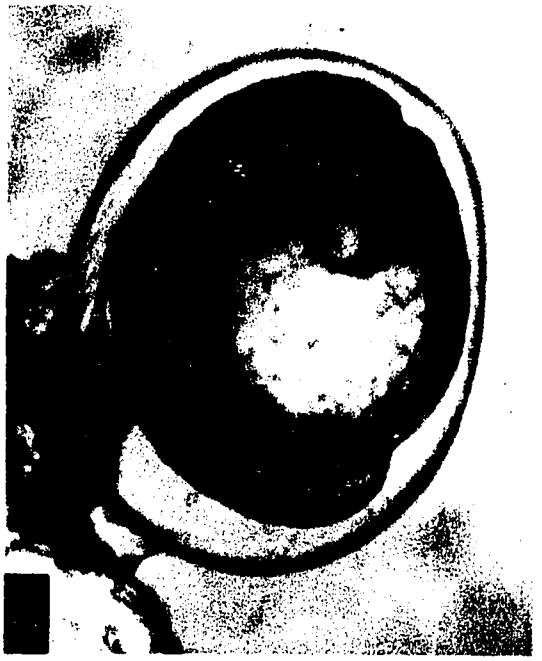
seen as the periblast begins spreading over the yolk mass. At the presumptive dorsal lip of the blastopore the embryonic bud begins forming; this gives rise to the embryonic shield.

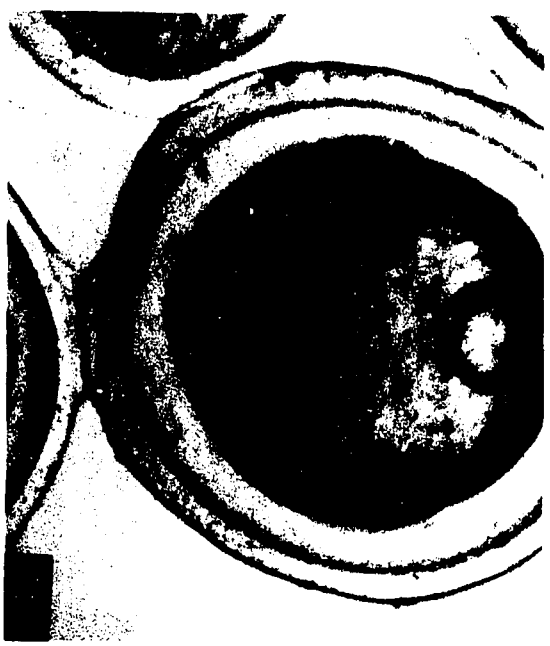
Stage 12. Early gastrula. (6:00-6:30, 8.9%) (Figure 7d)--The first gross changes indicating gastrulation now become evident. Approximately one-half of the yolk has been encompassed by the periblast. The caudal mass is set off from the yolk surface by an invagination at the site of gastrular movement. Primitive endoderm should now be forming and moving forward to underlie the presumptive ectoderm of the embryonic shield (Price, 1934).

Stage 13. Mid-gastrula. (7:30-8:00, 12.9%) (Figure 8a)--The future embryo extends over the upper half of the yolk mass. The anterior region of the embryonic shield has formed the cephalic area of the embryo. Development to this stage has been centered under the micropyle. If the micropyle is formed in the ovary by attachment to a capillary stalk, then the polarity is established in the ovary. Blaxter (1969) stated that the determination of polarity of fish eggs had been described in few fishes.

Figure 8. Gastrulation and closure of blastopore in D. petenense at 74° F. A. Mid-gastrula, 7:30 hours post-fertilization. B. Late gastrula, 11:00 hours post-fertilization. Note: chorion removed. C. Closure of blastopore, 14:00 hours post-fertilization. D. Expansion of the fore-brain, 15:00 hours post-fertilization.







Stage 14. Late gastrula. (10:00-12:00, 16.4%) (Figure 8b)--Usually during this period of development, the embryo rotates within the membranes. Removal of the chorion is required so that the egg can be repositioned. Increasing embryonic mass and the resultant change in center of gravity probably cause this shift. The neural keel, anlage of the central nervous system, can be seen as a thickening of the ectodermal area, especially in the cephalic region. The periblast has enclosed more than three-fourths of the yolk.

Stage 15. Closure of the blastopore. (14:00-14:30, 19.9%) (Figure 8c)--Closure of the blastopore is almost complete by 13 hours and is total by 14 hours. All portions of the germ ring contribute to the closure as judged by relative position of the oil globule. Warner (1940) came to the same conclusion for D. cepedianum. The three primitive areas of the brain are differentiated, and the neural keel is well developed.

Stage 16. Expansion of the forebrain. (15:00-15:30, 21.2%) (Figure 8d)--The embryo extends about three-fourths around the yolk. The prosencephalon is expanded laterally to form the optic bud, or optic primordia. Mesodermal differentiation has formed three to six somites in the mid-

region of the embryo. A notochord occupies the posterior one-third of the embryo.

Stage 17. Optic vesicles. (16:00-17:00, 23.3%) (Figure 9a)--The optic primordia becomes vesicular during this period. There are 14-18 pairs of somites, and the embryo has continued to encircle the yolk.

Stage 18. Auditory placode. (18:00-20:00, 27.4%) (Figure 9b)--Up to 26 somite pairs have formed by this period. Invagination of the optic vesicle has begun, and ectodermal thickenings form the precursors of the lens. Auditory placodes can occasionally be seen as thickenings of ectoderm on either side of the myelencephalon, and the metencephalon is differentiated.

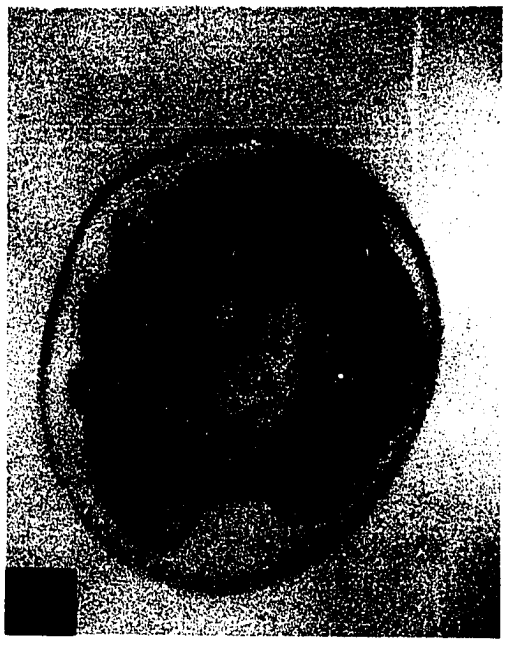
Stages 19-20. Nervous system cavitation. (21:00-23:00, 31.5%) (Figure 9c)--The embryo almost completely encircles the yolk, and 29-30 pairs of myomeres have formed. Auditory vesicles are well developed as are the lens precursors. Kupffer's vesicle was observed during this period of development. The caudal mass is raised above and appears to be separating from the yolk mass. The heart is a tubular mass which irregularly pulsates.

Stages 21-22. Motility; whole heart beat. (24:00-

Figure 9. Proliferation of the nervous system of D. petenense at 74° F. A. Optic vesicle stage of development, 16:00 hours post-fertilization. B. Auditory placode stage of development, 19:00 hours post-fertilization. C. Nervous system cavitation stage of development, 22:00 hours post-fertilization. D. Motility, heart beat stage of development, 26:00 hours post-fertilization.

Legend

O-Optic vesicle
A-Auditory placode
My-Myomere

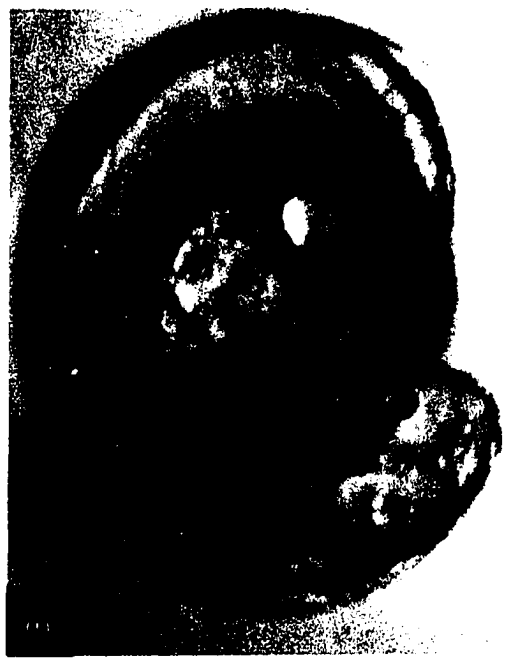


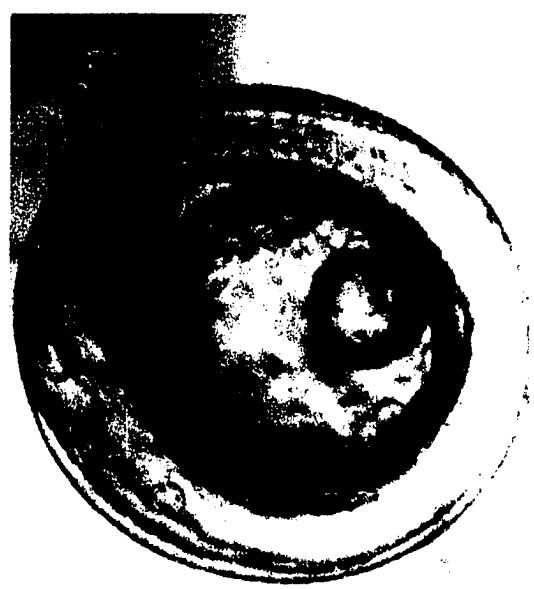
28:00, 38.4%) (Figure 9d)--By this period of incubation there exists a considerable range of development among individuals of the same group. This was reflected by a wide variation in hatching period. In most larvae, the embryo's head and tail meet, and the caudal mass is separate from the yolk surface. Muscular flexures occurred periodically. Heart contractions were regular at 70-80 b.p.m.; however, no blood pigment was apparent. Otocysts were developing in most individuals. The eyes still retained a prominent ventral choroid fissure, and the lenses were well differentiated.

Stages 23-26. Otoliths. (29:00-35:00, 47.9%) (Figure 10a)--The tail is free, flexed to one side, and extends back to the level of the auditory vesicle. Otoliths are well developed in each ear precursor. All five major areas of the brain can be easily identified. The optic lobes of the mesencephalon are prominent, having been differentiated at some earlier stage. The notochord extends to the anterior portion of the embryo near the level of the mid-brain. Heart beat had increased to 80-90 b.p.m.

Stage 27. Coiling stage-round fin. (36:00-40:00, 54.8%) (Figure 10b)--The embryo is coiled within the egg almost one and one-half times, and the caudal mass is taking

Figure 10. Advanced embryo of D. petenense at 74° F. A. Otolith stage of development, 30:00 hours post-fertilization. B. Coiling stage of development, 38:00 hours post-fertilization. C. Pigmentation stage of development, 50:00 hours post-fertilization. D. Pre-hatching stage of development, 58:00 hours post-fertilization.





on the characteristics of a tail region. Heart beat had further increased to 110-120 b.p.m. No pigmentation had developed.

Stage 28. Pigmentation. (41:00-55:00, 75.3%) (Figure 10c)--The embryo is coiled within the egg one and one-half to two times and repositions itself periodically. In the latter few hours of this period, pigment was seen in the eyes as dark gray shading. Some scattered melanophores were also seen on the surface membranes covering the brain. The lens had become spherical, and a corneal layer could be seen over the exterior of the eye. Pectoral fin buds could be seen in early development. The gut, posterior to the yolk, had also developed. Heart beat was about 150 b.p.m.

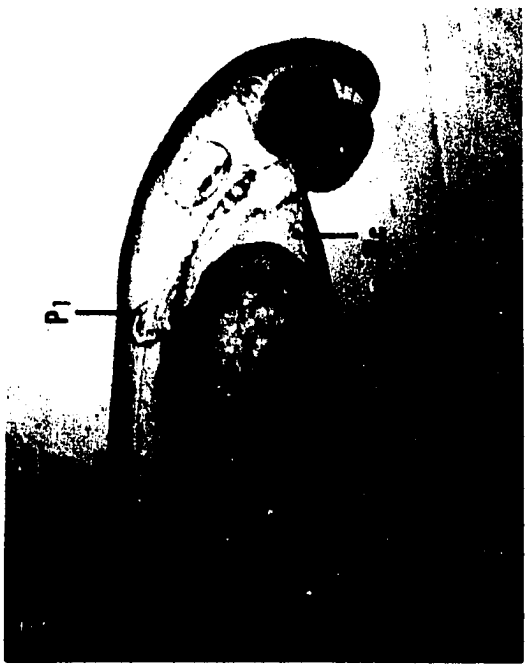
Pre-hatching stage. (56:00-61:00, 83.6%) (Figure 10d)--The embryo is very active, twirling within the egg frequently. The heart rate was up to 180 b.p.m. Precursors of the semi-circular canals were developing in the otic capsule. Olfactory placodes could be seen, although they were not obvious. Dark eye pigment was well developed. Some early hatching occurred in the latter hours of this period.

Stage 32. Hatching. (62:00-73:00) (Figure 11a)--Most hatching occurs during this interval. A larva hatches by pushing with the tail and forcing its head through both egg membranes. The chorion is still intact, although often noticeably thinner. Some stages of Oppenheimer (1937) could not be used (28-31) as D. petenense did not develop peritoneal pigment until post-hatching, and the swim bladder did not form until much later. The stomodaeum was not perforated at hatching although the gut posterior to the yolk was well developed. Pectoral fins are developed at hatching, but the period at which circulation in them began (Stage 29) was not determined. Also, no development of branchial arches was apparent at hatching. No vitelline circulation could be demonstrated but some must be present or soon develops because the yolk lies outside the gut in teleosts (Iwai, 1962). Seven to nine pairs of trunk neuromasts were present in the freshly-hatched larvae as reported by Stephens (1967). No cupulae were noted at hatching but they developed within a few hours. Total-length at hatching was 3.25-3.45 mm. Thirty-five to thirty-seven myomeres were present in the newly-hatched larvae. In the cranial portion of the yolk a prominent pericardial cavity can be seen (Figure 11b).

Figure 11. Hatching larvae of D. petenense at 74° F. A. Hatching stage, 68:00 hours post-fertilization. B. Freshly-hatched larva.

Legend

Pc - Pericardial cavity
P_1 - Pectoral fin bud



A finfold extends from the yolk, posterior around the caudal area, and anterior on the dorsal region to the level of its ventral origin. It is interrupted only by the posteriorly located anus. The yolk is globular in shape and remains essentially so until absorption. The head is flexed sharply down over the yolk, but straightens within the first 24 hours following hatching.

Embryogeny of Dorosoma cepedianum

Development of D. cepedianum was studied by Warner (1940), and much of his work was later incorporated by Miller (1960). Warner's series developed at 62° F; I used 74° F so a direct comparison could be made with D. petenense. No illustrations of D. cepedianum embryogeny are included as there were no visible structural differences, although developmental periods do differ (Table 1).

Dorosoma cepedianum appeared to have a more rapid rate of development, but on closer examination this proved to be slightly misleading. D. cepedianum does hatch earlier than D. petenense at any given temperature, but they reach the same stages at fairly equivalent times. The difference is in the degree of development at hatching as D. cepedianum

Table 1. Embryogenic developmental stages (Oppenheimer, 1937) of Dorosoma cepedianum and Dorosoma petenense.

D. petenense 74° F Post-fert. (hrs.:mins.)	%	Stage-Character	D. cepedianum 74° F Post-fert. (hrs.:mins.)	%	62° F[W] Post-fert. (hrs.:mins.)	%
0:10- 0:15	0.3	(2) Polar cap	0:10- 0:15	0.5		
0:30- 0:40	0.8	(3) Two-cell	0:30- 0:40	1.5		
0:45- 1:00	1.3	(4) Four-cell	0:45- 1:00	2.2	3:00	3.2
1:15- 1:30	2.1	(5) Eight-cell	1:15- 1:30	3.3		
1:35- 1:45	2.3	(6) Sixteen-cell	1:45- 2:00	4.3		
1:50- 2:00	2.7	(7) Thirty-two-cell	2:00- 2:30	5.4		
2:30- 2:45	3.8	(8) Early high blastula	2:45- 3:15	7.1	5:00	5.3
3:00- 3:30	4.8	(9) Late high blastula	3:30- 3:50	8.5		
5:00- 5:45	7.8	(10-11) Flat-expanding blastula	5:00- 5:30	12.0		
6:00- 6:30	8.9	(12) Early gastrula	6:00- 6:45	14.7	15:30	15.8
7:30- 8:00	12.9	(13) Mid-gastrula				
10:00-12:00	16.4	(14) Late gastrula	10:00-11:30	25.0	23:30	24.2
14:00-14:30	19.9	(15) Blastopore closure			25:30	26.3
15:00-15:30	21.2	(16) Expanding forebrain	14:00-14:30	31.5	33:30	34.0
16:00-17:00	23.3	(17) Optic vesicles	15:30-16:00	34.8	52:30	54.7
18:00-20:00	27.4	(18) Auditory placode	16:30-19:30	42.4		
21:00-23:00	31.5	(19-20)Nervous system cavitation				
24:00-28:00	38.4	(21-22) Motility; heart beat	20:00-24:00	52.2	60:00	63.2
29:00-35:00	47.9	(23-26) Otoliths*	28:00-33:00	71.7		72.9
36:00-40:00	54.8	(27) Coiling-round fin	35:00-38:00	82.6		
41:00-55:00	75.3	(28) Pigmentation*				
56:00-61:00	83.6	Pre-hatching				
62:00-73:00		(32) Hatching	41:00-46:00		95:00	

[W]Warner (1940)

* Omitted stages were not passed through by D. petenense prior to hatching. In addition, stages 24, fin bud; 28, pigmentation; 29. circulation in pectoral fin were not passed through by D. cepedianum prior to hatching.

is much less advanced. This is exemplified by the eyes, which, at hatching, lack pigment and still possess a choroid fissure, while D. petenense hatches with well developed, pigmented eyes. This can also been seen in the percentage of development completed at a particular level (Table 1). At any period of comparison D. petenense had completed a lesser percentage of total incubation than had D. cepedianum. Comparison of incubation periods of D. cepedianum at two different temperatures (74° and 62° F) produces comparable percentages except after the period of optical vesicle development. Eye development began later in Warner's series. Hayes, et al. (1953) noted that optic components seem to develop earlier at higher temperatures.

Stage 1. Unfertilized ovum.--As mentioned previously, there is little or no difference between the eggs of these two species. The intra-ovarian development of the two is not different (Bodola, 1966; Shelton, 1964). Also, the extruded egg, irregular at first, retains its degenerate follicular epithelium as the adhesive chorion. This feature was apparently overlooked by Bodola (1966). The layer is occasionally lost, and the egg is no longer adhesive. Outside diameter of a freshly extruded and rounded egg was 0.9-1.1

mm. Warner (1940) stated the diameter after fixation was 0.75 mm, and this value has often been quoted without stating that it was based upon preserved material (Mansueti and Hardy, 1967). D. cepedianum eggs have the funnel-shaped micropyle in the chorion as described in D. petenense eggs. Miller (1960) reported the presence of a micropyle in D. cepedianum eggs. The vitelline membrane and other described features of D. petenense eggs are also found in D. cepedianum with no distinguishing characteristics.

Stage 2. One-celled zygote. (0:10-0:15, 0.5%)--Following fertilization, cytoplasmic reorganization as described for D. petenense was observed in the eggs of D. cepedianum. The perivitelline space was formed as described for D. petenense. A cytoplasmic cap was evident 10-15 minutes following fertilization.

Stage 3. Two-celled zygote. (0:30-0:40, 1.5%)--The first division was noted after 30 minutes and was completed by 40 minutes.

Stage 4. Four-celled zygote. (0:45-1:00, 2.2%)--The second division was observed approximately 45 minutes post-fertilization. This division appeared to establish the longitudinal axis of the future embryo as described for

D. petenense.

Stage 5. Eight-celled zygote. (1:15-1:30, 3.3%)--The eight-cell stage of development was completed after 1.5 hours of incubation.

Stage 6. Sixteen-celled zygote. (1:45-2:00, 4.3%)--The sixteen-cell stage was completed two hours after fertilization, a slightly longer period than in D. petenense.

Stage 7. Thirty-two-celled zygote. (2:00-2:30, 5.4%) --The developing blastodisc was comparable to that in D. petenense, but required slightly longer. To reach this stage at 62° F five hours of development were needed (Warner, 1940).

Stage 8. Early high blastula. (2:45-3:15, 7.1%)--The early blastula stage of development apparently required about one-half hour longer for attainment than the comparable stage of D. petenense. This level of development required five hours at 62° F (Warner, 1940).

Stage 9. Late high blastula. (3:30-3:50, 8.5%)--The late high blastula was reached after almost four hours of incubation at 75° F.

Stages 10-11. Flat blastula-expanding blastula. (5:00 -5:30, 12.0%)--The blastoderm conformed more with the yolk contour, and epiboly had begun after five hours of incubation.

Stages 12-13. Early to mid-gastrula. (6:00-6:45, 14.7%)--The periblast had encompassed about one-half of the yolk by the end of this period. Signs of gastrulation were seen during the earlier portion. Warner (1940) illustrated this stage about 15 hours post-fertilization at 62° F.

Stages 14-15. Late gastrula-closure of blastopore. (10:00-11:30, 25.0%)--In the later portion of these stages the three primitive areas of the brain were differentiated and the neural keel was very well developed. This period of development was noted by Warner (1940) after 25 hours incubation at 62° F. D. petenense had attained stage 15 by 14 hours at 74° F (Table 1).

Stage 16. Expansion of the forebrain. (14:00-14:30, 31.5%)--After 14 hours of incubation the optic primordia were well developed. The notochord occupied the posterior one-half of the embryo which now covered about three-fourths of the yolk. Two to three somites were present in the mid-region.

Stage 17. Optic vesicles. (15:30-16:00, 34.8%)--Optic vesicles were well developed during this stage, Kupffer's vesicle could be seen, and there were about 17 pairs

of somites. Some muscular contraction was observed. The notochord had extended forward to about the level of the hindbrain.

Stages 18-20. Auditory placodes-cavitation of the nervous system. (16:30-19:30, 42.4%)--The embryo had grown around the yolk, its tail was almost free, and there were up to 23 somites. Lens placodes were developing a thickened ectoderm over the inpocketing of the optic vesicles. Auditory placodes were in evidence in the latter part of these periods as was an irregularly pulsating heart. A few larvae hatched prematurely during this time. Although only 2.75 mm (TL), they appeared to be normal.

Stages 21-22. Motility-whole heart beating. (20:00-24:00, 52.2%)--The head and tail overlapped slightly, and muscular activity was fairly regular. Auditory vesicles were well developed as were the lens precursors. The heart was weakly pulsating.

Stage 23. Otoliths. (28:00-33:00, 71.7%)--The larva was coiled one and one-half to two times in the egg; muscular activity was frequent. The lens had developed, and there were prominent choroid fissures in the aspect of the eyes.

Stage 27. Coiling-round fin. (35:00-38:00, 82.6%)--The embryo was coiled several times within the egg and was fairly active. No pigmentation was present.

Stage 32. Hatching. (41:00-46:00)--Several of Oppenheimer's stages could not be used to describe the later pre-hatching embryogeny of D. cepedianum as hatching occurred at an even lesser developed stage than in D. petenense. The eyes did not develop pigment and were presumably non-functional (Blaxter, 1969). No cornea was evident, but a prominent choroid fissure was still present. Pectoral fins were not developed. Total-length ranged from 3.25-3.45 mm. Hatching of D. cepedianum is accomplished by forcing the head through both investing membranes as described for D. petenense. Seven to nine pairs of trunk neuromasts were present in freshly-hatched larvae, but cupulae were not observed until later. Neuromasts presumably aid in avoidance of capture prior to development of the eye (Blaxter, 1969). The yolk is normally elongate although it may be transitorily globular in freshly-hatched larvae. Thus, the combination of yolk shape and eye pigmentation can be used to separate freshly-hatched larvae of D. cepedianum and D. petenense.

Embryogeny of Hybrid Dorosoma

Minckley and Krumholz (1960) described natural hybridization between sympatric species of Dorosoma. Natural hybridization occurs in Lake Texoma between D. petenense and D. cepedianum and will be discussed later.

Artificial hybridization, attempted on several occasions, was frequently successful. Crosses between D. petenense males and D. cepedianum females never resulted in development beyond late blastula. However, the reciprocal cross, D. cepedianum males with D. petenense females, was successful many times, developing through post-hatching larvae. Embryogenetic development will not be discussed as the sequence was the same as described for the parental types. Developmental time, however, was intermediate between the two. Hybrids developed pigment in the eye prior to hatching except at the lowest incubation temperature of 65° F. Development of eye pigment is generally more precocious at higher temperatures (Smith, 1957). At hatching the yolk was spherical and pectoral fins were developed. Therefore, the hybrid larvae were essentially like D. petenense except for the lack of pigmented eyes at lower incubation temperature.

Adult male and female hybrids, frequently captured with well developed gonads, produced germ cells that appeared to be viable. A cross between f_1 hybrids was not attempted as both sexes were never taken simultaneously. However, several crosses were made with males or females of both species. Only the cross between a hybrid female and a male D. petenense produced development through hatching (Appendix A, Table 8). Rate of development was equivalent to that observed for hybrids, and no undue mortality was apparent. Upon hatching, these larvae had eye pigment, globular yolk, and pectoral fins, thus more nearly resembled the larvae of D. petenense.

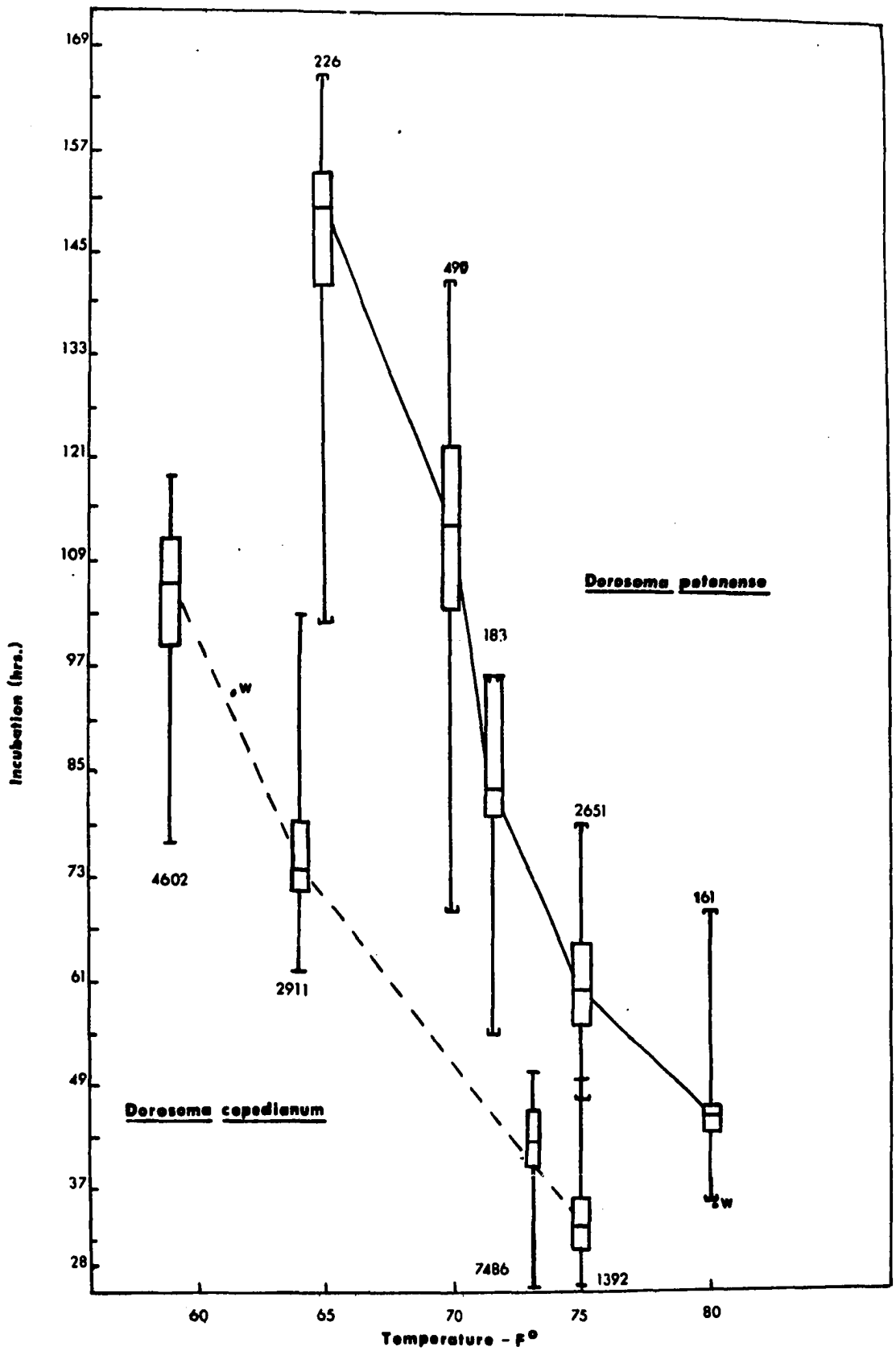
Developmental Period

The developmental period is defined as the interval between fertilization and hatching of one-half of the larvae; hatching period is the interval between the first and the last hatched larvae (Lagler, et al., 1962). Developmental period was determined for D. petenense and D. cepedianum over a range of temperatures as an aid in interpreting times of spawning from naturally spawned eggs. This information was only of general use, however, as the hatching period for

both species was found to be quite long--up to 50% of the total incubation period in some cases (Figure 12). Hatching period for D. petenense was usually longer than for D. cepedianum. I believe a 50% hatching interval is more useful; it is the shortest period of time during which 50% of the fish hatch. This represents a mode of hatching which includes the end of the developmental period.

The developmental period of D. petenense was greater than for D. cepedianum at any particular temperature (Figure 12). At a given temperature D. petenense required roughly twice the incubation to hatching as did D. cepedianum. In some cases the range, or hatching periods, overlapped but if the 50% hatching intervals or the end of the developmental periods are compared the relationship is more meaningful. Connecting the points that represent the developmental period at various temperatures results in a curvilinear relationship which is generally followed by both species. This relation was reported by Blaxter (1969) for various fishes and for two clupeiform fishes by Lasker (1964). It is interesting to note that for a decrease of only 10° F, the developmental period for both species roughly doubles. The much

Figure 12. Developmental period. Vertical line represents range or hatching period; rectangles represent the interval at which 50% hatch occurred; the horizontal enclosed line indicates the end of the developmental period for 50% of the larvae. Numbers are total number of larvae hatched. "W" data from Warner (1940).


169
157
145
133
121
109
97
85
73
61
49
37
28
Incubation (hrs.)
226
490
183
2651
161
4602
2911
7486
1392
♂w
♂w
Doresoma patenense
Doresoma copedianum
60
65
70
75
80
Temperature - F°

shorter developmental period of D. cepedianum can largely be explained by their hatching more prematurely than D. petenense.

Some of the temperature series experiments were dual in nature. A portion of the incubation chambers were exposed to a dark-light cycle while others were enclosed in several layers of black plastic to exclude the cycle. This was designed to test the possibility that the transition of light intensity at either dawn or dusk might provide a stimulus for hatching. The dual experiment for D. petenense was performed at 70° and 75° F (Appendix A, Tables 2 and 3).

In the 75° F series there appeared to be a difference between the two conditions. By 65 hours of incubation the cumulative hatch of both conditions had reached approximately 94%. The constant dark chambers had a uniformly increasing hatching rate up to this point, whereas in the chambers exposed to dark-light cycle, there was a marked increase (from 17% to 94%) in hatching rate in the 4-hour interval following darkness. Hatch was low in the 70° F series so a valid parallel cannot be made. The eyes of D. petenense have pigment prior to hatching and are functional. If there is

an adaptive value to hatching at night, then they have the ability to detect transition from light to dark. At the other temperature tests there seemed to be a tendency for the greatest number of larvae to hatch during darkness but the numbers involved were too small to add much emphasis to this idea. In the 75° F series, however, a large sample was collected which gave some evidence for this contention. Yolk-sac larvae, sampled in the lake on a diurnal schedule, appeared to be most numerous during the day but insufficient data prevented adequate comparison.

Dorosoma cepedianum was treated similarly to D. petenense, and a dual set of experiments was accomplished at 60° and 64° F (Appendix A, Tables 4 and 5). There appeared to be little difference between the two conditions at 60° F. Both conditions produced a 51% hatch by 107 hours and there was a gradual increase up to that time.

In the 64° F test, chambers exposed to constant darkness reached 50% hatch by 72 hours incubation, whereas chambers exposed to the dark-light cycle attained near 50% hatch by 78 hours of incubation. In both, there was a gradual increase to this point. There seemed to be no particular time

(dark vs. light) at which there was an abrupt peak in hatching. The eyes of D. cepedianum at hatching are not pigmented and thus presumably non-functional according to Blaxter (1969). This is not to say that some sensitivity to light is not possible by the larvae but the capability is certainly not as developed as in D. petenense. Since temperature was constant, there is a possibility that a temperature cycle might cue the larvae to an evolutionarily selected preferred-hatching time. Diurnal sampling of yolk-sac larvae did result in a definite hatching peak for D. cepedianum (Table 7). Maximum hatch, which correlates with maximum spawning activity, was probably a function of spawning time and incubation time at the existing temperature.

The incubation period for hybrids between D. cepedianum males and D. petenense females was tested at four temperatures (Appendix A, Table 8). Although the total number of larvae hatched was small, the trend was fairly constant. The developmental period falls between that of the parental types for each temperature. The only eggs successfully fertilized from a hybrid back-cross, a hybrid female with a D. petenense male, were incubated at 74° F. The development

period was about 61 hours, again within the intermediate range between the two species.

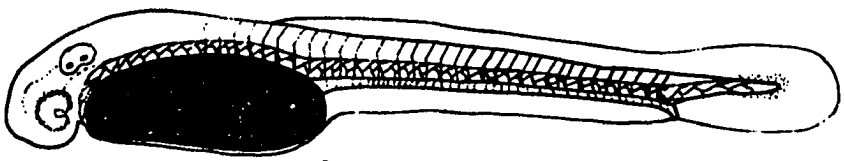
The developmental period for the two species over a range of temperatures was non-overlapping and bore a constant relationship. Influence of light on hatching time was less distinct. Variation in temperature, such as a decrease at night, might stimulate hatching and thus not require a high level of eye development. Observed hatching peaks from natural D. cepedianum spawns indicated that this or some other mechanism might be involved. There seemed to be an indication of a higher hatch rate by D. petenense during darkness.

Development at a constant temperature can only be used as a rough indicator of incubation under the natural oscillatory conditions. Shelford (1929) stated that in general organisms incubated under varying conditions around a particular mean will hatch eight to nine percent sooner than organisms exposed to the same mean but at a constant temperature.

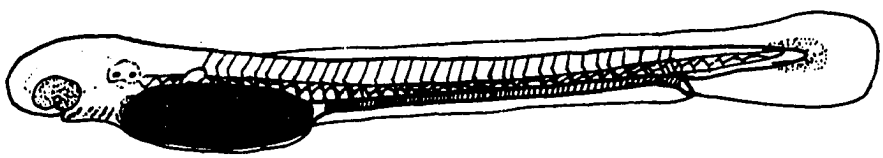
Development of Larvae and Young

Newly-hatched larvae - 74° F (Figures 13a and 14a)--

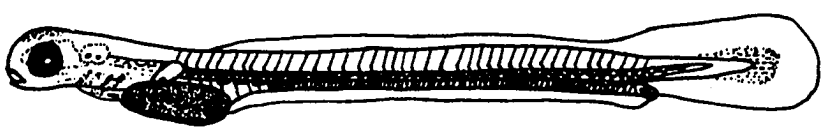
Figure 13. Dorosoma cepedianum larvae. A. Newly-hatched larva, 3.5 mm TL, 74° F. B. One-day larva, 4.5 mm TL, 74° F. C. Two-day larva, 5.1 mm TL, 74° F. D. Three-day larva, 5.5 mm TL, 74° F.



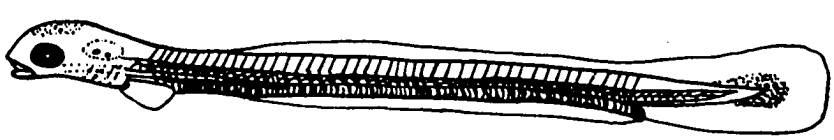
A 3.5 mm TL



B 4.5 mm TL

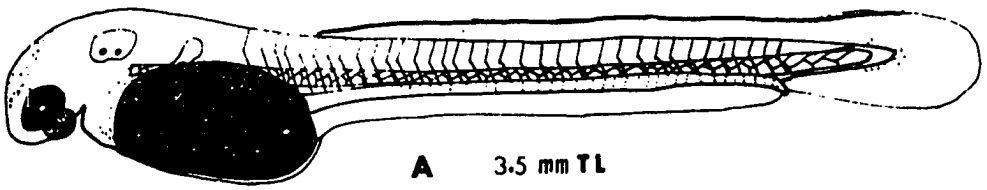


C 5.1 mm TL

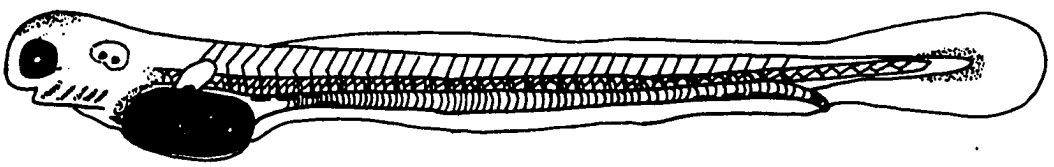


D 5.5 mm TL

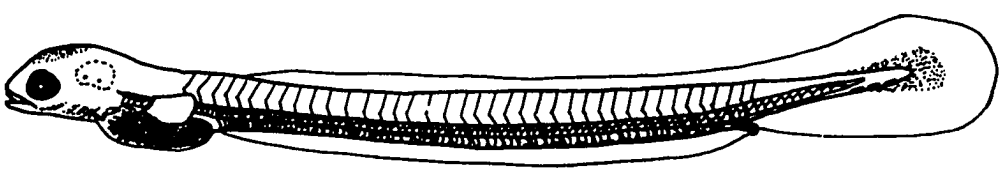
Figure 14. Dorosoma petenense larvae. A. Newly-hatched larva, 3.5 mm TL, 74° F. B. One-day larva, 4.5 mm TL, 74° F. C. Two-day larva, 5.1 mm TL, 74° F. D. Three-day larva, 5.5 mm TL, 74° F.



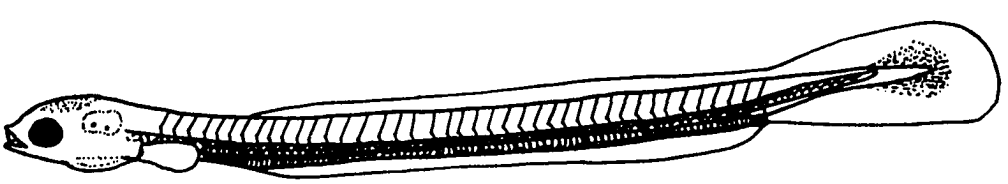
A 3.5 mm TL



B 4.5 mm TL



C 5.1 mm TL



D 5.5 mm TL

Dorosoma larvae hatch in a fairly undeveloped state. The digestive system is incomplete anteriorly--it has an unperforated oral plate and lacks pharyngeal and jaw development. The gut, posterior to the yolk, is well developed and terminates at the anus which is just anterior to the caudal finfold.

Dorosoma petenense has pectoral buds and the finfold upon hatching. The finfold arises in the mid-dorsal region above the yolk, extends caudally along the mid-line, forms the caudal, then extends forward to the posterior angle of the yolk, interrupted only by the anus. D. cepedianum has only the finfold as no pectoral fins are present at hatching (Figure 14a). The caudal area of both species is initially little expanded.

Sense organs include fairly well developed inner ears and eyes of differential development in the two species. D. petenense has darkly pigmented and functional eyes at hatching while D. cepedianum has less developed, non-pigmented and presumably non-functional eyes. Both possess a complement of seven to nine pairs of exposed trunk neuromasts which develop cupulae within a few hours.

In addition to eye pigmentation, D. petenense has scattered melanophores on the brain covering. D. cepedianum is completely devoid of pigmentation (Mansueti and Hardy, 1967). Freshly-hatched larvae of both species average about 3.45 mm total-length. At hatching myomeres were only developed anterior to the anus. D. cepedianum had approximately 32; D. petenense had 34-36. Between the downward flexed head and the large yolk is a transparent area, the pericardial cavity. The yolk of D. cepedianum is elongate, although it may be somewhat rounded immediately after hatching. In D. petenense the yolk is essentially globular and remains so until absorbed. In both species there is a posteriorly located oil globule. This permits rapid separation of Dorosoma from Morone chrysops yolk-sac larvae which have non-pigmented eyes, are slightly smaller, and have the oil globule anteriorly positioned.

Larval behavior of the two species differs only slightly. Yolk-sac larvae appear to have a negative geotactic and/or positive phototactic reaction which causes them to actively swim toward the surface. The propulsion is a result of rapid undulation of the caudal area. When

swimming activity ceases the larvae rotate 180 degrees and sink head downward due to high specific gravity of the yolk mass. Length of each phase of movement varied. The active phase often continued until the surface film was contacted, while the passive or sinking phase seemed to be of shorter duration. The net result was a concentration away from the substrate, which could represent an adaptive reaction to prevent suffocation in the bottom mud. This activity was observed under normal illumination and under very low intensity red-light illumination. Taber (1969) noted that yolk-sac Dorosoma were most numerous, day and night, in surface trawling samples.

Positive phototaxis could account for the same swimming behavior as natural light would normally be from above. D. cepedianum showed no strong attraction to light prior to pigmentation of the eyes; however, D. petenense congregated in the lighted end of aquaria within a few minutes of hatching.

Hatching abnormalities were noted in both species. The most common was a malformation of the notochord. The posterior portion of these larvae was variously coiled or

twisted. These malformed individuals were usually among the last to hatch. This abnormality probably impaired hatching as the tail is used in forcing the head through the membranes. Attempts to swim resulted in irregular twirling on the substrate. This condition has been reported in various hatchery-reared fishes, and the fry are called "spinners."

One-day larvae - 74° F (Figures 13b and 14b)--Larvae of both species averaged 4.5-4.7 mm total-length with a maximum of 5.0 mm after one day. Much of the increase was apparent growth as the head was not as flexed over the yolk. Most D. cepedianum still had no pigmentation although a few had a light-yellowish tint in the eye. This was subsequently masked by darker pigment, at least until a much larger size. The predominant eye color of juveniles and adults is yellow-gold while adult D. petenense have silvery eyes. If this character were obvious in preserved larvae, they could be easily separated. Dark eye pigment developed in one-day-old D. cepedianum larvae at 80° F, so at higher temperatures this character of identification must be correlated with yolk or jaw development. If more than one-half of the yolk is

absorbed and there has been some jaw development, D. cepedianum are likely to have formed pigmented eyes. D. petenense had developed isolated, dot-like melanophores along the intestine and anterior portion of the yolk by about 12 hours post-hatching. By the end of 24 hours these punctulations were elongate.

Pectoral buds were developed in the one-day-old D. cepedianum. Those of D. petenense had increased in size. In both cases the stomodaeum was perforated later in this period. The lower jaw was partially formed as a finger-like projection behind the stomodael concavity. The auditory capsules were relatively large and produced a large bulge on either side of the head. Only two otoliths were evident in each capsule. Yolk had been reduced by about one-third to one-half of the volume at hatching. The reticulate pattern of the notochord is a prominent feature of larval anatomy.

Behavior was little changed from that described in the freshly-hatched individuals. However, D. cepedianum was more attracted to light concomitant with the development of pigmented eyes. The alternate upward swimming and downward sinking was still the prominent feature of their movement.

Two-day larvae - 74° F (Figures 13c and 14c)--Total-length had increased only slightly to an average of about 4.9 mm with a maximum of 5.5 mm. Myomeres had increased to 37-39 in D. cepedianum and 36-37 in D. petenense. Approximately one-half to two-thirds of the yolk had been absorbed. The alimentary canal was complete as the stomodaeum had completely cavitated into the pharynx and the lower jaw had begun to form. The lower jaw was well developed in D. petenense, being about equal in length to the upper jaw. In D. cepedianum the lower jaw was not quite so well developed.

Pigmentation had increased in both species. D. petenense had an almost continuous line of pigment above the gut and posteriorly, below the gut. One large stellate melanophore was present above and surrounding the anus. The caudal fin had expanded slightly into a paddle-shaped organ and had radial striations emanating into the finfold from the notochord. Some pigment had developed on the ventral portion of the notochordal mass in the caudal fin area.

Dorosoma cepedianum had more prominent yellowish pigment in the eye and some melanophores were developing along the intestine as earlier described for D. petenense. This

stage of pigmentation was not reached until three to four days at 62° F (Warner, 1940) and at a greater length. This may represent another example of pigmentation being more precocious at higher temperatures. A Y-shaped area of pigmentation, consisting initially of three melanophores, had formed on the anterior ventral aspect of the yolk in D. petenense and D. cepedianum. The apex was anterior and culminated over the area where the cleithrum will subsequently develop.

Three-day larvae - 74° F (Figures 13d and 14d)--The larvae had increased to about 5.25-5.5 mm total-length. There was considerable variation in growth among fish from a single group. This reflects some of the range noted in the embryological development. The lower jaw of both species was well developed and functional. Those which hatched earlier were also able to begin feeding earlier and thereby increase their margin over the more slowly developing individuals.

Positive phototaxis, which seemed to develop as the eyes became pigmented, was now well developed in D. cepedianum. A greater amount of dark pigment had partially masked the former yellow color. The yolk was absorbed in most of the

individuals of both species, and the tendency to sink was much less pronounced. Sinking was still head downward, but only at a slight angle from the horizontal. Larvae of both appeared to collect near the surface with heads upward. Eel-like undulations characterized swimming at this size. Larvae still moved independently with no tendency toward schooling.

Five-day larvae - 74° F--Most individuals of both species were about 6.0 mm total-length, but some were as large as 9.0 mm. Pigmentation of D. cepedianum was nearly a continuous line above and below the intestine. A large stellate melanophore had developed near the anus of D. cepedianum as described previously for D. petenense. The pectoral fins of both were paddle-shaped and the developing cleithrum could be seen beneath and between them. The pectorals were frequently observed vibrating rapidly and may be of considerable importance to supplement the eel-like swimming. They were capable of rapid, elusive darting behavior at this size. No caudal rays had developed and the notochord had not yet turned upward. Schooling behavior was still not apparent.

High mortality was experienced by the larvae of both species following this period. This was probably associated with failure to begin feeding under laboratory conditions. Numerous and varied attempts to rear larvae beyond this size failed. If feeding is not initiated within a certain period following yolk absorption, larvae die even though feeding is subsequently begun. This was described as the "point of no return" by Blaxter (1969). Mortality was delayed until 10-11 days at 65° F. Bodola (1966) reported this mortality at 10-11 days for D. cepedianum. There may be a comparable high rate of mortality under natural conditions associated with the transition from yolk nutrition.

10-13 mm larvae, ca. 7-14 days - 75° F--Larvae of neither species had definitive fin development up to this point other than the paddle-shaped pectoral fins, and these were not supported by rays. The caudal fin was the first to show ultimate development. The developing vertebral column tilted upward to form the urostyle at 11.5-12.5 mm total-length. (To this point total- and standard-lengths have been essentially the same. Unless specified, subsequent

lengths will all be standard-length.) Ventral elements of the future caudal fin began to form and will be the bases of attachment for the caudal fin-rays. Ossification of the vertebral column proceeded from the mid-posterior region, anteriorly; as postanal myomeres and vertebrae are added there will be additional posterior sites of ossification. This pattern of ossification was reported for Plecoglossus altivelis by Iwai (1962) and for Elops saurus by Gehringer (1959). Myomeres have increased to 39-43 in D. cepedianum and 36-40 in D. petenense. There are few postanal myomeres but subsequent additions will increase the total amount.

The dorsal fin first appeared as a lobe, two-thirds of the distance from the head to the caudal area, and subsequently developed four to seven rays prior to 12.5 mm total-length (Appendix B, Table 1).

13-15 mm larvae, ca. 14-21 days - 75° F--During this growth phase several changes were apparent in the anatomical features of these species. The operculum was partially developed at 13-14 mm, growing backward over the newly-forme gills. The hypural plate was formed by 13 mm, and at 14 mm the caudal was well developed. The dorsal fin of both had

10-14 rays by 13 mm and the last ray was doubled. By 15 mm D. petenense had 14-15 rays in the dorsal fin while D. cepedianum had only 12-13. In both species pectoral fins developed three to four rays by 15 mm and the earliest pelvic buds appeared about midway between the pectorals and anus. The anal fin was also somewhat retarded in its development. A lobe was present in the 14-mm larvae with a variable number of rays having developed by 15 mm. As few as eight total were formed and as many as 22 in D. petenense and 28 in D. cepedianum (Appendix B, Table 1).

The initial changes which altered the larval form began as gut alterations. At 14-15 mm the gut began to form the first of several loops. The first loop later became the gizzard and produced the evagination that forms the swim bladder. Bodola (1966) illustrated the sequential development for D. cepedianum.

The bones of the mouth were differentiating and ossifying during this period. The supramaxillaries of both had formed by 15 mm although not yet characteristic of the species. No difference in growth rate was noted between the two species to this point.

15-20 mm larvae, ca. 2-4 weeks - 75-78° F--The full complement of dorsal rays had developed in D. cepedianum and D. petenense by 16 mm. D. cepedianum had 12-14 while D. petenense had 15-16. These counts appear high but were total counts and not as defined taxonomically. By 15-16 mm both species had sufficiently developed the elongate last dorsal ray which identified them as Dorosoma.

Dorosoma petenense attained its full anal ray complement by 17-18 mm, while that of D. cepedianum was fully formed by 16-21 mm. In both, the anterior rays were the last to develop which necessitated including all in the counts. This procedure was followed for the anal fin until the counts were characteristic of the species.

In some larvae there was a noticeable lag in attaining full ray complements. This was correlated somewhat with rate of development. Larvae from the same spawn that grew more rapidly attained their full complement of rays at a larger size. This was especially marked in anal rays (Appendix B, Tables 2 and 3) but other characteristics also altered. Rapidly growing D. cepedianum often attained a length of 20-21 mm before all anal rays developed and the larval

form was lost. The more slowly developing larvae appeared to attain their complement of rays and to transition from the larval form at a smaller size. Transformation consists of the following: an increase in body depth as a result of gut reorganization and air bladder formation; development of scales; and complete acquisition of meristic elements. Transformation was not noted in either species in individuals smaller than 15-16 mm, whereas some D. petenense as large as 17 mm and D. cepedianum as large as 20 mm retained their larval form. Judging from the upper range, it would appear that D. cepedianum transform at a larger size than D. petenense and this often, but not always, occurs (Appendix B, Tables 4 and 5).

Evidence of the swim bladder can normally be detected in cleared specimens of both species between 15-16 mm. This is in conjunction with the first flexure of the gut.

Scale formation was noted for larvae as small as 16 mm in both species. The deciduous nature of scales made determination of early development difficult. The most frequent areas of early scale development were behind the operculum dorsal to the pectoral fins and in the region of developing scutes along the belly. This pattern of development is

contrary to many other teleosts but was also reported for Alosa mediocris by Mansueti (1962).

Rays in the pectoral fin were developed by 17-18 mm. Therefore, in spite of the early appearance of the buds they are latent in their definitive development.

Myomeres had increased to 47-48 in D. cepedianum and 42-44 in D. petenense. Considerable variation in myomere counts can result from varying methods of counting. In this study all myomeres were included. There was a trend for D. cepedianum longer than 10 mm (TL) to have consistently greater numbers of myomeres than D. petenense, but my counts for D. petenense were higher than reported by Kersh (1970).

The bones of the mouth have ossified to the point of being unique to the species by 17-18 mm. In general, the bones of the mouth contribute individually to the overall morphology of the head region. The mouth bones of D. petenense are usually longer than those of comparably sized D. cepedianum. This results in a larger gape in the former species.

Position and shape of the premaxillaries are primarily responsible for the difference in mouth position and snout shape. In D. cepedianum these bones form a blunt

snout by projecting ventrally into the gape, while in D. petenense they conform to the sloping contour of the snout and contribute to a more terminal mouth. This form is acquired gradually between 20 and 24 mm.

The maxillaries of D. petenense are longer and slightly different in shape than those of D. cepedianum. Both have teeth on the posterior portion of the maxillary bones.

Supramaxillary bones are supporting bones and are located in the membranes at the side of the mouth. There are two pairs of supramaxillaries in Dorosoma. There is little difference between the smaller supramaxillaries (Sm_1) of the two species. The larger supramaxillaries (Sm_2) are species characteristic in shape and size (Figure 15). They project anterio-dorsad from the posterior portion of the maxillaries. The fully developed supramaxillary$_2$ bones of D. petenense are paddle-shaped at their bases, elongate and needle-like at the opposite end, and are generally symmetrical. D. cepedianum have supramaxillaries$_2$ which are asymmetric at their bases, being enlarged on the aspect nearest the gape. The pointed portion of each is not as elongate as that in D. petenense. Their unique shape is gradually

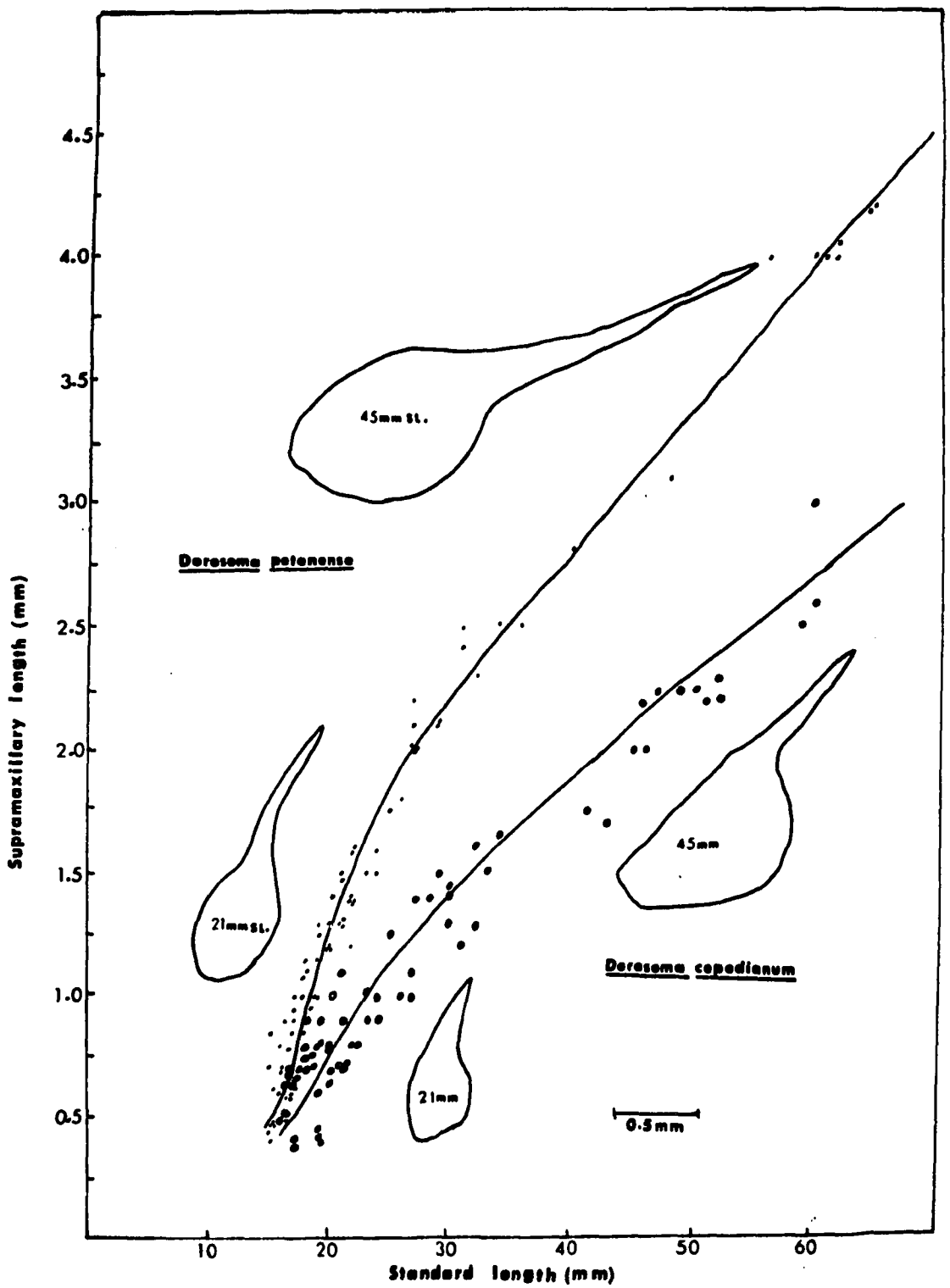


Figure 15. Comparison of supramaxillary$_2$ lengths with standard lengths.

acquired and is distinct in larvae larger than 18 mm.

20-25 mm larvae, ca. 6 weeks - 75° F--During this phase of growth the larval transformation was completed. Most characteristics approached the adult condition. The blunt snout of D. cepedianum developed as described previously. In addition, another character often used to separate adults was acquired. This is the maxillary notch, an indentation in the margin of the upper jaw profile; it forms in the membrane adjacent to that portion of the maxilla which contributes to the gape. This never develops in D. petenense and is variable in hybrids. In D. cepedianum the notch is weakly developed by 20 mm but well developed by about 30 mm.

During this and the previous growth periods the gut lengthened and the relative body depth increased. Young have now attained a characteristic shape--D. petenense are lanceolate whereas D. cepedianum have heavier anterior profiles and relatively deeper bodies. The yellow color of the caudal fin, which is characteristic of adult D. petenense, developed somewhat later (about 30 mm). Various larval stages of D. petenense were illustrated by Taber (1969), and Miller (1960) illustrated various stages of D. cepedianum. My observations

and those of Swingle (1969) indicate that there is normally no difference in the early growth rate of the two species.

CHAPTER IV

SPAWNING

Gonadal Somatic Index

A gonadal somatic index (GSI) is a useful and relatively easy method to assess the spawning season of fishes. Generally ovaries are used since changes are large and obvious, whereas seasonal changes in testes are much less conducive to quantitative evaluation (Appendix C, Tables 1, 2, and 3). Johnson (1971) concluded that testes might be better indicators of the end of spawning season because they lack residual material, but from a quantitative point of view, I believe they are less desirable. To use a GSI effectively one should know the age of maturation, whether size variation is a factor, and if migration affects collections at a particular site.

Age of maturation was determined for D. cepedianum in Ohio by Bodola (1966). He found that males tended to mature slightly younger than females. A few males matured at age-

group I and as small as 9.4 inches TL, but most matured by age-group II. Fewer age-group-I females matured; most were age II or III and greater than 9.6 inches TL. In Lake Texoma I found some age-group-I D. cepedianum males as small as 8.2-8.5 inches TL to be mature. Mature age-group I females were larger than 8.7-9.0 inches TL. The majority of both sexes matured by age-group II, the third year of life. Thus, fish larger than 8.5-9.0 inches TL were included in the gonadal evaluation, although the majority of spawning fish were larger.

Dorosoma petenense matured at a smaller size than D. cepedianum and possibly at a younger age. Some may mature at age 0 (Carlander, 1969). D. petenense females larger than 2.4 inches TL (1.8 inches SL) were found to be mature and were included in gonadal elaboration. There are indications that in springs following severe winters young-of-year may mature and spawn the same season, presumably in response to decreased intraspecific competition. In late July, 1963, following the particularly cold winter of 1962-1963 (Figure 16), I observed flowing-ripe male and female D. petenense in Lake Texoma. Some were as small as 2.7 inches TL (2.1 inches SL). The 1963 growth of D. petenense

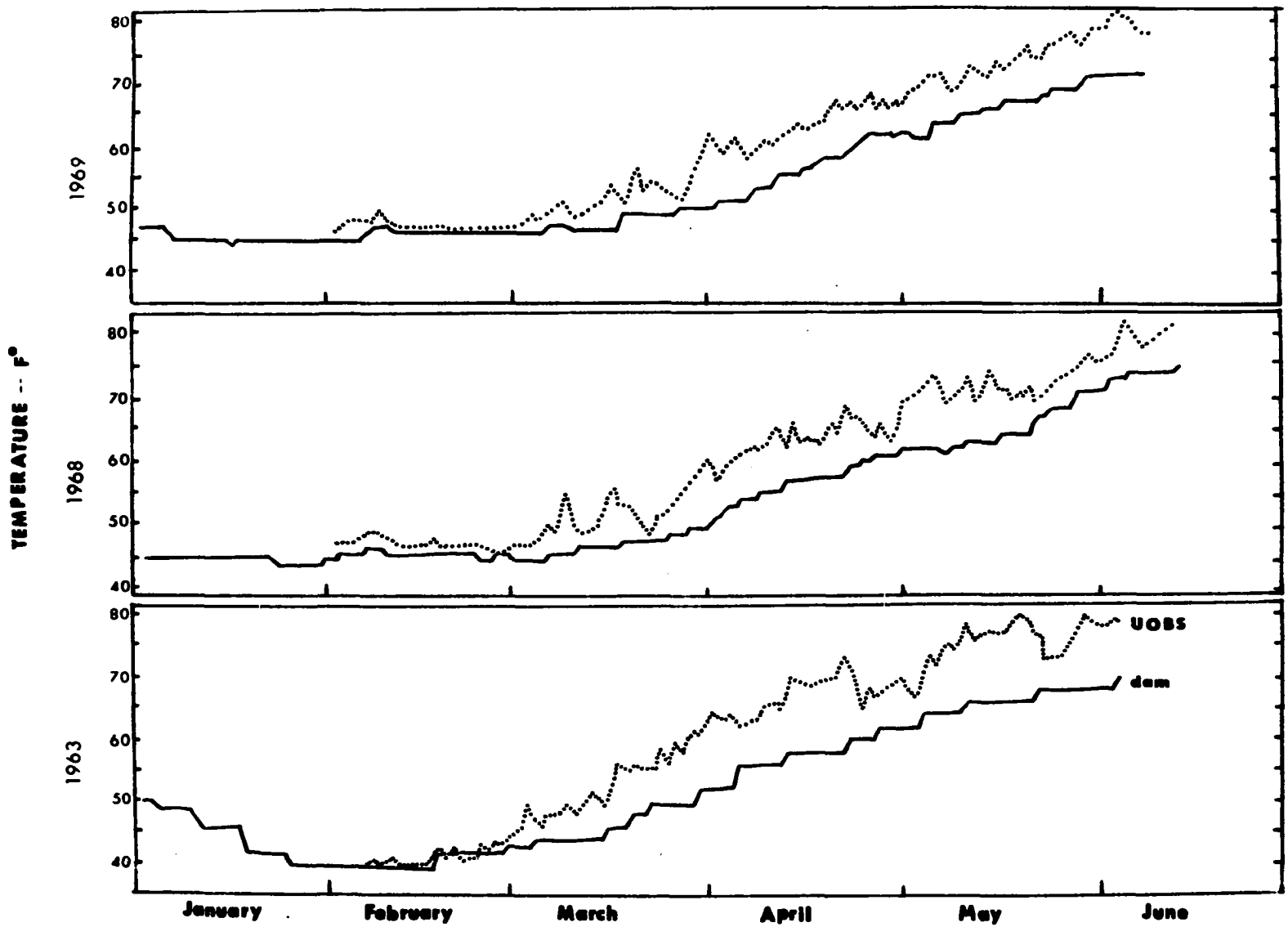


Figure 16. Mean-daily water temperatures, surface at University of Oklahoma Biological Station and sub-surface from Denison Dam.

in Bull Shoals Reservoir, Arkansas, was high, possibly indicating an expanding population (Bryant and Houser, 1968). Houser (personal communication) believes this might also have occurred in Beaver Reservoir, Arkansas. The winters of 1967 through 1971 were milder, and this phenomenon was not observed during these years. Johnson (1971) reported no spawning young-of-year in Arizona and believes that reports of such were probably age-group-I fishes.

Fish as small as 2.4 inches TL were collected during the early part of the spawning season. Length-frequency analysis of spawning aggregations for 1968 indicated a tendency for aggregations in the early spawning season to be composed of about equal numbers of small and large males (Figure 21). As the season progressed smaller males predominated in the spawning aggregations. Females were not as numerous in these spawning groups. Small and large females were present in all collections but relative abundance of size groups varied (Figure 21). Johnson (1971) reported a tendency for smaller fish to spawn later in the season in Arizona. In Lake Texoma the early aggregations were composed of age-groups I, II, and III, and probably IV. The

modes for II and III were indistinguishable except in the mid-April collection. In Bull Shoals Reservoir male and female D. petenense attained an average length (TL) of about 2.6 inches by age-group I, and 4.6 inches by age-group II. Age-group-III males and females reached an average length (TL) of 4.7 and 5.2 inches, respectively (Bryant and Houser, 1968). A slower growth rate in Arizona was indicated by Johnson (1970). Length-frequency data of spawning aggregations indicated a growth rate in Texoma more comparable to that in Bull Shoals.

Gonadal variation among size-groups and between different areas was indicated. Early in the season there was a tendency for larger fish to have a higher index; a decrease in GSI generally occurred in these fish first (Appendix C, Table 4). This trend was not always statistically significant. The small number of fish analyzed which were less than five inches decreased the significance of this comparison. The presence of small fish in early spawning aggregations appears to contradict these data, but length-frequencies only indicated extent of participation by various sizes and not the individual's GSI.

Length-frequency data were not accumulated for D. cepedianum as spawning aggregations in different seasons and in sufficient numbers could not be readily collected. Likewise, the gonadal indexes of the two size-groups analyzed did not reflect the trend (Appendix C, Table 4). The most frequently collected spawning-size fish were 10-14 inches TL in age-group III or older. Baglin and Kilambi (1968) noted that age-group-III and -IV fish in Beaver Reservoir showed no seasonal difference in GSI while fish in age-group II were somewhat slower in development. Bodola (1966) reported a higher index for age-group-II D. cepedianum in Lake Erie but did not refer to a seasonal difference.

A variable locational difference in GSI was noted for both species (Appendix C, Table 5). A significant difference between sites might indicate a spawning movement. For locational comparison two gill net sites were selected. One, near the mouth of the creek, was designated upper Buncombe; the other, near the mouth of the arm, was designated lower Buncombe. Collections made at these sites were compared during the spawning period. Generally the GSI for D. petenense was higher in the lower Buncombe area. It was

significant only once and this was prior to commencement of spawning. There was one significantly higher GSI mean at the upper set on 30 May 1968. Spawning was heaviest in the shallow water adjacent to deep water which is more prevalent near the main body of the lake. This might explain the general trend for the higher GSI in the lower Buncombe area.

In the upper portion until mid-April the GSI for D. cepedianum tended to be higher, though not always significantly so. After this date there was practically no difference in subsequent samples (Appendix C, Table 5). Since D. cepedianum spawned earlier in tributaries, the tendency for the GSI to be higher in the upper end during March and early April was probably a result of movement toward these tributaries. Later in the season, spawning was occurring throughout the lake and no real difference was apparent in the two regions.

To further substantiate this idea, during early April I took samples from the creek mouth and well up in the creek. The GSI was highest at the mouth but both were higher than the main lake samples (Appendix C, Table 5). D. cepedianum move into creeks to spawn and are most active at night.

Although some spawning continues throughout the morning most retreat to the lake during the day. They probably concentrate near the creek mouth and upper reaches of the arm. GSI area comparison data seem to confirm this consideration. Although Bodola (1966) did not discuss tributary spawning, he did mention shoreward movement of spawning D. cepedianum in Lake Erie.

Relating gross structure to microscopic structure gives a better understanding of the changes connected with gonadal development. In early February the ovaries of both species contained small oocytes in early stages of development. No yolk deposition had occurred and the follicular epithelium of the individual oocyte was represented only by scattered cells on its surface. The ovary was translucent.

Dorosoma cepedianum ovaries began to change earlier than those of D. petenense. By late February yolk deposition had begun in some D. cepedianum. The follicular epithelium had become a distinct layer surrounding the eggs. Ovarian color was an opaque yellowish-pink. The GSI averaged one to two percent in both species with D. cepedianum having a slightly higher average (Figure 17).

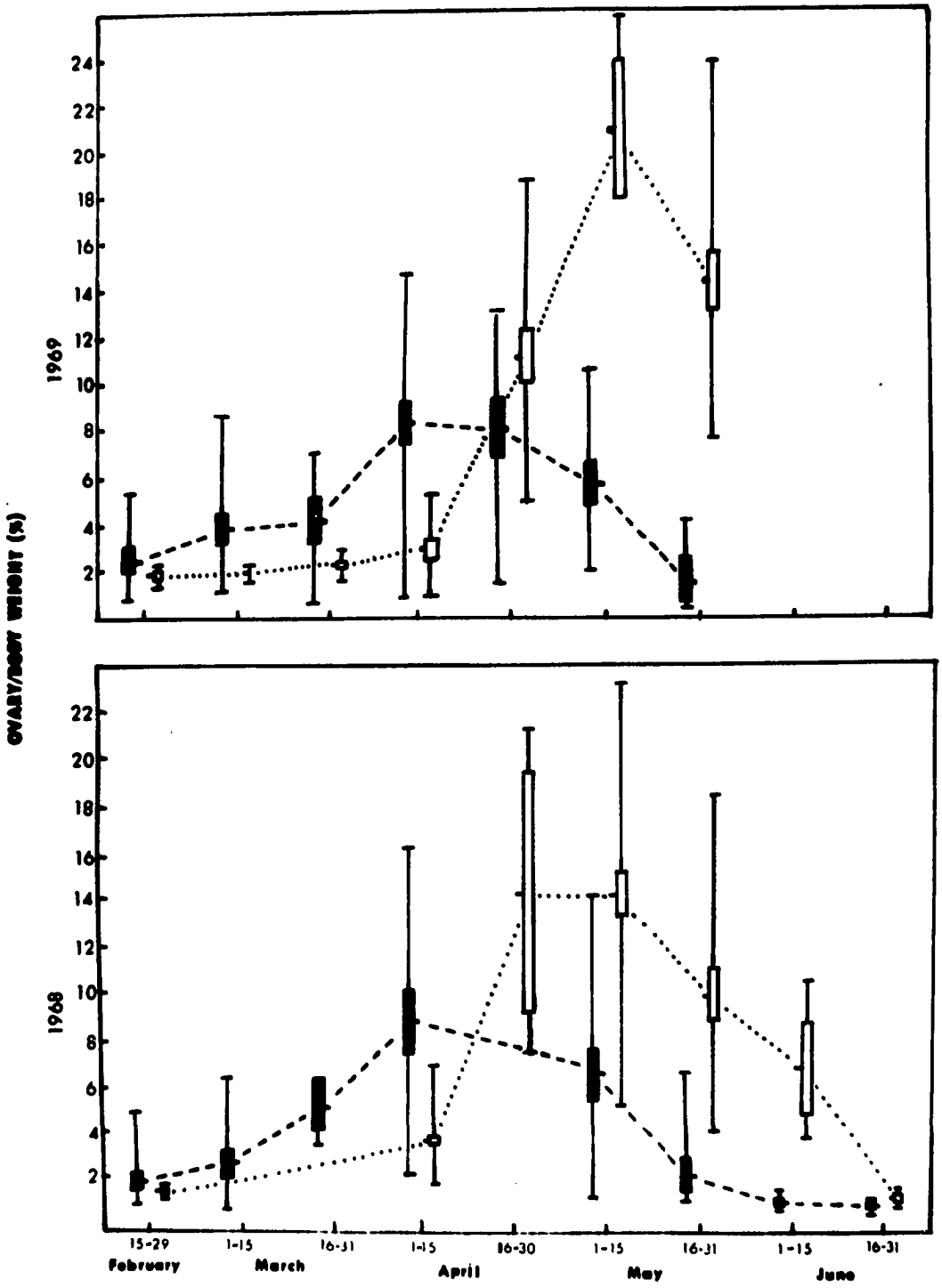


Figure 17. Gonadal somatic indexes for D. cepedianum (solid rectangle) and D. petenense (open rectangle).

Yolk deposition increased in D. cepedianum during March. Individual oocytes enlarged, resulting in an ovarian increase. The GSI for D. cepedianum averaged two to three percent early in the month and four to six percent later. Ovarian color had transitioned to a deeper yellow, due in part to increasing vacuolization of the eggs. The follicular epithelium became very thick and prominent. A vitelline membrane developed during this phase but was not apparent in unsectioned material.

The transition observed in ovaries of D. cepedianum during late February occurred in those of D. petenense during March. Early yolk deposition did not occur until mid- to late March. Average GSI was about two to three percent. By late March and early April the GSI averaged about four percent and ovarian development had proceeded to the stages attained by D. cepedianum in early to mid-March.

In late March and early April ovulated eggs had collected in the ovarian lumen of D. cepedianum. Spawning had begun in the more rapidly warming tributaries. GSI averaged 8-10%, ranging as high as 16-18%. D. petenense had ripe eggs in the lumen after mid-April. The average GSI of

D. petenense in late April to early May was 16-20% with some as high as 26%.

During May, after a portion of the eggs had been deposited, the GSI of D. cepedianum began to decline. Ensuing maturation of additional eggs prolonged the period of gonadal enlargement, but at the end of the spawning season the ovary was flaccid and contained only a few residual yolked eggs and many small oocytes. The GSI had returned to about one to two percent by the end of May.

The same pattern was observed for D. petenense during late May and early June. The release of matured eggs was reflected by a gradual decline in the GSI. Retention of a large group of mature eggs as reported by Johnson (1971) was not observed in Lake Texoma D. petenense; only rarely were there more than a few residual yolked eggs in the flaccid ovary at the end of the spawning season. It is evident, however, that eggs that develop beyond yolk deposition are resorbed if they are not voided. Johnson (1971) also reported a large number of abnormal ovaries encountered during his study. No such anomalies were observed in Lake Texoma.

Gonadal somatic index as an indication of spawning season should be interpreted in relation to the most plausible

controlling physical parameters. In temperate regions the most influential factors are probably light and temperature (Aronson, 1965). The cycles coordinate gonadal development among individuals of a species, culminating in reproduction during the optimum season for survival of young.

Photoperiod steadily increases in the Northern Hemisphere from December to June and affects the gonads through the pituitary. Increasing day length regulates seasonal gonadal development while the diurnal cycle establishes a circadian rhythm which coordinates daily spawning activity. Early in the spring gonads of both species underwent a gradual increase in size which paralleled the increasing day length. Photoperiod increase from December to early February is small and very gradual. The change in GSI of both species was very slight during this interval but indicated an end to a relatively inactive period. Gonadal development in D. cepedianum preceded that in D. petenense by several weeks.

Effects of the lengthening photoperiod are difficult to separate from temperature effects which increase concomitantly. In the Northern Hemisphere the coldest calendar

period is from December to early February. Minimum water temperature varies from year to year depending upon the severity and duration of winter. A colder than normal winter does not necessarily result in a later spring. The water may warm rapidly and reach spring temperatures equivalent to those following a milder winter. This occurred following the severe winter of 1963 when a warm spring brought temperatures in line with those observed in springs following the mild winters of 1968 and 1969 (Figure 16).

The minimum water temperature normally occurs in late January or early February. Primary oocytes have been present in the ovary throughout the winter, but yolk deposition does not occur until spring. Vitellogenesis results in enlargement of individual oocytes which produce the gradual enlargement of the ovary.

Gonads of D. cepedianum appeared to enlarge only slightly prior to temperature increase, as exhibited by mean daily surface water temperature. Fluctuations of temperature in the spring may carry information to the species before it is reflected in a mean temperature increase. Yolk deposition accelerated in mid-March in conjunction with increasing mean water temperature (Figures 16 and 17).

Increasing photoperiod and changing temperatures may physiologically prepare the fish for a subsequent temperature increase which will initiate vitellogenesis.

Gonadal development in D. petenense was delayed until a warming trend was well established. Yolk deposition was not initiated until late March or early April. Early gonadal development of both species was most certainly under the influence of the photoperiod. Gradual increase in day length probably initiates changes prior to vitellogenesis which do not appear until a temperature increase has been established.

Relationship of temperature and gonadal maturation can be indicated by comparing D. cepedianum in its southern and northern ranges (Bodola, 1966). His data show a GSI increase in late April with spawning not occurring until June in Lake Erie. Lake Texoma D. cepedianum spawn six to eight weeks before their northern counterparts. This can be attributed to latitudinal difference in season. A two percent increase in GSI was not noted in Lake Erie until mid-April when water temperatures were in the low 50's. In Lake Texoma the increase above two percent was recorded in early March when the mean surface water temperature was about

50° F. Maximum average GSI (9-10%) occurred in Lake Erie in early June when the water temperature was in the low 60's. A comparable GSI in Lake Texoma was reached in early April with mean surface water temperatures in the low 60's. A similar comparison cannot be made for D. petenense as it has not been studied over its north-south range. It would be interesting to compare the spawning cycle in this latitude with the cycle of D. petenense in its southernmost range, British Honduras.

If day length were the only factor, GSI increase should be very uniform from year to year. Temperature increase in the spring is not constant within or between years due to meteorological variation so it would be expected that some variation would occur in the GSI increase from year to year. Water temperatures for 1968 and 1969 were comparable for the winter and for the early warming schedule in the spring. During these two years the GSI for D. cepedianum was analogous as was the temperature history for the time of rapid gonadal development.

The D. petenense GSI appeared to increase to a greater degree in the last half of April, 1968, than for the same

period in 1969. However, there was a slight difference in temperature history for the period of rapid gonadal development. In 1968 a steadily increasing temperature was apparent until late April. This coincided with maximum gonadal development. In 1969, however, the warming trend in early April was more erratic and slightly slower, possibly affecting gonadal development rate during this period. Gonadal development of D. petenense for 1963 may be included for comparison (Shelton, 1964). Rapid warming more than compensated for the lower winter temperatures. D. petenense GSI increased earlier in 1963 than in either 1968 or 1969 but was intermediate after mid-April.

In both species it appears that gonadal development is closely correlated with particular environmental parameters, especially photoperiod and temperature. It is most probable that the effects of temperature and day length on Dorosoma are not independent but are interrelated and sequential. A particular photoperiod increase is apparently necessary to establish a gonadal condition conducive to subsequent stimulation by temperature increase and the resultant vitellogenesis. Yolk deposition, once initiated, is not

reversible; the eggs develop to ovulation and shedding, or else they are resorbed at some intermediate stage.

There is a difference between the two species at the same location. The GSI for D. cepedianum precedes that of D. petenense by three to four weeks (Figure 17). The spawning season for D. petenense and D. cepedianum in Lake Texoma, as interpreted by GSI, overlaps at the peak. D. cepedianum gonadal development indicates an onset of spawning from late March to the first of April, continuing until mid-May, and peaking in late April. These data indicate a spawning period of about six to seven weeks. Bodola (1966) reported an approximate 4-week spawning period from June to July in Lake Erie. Miller (1960) recorded spawning principally from April to June (50-70° F) in temperate waters of the United States. Baglin and Kilambi (1968) reported spawning for D. cepedianum from mid-April through May in Beaver Reservoir, Arkansas, and Taber (1969) indicated spawning from late March until late May in Lake Texoma.

The gonadal development data for D. petenense indicate an 8-10 week spawning period, from mid-April to mid- or late June, with a peak around the first of May. This does not

include the possibility of late spawning in July by smaller size-groups whether they be young-of-year or late maturing age-group-I fish. Based on trawling samples, Taber (1969) indicated a spawning period of mid-April to September in Lake Texoma. Johnson (1969) found that April to June was the spawning period in Arizona reservoirs.

Egg Sampling

A program of egg sampling was designed to gather information concerning spawning period, spawning sites, and diurnal spawning variation for D. cepedianum and D. petenense. Egg samplers (Figure 3) were tested initially to see if they sampled adequately. Green and yellow tulle was used for the surfaces. Material of each color was placed on separate shallow-set samplers in one to two feet of water where spawning was in progress and could be observed. D. petenense utilized the samplers considerably. Groups spawned over the horizontal surfaces or rushed toward and spawned on the vertical surfaces. In addition, the same group would repeatedly circle around the sampler and deposit several successive times before departing, indicating a degree of selectivity as to spawning substrate. D. cepedianum were tested in the same

manner. They used the samplers but deposition density was lower.

The highest deposition density by D. petenense was on the yellow surfaces (Appendix D, Table 2). However, this was the sampler the fish encountered first as they moved along the shore. This may have been more important than the color. D. cepedianum deposited most heavily upon the green surfaces. There also appeared to be a slight tendency for both to deposit on the vertical surfaces, which is significant since more effort would be required to deposit demersal eggs on a vertical surface.

Following this preliminary test, it was decided the samplers would provide an adequate means to sample spawning as they seemed to present significant stimulus as a spawning substrate. Green tulle was used as it resembled natural substrate in color and was utilized by both species. Utilization of samplers probably depended upon the substrate being a sight-releaser mechanism where appropriate substrate is "selected" by the spawning fish. It would be futile to hope that collection of eggs would occur on the small surface areas if random distribution of eggs were the mode of spawn-

ing. Samplers collected eggs of several species of fish other than Dorosoma (Table 2). Most were easily separated, if not identified. All were comparable in that they were demersal and adhesive, or at least had some attachment structure.

Dorosoma eggs are not separable as all characteristics are essentially the same. Thus, it was necessary to incubate the eggs to hatching for identification. Separation was possible based upon eye and yolk characters as described in the section on embryogeny.

Obvious problems were associated with this sampling technique. Laborious removal of eggs from sampler surfaces and mortalities prior to hatching were the most common. The latter proved to be the most serious as many thousands of eggs were collected which could only be identified as Dorosoma (Table 3). This table summarizes the total number of eggs collected during routine sampling and the number of larvae which hatched. Only data from sets which included all three samplers were used; thus, creek samplers and unassociated floating samplers were not included.

In 1968 and 1969 the first Dorosoma eggs were collected

Table 2. Fishes' eggs collected on samplers.

Species	Egg diameter (mm)	Description
Dorosoma cepedianum	0.8 -1.1	opaque, extremely adhesive
Dorosoma petenense	0.8 -1.1	opaque, extremely adhesive
Morone chrysops	0.9 -1.0	pale yellow slightly adhesive
Menidia audens	0.95-1.0	clear, with elastic filament
Cyprinus carpio	1.5 -1.6	sandy brown adhesive
Ictiobus sp.	2.0 -2.5	sandy brown adhesive
Lepisosteus sp.	3.5 -3.8	gray-green very adhesive

Table 3. Summary of Dorosoma eggs collected on lake samplers during 1968 and 1969.

	1968-69			
	Shallow	Floating	Bottom	
Eggs	61,483	2,917	2,331	66,731
D. cepedianum	808	138	338	1,284
Percent	62.9	10.7	26.3	
D. petenense	1,863	375	31	2,269
Percent	82.1	16.5	1.4	

from the lake during the period 1-15 April (Appendix D, Tables 3 and 4). All eggs identified were D. cepedianum. Apparently, no. D. petenense eggs were collected. During the period 16-30 April, eggs of both species were collected. The 26 April 1968 sample was small, which was probably due to the cold weather from 22-29 April. This may have slowed or suspended spawning of D. petenense and possibly that of D. cepedianum. Eggs of both species were collected throughout May. The 15 May 1968 sample was small because almost all samplers were lost due to rapidly rising water. Only D. petenense eggs were identified from the June collection.

The spawning season of D. cepedianum, as indicated from these data, would appear to have been April through May, or a period of approximately seven to eight weeks. This was slightly longer than judged from the GSI. In addition, observations of spawning and collection of eggs on 27 March 1968 indicated an additional week if tributary spawning is included. Tributary spawning can be substantial and is not restricted to the initial early season.

The spawning period of D. petenense appeared to extend from mid-April throughout June for a period of approximately

nine to ten weeks. This was about the same as judged from the GSI. D. petenense presumably do not ascend streams to spawn. No evidence was found to suggest that they might (Appendix D, Table 5). Additional evidence to substantiate this contention will be presented from larvae sampling data.

Contrasting vertical and horizontal surfaces, as mentioned in the sampler-testing experiment, suggest a slightly higher utilization rate of the vertical surface. Additional data from routine egg sampler series supplemented this contention (Appendix D, Table 7). Wave action was not a factor for the dates and/or locations cited. Floating sampler data was not included as the sampler often floated at a slight angle. If the surfaces were used only equally, it would still be interesting as some additional effort must be required to deposit on the vertical rather than the horizontal surface. Probably the horizontal position of females at the time of egg deposition contributed to this distributional pattern. It seemed that D. petenense had an apparently stronger tendency to spawn on the vertical surface (Appendix D, Table 7). D. petenense, observed spawning, usually turned on their sides to deposit eggs. This tendency was not so

constant during the spawning act of D. cepedianum. Data from egg sampler surfaces seemed to affirm this observation.

Egg sampling data also suggest a differential deposition pattern between samplers of a standard set (Table 3; Appendix D, Tables 3 and 4). The greatest number of eggs of both species was deposited on the shallow-bottom sampler. D. petenense utilized the shallow-bottom samplers more on a numerical and percentage basis than did D. cepedianum (Table 3). Floating samplers collected the second largest number of D. petenense eggs, whereas bottom samplers collected the second largest number of D. cepedianum eggs. D. petenense used the deeper bottom samplers very little; it is possible that the relatively small number of eggs might have drifted from above. D. cepedianum used the floating samplers proportionately more than D. petenense used the bottom samplers. It was not determined if eggs were deposited on the bottom at depths greater than five feet.

Spawning observations aided interpretations of these data. D. petenense spawned heavily in water less than one to two feet deep and most of the activity appeared to be

directed toward the surface. They also spawned on floating objects in deep water. Their primary orientation, therefore, seemed to be toward the surface and since objects close to the surface are more frequently found at the edge, their activity was usually concentrated there. A variety of floating objects was observed to be used--boathouses, boats, buoys, and floating debris. Concentration of eggs on shallow samplers and to a lesser degree on floating samplers together accounted for over 98% of the D. petenense eggs collected on the routine series. In addition, tremendous numbers of eggs, exclusively D. petenense, were collected on floating samplers at the boathouse during 1968 (Table 4). This is not to imply that all spawning is on surface objects for much spawning occurred on substrate not in contact with the surface. But, this was mostly in water less than one to two feet deep, so in effect the substrate was near the surface. May (1969) noted this same concentration of D. petenense eggs in water less than one foot deep.

Observations of spawning D. cepedianum suggested that their primary orientation was toward the bottom and objects on the bottom. Their spawning was accompanied by much less

surface disturbance as they turned abruptly and returned to deeper water along the bottom. These observations agree with the distribution of eggs among samplers. Over 88% of the D. cepedianum eggs collected during 1968 and 1969 were on the two bottom samplers. Only about 11% were deposited on the floating samplers (Table 3). This pattern conforms to the observed spawning behavior of moving along the bottom toward the shore, turning abruptly, and retreating to deeper water. Some unobserved surface activity may have occurred at night, possibly accounting for the low but fairly regular deposition on the floating samplers.

Vertical sampler series were employed to gain some additional information on surface activities of D. petenense. One series was at the boathouse and the other was located at some buoys 25-50 yards offshore in 35-40 feet of water. Both consisted of a floating sampler and additional samplers at 5-foot intervals down to 15 feet. Most eggs were collected at the surface. Only a small number were taken at five feet, fewer still at 10 feet, and none were collected in either series at 15 feet (Appendix D, Table 5). The set in open water had fewer eggs, but all were D. petenense as were

the eggs collected from the Cladophora on the buoys. All eggs collected at the boathouse set were also D. petenense.

A continuous series of samples was taken at the University of Oklahoma Biological Station boathouse during the spring of 1968 to compare the occurrence of spawning at the boathouse with other areas (Table 4). Two floating samplers were continuously set, one at either end of the boathouse. The surfaces were checked each morning, usually prior to sunrise, and at varying intervals throughout the day. Any surface that was found to bear eggs was replaced. During 1968 all spawning at the boathouse was after sunrise so that the morning's first spawn at this location was frequently observed. The samplers were also used as a form of positive check for spawning which occurred in my absence. The boathouse samplers seemed to be very good indicators of D. petenense spawning elsewhere. Only twice, 28 May and 4 June, was spawning observed elsewhere in the arm when no eggs were found on the boathouse samplers. If a similar series had also been monitored on the riprap, a check of spawning would have been more efficient as spawning was often moderate to heavy along the edge but only light under the boathouse.

Table 4. *Dorosoma* eggs collected on University of Oklahoma Biological Station samplers during 1968 compared with actual spawning observations.

Date	1968 Eggs	Number Hatched*	Spawning also observed elsewhere
April 15-17	0	0	-
18	5	3	+
19	0	0	-
20	12	7	+
21	15	10	+
22	19	18	+
23-25	0	0	-
26	212	79	+
27-28	0	0	-
29	45	20	+
30	50	20	+
May 01	46,600	1,945	+
02	4,216	597	+
03	564	216	+
04	60	42	+
05	12	1	+
06-07	0	0	-
08	247	63	+
09	5,000	1,003	+
10	3	0	+
11	225	59	+
12	52	21	+
13	8	7	-
14	0	0	-
15	3	2	+
16	5	3	+
17	0	0	-
18	72	39	+
19-21	0	0	-
22	2,000	100	+

Table 4 (cont'd.)

Date	Eggs	1968 Number Hatched*	Spawning also observed elsewhere
23	4,000	76	+
24-27	0	0	-
28	0	0	+
29-30	0	0	-
31	12	9	-
June 01-04	0	0	+
05	9	4	-
	63,446	4,344	

* All larvae were D. petenense.

Furthermore, the riprap area south of the boathouse appeared to be one of the most frequently used areas as well as one of the first areas used in the morning.

A surface water temperature of 67° F was plotted (Figure 18) because of the apparent close correlation with initiation of D. petenense spawning activity. During 1968 a surface water temperature of 66° F was exceeded on four or five days prior to 18 April, but all were in the afternoon. On 18 April, 66° F was reached at 0800; spawning was observed at 0900. Subsequent drops below 66-67° F appeared to suspend spawning which resumed when this range was again exceeded. This phenomenon was observed for M. chrysops by Webb and Moss (1967). If the range was not reached or exceeded during the morning hours, spawning was very infrequent. On some days the temperature never reached 67° F. For example, on 19 April, no spawning was observed or indicated even though heavy spawns occurred on the 18th and 20th of April. The egg sampler series of 26 April in the entire arm (Appendix D, Table 3) also reflected the effect of possible water cooling on spawning. On 26 April, the surface water temperature reached 67° F at 1000 and light spawning was observed

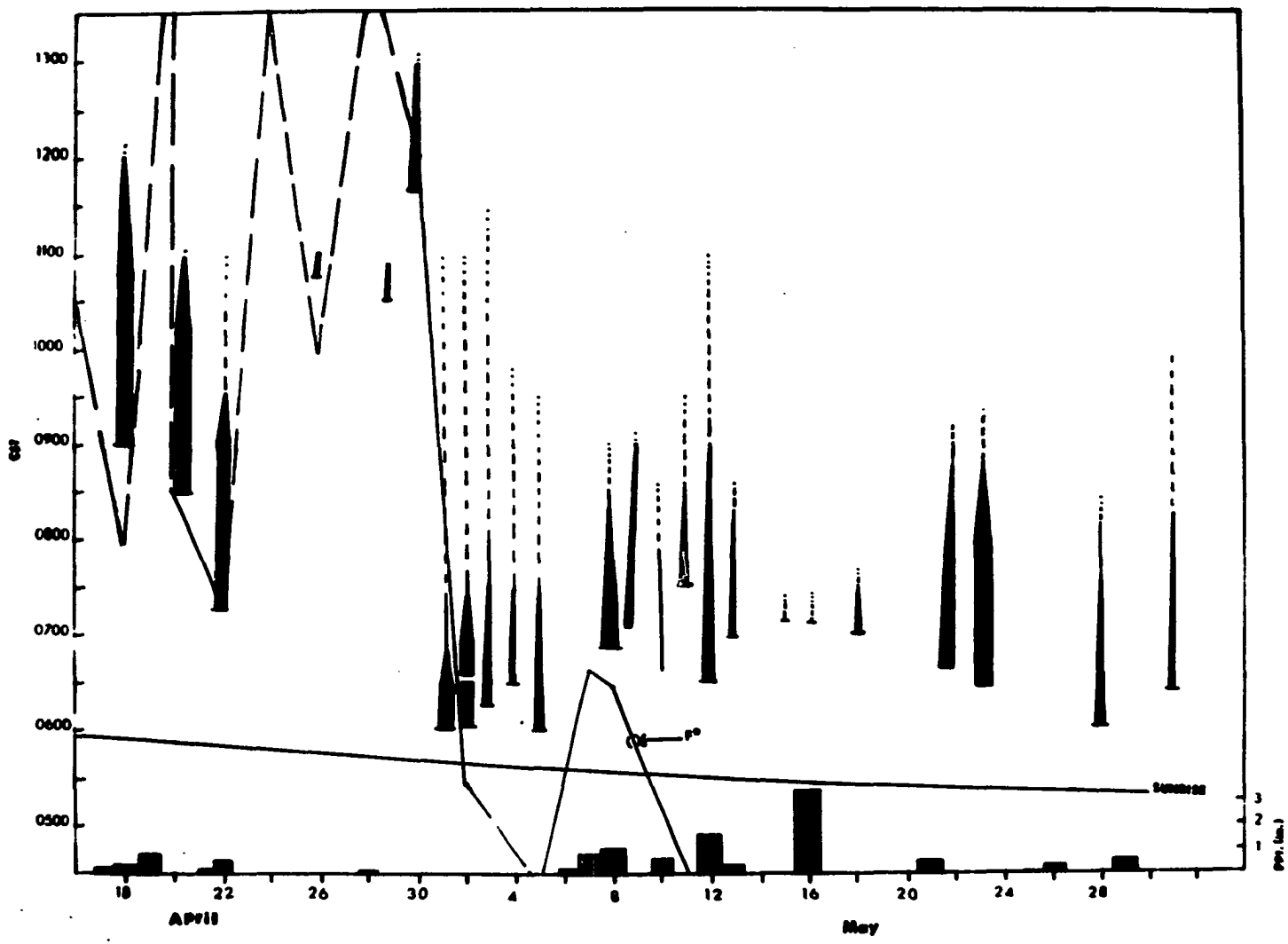


Figure 18. Spawning observation of D. petenense compared with various meteorological conditions. Width of spawning plot roughly indicates intensity. Temperature line (67° F) indicates time attained.

from 1045-1100. Subsequently, the temperature did not exceed 65° F until the 29th and no spawning was observed or indicated during the interval. On 29 April, the water temperature did not reach 67° F until the afternoon, but spawning was observed between 1030 and 1100 and at a water temperature of 63-64° F. This was the only time I had any indication of spawning at less than 66° F. Rawston (1964) reported observing spawning of D. petenense at 58° F and 64° F. Johnson (1969) reported spawning once at 17° C (62.6° F).

Following 29 April, the weather warmed and 66-67° F was thereafter always exceeded in the morning by 0700-0800. After 2 May, the temperature did not drop below 66° F. Spawning was fairly predictable for about the next week. The first activity would begin around 0630 with intensity varying from day to day and during the day. Spawning would be very active about 30 minutes to one hour after sunrise, continue about one to two hours, then would be sporadic until almost noon. Egg samplers and diurnal observations indicated spawning was generally restricted to this envelope with only an occasional exception. These will be discussed

in relation to spawning behavior. From these observations it seems that the light cycle influences diel activity more than a particular light intensity. Activity is restricted to the post-sunrise to pre-midday hours. Imposing the previously discussed temperature minimum, which apparently must normally be exceeded in this time envelope, restricts the diel spawning activity.

After mid-May, several consecutive days passed when no spawning was observed even though suggested prerequisite physical conditions had been met. It could be that in fishes which spawn in very large aggregations there are lapses in spawning due to a mass, temporary spent condition or perhaps there might be no spawning in that particular area. Neither explanation appears satisfactory due to the unlikelihood of either occurring in the tremendous population of D. petenense which is present in Lake Texoma.

There was never an indication of night spawning by D. petenense and only a few examples of afternoon spawning. During 1968 more than 60,000 eggs were collected on the boathouse floating samplers; all were collected within the previously mentioned time interval. Only about seven percent of

the eggs hatched for positive identification (Table 4). These were all D. petenense.

Another facet of egg sampling considered was the hazard of depositing eggs in shallow water (less than six inches) in reservoirs exposed to water level fluctuations. Rapid subsidence can expose large numbers of eggs. This potential mortality was noted in both species but was much less pronounced in D. cepedianum. D. cepedianum deposited eggs in shallow water but appeared not to concentrate them there. Also, most of their spawning was completed before the heaviest rains and thus before the major lake fluctuation. Their tributary-spawned eggs might be slightly more prone to exposure, however. There are indications that they ascended streams partially under the influence of runoff water. Eggs deposited under these conditions could be exposed following rapid subsidence of the stream. This was noted in Glasses Creek on two separate occasions when large numbers of eggs were exposed. D. cepedianum have a shorter incubation time than D. petenense but the minimum time needed to hatch was about 1.5 days. It was only in tributary spawns that the concentration of D. cepedianum eggs approached the density

of D. petenense eggs in the lake. The amount of tributary spawning by D. cepedianum, as compared to the total spawn, might not be proportionately large enough to have a major impact on the population; nevertheless, it must be a factor.

Dorosoma petenense frequently deposited 10,000-15,000 eggs on a 6-inch-square surface while D. cepedianum lake spawns rarely exceeded 150-200 eggs on an equivalent area. D. petenense concentrated their spawn in extremely shallow water. Normal wave action often exposed large quantities of eggs, but if the lake level declined the situation was magnified. Minimum time required for D. petenense eggs to hatch at the highest temperature investigated was about two days. At the prevalent temperature probably three days would be required. Rapid drawdowns are frequently necessary to prevent flooding from heavy spring rains. D. petenense normally spawned during this period and were apparently stimulated further by runoff water; at least allocthonous debris was utilized heavily as spawning substrate. Spawning was often heavy during rising water levels which could result in egg exposure in subsequent drawdowns. This occurred during mid-May of 1968 and 1969 when drawdowns averaged

about 0.35 feet per day (Table 5). In a 2-day period, a vertical drop of nearly three-fourths of a foot exposed greater horizontal distances and thereby tremendous numbers of eggs.

The amount of horizontal surface exposed varied with the slope of the terrain. Around the boathouse area where spawning was heavy and the slope was moderate, a vertical decline exposed five feet horizontally in two days. In the upper areas of the arm, 25-30 feet were exposed during the same two days. At the boathouse, spawn was heavy to a depth of about 2.5 feet but was concentrated in less than six inches of water. This entire area would be exposed in the 2-day minimum required for hatching; therefore, near total mortality would occur for that particular spawning interval. Heavy spawns at the boathouse, i.e., about 50-55 eggs per square inch or about 8,000 eggs per square foot, were recorded for 22 and 23 May 1968. Extrapolating from this data a tremendous number of eggs must have been exposed in the entire lake during this period.

Effects of high concentrations of eggs on hatching success were not investigated but are worth some speculation.

Table 5. Lake levels during a portion of spring, 1968 and 1969.

1968			1969		
Date	Lake level	Drop/Day (ft.)	Date	Lake level	Drop/ Day (ft.)
March-April	616-617 ft. msl		March-April	614-615 ft. msl	
13 May	617.25	--	6 May	614.90	--
14 May	617.27	--	7 May	616.17	--
15 May	618.77	--	8 May	617.30	--
16 May	619.64	--	9 May	618.40	--
17 May	620.79	--	10 May	619.20	-0.20
18 May	621.08	--	11 May	619.60	--
19 May	622.20	--	12 May	619.48	-0.12
20 May	622.05	--	13 May	619.33	-0.15
21 May	621.71	-0.34	14 May	618.95	-0.38
22 May	621.26	-0.45	15 May	619.86	--
23 May	620.80	-0.46	16 May	620.27	--
24 May	620.41	-0.39	17 May	620.57	--
25 May	620.00	-0.41	18 May	620.66	--
26 May	619.66	-0.34	19 May	620.45	-0.21
27 May	619.25	-0.41	20 May	620.10	-0.35
28 May	618.92	-0.33	21 May	619.57	-0.53
			22 May	619.11	-0.46
			23 May	618.65	-0.46
			24 May	618.24	-0.41
			25 May	617.83	-0.41
			26 May	617.46	-0.37
			27 May	617.25	-0.21

D. petenense eggs were usually found in dense concentrations since many fish deposited repeatedly at the same site. Eggs were often massed up to an inch in depth. It is very likely that decreased hatching success occurred as a result of oxygen competition, waste buildup, fungus spread, etc. The concentration of eggs also made them more vulnerable to predation. Centrarchids, especially Lepomis macrochirus and L. megalotis, were observed actively feeding on recently spawned eggs. Confirmation was made on several occasions--400-500 Dorosoma eggs were found in the stomach of one 4.5 inch L. macrochirus.

Dorosoma cepedianum eggs were less densely deposited in the lake. Concentration of eggs is probably a function of the size of spawning groups as much as any other factor. Thus, the dispersion of their eggs may enhance chances for survival.

Substrates were collected on an irregular basis to supplement egg samples. The material on which eggs were found varied. D. cepedianum often used submerged vegetation, such as Cladophora, Eleocharis, inundated Bermuda grass, and a range of exposed plant roots. A variety of

nonliving material was used, such as brush, sticks, rocks, etc. In several areas, deposition directly upon sand was observed.

The main difference in spawning substrate between the two species appeared to be the extensive use of floating objects by D. petenense. Rocky shores with short, filamentous algal mats were often used to the extent that the algae resembled miniature bunches of grapes. The array of floating objects offered an otherwise little used spawning substrate. Floating docks with attached barrels, algae, and boats, as well as buoys and runoff debris, were frequently and often heavily used as spawning substrate by D. petenense. In the boathouse, eggs were often found on the sides of boats above the splash board, up to six to ten inches above the water line, and on the sides of the metal boathouse to an equivalent height. Of course, these eggs soon desiccated but were evidence of the extreme activity which accompanied D. petenense spawning. It was characteristic of D. petenense to deposit eggs very densely at a particular location which reflects their mass spawning behavior. Inundated vegetation, such as Bermuda grass, willows,

salt cedar, and pepperweed (Polygonum) were frequently spawned upon.

Some information concerning areas of spawning or general preferred habitats was obtained with the egg collection program (Appendix D, Tables 8 and 9). The number of samples that could effectively be examined and the low hatch limited the effectiveness of this particular aspect. The number of times each area was sampled was about the same, although on an area comparison small bays, etc., received more sampling per unit area (Appendix D, Table 1).

As discussed in the habitat descriptions, the arm was divided into eight areas and two major bays. Much of the lower west shore and the middle portion of the east shore was underlain by limestone which produced a shore of moderate to steep slopes. This describes areas 2, 3, 4, and 5 with some slight variation. Areas 2, 3, and 5 had mostly moderate slope, whereas area 4 had a very abrupt slope. The lower bay (0), part of the mid-bay (Beaver Bay), and areas 6, 7, and 8 had moderate to low profiles and primarily sand substrate. The samplers were variously located within the areas but often success was determined by the microhabitat.

For example, one spawn in the north bay of area 4 produced over 40,000 eggs on the three samplers. The vegetation of this area was also thickly covered following this spawn. Had the sampler been placed at some adjacent position, this deposition might not have been nearly so large. Thus, the problem of trying to elaborate on the area of spawning was made more difficult by the fact that microhabitats within each area were frequently differentially utilized.

In general, D. cepedianum eggs were more commonly collected in the upper arm (areas 7 and 8), the creek, and embayments. D. petenense, on the other hand, seemed to spawn more frequently and heavily in the lower reaches of the arm and on points of land at the mouth of bays. This is not to say that they did not enter bays and spawn, as the boat harbor was heavily used and the entrance was narrow.

The asterisks on the map (Figure 19) denote areas of very heavy and frequent spawning by D. petenense. These represent a variety of substrate types but generally all are adjacent to fairly unconfined, open water with some amount of moderate slope at or near the edge. Less spawning was indicated in areas predominantly near vertical shores, which are common in area 4. This might be due to a lack of

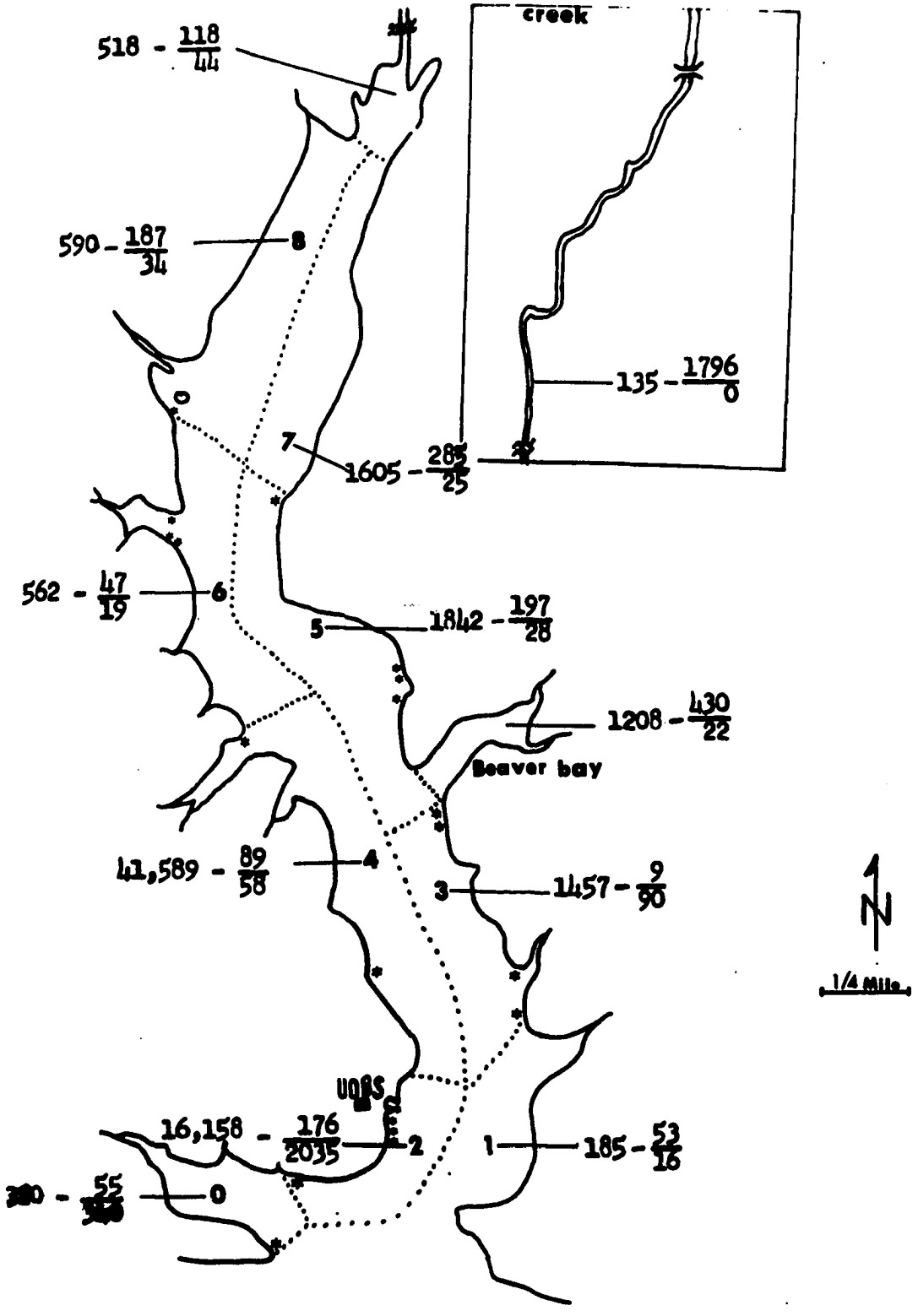


Figure 19. Eggs and larvae collected in areas of Buncombe Creek arm. Numbers represent: eggs collected-eggs and larvae of Dorosoma cepedianum / eggs and larvae of D. petenense. Asterisk indicates areas of frequent D. petenense spawning.

vegetation or other preferred substrate.

Areas 2 and 4 had large total egg counts, and in area 2 the eggs were identified predominantly as D. petenense. D. petenense spawned regularly in this area and spawnings were frequently heavy.

Larvae Sampling

A third means of defining spawning period for Dorosoma was collection of freshly-hatched larvae. A modified meter net was used to sample for yolk-sac larvae during spring and summer. Yolk-sac larvae were evidence of spawning within the previous two to five days, depending upon the species and temperature. Trawling was concentrated along the shoreline, the area of assumed greatest spawning activity. Trawling was accomplished within each area at about 2-week intervals (Appendix E, Table 1).

No yolk-sac larvae were collected in the lake prior to 1 April, but D. cepedianum larvae were collected in upper Buncombe Creek approximately 1.5 miles from the mouth on 27 March 1968 (Appendix E, Table 2). Surface water temperature in the lake was 55° F at the same time that creek water temperature was 62° F. A few larvae were collected indicating

light spawning had occurred probably two to three days previously. Heavy rains and snow around the 20th and 21st increased the creek volume and may have stimulated movement into the creek. Larvae were not collected in the creek when sampled on 20 March.

During the period 1-15 April 1968 no D. petenense or D. cepedianum larvae were collected from the lake, but D. cepedianum larvae were commonly taken in the creek. The fact that D. cepedianum spawning occurred in the lake during this period was indicated by the collection of eggs. This indicates the desirability of more than one criterion for determining fishes' spawning periods.

Dorosoma cepedianum larvae were well represented in the collections taken from 16-30 April 1968 and those of D. petenense were taken for the first time during this period Two trawling series were made during this interval, one on 18 April and the other on 24 April. The 18 April series included only D. cepedianum. The 24 April series included the season's first D. petenense which agreed with the first observed spawning activity on 18 April. Larvae from this spawn would not have appeared until about three to four days

later. Larvae taken during the 24 April series were probably spawned during the period 20-21 April as the egg data from the University of Oklahoma Biological Station boathouse indicated no spawning on the 19th and the larvae from the 18th would have hatched and absorbed most of the yolk by the 24th.

During the period 1-15 May, the majority of larvae collected were D. petenense, although D. cepedianum was still actively spawning as indicated by egg sampling in the arm. From 16-31 May, the numbers of D. cepedianum and D. petenense were low. This interval was one of rising water. Large amounts of floating debris fouled the trawl, and the trash in the samples increased the probability of overlooking yolk-sac larvae.

Dorosoma petenense was frequently collected from 1-15 June, but no D. cepedianum was taken. Trawl collections in the last half of June resulted in no larvae of either species although eggs of D. petenense were collected on egg samplers. Subsequent samples produced no larvae.

Larvae data for 1969 agree in general with those for 1968 even though the former collections were much smaller.

Possibly the trawl was worn, resulting in inefficient collection. Holes were always patched but loosening of the weave in the cod-end may have permitted enough flexibility so that small yolk-sac larvae were forced through the stretched meshes.

The data indicate a spawning period for D. cepedianum, if tributary data are included, from late March until late May, or about seven to nine weeks. D. petenense had an indicated spawning period from late April to late June, a 9 to 10 week period. These data agree with those from egg collections which, as mentioned, give a slightly longer estimated period of spawning than was judged from GSI.

Table 6 summarizes the information from larvae and egg sampling. The spawning period of D. cepedianum was indicated to be late March in the tributaries and early April through May in the lake. The peak was from mid-April until mid-May. The spawning period of D. petenense was from mid-April to late June with the peak between the first and last of May. Thus, the peak periods of spawning for the two species overlapped.

Diurnal spawning period was investigated during both egg and larvae sampling. Observations on actual spawning

Table 6 Combined eggs and larvae of Dorosoma cepedianum and Dorosoma petenense collected during 1968 and 1969.

	1968							
Species	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	16-31 May	1-15 June	16-30 June
D. cepedianum	-	5	581	1775	420	2	0	0
D. petenense	-	0	0	28	395	36	510	47

	1969							
Species	1-15 March	16-31 March	1-15 April	16-30 April	1-15 May	16-31 May	1-15 June	16-30 June
D. cepedianum	0	0	270	20	330	26	0	-
D. petenense	0	0	0	25	109	1561	16	-

indicated that D. cepedianum spawned most actively at night but continued throughout the morning with some spawning in the late afternoon. D. petenense spawned almost exclusively in the early morning hours. This was well exemplified by the 1968 boathouse egg sampling series (Figure 18). A short-term series was attempted on the adjacent shore so that D. cepedianum spawning might be included, and plankton net tows were also taken for larvae (Table 7). Larvae samples were insufficient to establish a distinct pattern for the lake. The egg deposition pattern in this experiment compares with spawning observations of D. cepedianum in tributaries (Table 7). Peak D. cepedianum egg deposition was from 2200-0200 while peak spawning for D. petenense was from 0500-1030. Thus, the peaks of diel spawning did not overlap, although D. cepedianum continued to spawn on into the spawning time of D. petenense. This diel separation may be one of the important factors in maintaining minimal hybridization.

Another factor discussed under egg sampling was the apparent stratification observed in spawning. Spawning of D. petenense appeared to be directed toward the surface and was usually in shallow water, thus concentrating the spawn

Table 7. Comparison of observed spawning time with hatching time in the lake and creek.

Lake - 4-6 May 1970 Temp. 69-74° F

	Boathouse Area Eggs		Plankton Net Larvae	
Time	D.c.	D.p.	D.c.	D.p.
2200-2400	50	0	20	50
2400-0200	170	0	--	--
0200-0500	1	0	4	13
0500-0800	0	350	0	3
0800-1030	0	380	5	71
1030-1900	0	0	11	53
1900-0530	498	0	8	73

Glasses Creek

Temp. 63-69° F

	Spawning Observed	Larvae Drift Net
21-22 April (± 15)	D.c.	D.c.*
0800	active	0
1000	moderate	0
1200	moderate	6
1400	moderately light	31
1600	intermittent	79
1800	none	2,363
2000	started activity	2,371
2200	very active	1,658
2400	very active	2,378
0200	very active > greatest	5,817
0500	very active > greatest	3,966
0700	active	753
0900	active	870
		20,292

D.c. incubation 72° F = 48 hrs. Probable spawn: 2400 on 19th
70° F = 52 hrs. 2000 on 19th

Rain caused river to rise 1700 18 April, falling until 22 April.
* No D. petenense larvae collected nor was spawning observed.

in one strata. D. cepedianum utilized the shallow water also, but seemed to orient more toward the bottom. This may have the effect of stratifying the two species. Therefore, three possible mechanisms have been discussed which could help maintain species integrity: (1) seasonal difference in spawning but with overlap; (2) diel difference in spawning with some overlap; and (3) stratification in spawn with considerable overlap.

A fourth possibility that has been mentioned briefly in connection with egg sampling is the segregation of spawning habitat. One of the most obvious differences in spawning habitat was the tendency for many D. cepedianum to ascend small streams to spawn and the apparent lack of this response in D. petenense. D. petenense do move into streams as they are frequently collected in these and backwater areas and they probably spawn in larger riverine situations. But, I have gathered no evidence to indicate any spawning of D. petenense upstream from the mouth of small tributaries. During 1968, 1,509 D. cepedianum were identified from eggs and larvae taken in Buncombe Creek at least 0.5 miles upstream; in 1969, 287 D. cepedianum were identified from

larvae or eggs. No D. petenense larvae were collected in either year. In the spring of 1970 the lake level was too low to permit upstream movement in Buncombe Creek so samples were taken in Glasses Creek on the Washita arm. The substrate is mainly limestone and sedimentation has not formed at the mouth to prevent upstream migration. D. cepedianum spawning was observed on 21-22 April and larvae samples were taken. Direct observation was efficient as the stream was clear and shallow. Spawning was most active from 2200-0500 (CST) with active spawning continuing until about 0900 (Table 7). Moderate spawning continued until about noon, was intermittent until 1600, then stopped until about 2200. Activity abruptly began about 2000 and increased until 2200.

M. chrysops were spawning heavily and with much the same schedule as D. cepedianum. The larvae hatching pattern closely followed the above mentioned spawning schedule. A 30-minute drift net sample was taken every two hours for a period of 25 hours (Table 7). A large number of larvae were captured between 1800-1500 with the peak around 0200 when 5,817 drifted into the plankton net in the 30-minute sample. The total number of larvae collected was 20,292, all

of which were D. cepedianum. Back calculations placed the most probable spawning time of these larvae between 2200-2400 on 19 April. The creek had risen on 18 April about 1700 and might have stimulated upstream migration of spawning adults.

The area of spawning, which was within a few hundred yards of the creek mouth, was relatively narrow and shallow and had a moderate current. D. petenense were spawning in the lake at this time so had they normally moved up this stream, they would probably have done so during one of these sampling periods.

Area comparison in the lake was slightly more problematical. Yolk-sac larvae were collected in abundance in only a few areas. The Buncombe Creek collection resulted in the largest number of larvae. Areas 7, 8, and 0 were also productive sampling areas (Appendix E, Tables 3 and 4). The number of larvae collected was not always indicative of the spawning activity in any particular area. For example, areas 2, 3, and 5 were sites of frequent spawning, especially by D. petenense; however, fewer larvae were collected than expected. Conversely, D. petenense spawning in area 0 was

less frequently observed than in area 2, but a much larger number of yolk-sac larvae was collected in the former area.

Larval movement reduces the effectiveness of estimating spawning sites from trawling data. Swimming activity of yolk-sac larvae was primarily vertical, but currents would affect horizontal distribution. As an example, area 0 had what appeared to be a disproportionate number of larvae, but the prevailing wind during the spring is southerly and usually quite strong. Larvae which hatched in parts of area 2 could easily be concentrated in area 0 by wave action.

Another problem associated with trawling data as a determinate of spawning areas lies in collection efficiency. Areas where larvae were adequately collected are characterized by smooth, unobstructed substrate. Conversely, in much of the lower arm areas the shoreline and bottom were very irregular. Even though laboratory observations of yolk-sac larvae indicated they concentrated near the surface, an irregular substrate made sampling less effective. In addition, wave action probably alters the inshore larval distribution. Thus, it seems that for yolk-sac larvae, trawling was a very inefficient means of collection.

If eggs and larvae data are combined, a better analysis of spawning habitat can be offered (Figure 19). The upper half of the arm was the most heavily utilized spawning area of D. cepedianum. The large number of D. cepedianum yolk-sac larvae collected in the upper reaches, especially in the creek, was indicative of greater spawning in that area. If the numbers were a result of concentration by wave action, more larvae would have been collected near the mouth of the creek than in the upper reaches. However, the converse was true indicating movement downstream. Bay areas were comparably utilized by D. cepedianum, especially Beaver Bay.

Spawning sites for D. cepedianum were also located within areas 2 and 5. These areas have very little similarity to areas 7 and 8. Overall D. cepedianum seemed to be less specific as to spawning site since some spawning was indicated within all areas.

As previously discussed, only in area 0 were D. petenense larvae collected in large numbers. Very few larvae were collected in other areas. Egg deposition patterns and especially observations of spawning indicated that in the lower reaches of the arm exposed shorelines and points of

land at the mouths of bays were the most frequent sites of spawning. The entrance to the bay in area 6, for example, was the site of heavy D. petenense spawning on at least three separate days. At this location on 20 April 1968, 768 eggs were collected within two hours on two samplers. Tremendous numbers of eggs were regularly spawned along the riprap in area 2 near the University of Oklahoma Biological Station boathouse. Several other areas where D. petenense spawning frequently occurred are marked with an asterisk (Figure 19). Much of the egg data collected on unscheduled collection days are not included in the egg summaries.

If the total numbers of larvae and eggs collected in various areas are combined, some generalizations can be made. If collection data from areas 6, 7, and 8, the creek, and Beaver Bay were combined, and data from areas 1 through 5 were combined, the pattern, as mentioned previously, is again evident (Figure 19). D. cepedianum spawned primarily in the upper end of the arm, areas 6 and above. D. petenense spawned mainly in the lower reaches of the arm (areas 0-5).

These combined data agree with the observed spawning pattern for each species. D. petenense appeared to move in

from open water toward the shoreline. They seemed to follow the bottom contour but not in water which was too shallow. Close proximity to the shoreline was maintained. Small groups broke off, made runs almost perpendicular to the shore, and spawned on appropriate substrate. In an area with a very gradual slope, the aggregation maintained a greater distance from the edge, possibly resulting in less near-shore spawning.

Dorosoma cepedianum seemed to move less within an area although there was some movement toward and into tributaries. In the lower reaches of the arm, they appeared to orient over much the same spawning substrate as did D. petenense. Large, moving aggregations were not formed, at least not at the surface where they could be seen. Observations of spawning behavior suggested that they may congregate offshore, as they did in tributary pools. Small groups would then depart, move somewhat perpendicular to the shoreline, and along the bottom which would be comparable to the run from pool to riffle. Offshore undertow-type currents or the slope of the bottom might form orienting references. All spawning observed in the lake could be placed into this model. There could be large schools moving parallel to shore and away from the

surface. If this were the case, there would probably be much more inshore activity and a greater concentration of eggs in particular locations than was observed. This pattern of inshore movement along the bottom with abrupt turns and a return to deeper water could explain egg deposition on egg samplers and the relatively small amount of surface activity in D. cepedianum spawning. This behavior and the predominance of nocturnal spawning would both contribute to the infrequent references to actual observation of D. cepedianum spawning.

CHAPTER V

SPAWNING BEHAVIOR

Spawning of Dorosoma cepedianum

Description of spawning behavior in gizzard shad has been incomplete and somewhat contradictory. Many workers, concentrating on various other aspects of the life history, have made chance observations of spawning. Warner (1940) reported spawning around midday at 60° F. Bodola (1966) believed spawning occurred mainly after midnight beginning at water temperatures between 66-68° F. Other workers mentioned the occurrence of spawning at various times of the day and within this temperature range. Clupeids of the genus Alosa have also been reported to spawn throughout the diurnal cycle but the greatest activity is reputedly at night. Many species of Alosa are potamodromus, moving upstream to spawn.

In Lake Texoma, D. cepedianum spawning activities were difficult to observe and would have been incomplete if

certain habitats had not been explored. Spawning occurred in the lake proper, but observations there were difficult and a matter of chance. On numerous occasions while observing D. petenense spawn, a small group of D. cepedianum was seen to rush shoreward deposit, and retreat. Usually there was little if any surface agitation. Without observation in tributaries, spawning behavioral information would have been extremely disjunct. Fortuitously, many D. cepedianum ascend streams to spawn. They appear to do so primarily during the early spring when the stream temperature is increasing at a greater rate than the main lake and possibly under the influence of increased runoff from precipitation. Thus, a portion of the population ascends tributaries to spawn well in advance of others in the lake, making possible a more complete description of spawning habits and diurnal cycle. If D. cepedianum were as mobile as D. petenense, perhaps much greater numbers would ascend streams. Extrapolating from these observations, certain assumptions on lake spawning might be made.

This study was conducted primarily in Buncombe Creek arm, but during 1970 when the lake level was less than 610

M.S.L. some work was done in Glasses Creek on the Washita arm. Glasses Creek has a limestone substrate and a fairly continuous flow whereas Buncombe Creek is mainly sandy substrate and sedimentation effectively blocks the mouth at water levels below 610 M.S.L. Clarity and uniform flow of Glasses Creek permitted the best observations of spawning.

Spawning was observed in Buncombe Creek in 1968 on 27-28 March. The lake level was 611 or above during this spring, permitted passage upstream by the fish. There had been no runoff immediately prior to these dates and the water was clear but considerable runoff had occurred the previous week. Afternoon temperatures taken within a 15-minute period illustrated the temperature relationship. Surface water temperature in the lake was 55° F; at the creek mouth it was 58° F; and at the spawning site, 1.5 miles upstream, the surface water temperature was 62.5° F. Air temperature was 75° F. The sky was partially overcast and winds were southerly at 5-10 k.

The area of observation was a riffle-pool situation. The pool was about 20-25 feet long, five feet wide, and three feet deep in the deepest portion. The riffle was sandy

bottom and abruptly sloped into the pool. One bank was shallow and sandy while the other sloped steeply into the water. The steeper slope was stabilized by roots from terrestrial vegetation and patches of Eleocharis sp. The top of this bank was approximately 15 feet above the water which permitted observation with minimal surface glare.

Spawning was reported in mid-morning by C. Taber. My observations began prior to noon and continued until noon of the following day. A plankton net was set as a drift net during the period of observation. Only a few larvae were collected, indicating spawning had probably begun within the previous 48-72 hours.

The spawning aggregation consisted of 40-50 adult fish, eight to 14 inches (TL). Most were congregated in the pool, oriented upstream and maintaining their position in the current over the same general bottom area. The homogeneity of the aggregation varied as small groups of three to five fish occasionally left or entered. Sex ratios of spawning aggregations favored males at about 3-4:1. At the end of the observation period several spawning aggregations were collected. The ratio was 125 males to 34 females and 1

hybrid male (ripe). Two subsequent collections of spawning aggregations produced ratios of 19:7 and 33:7.

Sexual dimorphism does not exist in Dorosoma so females could be identified only by their distended sides or slightly different behavior. A female was usually near the front of the aggregation. She would maintain her position there for a period of time, then either turn slightly and be carried downstream by the current or depart rapidly upstream. In the first instance she usually re-entered the aggregation in the posterior portion. In the second instance she would usually be accompanied by one to three males and would swim rapidly upstream or to the side. Only those fish which left the larger aggregation were actually spawning. The female's rate of departure may have been a cue to the males as she was only accompanied when she abruptly left the aggregation. Males pursued the female slightly below and behind. The rate of swimming rapidly accelerated as the deposition site was approached.

The increased velocity appeared to further stimulate the males as they crowded closer during this phase of spawning. If deposition was in the riffle area or directly on the bottom, the female tilted 20-45 degrees to one side.

Males crowded closest at this time and presumably deposited milt. Deposition on vegetation or other material off the bottom was accomplished by swimming more or less directly toward the substrate and abruptly turning as it was reached. This often resulted in a disturbance of the water surface either by a net upward movement or by the males being crowded between the turning female and the water surface. Following actual spawning, the group returned to the posterior portion of the aggregation.

As mentioned, the abrupt departure movement by the female appeared to have a releasing effect on the males. On several occasions apparent "mis-cues" were observed, i.e., males following fish of other species. This was observed on several occasions with Morone chrysops (12-16 inches TL) and on other occasions with spawning D. petenense. The observations with D. petenense were made only in the lake, and it is possible that the presumed male was actually participating in spawning.

Morone chrysops spawned during the same period and in the same stream as D. cepedianum and thus were often abundant in the same areas. On numerous occasions some D. cepedianum

males would be attracted by a passing M. chrysops. Abrupt movement by the departing M. chrysops appeared to increase the pursuing males' tenacity. D. cepedianum males would usually not return until they had followed a considerable distance.

Eggs were easily detected at the spawning sites, especially on Eleocharis sp. Sticks, roots, and leaves were also frequently utilized substratum. Eggs deposited over sandy bottom were more difficult to locate as the adhesive outer membrane rapidly collected a layer of sand grains. Areas of deposition in sand could often be located, however, by the presence of scattered deciduous shad scales. Dorosoma eggs could be differentiated from Morone eggs even though they are approximately the same size. Shad eggs are very adhesive and regardless of substrate accumulate a layer of debris, while white bass eggs are only slightly adhesive initially and appear clear throughout incubation.

Spawning was extensively observed in Glasses Creek near its mouth on 21-22 April and 6 May 1970. The activity was not too different from that observed in Buncombe Creek. Pools and riffles were large and the current more swift but the depth was roughly the same. Much larger aggregations

collected in the pools which increased the total spawning activity and resulted in concentration of deposited eggs. D. cepedianum and M. chrysops were both spawning upon arrival at 0500 on 21 April. The water temperature was 60° F and the sky was clear to partly cloudy with winds less than 10 k. The creek was up from a rain on the 19th but was clear. The water level in the creek gradually decreased six to ten inches throughout the two days of observation. Intensity of spawning was high and continued so throughout the morning, gradually decreasing until 1330 and essentially ceasing at 1600. The water temperature had increased to 79°F.

Spawning commenced again abruptly at 1950, 45 minutes after sunset and 15 minutes before dark. Spawning also suddenly began on 5 May at 2005 (CST) just 55 minutes after sunset and 10 minutes before dark. Light intensity was less than one foot-candle 20 minutes after sunset (Figure 20). D. cepedianum spawned with increasing intensity until 2000-2100. Activity during darkness was partially judged by audible surface agitation. Activity was very high throughout the night and until one hour post-sunrise at 0630. Activity continued through 1200 and gradually tapered afterwards.

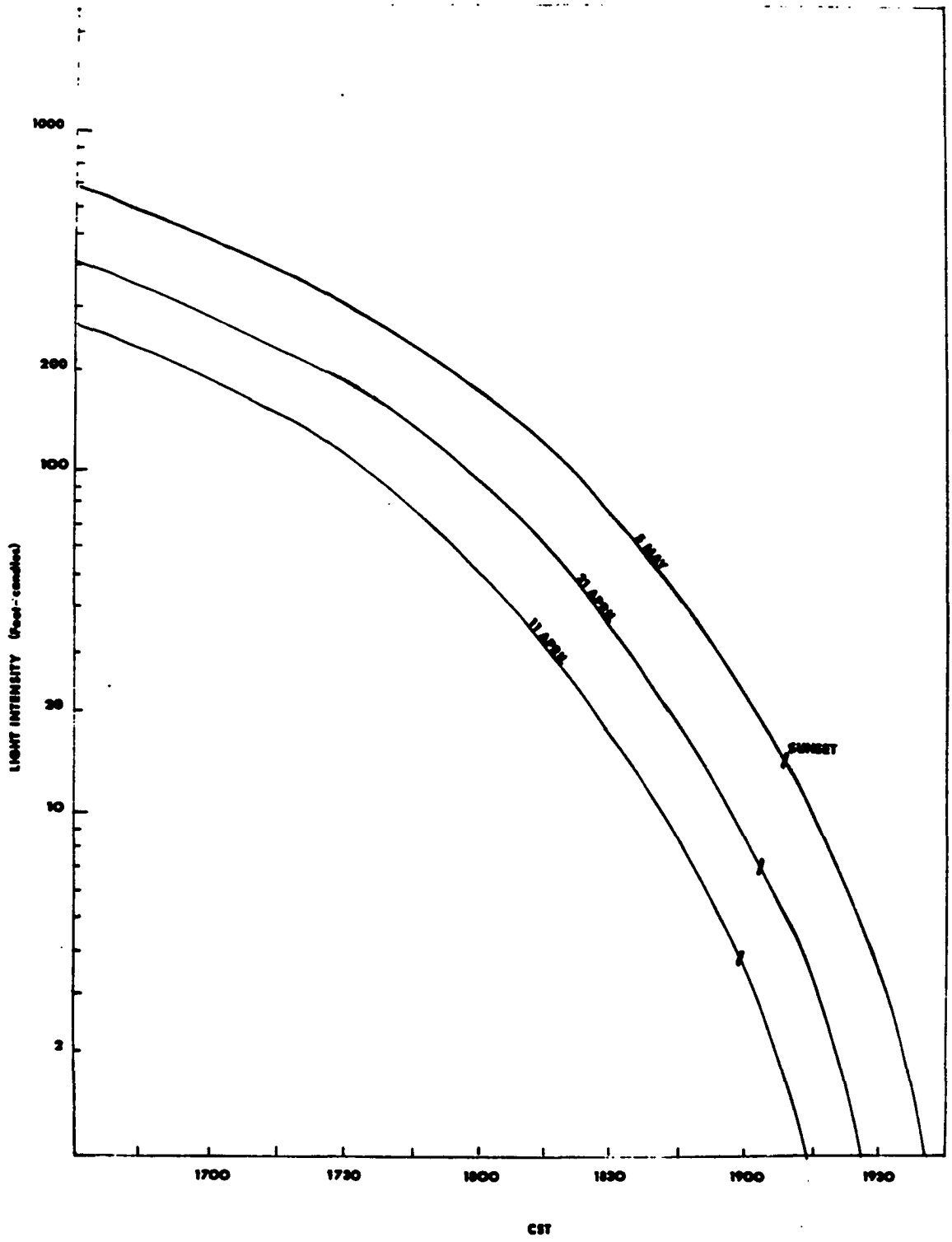


Figure 20. Afternoon light intensity at Lake Texoma on clear days, 1970.

These observations are summarized in Table 7, and peak spawning is closely compared with larval hatching pattern.

A plankton net was anchored in the current and a 30-minute sample was taken each two hours during this period of observation. Peak hatching as indicated by number of larvae captured occurred between 2400 and 0500. Back calculations of the laboratory-determined incubation periods indicated that probable spawning was on 19 April between 2200 and 2400 which agreed with the observed spawning peak of 21 April.

Lab experiments indicated no clear hatching peak associated with light intensity but it seems plausible that larvae hatched at night might be less vulnerable to predation, thus possibly having a higher survival rate. If these larvae are the progeny of night-spawning adults, this, as a selective force, might perpetuate night spawners.

The larger size of this creek apparently gave greater latitude of movement and the spawning group appeared to swim erratically as if searching until an appropriate site was located. The female would then abruptly turn toward it and deposit. During the searching phase, accompanying males

appeared to press against the female, often forcing her caudal fin near the surface. Males were apparently not instrumental in stimulating the female to initiate a spawning run. On a few occasions a single female was observed to abruptly depart the group unaccompanied by males. She continued through the search phase and appeared to deposit although the latter was not confirmed.

Spawning in scattered areas of the lake was fortuitously observed on various occasions. One such time was 3 May 1968 at 0645 (CST) along the riprap near the University of Oklahoma Biological Station boathouse. The riprap is composed of large rocks, one to four feet in diameter, placed along the shoreline, which is exposed to excessive wave action. The sky was clear and there was only a slight breeze. Water temperature was 69° F and D. petenense were actively spawning at the time. Three to four D. cepedianum, 10-12 inches TL, appeared out of the adjacent deeper water and rapidly swam along the bottom toward the shoreline. They abruptly turned just short of the edge and swam directly back to the deeper water. A single splash was audible as they turned and presumably spawned. This sequence of events was repeated three more times at short intervals.

On 21 April 1969 at 0900, D. cepedianum were again observed spawning in the same area adjacent to D. petenense. The lake was lower and a submerged limestone outcrop was visually exposed east of the riprap. The sky was clear, a slight wind blew from the south, and water temperature was 68-69° F. Groups of four to five adults, always less than 10, repeatedly spawned over this outcropping in three to four feet of water. It was exposed to southerly wave action but it could not be definitely established if the fish were orienting into the current. Again, the movement was out of deeper into shallower water, followed by subsequent retreat. In the three to four hours during which they were observed spawning, all activity was on the borrom and no surface disturbances were noted.

Extrapolating from observations in the creeks, it seems plausible that aggregations of adults collect in the deeper offshore water, at least out of sight. As in creek spawning, splinter groups, composed of a female and several males, depart and move along the bottom, spawning on submerged objects. This spawning run may or may not carry them into shallow water where they could be observed or

possibly heard. The returning "undertow" from waves contacting the shore may be an orienting stimulus and may account for the perpendicular movement. The bottom slope toward shallow water might also be used for orientation. If this interpretation is correct, it may partially explain the scarcity of spawning observations on this much studied fish. The fact that maximum intensity of spawning, at least in creeks, was at night would also be a factor. The apparent orientation toward the bottom and the direction of movement might tend to explain egg deposition patterns on egg samplers--28% and 61% respectively, on bottom and shallow sets. Floating samplers collected only about 10% of the total number of eggs.

Spawning of Dorosoma petenense

Spawning descriptions for D. petenense have been offered by various workers. Kimsey, et al. (1957) briefly described the surface activity. Gerdes and McConnell (1963) and Lambou (1965) offered more detail and essentially agreed, except for the mention by Lambou that spawning ceased when the sun fell on the spawning site. May (1969) included some additional observations. The description by Johnson (1969) was

comprehensive and agrees with many observations made in the present study. This study adds to the detail of spawning behavior and associated factors but principally compares D. petenense spawning with that of D. cepedianum.

In contrast to D. cepedianum, spawning of D. petenense was not difficult to see. Anyone in the vicinity of spawning D. petenense will be well aware of the event. There was so much surface activity that the disturbance could be seen even when the water was fairly rough and the sound which resulted from splashing was audible for a considerable distance.

Interpretation of the activity was another matter. Spawning groups swam rapidly and erratically so that it was difficult to follow their movements. They moved into and out of an area in a matter of minutes. On some occasions such tremendous numbers were involved that for hours there was little interruption of activity at a particular site; at other times, only scattered small groups were active. In general, there were movements of extremely large surface schools parallel to the shore and at varying distances from the edge. The enormous amount of inshore activity was

usually so intense that the offshore movement was easily overlooked. The offshore flow was in one direction at any one time, but the large school appeared to be an aggregate of more compact subgroups. Spawning has been observed many times near the University of Oklahoma Biological Station boathouse and the major movements were invariably from the main lake. Usually, the aggregation moved along the west shore toward the upper reaches of the arm. Apparently the schools moved shoreward from open water, then generally followed parallel to the shore. Johnson (1969) reported this behavior for spawning D. petenense in Arizona.

Sub-groups of six to ten fish occasionally departed the main flow and moved shoreward. These small groups usually consisted of one female and several males. As in other clupeids, sexual dimorphism is limited to body proportions--females being generally larger in the spawning aggregations (Figure 21). Males were normally smaller than females although a few males did get fairly large, but proportionally less frequently. Males and females matured by age-group I, 2.4 inches TL or larger, with some reported to have matured by age-group 0. Thus, the general spawning

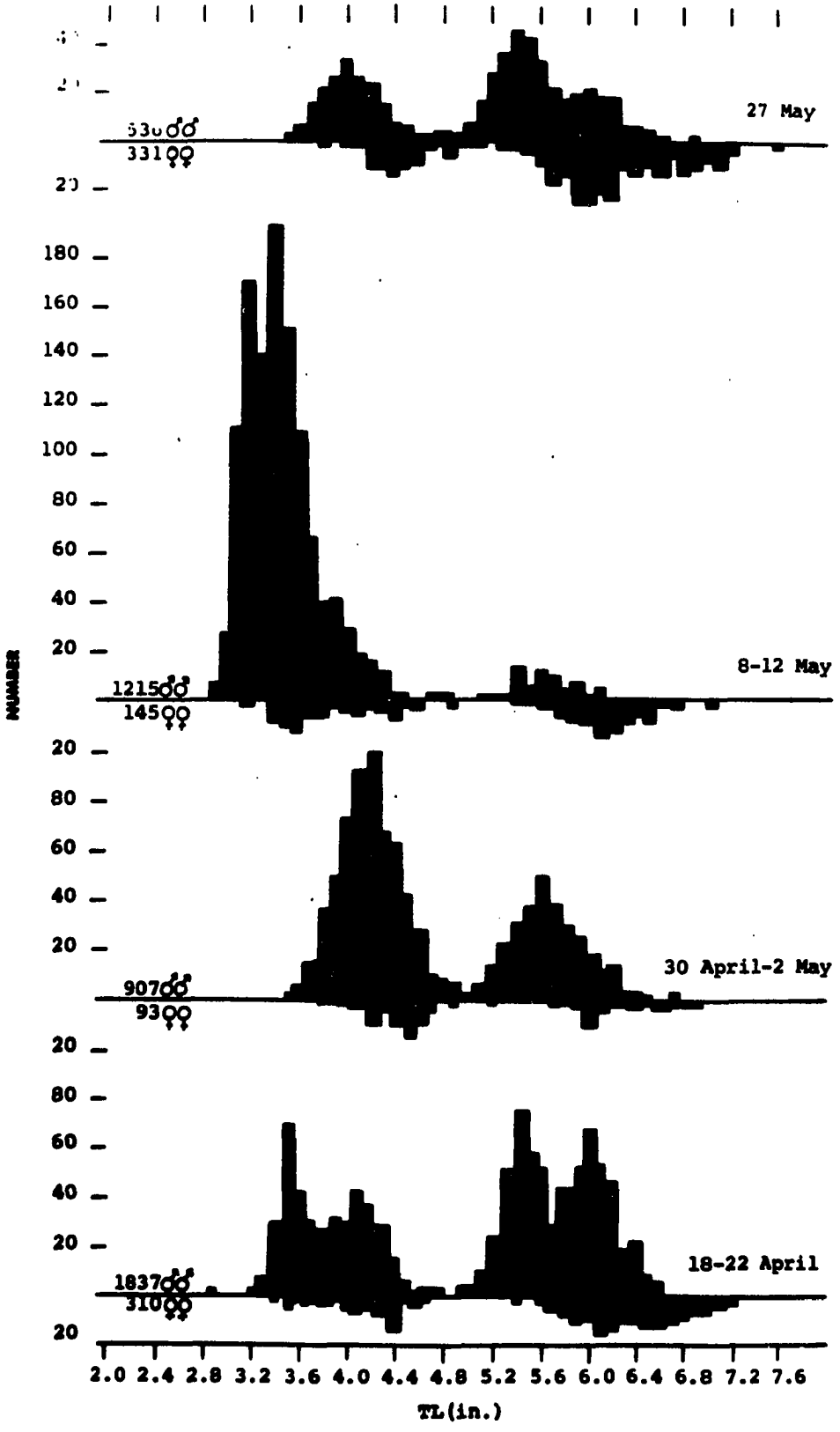


Figure 21. Length-frequencies of D. petenense taken from spawning aggregations, 1968.

group consisted of one relatively larger female and several smaller males. Small groups were often in close proximity to one another but they invariably moved independently.

The sex ratio in these aggregations was very biased in favor of males--normally 3-8:1 but as high as 50:1. The higher ratios were probably not representative of the actual spawning aggregation. After spawning had begun in an area there were usually variable numbers of fish randomly swimming adjacent to shore. Based on their behavior, these were judged to be males since they joined with spawning groups moving shoreward on a spawning run. Thus, a sample taken in shallow water with a seine or shocker could have a great number of males and very few females.

When a female broke away from the main flow of the school and moved rapidly shoreward, males attempted to stay as close as possible to the erratically swimming leader. Females, upon encountering an object, abruptly turned, moved upward, and usually broke the water surface almost horizontally. Subsequently, the groups continued following the shoreline, periodically turning abruptly to spawn when encountering appropriate sites. Spawning groups would proceed

along the shoreline in a loop-like fashion. The tight inshore portion of the loop was the culminating rush at the surface. Return to the main school was often delayed as a group would continue to spawn in the area for some time. This could possibly be a factor in the diminished activity after mid-morning as the main group would be continually depleted when a spawning aggregation did not rejoin immediately.

The momentum and force of pursuing males and the female's terminal acceleration often carried individuals of the spawning group well out of the water and sometimes completely stranded them. Several other workers have reported this phenomenon. Sizeable mortality of stranded individuals was often observed. Following one spawn, 351 dead adult D. petenense that had stranded themselves and succumbed were collected along 300-500 yards of riprap. Berry, et al. (1956) reported D. petenense spawning mortality in Florida but it was apparently due to some other factor.

In the University of Oklahoma Biological Station boat harbor, spawning was frequent and it appeared that on some occasions the major flow of the school had entered the harbor. One such event occurred on 2 May 1968 when spawning

began abruptly at 0600 (CST). The school was at least 20-30 feet wide; the fish overlapped head to tail and were only a few inches apart. This flowing school continued for 15 uninterrupted minutes. Spawning occurred along the edge as female-led groups broke away, spawned, and rejoined the mass. The entire water area adjacent to shore and any nearby submerged or floating objects were agitated as if there were submerged air pumps. There was no spawning for approximately 15 minutes, then the above sequence was repeated. The numbers of fish involved were unbelievable.

Even more remarkable was the density of deposited eggs. Following such a mass spawning, practically any object in or near the water was covered with eggs, often up to an inch deep. Egg samplers had as many as 20,000 eggs on the 6-inch-square surface. Extreme concentration of eggs was partially due to repeated use of suitable objects. A substrate which projected out from the general bottom contour or edge was used time after time by different groups in their turn. The projecting stern and motor of a beached boat were heavily covered with eggs after the above mentioned spawn.

Although movement characterized these mass spawns, individual groups often lingered in a single area for a fairly

extensive period of time. This was more common in the less frenzied spawning of smaller groups which were characteristic of later morning spawns. In these instances, the loop-like pattern was compressed to form a figure eight swimming pattern. The deposition site was at the intersection of the pattern and the typical surfacing occurred here. Each lobe of the pattern was characterized by diving away from the surface, regrouping as they turned toward the spawning object, and again accelerating upward toward the surface. The latter phase culminated in spawning and the horizontal body position at the surface. Thus, two passes would be made during each figure eight pattern interspersed with two regrouping phases. This was also the sequence in groups that moved from object to object in the looping pattern.

The length-frequencies of fish collected from spawning aggregations during 1968 indicated an interesting pattern (Figure 21). These data indicate participation in early spawning activity by all age-groups. The larger size-groups are slightly more numerous than the smaller size-groups in the earliest spawning collections. This was more evident for females even though they were less numerous than males.

Spawning aggregations collected around the last of April and first of May indicated greater participation by the smaller, age-group-I fish of both sexes. This trend was even more apparent in the early portion of May, particularly with respect to males. There also seemed to be a shift to a slightly smaller age-group-I fish. It may be that there was a delay in maturity by some of the smallest yearling fish.

The late-May sample had a more equitable distribution but with greater proportions of older age-groups. Perhaps they have a more rapid recovery rate and are better able to participate in multiple spawnings. One of the most obvious characterizations of spawning aggregations, aside from the sex ratio, was the tendency for females to be larger than the participating males. According to Bryant and Houser (1968) females attain a greater size and live longer than males.

The GSI seemed to indicate a late maturation of the younger fish, and this was the interpretation given by Johnson (1971). But, length-frequency data for spawning groups seem to suggest participation by age-group-I fish

from the very earliest spawning. These yearling fish increased in abundance near the spawning peak and became less of a factor later.

Spawning was observed only once at surface water temperatures lower than 66-67° F. Rawston (1964) reported observing spawning at surface water temperatures of 58° F and 62° F on the same day. The only occasion I had evidence of spawning at a temperature lower than the 66-67° F range was on 28 April 1968 when a short period of spawning occurred at a water temperature of 63° F (Figure 18). This was observed at 1030 (CST) after a period of cool weather. Earlier, a cold front passage had dropped the water temperature and suspended spawning for several days.

Spawning had occurred regularly from 18 to 22 April on mornings when water temperature exceeded 66° F. On 23 April the cold front reduced the water temperature to the low 60's. Until 30 April water temperature exceeded 66° F only once before noon. On 26 April the water temperature reached 67° F at 1000 and spawning was observed from 1045 until 1100. On the 30th, spawning was observed when the water temperature reached 66° F. Thereafter, spawning occurred regularly.

As the season progressed and the minimal temperature was reached earlier in the morning, active spawning was soon almost confined to the hour or two following sunrise. Egg samplers and gill nets which were periodically checked yielded no information to indicate spawning activity other than at observed times. A specially constructed small mesh experimental net (3/8-, 1/2-, and 3/4-inch mesh by 50 feet) was frequently suspended from the boathouse to collect spawning D. petenense. The catch pattern as presented in Table 8 was typical and indicates the diel pattern of spawning. The same sequence can be seen in the egg deposition pattern for May 1960 (Table 7).

The diel pattern for D. petenense spawning was much more compressed than that for D. cepedianum. Spawning at night was not observed nor did any data collected indicate such. Only rarely was spawning observed in the late afternoon and this was very early in the season. One such occasion was on 21 April 1969 when the activity continued all afternoon. This was probably the first spawn of the season as afternoon spawning was observed very infrequently.

The apparent strict morning spawning schedule would suggest a close relationship with light intensity. However,

Table 8. *Dorosoma petenense* netted at the University of Oklahoma Biological Station boathouse on 5 and 6 May 1968.

Time (CST)	Number Captured
2400-0530	5
0530-0700	1890
0700-0930	300
0930-1800	5
1800-2300	3
2300-0400	0
0400-0530	6
0530-0700	46
0700-1400	5
1400-2100	3
2100-2400	6

this may be true only in so far as the day-night cycles have an influence on the circadian rhythm. Light intensity readings at various observed spawnings resulted in no particular pattern. Spawning was observed to begin actively on 22 April 1969 at 0900 when the water temperature reached 66° F. The weather was clear and calm. On 22 April 1967, heavy spawning began at 0700 (68° F), a calm day with fog-restricted visibility of less than one-half mile. Activity was also observed during heavy rain showers with gusty winds and overcast sky on 22 April 1968 at 0645 (67° F). Actual level of light intensity seemed less important than the time of morning. Times of spawning did not vary appreciably from one climatological condition to the other as might be expected if a certain light level was a triggering mechanism. The delay in morning spawning in 1969 was apparently due to the temperature.

To illustrate this point further, spawning was recorded between 5 and 8 May for five consecutive years, plus one disjunct year. The time of day spawning was nearly the same despite different climatological conditions and, thus, light intensity. Table 9 briefly compares these years.

Table 9. Comparison of Dorosoma petenense spawning for comparable dates over a 6-year period.

Date	Earliest Daily Spawn*	Water Temperature	Climatological Conditions
8 May 1963	0600	73° F	Clear, wind 5-15 k
5 May 1967	0830	67° F	Overcast, rain showers
5 May 1968	0615	67° F	Clear, calm
6 May 1969	0630	70° F	Overcast, calm
5 May 1970	0625	69° F	Clear, calm
8 May 1971	0630	67° F	Clear, calm

*CST

In general, spawning was most active about 15 to 30 minutes after sunrise. Exceptions mentioned above, such as 5 May 1967 and 22 April 1969, were probably retarded because of low temperatures. Light intensity for 5-8 May from 0600 to 0630 on a clear day would have been between 300 and 900 foot-candles. For 22 April 1969 from 0645 to 0700 light intensity would have been about 300-500 foot-candles. The light intensity would certainly not be comparable on 5 May 1968 and 6 May 1969. The former day was clear; the latter was fogbound. Spawning occurred at approximately the same time on both dates. Comparative light intensity readings were taken on a clear day and a day with a thin overcast (Figure 22). A thin overcast reduced the light intensity at comparable times, thus a heavy fog would reduce the intensity proportionately more.

Factors affecting the actual value of light intensity which reached a fish's eye would be dependent upon variables that affect light penetration. Some sub-surface readings were taken along with one series of surface intensity readings. The percentage of light which penetrated the water surface varied with the changing angle of solar rays.

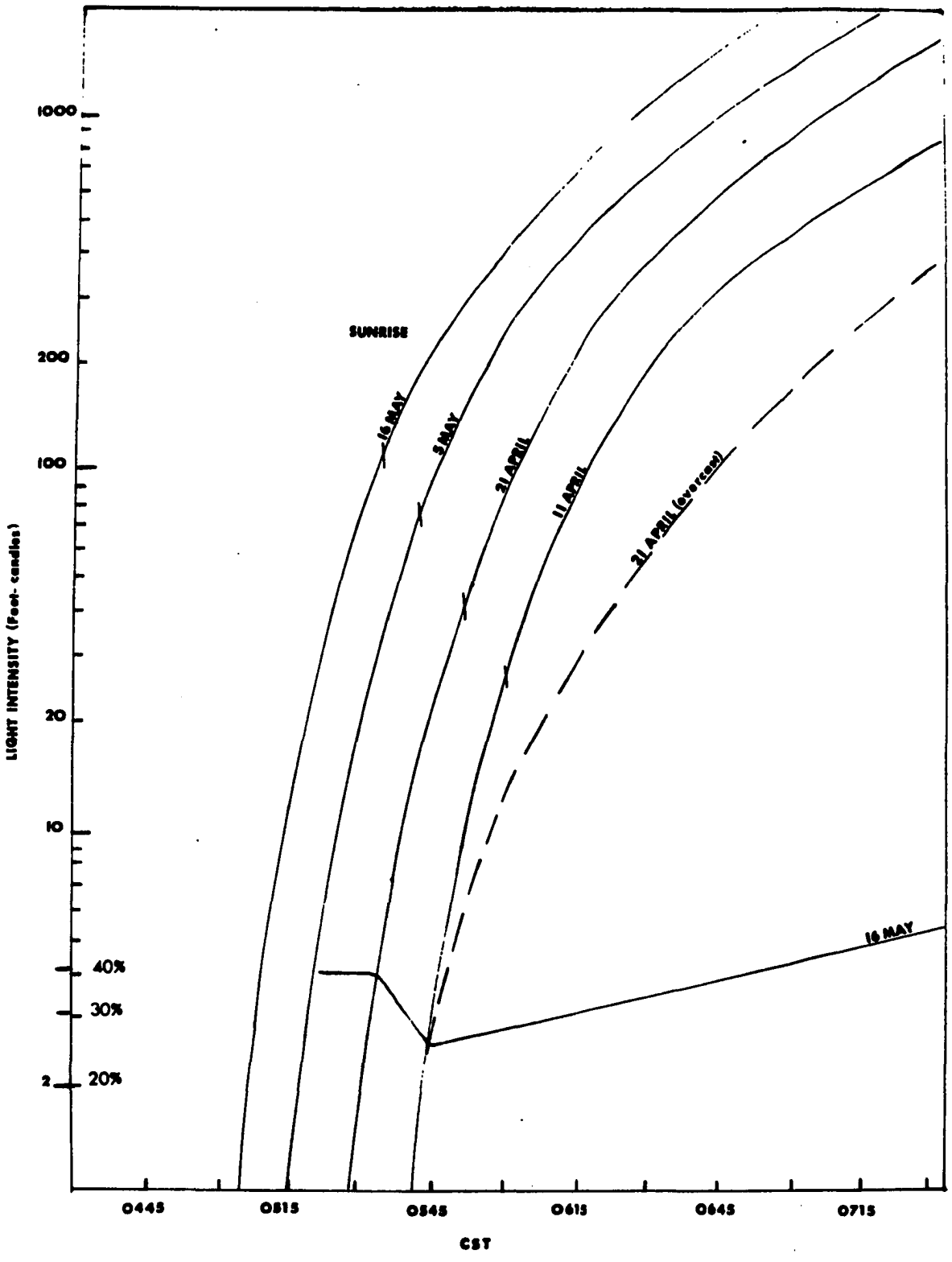


Figure 22. Morning light intensity at Lake Texoma on clear days, 1970, and percent of incoming light that penetrated the water surface.

Lambou (1965) reported that D. petenense almost ceased spawning after sunrise. Observations in Lake Texoma indicated that most active and regular spawns occurred just after sunrise and continued actively for an hour or two after which spawning usually was scattered and intermittent until near noon. Early in the season spawning was active only in the later morning hours after the apparent minimum temperature had been reached. There were occasional scattered spawnings in the afternoon but these were not the rule. Rawston (1964) observed afternoon spawning on 23 April. The only time I observed active spawning in the afternoon was 22 April 1969; this appeared to be the first spawn of the season. Spawning commenced at 0900 (66° F) and continued until 1800. It seems possible that some initial spawning might be considered somewhat atypical in that this pattern was not observed during any other spawning years.

Spawning correlation with precipitation can only be suggested. It may not be a necessary stimulus, but observations indicated it often increased the pitch of spawning Some of the heaviest spawns observed during 1968 were during heavy rains and frequently correlated with precipitation

data (Figure 18). The temperature of runoff water was usually a few degrees cooler than surface water temperature. Either the temperature differences or the inflowing current could have been the stimulus. Very active spawning was frequently seen during rain storms at points where runoff carried large quantities of debris into the water. Other workers have noted active spawning on rafts of floating debris, and May (1969) suggested that there seemed to be a correlation between rising reservoir water levels and intensive spawning.

Strong, gusty winds are typical to thunderstorms in the Midwest. Spawning did not appear to be impaired by the resulting wave action. In fact, the area of the most regular and active spawning was on riprap near the Biological Station. This was constructed to protect the shoreline which was fully exposed to prevailing southerly winds. During the spring, this part of the lake is frequently exposed to winds 15-30 k which may produce waves four to five feet high. The frequency of spawning under such conditions was not recorded but D. petenense were observed spawning on this wave-swept shoreline when it was virtually impossible to negotiate a

boat inshore. Thus, although spawning observation was enhanced by calm water and the fish and their eggs were certainly less likely to be stranded, heavy wave action did not prevent spawning in Lake Texoma. However, Johnson (1969) reported spawning suspension during wave action in Arizona.

Spawning appeared to occur primarily in the lake. D. cepedianum were observed spawning numerous times in the tributaries but no D. petenense were seen to spawn above creek mouths. In addition, neither D. petenense eggs nor larvae were identified out of a total of over 22,000 collected from Buncombe Creek during 1968 and 1969 and from Glasses Creek during 1970 (Appendix D, Table 5).

Spawning orientation appeared to be toward the surface even though submerged objects were heavily utilized. Usually these objects were in shallow water, six to twelve inches deep. This effectively concentrated eggs along the margins where they might be exposed during water level drops. During May of 1968 and 1969, heavy rains rapidly raised the lake level and drawdowns were necessary to prevent flooding. The lake level declined four to six inches vertically every day. This exposed 15-20 feet of shore (horizontally)

depending upon the slope. Thus, most of the eggs spawned during that period were exposed.

Much spawning was also directed at objects floating at the surface, such as runoff debris, logs, etc. These eggs would not be exposed by water fluctuations. The use of floating objects, such as marker buoys, was observed at considerable distances from shore and in water 30-50 feet deep. Apparent surface activity was occasionally observed away from floating objects--in some cases, shadows on the water might have appeared as floating objects to a sub-surface eye. Egg samplers placed in the boathouse stalls from April through June 1968 received regular and occasionally heavy egg deposition; 63,446 eggs were collected--4,344 were identified as D. petenense, none as D. cepedianum. In effect, the boathouse, including the Cladophora-laden barrels, boats, and objects projecting into the water, was heavily utilized by D. petenense as spawning substrate. It was not unusual to find eggs six to twelve inches above the water surface on both sides of boats. The boathouse was sheltered and was exposed to little, if any, wave action which might have washed the eggs to these heights.

The spawning pattern observed in deeper water, such as at the boathouse, was like that described for shallow spawns, i.e., typically figure eight or looping erratically from object to object. Depth of water was not restrictive, however, and in the ascending phase prior to deposition the female would often appear to have risen from several feet to suddenly appear near the surface. Deposition would be followed by a diving arc of one to two feet in diameter and to a depth of six to twelve inches.

Pursuit of other species by male D. cepedianum during spawning was previously discussed, and M. chrysops was the species most frequently pursued. As mentioned, the acceleration or erratic swimming of the fish appeared to be particularly stimulating to the males. May (1969) speculated that erratic swimming by female D. petenense was a possible factor in sex recognition. Johnson (1969) also discussed this and mentioned that D. petenense males followed Lepomis macrochirus when they swam rapidly and erratically away.

In Lake Texoma, D. petenense was observed to pursue spawning Menidia audens. The spawning pattern of M. audens was very comparable to that of D. petenense. Males often congregated in extremely shallow water and pursued a female

when she moved into the area. Her movement was rapid, erratic, and darting as described for D. petenense females, and to a lesser extent for D. cepedianum females. On numerous occasions male D. petenense and M. audens were observed milling about in shallow water only to actively pursue a female Menidia when she entered the area. The following of other species by D. cepedianum and D. petenense involved aligning with fishes more compatible to their respective sizes.

Even though D. petenense have tremendous reproductive potential, it appeared that several factors may work to prevent overpopulation. Densely massed eggs in heavy spawns probably have reduced hatch success, and spawning in shallow water may result in tremendous egg mortalities. Thus, although the D. petenense population has increased enormously since first observed in 1957, D. cepedianum appears to have withstood the initial population explosion and the two species will probably continue to coexist. Differences noted in spawning season, diurnal pattern, and habitat separation--including stratified and horizontal separation--might be sufficient to perpetuate coexistence.

Hybridization

It appears that several possible mechanisms might be instrumental in Lake Texoma to reproductively isolate D. petenense and D. cepedianum (Table 10). Mayr (1966) discussed isolating mechanisms and various degrees of breakdown. There are many locations where D. cepedianum has existed in the absence of D. petenense, but some of these have recently been invaded. Lake Texoma is such an example and thus sympatry of the species is relatively new to the lake.

Spatial difference in spawning was suggested in two modes, one being habitat preference. D. petenense seemed to spawn less in backwater areas and not at all upstream in small tributaries. There appeared to be a stratified spatial difference in spawning in areas where they overlapped. D. petenense appeared to spawn heaviest in very shallow water and at the surface whereas D. cepedianum oriented more to the bottom and in somewhat deeper water. But, again there was an overlap.

The temporal aspect of segregation was evident seasonally as D. cepedianum spawned earlier, but the peaks of

Table 10. Comparison summary of Dorosoma cepedianum and Dorosoma petenense spawning.

	D. cepedianum	D. petenense
Temperature:	>60°-62° F	>66°-67° F
Seasonal:	Late March to mid-May (ca. 6-8 wks.)	Mid-April to mid-June (some in July) (ca. 8-11 weeks)
Diel:	Entire 24 hrs. (max. - 2000-0800)	Post-dawn - 1200 (max.- 0600-0900)
Sites:		
Lake	Variety of substrate Edge to deeper water. Bottom oriented.	Variety of substrate Shallow water and on floating objects.
Tributary	Ascends and congregates in pools. Spawns in riffles.	Mouth only.
Sex Ratios:	2-4 males:1 female	5-15 males:1 female
Habits:	Smaller aggregations. Probably little parallel movement. Inshore movement along bottom. Abruptly turning in shallow water. Little surface agitation except in tributaries.	Large aggregations moving parallel to shore near surface. Shoreward movement in smaller groups Much surface agitation.

Table 10 (cont'd.)

	D. cepedianum	D. petenense
Maximum Spawn Density: (Lake)	1800 eggs per sq. ft. or less	>96,000 eggs per sq. ft. Often completely covering submerged objects to thickness of nearly 1 inch.
Tributary	Higher concentration. May approach D. petenense density.	None
Miscues:	Males observed following M. chrysops and D. petenense	Males observed following spawning M. audens.

both species overlapped. Also, there was a separation in diurnal spawning as D. cepedianum tended to be most active at night although their activity tapered into the peak spawning period of D. petenense.

Behavioral separation was evident from the differences in spawning so far described but the basic mechanistic stimuli of the spawning act seemed very similar and potentially capable of breakdown. This is perhaps exemplified by the miscues between male Dorosoma and other genera of fishes. If these mechanisms should break down, and in the case of D. petenense and D. cepedianum they do, maintenance of distinct species may be perpetuated by incompatible gametes, embryonic death, or sterility to low fertility in offspring.

Hybridization between D. cepedianum and D. petenense was first reported by Minckley and Krumholz (1960). They cited as the probable cause the lesser abundant D. petenense joining spawning groups of D. cepedianum. The D. petenense population in Lake Texoma is far from small and hybridization has occurred to the present from its first report by C. D. Riggs and G. A. Moore in 1960 (personal communication). During 1968 and 1969, 36 identifiable hybrids were collected

from a total of 2,072 recorded Dorosoma. This is an average of 1.7% hybrids for these two years. Nine were males, seventeen were females, and ten were immature. Thus, there appears to be no asymmetry in sex ratios.

It seems that there are at least two possible means by which hybrids have been produced in Lake Texoma, and possibly both occur. The first is chance or accidental union of eggs and sperm because of overlap in spawning areas and time. This is not unlikely as both species have been observed spawning simultaneously at the same site. The second possibility is that of one of the species actually spawning with the other. D. petenense was never observed participating in spawning activities of D. cepedianum but the lack of D. petenense spawning in creeks and the scarcity of observation in the lake make this contention superficial. On the other hand, small D. cepedianum were observed actively participating in spawning with D. petenense and on 22 April 1968 a ripe male D. cepedianum was collected among spawning D. petenense. It is suggested that this is the likely natural cross. A small D. cepedianum male is more comparable in size to D. petenense females than any

size D. petenense male is even to the smaller, mature D. cepedianum females. In addition, the data discussed under egg collection make it seem more likely for a male D. cepedianum to be in an area of spawning D. petenense females than vice versa. As an additional bit of evidence, this cross was the only one to have been successful in the laboratory.

Hybrid offspring are apparently fertile but the level of fertility has not been investigated. Most of the natural hybrids collected were mature males or females and were frequently classed as ripe. A hybrid male was collected among a spawning aggregation of D. cepedianum on 28 March 1968. Viable larvae were produced from a back-cross of a male D. petenense and a hybrid female, thus indicating at least some fertility. Hybrids have been produced artificially by crosses between D. cepedianum males and D. petenense females. These crosses have produced 450 viable yolk-sac larvae. The reciprocal cross, however, has repeatedly failed; the eggs rarely developed beyond gastrulation.

CHAPTER VI

SUMMARY

1. Dorosoma cepedianum and D. petenense have been sympatric in Lake Texoma at least since 1957; prior to the appearance of D. petenense, D. cepedianum had been the most abundant fish. In the subsequent years, D. petenense has superseded D. cepedianum in abundance.

2. The embryogeny of D. petenense at 74° F generally followed previous descriptions of fish development. The egg included a chorion and vitelline membrane; the chorion (degenerate follicular epithelium) remained adhesive throughout larval development. Sperm penetrated through a micropyle which was located in the outer membrane. At fertilization a perivitelline space formed beneath the vitelline membrane. Cleavage and organogenesis proceeded through stages as described by Oppenheimer (1937), except in the pre-hatching stages. D. petenense hatched relatively prematurely, i.e.,

lacking a complete digestive system, swim bladder, and incompletely formed branchial arches. Well developed, pigmented eyes and pectoral fin buds were present.

3. Embryogeny of D. cepedianum was studied at 74° F and was comparable to that of D. petenense until the latter portion of the developmental period. The egg and fertilization were not different; cleavage and organogenesis differed in that D. cepedianum proceeded at a more rapid rate. Hatching was at an even more abbreviated condition than that of D. petenense. Eyes of D. cepedianum were poorly developed; they lacked pigment and still retained a choroid fissure. No pectoral fin development was evident.

4. Embryogeny of laboratory-reared hybrids was intermediate between the parental types. Viable larvae hatched and were generally intermediate in development between D. petenense and D. cepedianum larvae.

5. Developmental period for each species was determined over a range of temperatures. D. cepedianum hatched in less time than D. petenense at any particular temperature. Developmental period for D. petenense was roughly double that for D. cepedianum. The more premature hatching

of D. cepedianum partially accounted for the differences. The hatching period of both species was very protracted and was occasionally equal to 50% of the total developmental period. Effect of light on hatching was not definitely determined, although it seemed there might be a tendency to hatch during darkness.

6. Development of the larvae of both species was comparable. No difference in growth was found during the larval stages. Pigment developed in the eyes of D. cepedianum 24-36 hours post-hatching at 74° F. In both, the mouth was developing. General pigmentation for D. cepedianum was also delayed when compared to D. petenense, but after five days of development both were equally pigmented. Fins were developed in the following order: caudal, dorsal, pelvics, and anal. The pectorals developed definitively near the end even though the bud was present shortly after hatching. Transformation from the larval form was begun after two to three weeks of growth. Scales and swim bladder were developed and the body shape gradually changed until the juvenile form was attained at about 25 mm SL.

7. Several approaches were used to compare spawning.

The gonadal somatic index (GSI) was used as an indication of spawning season. D. cepedianum was found to mature at sizes larger than 8.2-9.0 inches TL. D. petenense matured at sizes in excess of 2.4 inches TL. The GSI for mature D. cepedianum began to increase in early March, reached a maximum during early to late April, and subsequently declined. The average GSI during the peak was eight to ten percent with the maximum ranging from 16-18%. The GSI for D. petenense gradually increased during March to a peak in mid-April to mid-May and declined thereafter. The average D. petenense GSI during the peak was 16-20% with a maximum of 26%. This sequential description of the GSI indicated an overlap during the peak gonadal development and probably indicated spawning periods. The gonadal development appeared to be under the influence of photoperiod and temperature. The estimated spawning periods from these data were late March to mid-May for D. cepedianum and mid-April to late June for D. petenense.

8. Collection of naturally spawned eggs yielded information on the spawning period, diurnal cycle, and spatial relation of the two species. Identification required incubation to hatching. D. cepedianum eggs were first

collected in tributaries as early as mid-March. Shortly afterward lake spawning was indicated by egg collections. D. petenense eggs were first collected in mid-April and only in the lake. D. cepedianum eggs were collected until late May, while D. petenense eggs were taken throughout June. These data indicate the same spawning period as judged from gonadal data, except for a slightly longer D. petenense spawning period.

9. Egg deposition patterns indicated a spatial difference between the two species. D. cepedianum spawned in small tributaries; D. petenense apparently never spawned above the mouth of small creeks. D. cepedianum eggs were more abundant in the upper arm, those of D. petenense in the lower reaches of the arm. D. petenense eggs were more concentrated near the shore and on floating objects whereas D. cepedianum eggs were more frequently collected on the bottom, either deep or shallow. D. petenense deposited eggs at a much greater density than D. cepedianum which probably resulted from the mass spawning behavior of the former. Substrate was comparable except for the difference in utilization of floating objects by D. petenense.

10. A difference was noted in the diel egg deposition pattern. D. petenense spawned almost exclusively between sunrise and noon while D. cepedianum spawned primarily around midnight but were active at other hours except late afternoon. Egg deposition for D. petenense was usually recorded at water temperatures above 66° F; D. cepedianum egg deposition occurred at water temperatures above 60° F.

11. Collection of yolk-sac larvae indicated a spawning season from late March to late May for D. cepedianum and from late April through mid-June for D. petenense. No D. petenense larvae were collected in the tributaries while D. cepedianum larvae were most commonly collected there. A diurnal hatching pattern was determined adequately only for D. cepedianum. The maximum hatch was during the night and coincided with maximum observed spawning activity. Trawling was the least effective method for determination of spawning. This may have been related to the swimming behavior of yolk-sac larvae.

12. Spawning behavior of D. cepedianum was described primarily from observations made in tributaries. Spawning began when the water temperature exceeded 60° F. Spawning

commenced first in the tributaries which warmed more rapidly than the lake. Runoff precipitation was possibly an additional stimulus to ascend streams. Aggregations of large numbers of males and fewer females congregated in pools. Periodic spawning runs were initiated by a female; several males accompanied her when she departed the main group. A run culminated in an abrupt turn, egg deposition, and fertilization. The rate of departure by the female appeared to have a releasing effect on the males as females that departed slowly were not followed. In addition, male D. cepedianum apparently were miscued by abrupt movements. of other fishes in the area. Both Morone chrysops and D. petenense were pursued at various times by spawning D. cepedianum males.

13. Dorosoma cepedianum spawning activities extended over most of the diurnal period but maximum spawning was during the night. The least amount of activity was observed in the late afternoon and early evening prior to dark. Spawning in the lake was observed only a few times but the pattern was like that described for stream spawning, except offshore currents or bottom slope were possibly orienting stimuli. Bottom orientation with minimal surface disturbance

was characteristic.

14. Dorosoma petenense spawning was observed extensively over several years. All was in the lake; no spawning was observed or indicated in small tributaries. Spawning was very active and usually included thousands of individuals. Mass movement was parallel to the shore but smaller groups of eight to ten fish left the main flow to move perpendicular to the shore. The normal ratio of males to females in spawning aggregations was 3-8:1. A small group consisted of one female and several males moving erratically along the shore and spawning on substrate that they encountered. D. petenense males were observed to pursue spawning Menidia audens females. Most D. petenense spawning activity appeared to be directed toward surface objects or objects on the bottom in very shallow water. The tremendous number of fish involved resulted in very thick egg deposition on substrate that extended from the general bottom contour or floated at the surface.

15. Dorosoma petenense spawning activity was concentrated in the early morning hours, primarily one to two hours following sunrise. Activity then tapered until midday.

Afternoon spawning was observed very few times and no night spawning was indicated. The early morning spawning schedule was representative of the peak spawning period. Earlier in the season, spawning did not occur until the water temperature exceeded 66° F during the morning hours. Precipitation runoff was possibly an additional stimulus as some of the most active spawning was observed during heavy rain storms. Exposure of concentrated eggs in very shallow water was considered as a plausible mortality factor.

16. Isolating mechanisms, other than geographical, have been indicated. These might be instrumental in maintaining species identity. Temporal differences in spawning were demonstrated by two modes, seasonal and diurnal. Spatial separation was suggested horizontally and vertically. Behavioral separation was reflected in the modes just discussed but there was very little difference in the spawning behavior which could insulate the two species, unless size was a factor.

17. Natural hybridization has occurred in Lake Texoma since at least 1960; during the years of this study a level of two percent hybridization was not exceeded. Hybrids

were produced in the laboratory only by crosses between D. cepedianum males and D. petenense females. Most of the adult hybrids had well developed gonads and there appeared to be no unusual sex ratio imbalance. Viability of hybrid gametes was indicated by a back-cross that produced viable larvae.

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APPENDIX A

Table 1. Hatching rate for *D. petenense* at 65° F, 71° F, and 80° F.

A.T. = 63-67 F W.T. = 64-66 F Dark Period = 11 hrs.			A.T. = 70-75 F W.T. = 71-72 F Dark Period = 10 hrs.			A.T. = 78-83 F W.T. = 79-81 F Dark Period = 10 hrs.		
	65° F			71.5° F			80° F	
Hrs. post-fert.	larvae	Cumul. %	Hrs. post-fert.	larvae	Cumul. %	Hrs. post-fert.	larvae	Cumul. %
102	0	0.0	55.5	5	2.7	31.0	0	
117	3	1.3	61.5	24	15.8	[36.0]	12	7.9
122	3	2.6	[70.5]	8	20.2	[38.0]	0	
127	1	3.1	76.5	28	35.5	45.0	6	11.1
[131]	0	--	79.5	6	38.8	47.0	128	90.6
140	6	5.7	[96.5]	112	100.0	50.0	7	95.0
[154]	150	72.1	101.0	0		55.0	0	
[162]	47	92.9				57.5	0	
165	16	100.0				[61.5]	7	99.4
						69.0	1	100.0
						74.0	0	
	226			183			161	
Developmental period = 149.5 50% hatch interval = 140-154 hrs.			Development period = 83 hrs. 50% hatch interval = 79.5-96.5 hrs.			Development period = 46 hrs. 50% hatch interval = 45-47 hrs.		

[ ] Indicates dark

APPENDIX A

Table 2. Comparison of hatching rate for *D. petenense* at 70° F exposed to diurnal light cycle and under constant darkness.

A.T. = 68-72 F
W.T. = 69-71 F
Dark Period = 10 hrs.

Hrs. post-fert.	Constant Dark				Dark-Light Period							
	Larvae		Σ	Cumul. %	Larvae				Σ	Cumul. %	ΣΣ	Overall cumul. %
69	0	0	0		10	12	0	7	29	8.6	29	5.9
71	0	0	0		0	0	0	0	0		0	
73	0	0	0		2	1	0	0	3	9.5	3	6.3
75	0	0	0		3	0	2	0	5	10.9	5	7.3
80	1	1	2	1.3	4	1	0	0	5	12.5	7	8.7
[84]	0	0	0		32	0	0	0	32	21.9	32	15.3
94	0	5	5	4.6	2	0	0	1	3	22.9	8	16.9
96	0	7	7	9.2	0	0	0	0	0		7	18.3
100	0	6	6	13.3	0	0	0	0	0		6	19.6
104	1	6	7	19.3	9	3	0	0	11	26.4	18	23.2
[108]	0	5	5	21.1	27	29	0	0	56	43.0	61	35.6
118	4	42	46	51.9	0	24	45	0	69	63.5	115	59.1
123	3	0	3	53.3	11	68	3	0	82	87.8	85	76.4
126	0	0	0		15	3	2	0	20	93.8	20	80.0
128	3	41	44	82.0	0	0	0	0	0		44	89.4
[132]	4	18	22	96.8	13	4	0	0	17	95.3	39	97.4
[140]	0	0	0		4	2	0	0	6	100.0	6	98.6
141	0	7	7	100.0	0	0	0	0	0		7	100.0
			152						338			

Development period = 113.5 hrs.
50% hatch interval = 104-123 hrs.

APPENDIX A

Table 3. Comparison of hatching rate for D. petenense at 75° F exposed to diurnal light cycle and under constant darkness.

A.T. = 73-77 F
W.T. = 74.5-75.5 F
Dark Period = 9 hrs.

	Constant Dark				Dark-Light Period							
Hrs. post-fert.	Larvae		Σ	Cumul. %	Larvae			Σ		Cumul. %	ΣΣ	Overall cumul. %
48	0	0	0	0.0	0	0	0	0	0	0.0	0	0.0
50	4	170	174	10.5	47	1	9	7	64	6.4	238	9.0
53	31	233	264	26.5	57	0	8	17	82	14.6	346	22.0
56	29	205	234	40.6	3	0	2	5	10	15.6	244	31.2
59	23	320	343	61.4	6	0	2	3	11	16.6	354	44.6
[65	22	509	531	93.5	221	8	104	444	777	94.1	1308	93.9
[73	26	44	70	97.7	2	0	2	51	55	99.6	125	98.6
79	30	2	32	100.0	3	0	0	1	4	100.0	36	100.0
85	0	0	0		0	0	0	0	0		0	
			1648						1003		2651	

Development period = 59.5 hrs.
50% hatch interval = 59-65 hrs.
(Dark 56-65)

APPENDIX A

Table 4. Comparison of hatching rate for D. cepedianum at 60° F exposed to diurnal light cycle and under constant darkness.

A.T. = 58-62 F
W.T. = 60-61 F
Dark Period = 12 hrs.

	Constant Dark					Dark-Light Period						
Hrs. post-fert.	Larvae			Σ	Cumul. %	Larvae			Σ	Cumul. %	ΣΣ	Overall Cumul. %
71	0	0	0	0	0.0	0	0	0	0	0.0	0	0.0
78	0	6	0	6	0.2	0	0	0	0	0.0	6	0.1
80	2	8	2	10	0.4	0	1	0	1	0.1	11	0.3
[83	0	1	0	1	0.5	7	0	0	7	0.9	8	0.5
[90]	100	64	7	171	5.1	68	3	6	77	9.3	248	5.9
94	48	26	18	92	7.6	17	1	13	31	12.7	123	8.6
97	109	37	101	247	14.3	23	0	21	44	17.5	291	14.9
101	127	31	398	556	29.4	45	0	60	105	29.0	661	29.3
104	93	32	315	440	41.3	35	1	85	121	42.4	561	41.5
[107	93	13	269	375	51.5	35	0	48	83	51.3	458	51.4
[112]	665	30	674	1369	88.6	102	0	114	216	75.0	1585	85.9
119	178	73	170	421	100.0	77	0	152	229	100.0	650	100.0
				3688					914		4602	

Development period = 106.5 hrs.
50% hatch interval = 101-112 hrs.

APPENDIX A

Table 5. Comparison of hatching rate for D. cepedianum at 64° F exposed to diurnal light cycle and under constant darkness.

A.T. = 62-66 F
W.T. = 64-65 F
Dark Period = 11 hrs.

	Constant Dark					Dark-Light Period						
Hrs. post-fert.	Larvae			Σ	Cumul. %		Larvae		Σ	Cumul. %	ΣΣ	Overall cumul. %
[58]	0	0	0	0	0.0	0	0	0	0	0.0	0	0.0
[61]	16	5	3	24	1.5	2	1	3	6	0.4	30	1.0
[64]	61	3	13	77	6.5	17	2	1	20	1.8	97	4.4
[67]	68	10	20	98	12.8	52	2	4	58	6.2	156	9.7
[69]	105	15	34	154	22.7	79	5	12	96	13.3	250	18.4
72	360	49	98	507	55.2	192	15	41	248	31.6	755	44.2
74	45	41	31	117	62.7	39	3	4	46	35.0	163	49.8
76	5	10	30	45	65.6	40	3	2	45	38.4	90	52.9
78	13	15	14	42	68.3	104	6	6	116	46.9	158	58.4
[82]	32	14	24	70	72.8	430	3	10	443	80.0	513	76.0
[85]	115	11	49	175	84.2	164	11	8	183	93.2	358	88.3
[91]	41	26	57	124	92.0	26	8	3	37	95.9	161	93.8
95	29	18	19	66	96.2	28	2	3	33	98.4	99	97.2
99	6	9	16	31	98.1	6	2	1	9	99.0	40	98.6
103	3	3	2	8	98.7	4	1	0	5	99.4	13	99.0
[107]	5	0	15	20	100.0	8	0	0	8	100.0	28	100.0
				1558					1353		2911	

Development period = 74.2 hrs.
50% hatch interval - 69-82 hrs.

APPENDIX A

Table 6. Hatching rate for D. cepedianum at 74° F and 75° F exposed to constant condition.

A.T. = 72-76 F
W.T. = 73-75 F
Constant light

74° F

Hrs. post-fert.	No.	Cumul. %
20	1	0.0
25	0	0.0
33	12	0.2
41	732	9.9
46	6021	90.0
47	500	96.9
52	200	99.3
52	20	100.0
	7486	

Development period = 42 hrs.
50% hatching interval = 41-46 hrs.

APPENDIX A

Table 7. Hatching rate for D. cepedianum exposed to diurnal light cycle.

A.T. = 72-78 F
W.T. = 74-76 F
Dark cycle = 9 hrs.

75° F

Hrs. post-fert.	No.	No.	No.	No.	Σ	Cumul. %
30	0	0	0	0	0	0.0
36	236	47	604	18	904	64.9
38	43	7	30	0	80	70.7
40	7	0	15	0	22	72.3
43	37	0	0	13	50	75.8
44	137	2	151	0	290	96.8
47	0	4	0	1	5	97.1
49	2	0	0	0	2	97.2
50	0	0	0	39	39	100.0
					1392	

Development period = 32.8 hrs.
50% hatch interval - 30-36 hrs.

APPENDIX A

Table 8. Developmental period at various temperatures for hybrids between D. cepedianum males and D. petenense females.*

Temperature (F)	Development Period (hrs.)	Number	Range(hrs.)
65°	83	331	81-87
70°	72	18	69-75
72°	56	76	56-71
75°	41	25	39-59

* No development from 15 attempts for the reciprocal cross.

Crosses between D. petenense males and hybrid females were unsuccessful three times while two attempts were successful and produced 45 larvae.

APPENDIX B

Table 1. Meristics for D. petenense and D. cepedianum reared in ponds at 75-78° F.

MERISTICS									
		D. petenense				D. cepedianum			
SL	(TL)	Myomeres	Anal Rays	Dorsal	No.	Myomeres	Anal Rays	Dorsal	No.
8	(8)	38			2	43			2
9	(9)			0					
10	(10)		0	0		43			2
11	(11)		0	0			0		
12	(12)		0	4-11	2	43	0	4-11	2
13	(14)	38-41	9T	14	2	44	0	10-13	3
14	(16)		11-12T	15	2	45	8T-18	11-14	8
15	(17)	41	8T-22	14-15	6		4T-28	12-13	6
16	(18)	41-43	15T-24	14-16	6	45-48	7T-32	12-14	10
17	(20)	40-43	17T-23	15-16	15	45-48	9T-34	12-14	10
18	(21)	43-44	20-23	15-16	11	46	21-34	13-14	10
19	(22)	41-42	21-24	15-16	7	47	21-33	13-14	5
20	(24)	40-45	21-24	16	6	47	29-33	13-14	5
21	(25)	40-45	21-23	16	7		30-32		5
22	(26)		21-24	16	7	47-48			2
23	(28)		21	16	1		30-31		2
24	(30)		22	16	1		32-33		2
					75				74

T = Total count

APPENDIX B

Table 2. Anal ray counts for Dorosoma petenense reared at 75-78° F.

N	SL (mm)	24 May	26 May	28 May	2 June	11 June	18 June	24 June
1	13	--	--	9T*	--	--	--	--
2	14	--	11-12T	17T	--	--	--	--
6	15	8T	--	--	--	22	20	21-22
6	16	15T	18-21	20	24	22	--	--
15	17	17T	18-22	20-23	23	21-22	23	21
11	18	--	20-21	21-23	20-22	21-22	22	21
7	19	--	--	--	24	--	21-23	--
6	20	--	--	--	--	--	21	24

* = Total count

APPENDIX B

Table 3. Anal ray counts for Dorosoma cepedianum reared at 75-78° F.

N	SL (mm)	20 May	22 May	24 May	26 May	28 May	31 May	2 June	11 June	18 June
2	13	0	0	0	0	0	--	--	--	--
8	14	--	0	0	7-14T*	8T	--	17-19	18	--
9	15	--	4-9T	10	16-17T	17T	20	--	27-28	--
10	16	0	7-11T	16T	21	--	29-30	32	30	30-31
10	17	--	9T	18T	22-23	--	--	33	34	30-33
10	18	--	--	--	--	--	--	--	34	31
5	19	--	21-32	--	--	--	--	30	--	29-33
5	20	--	--	--	--	--	--	--	--	--

* = Total count

APPENDIX B

Table 4. Indexes of various measurements (structural length divided by standard length) of D. cepedianum.

		D. cepedianum				
SL	(TL)	Maxillary	Mandible	Body Depth	Sm_2	No.
13	(14)	18.6-20.0	13.0-13.7	10.0-10.8L	V	2
14	(16)	15.6-20.0	10.3-13.5	8.8-11.7L	V	8
15	(17)	12.5-18.8	9.4-12.5	5.6-10.7L	V	6
16	(18)	12.8-16.1	8.0-11.4	4.7-10.0L	26.7-45.7	10
17	(20)	12.1-18.9	8.5-13.4	4.3- 8.9L	18.9-42.5	10
18	(21)	12.0-12.9	7.5- 8.8	3.6- 9.4L	20.0-25.0	10
19	(22)	12.7-15.6	7.9- 9.1	3.8- 8.3L	21.1-47.5	5
20	(24)	12.5-15.6	7.7- 9.1	3.6- 5.3	20.0-30.8	5
21	(25)	11. -16.2	7.0- 9.5	3.5- 5.0	19.1-30.0	5
22	(26)	14.7	7.9	3.8	27.5	2
23	(28)	12.1-12.8	7.2- 7.7	3.0- 3.8	23.0-25.6	2
24	(30)	11.4-15.0	6.8- 8.6	6.5- 7.2	24.0-26.7	2
25	(31)	11.6	7.2	6.8	26.0	1
26	(32)	13.0	8.7	3.5	26.0	1
27	(33)	12.9-15.0	7.7- 9.0	3.0- 3.4	24.5-27.0	2
28	(34)	12.5	7.8	3.2	25.0	1
29	(36)	12.1	7.4	3.0	24.2	1
30	(38)	12.0	7.5	3.0	23.1	1
60	(78)	12.5	7.6	2.7	20.0	1
						75

L = Larval forms
V = Vestigial

APPENDIX B

Table 5. Indexes of various measurements (structural length divided by standard length) of D. petenense.

SL	(TL)	Maxillary	Mandible	Body Depth	Sm_2	No.
13	(14)	18.6	13.0	10.0L*	V**	1
14	(16)	6.1-19.3	10.4-11.2	9.1-9.7L	V	4
15	(17)	7.9-11.5	6.0- 7.5	4.0-8.0L	V	6
16	(18)	10.7-16.0	8.4-10.0	5.7-8.0L	20.0-53.3	6
17	(20)	10.6-18.9	7.7-10.0	4.3-7.6L	17.0-42.5	15
18	(21)	9.5-15.0	7.2-10.3	3.8-7.2	15.6-36.0	11
19	(22)	10.6-14.2	7.6- 9.7	3.8-5.4	16.5-19.0	7
20	(24)	9.1-10.0	6.7- 7.4	3.5-4.0	14.3-16.7	6
21	(25)	9.5-10.5	7.1- 7.8	3.5-4.2	14.0-16.2	7
22	(26)	8.8-10.0	6.7- 7.7	3.3-3.7	13.8-18.3	7
23	(28)	9.6	6.5	3.3	15.3	1
24	(30)	9.6-10.4	6.5- 7.5	3.4	15.0-16.0	4
25	(31)	9.2	6.3	3.4	14.9	1
26	(32)	8.7	6.3	3.3	14.4	1
27	(33)	8.6	6.2	3.2	14.0	1
28	(34)	8.5- 9.3	6.0- 7.0	3.1-3.2	13.2-14.0	5
29	(36)	9.1	6.2	3.1	13.8	1
30	(38)	8.9	6.2- 6.5	3.1	12.4-12.9	2
60	(78)	8.8- 9.2	6.7- 6.9	3.0	14.0	2
						88

* = Larval form.
**= Vestigial

APPENDIX C

Table 1. Summary of female GSI for 1968.

	D. cepedianum				*D. petenense*			
Date	$\bar{y}$	Range	$S_{\bar{y}}$	n	$\bar{y}$	Range	$S_{\bar{y}}$	n
15-29 Feb.	1.87	0.82- 4.8	0.170	37	1.38	1.09- 1.67	0.045	14
1-15 March	2.56	0.55- 6.25	0.287	27	--	--	--	0
16-31 March	5.1	3.41- 5.78	0.54	7	--	--	--	0
1-15 April	8.7	2.04-16.10	0.62	36	3.58	1.67- 6.78	0.048	63
16-30 April	--	--	--	0	14.2	7.42-21.21	2.56	5
1-15 May	6.4	1.07-14.05	0.51	54	14.1	5.14-23.13	0.43	53
16-31 May	2.0	0.88- 6.48	0.35	21	9.8	3.89-18.39	0.54	83
1-15 June	0.73	0.50- 1.34	0.064	12	6.7	3.70-10.40	0.95	7
16-30 June	0.62	0.35- 0.85	0.103	4	0.98	0.63- 1.50	0.074	14

APPENDIX C

Table 2. Summary of female GSI for 1969

Date	*D. cepedianum* $\bar{y}$	Range	$S\bar{y}$	n	*D. petenense* $\bar{y}$	Range	$S\bar{y}$	n
15-29 Feb.	2.52	0.78- 5.39	0.289	19	1.78	1.20- 2.26	0.083	17
1-15 March	3.83	1.12- 8.57	0.278	33	1.48	1.56-2.20	0.147	4
16-31 March	4.2	0.50- 6.97	0.48	20	2.24	1.59- 2.86	0.064	34
1-15 April	8.3	0.93-14.56	0.40	65	3.01	0.87- 6.32	0.148	69
16-30 April	8.0	1.50-13.11	0.62	26	11.1	5.00-18.75	0.52	40
1-15 May	5.7	2.01-10.62	0.41	26	21.0	19:00-26.67	1.48	5
16-31 May	1.6	0.53- 4.14	0.30	14	14.4	7.69-24.00	0.61	37
1-15 June	--	--	--	0	--	--	--	0
16-30 June	--	--	--	0	--	--	--	0

APPENDIX C

Table 3. *D. cepedianum* males GSI for 1968.

Date	$\bar{Y}$	Range	$S_{\bar{y}}$	n
19 Feb.	0.97	0.15-2.0	0.131	18
8 March	0.98	0.22-2.40	0.170	15
22 March	2.0	1.43-2.94	0.35	4
8 April	2.43	0.80-4.03	0.240	14

APPENDIX C

Table 4. Size comparison of female GSI during 1968 and 1969.

Date	*D. petenense* 3-5 in.	5-6 in.	6 in. +	F	Significance
8 April 1968	--	3.04(34)+	2.98(33)	0.04 (1,65)	n.s.
9 April 1969	--	3.09(20)	3.78(44)	4.754(1,62)	*
22 April 1969	--	8.94(10)	11.25(30)	3.43 (1,38)	n.s.
2 May 1968	8.13(4)	15.12(23)	12.56(32)	6.681(2,56)	**
27 May 1969	18.03(8)	13.87(14)	12.99(15)	6.636(2,34)	**
30 May 1968	--	12.20(41)	10.09(29)	6.757(1,68)	**

Date	*D. cepedianum* 10-12 in.	12-14 in.	F	Significance
10 March 1969	3.60(12)	4.26(16)	0.95 (1,26)	n.s.
24 March 1969	4.93(12)	3.00(8)	4.732(1,18)	*
8 April 1969	7.50(27)	9.74(25)	7.789(1,50)	**
21 April 1969	7.68(14)	9.66(8)	2.407(1,20)	n.s.
13 May 1968	5.45(23)	6.86(14)	2.108(1,35)	n.s.

+ = $\bar{y}(n)$
** Significant at ≤0.01%
* Significant at ≤0.05%

APPENDIX C

Table 5. Area comparison of female GSI during 1968 and 1969.

Date	Upper	Lower	F	Significance
		D. petenense		
9 April 1968	3.27(20)+	4.29(20)	8.772(1,38)	**
9 April 1969	3.01(19)	3.01(50)	--	n.s.
22 April 1969	8.34(4)	11.45(36)	3.43 (1,38)	n.s.
2 May 1968	12.56(25)	15.03(25)	4.33 (1,48)	n.s.
30 May 1968	14.50(25)	9.33(25)	57.25 (1,48)	**
		D. cepedianum		
8 March 1968	3.53(14)	1.49(14)	24.66(1,26)	**
10 March 1969	3.86(14)	3.33(9)	0.585(1,21)	n.s.
24 March 1969	4.94(12)	3.00(8)	4.732(1,18)	*
9 April 1968	8.46(8)	7.95(8)	0.149(1,14)	n.s.
9 April 1969	9.12(38)	7.22(27)	5.805(1,63)	*
22 April 1969	7.83(6)	8.06(20)	0.023(1,24)	n.s.
2 May 1968	7.58(13)	7.69(13)	--	n.s.
30 May 1968	2.30(10)	1.73(10)	0.612(1,18)	n.s.

+ = $\bar{y}(n)$
**=Significant at $\leq$ 0.01%
* = Significant at $\leq$ 0.05%

APPENDIX C

Table 5 (continued)

Date	*D. cepedianum* Upper Creek	*D. cepedianum* Creek Mouth	F	Significance
9 April 1969	9.28(8)	11.18(6)	1.238(1,12)	n.s.

+ = $\bar{y}(n)$
** = Significant at ≤ 0.01%
* = Significant at ≤ 0.05%

APPENDIX D

Table 1. Number of egg samplers set during 1968 and 1969.

1968

Date	Areas 0-8	Beaver Bay	Buncombe Creek Mouth	Buncombe Creek Arm	
20 March	27	3	1	1	
10 April	27	3	1	1	
24 April	27	3	1	1	
1 May	27	3	1	1	
15 May	9	3	--	--	
4 June	27	3	1	1	
18 June	27	3	1	1	
12 July	27	3	1	1	
	198	24	7	7	236 samplers

Two samplers per day at boathouse from 16 April to 5 June = 100 samples.

1969

Date	Areas 0-8	Beaver Bay	Buncombe Creek Mouth	Buncombe Creek Arm	
10 March	27	3	1	1	
23 March	27	3	1	1	
8 April	27	3	1	1	
21 April	27	3	1	1	
6 May	27	3	1	1	
26 May	27	3	1	1	
	162	18	6	6	192 samplers

APPENDIX D

Table 2. Egg deposition on artificial surfaces of different colors, horizontal vs. vertical placement.

D. petenense - 20 April 1968, Area 6-Bay, 0800-1000, 68-71° F.

	V	H	Total	Percent
Green	139	140	279	36.3
Yellow	298	191	489	63.7
	437	331	768	
Percent =	56.9	43.1		

D. cepedianum - 27 March 1968, Buncombe Creek, 1200-1400, 74-76° F.

	V	H	Total	Percent
Green	14	6	20	62.5
Yellow	4	8	12	37.5
	18	14	32	
Percent =	56.3	43.7		

APPENDIX D

Table 3. Egg sampler summary for 1968, lake only.

Date	Eggs Collected				Eggs Identified							
					D. cepedianum				D. petenense			
	S	F	B	Σ	S	F	B	Σ	S	F	B	Σ
20 March	0	0	0	0	0	0	0	0	0	0	0	0
10 April	431	17	86	534	431	17	86	534	0	0	0	0
26 April	14	15	25	54	0	0	2	2	6	8	2	16
1 May	1,736	266	1,268	3,270	95	31	208	334	82	8	6	96
15 May	58	16	19	93	0	0	1	1	15	3	4	22
4 June	403	0	0	403	0	0	0	0	403	0	0	403
18 June	0	47	0	47	0	0	0	0	0	47	0	47
15 July	0	0	0	0	0	0	0	0	0	0	0	0
	2,642	361	1,398	4,401	526	48	297	871	506	66	122	584

APPENDIX D

Table 4. Egg sampler summary for 1969, lake only.

Date	Eggs Collected				Eggs Identified							
					D. cepedianum				D. petenense			
	S	F	B	Σ	S	F	B	Σ	S	F	B	Σ
10 March	0	0	0	0	0	0	0	0	0	0	0	0
23 March	0	0	0	0	0	0	0	0	0	0	0	0
7 April	49	0	0	49	49	0	0	49	0	0	0	0
21 April	42,720	1,117	660	44,497	14	0	4	18	25	0	0	25
6 May	1,940	189	169	2,298	193	90	37	320	97	11	1	109
26 May	14,132	1,250	104	15,486	26	0	0	26	1,235	298	18	1,551
	58,841	2,556	933	62,330	282	90	41	413	1,357	309	19	1,685

APPENDIX D

Table 5. Location comparison of *D. cepedianum* and *D. petenense* eggs and larvae.

	Eggs	*D. cepedianum*	*D. petenense*
Creek Mouth	432	27	41
Upper Creek	229	216	0

VERTICAL SET - Eggs-Larvae*

	Surface	5'	10'	15'
26 April - Boathouse	136-25	63-45	13-9	0-0
6 May - Buoy	16- 6	6- 3	0-0	0-0

*All larvae were *D. petenense*, no *D. cepedianum*.

LARVAE

	Creek Mouth		Upper Creek*	
Year	*D. cepedianum*	*D. petenense*	*D. cepedianum*	*D. petenense*
1968	57	37	1,442	0
1969	0	0	221	0
1970+	-	-	20,292	0

* 1/2 mile from mouth
+ Glasses Creek

APPENDIX D

Table 6. Total number of Dorosoma eggs collected.

1968

	V	H	Total	Percent
Shallow	1,742	900	2,642	60.03
Floating	154	207	361	8.20
Bottom	586	812	1,398	31.77
	2,482	1,919	4,401	
Percent =	56.40	43.60		

1969

	V	H	Total	Percent
Shallow	27,993	30,848	58,841	94.40
Floating	1,328	1,228	2,556	4.10
Bottom	422	511	933	1.50
	29,743	32,587	62,330	
Percent =	47.72	52.28		

1968-1969 All Egg Comparison Surfaces

	V	H	Total	Percent
Shallow	29,735	31,748	61,483	92.13
Floating	1,482	1,435	2,917	4.37
Bottom	1,008	1,323	2,331	3.49
	32,225	34,506	66,731	
Percent =	48.29	51.70		

APPENDIX D

Table 7. Comparison of eggs collected on the vertical (V) and horizontal (H) surfaces of egg samplers.

1968

D. cepedianum			*D. petenense*		
	V	H		V	H
3 April	25	24	20 April	486	416
10 April	349	168	1 May	400	300
1 May	171	174	15 May	316	73
3 May	280	246	4 June	329	74
	825	612		1,531	863
N = 1,437			N = 2,394		
$\bar{y}$ =	206.3	153.0	$\bar{y}$ =	382.8	215.7
Percent =	57.4	42.6	Percent =	63.9	36.1
Chi square = 34.97**			Chi square = 157.27**		
$P < .005$			$P < .005$		

APPENDIX D

Table 8. Area comparison of eggs collected on samplers for 1968. (Eggs - eggs identified as D. cepedianum/ D. petenense.)

Area	1968								
	20 March	10 April	26 April	1 May	15 May	4 June	18 June	12 July	Σ
0	0-0/0	3- 3/0	0-0/0	205- 8/ 9	1-0/ 0	0-0/ 0	0-0/ 0	0-0/0	209- 11/ 9
1	0-0/0	44- 44/0	8-1/ 2	119- 4/ 0	Lost	14-0/ 14	0-0/ 0	0-0/0	185- 49/ 16
2	0-0/0	14- 14/0	0-0/ 0	185- 2/ 1	Lost	389-0/389	47-0/47	0-0/0	635- 16/437
3	0-0/0	8- 5/0	16-0/ 6	737- 1/ 77	52-0/ 6	0-0/ 0	0-0/ 0	0-0/0	813- 6/ 89
4	0-0/0	7- 7/0	0-0/ 0	0- 0/ 0	5-0/ 0	0-0/ 0	0-0/ 0	0-0/0	12- 7/ 0
5	0-0/0	8- 8/0	3-1/ 1	559- 180/ 5	Lost	0-0/ 0	0-0/ 0	0-0/0	570-189/ 6
6	0-0/0	15- 15/0	17-0/ 5	43- 18/ 1	Lost	0-0/ 0	0-0/ 0	0-0/0	75- 33/ 6
7	0-0/0	3- 3/0	0-0/ 0	328- 1/ 0	Lost	0-0/ 0	0-0/ 0	0-0/0	331- 4/ 0
8	0-0/0	35- 35/0	10-0/ 2	269- 84/ 0	Lost	0-0/ 0	0-0/ 0	0-0/0	314-119/ 2
B.B.[1]	0-0/0	397- 397/0	0-0/ 0	777- 29/ 3	35-1/16	0-0/ 0	0-0/ 0	0-0/0	1,209-427/ 19
B.C.M.[2]	0-0/0	0- 0/0	0-0/ 0	30- 7/ 10	Lost	0-0/ 0	0-0/ 0	0-0/0	30- 7/ 10
B.C.[3]	0-0/0	49- 49/0	0-0/ 0	18- 18/ 0	Lost	0-0/ 0	0-0/ 0	0-0/0	67- 67/ 0
	0-0/0	583-580/0	54-2/16	3,270-352/106	93-1/22	403-0/403	47-0/47	0-0/0	4,450-935/594

[1]Beaver Bay
[2]Buncombe Creek Mouth
[3]Buncombe Creek

APPENDIX D

Table 9. Area comparison of eggs collected on samplers for 1969. (Eggs - eggs identified as D. cepedianum/ D. petenense.)

Area	1969						
	10 March	23 March	7 April	21 April	6 May	26 May	Σ
0	0-0/0	0-0/0	0- 0/0	111- 0/ 0	0- 0/ 0	0- 0/ 0	111- 0/ 0
1	0-0/0	0-0/0	0- 0/0	0- 0/ 0	0- 0/ 0	0- 0/ 0	0- 0/ 0
2	0-0/0	0-0/0	0- 0/0	347- 4/25	322-124/ 30	14,854-26/1,531	15,523-154/1,586
3	0-0/0	0-0/0	0- 0/0	644- 0/ 0	0- 0/ 0	0- 0/ 0	644- 0/ 0
4	0-0/0	0-0/0	0- 0/0	41,274- 0/ 0	293- 58/ 53	0- 0/ 0	41,567- 58/ 53
5	0-0/0	0-0/0	0- 0/0	1,095- 0/ 0	81- 0/ 1	132- 0/ 20	1,308- 0/ 21
6	0-0/0	0-0/0	0- 0/0	466- 0/ 0	21- 6/ 1	0- 0/ 0	487- 6/ 1
7	0-0/0	0-0/0	0- 0/0	21- 0/ 0	1,253- 71/ 17	0- 0/ 0	1,274- 71/ 17
8	0-0/0	0-0/0	0-00/0	22- 0/ 0	254- 5/ 0	0- 0/ 0	276- 5/ 0
B.B.[1]	0-0/0	0-0/0	0- 0/0	0- 0/ 0	0- 0/ 0	0- 0/ 0	0- 0/ 0
B.C.M.[2]	0-0/0	0-0/0	0- 0/0	402- 0/ 0	86- 53/ 7	0- 0/ 0	488- 53/ 7
B.C.[3]	0-0/0	0-0/0	49/49/0	15-14/ 0	4- 3/ 0	0- 0/ 0	68- 66/ 0
	0-0/0	0-0/0	49/49/0	44,397-18/25	2,314-320/109	14,986-26/1,551	61,746-413/1,685

[1]Beaver Bay
[2]Buncombe Creek Mouth
[3]Buncombe Creek

APPENDIX E

Table 1. Number of trawling samples* taken during 1968 and 1969.

	Area											
1968	0	1	2	3	4	5	6	7	8	B.B.[1]	B.C.M.[2]	B.C.[3]
22 March	4	2	1	3	5	3	3	3	3	4	1	1
3 April	4	2	1	3	5	3	3	3	3	4	1	1
18 April	4	2	1	3	5	3	3	3	3	4	1	1
24 April	4	2	1	3	5	3	3	3	3	4	1	1
12 May	4	2	1	3	5	3	3	3	3	4	1	1
28 May	4	2	1	3	5	3	3	3	3	4	1	1
10 June	4	2	1	3	5	3	3	3	3	4	1	1
22 June	4	2	1	3	5	3	3	3	3	4	1	1
15 July	4	2	1	3	5	3	3	3	3	4	1	1
29 Aug.	2	2	1	3	3	2	3	2	2	4	1	1
	38	20	10	30	48	29	30	29	29	40	10	10

1969	0	1	2	3	4	5	6	7	8	B.B.[1]	B.C.M.[2]	B.C.[3]
10 March	1	1	1	1	2	1	1	1	1	1	1	1
23 March	1	1	1	1	2	1	1	1	1	1	1	1
8 April	1	1	1	1	2	1	1	1	1	1	1	1
21 April	2	1	1	2	6	2	2	2	2	3	1	1
8 May	2	1	1	1	3	1	1	1	1	2	1	1
27 May	2	1	1	1	2	1	1	1	1	2	1	1
14 June	1	1	1	1	2	1	1	1	1	2	1	1
	10	7	7	8	19	8	8	8	8	12	7	7

* 3-minute hauls

[1]Beaver Bay

[2]Buncombe Creek mouth

[3]Buncombe Creek

APPENDIX E

Table 2. Larvae collected by trawling during 1968 and 1969.

1968

Date	D. cepedianum	D. petenense
22 March	5*	0
3 April	1	0
18 April	44	0
24 April	1,729	12
11 May	86	289
28 May	1	14
10 June	0	107
22 June	0	0
15 July	0	0
29 August	0	0
	1,861	422

*28 March

1969

Date	D. cepedianum	D. petenense
10 March	0	0
23 March	0	0
8 April	221	0
21 April	2	0
8 May	10	0
27 May	0	10
14 June	0	16
	233	26

APPENDIX E

Table 3. Area comparison of larvae collected by trawling during 1968 (D. cepedianum/D. petenense.)

	1968										
Area	22 Mar	3 Apr	18 Apr	24 Apr	11 May	28 May	10 Jun	22 Jun	15 Jul	29 Aug	Σ
0	0/0	0/0	10/0	15/ 0	15/220	1/ 2	0/107	0/0	0/0	0/0	41/329
1	0/0	0/0	4/0	2/ 0	0/ 0	0/ 0	0/ 0	0/0	0/0	0/0	6/ 0
2	0/0	0/0	0/0	1/ 0	5/ 9	0/ 0	0/ 0	0/0	0/0	0/0	6/ 9
3	0/0	0/0	0/0	1/ 2	3/ 3	0/ 2	0/ 0	0/0	0/0	0/0	4/ 7
4	0/0	0/0	6/0	0/ 1	18/ 2	0/ 1	0/ 0	0/0	0/0	0/0	24/ 4
5	0/0	0/0	1/0	2/ 1	5/ 0	0/ 0	0/ 0	0/0	0/0	0/0	8/ 1
6	0/0	0/0	1/0	1/ 1	5/ 7	0/ 0	0/ 0	0/0	0/0	0/0	7/ 8
7	0/0	0/0	5/0	195/ 6	10/ 2	0/ 0	0/ 0	0/0	0/0	0/0	210/ 8
8	0/0	0/0	17/0	30/ 1	8/ 15	0/ 0	0/ 0	0/0	0/0	0/0	55/ 16
B.B.[1]	0/0	0/0	0/0	2/ 0	3/ 3	0/ 0	0/ 0	0/0	0/0	0/0	5/ 3
B.C.M.[2]	0/0	1/0	0/0	57/ 0	0/ 28	0/ 9	0/ 0	0/0	0/0	0/0	58/ 37
B.C.[3]	5/0*	0/0	0/0	1,423/ 0	14/ 0	0/ 0	0/ 0	0/0	0/0	0/0	1,442/ 0
	5/0	1/0	44/0	1,729/12	86/289	1/14	0/107	0/0	0/0	0/0	1,866/422

[1]Beaver Bay
[2]Buncombe Creek mouth
[3]Buncombe Creek
*28 March

APPENDIX E

Table 4. Area comparison of larvae collected by trawling during 1969 (D. cepedianum/D. petenense).

	1969							
Area	10 Mar	23 Mar	8 Apr	21 Apr	8 May	27 May	14 June	Σ
0	0/0	0/0	0/0	1/0	0/0	0/ 3	0/ 0	1/ 3
1	0/0	0/0	0/0	1/0	0/0	0/ 0	0/ 0	1/ 0
2	0/0	0/0	0/0	0/0	0/0	0/ 3	0/ 0	0/ 3
3	0/0	0/0	0/0	0/0	0/0	0/ 0	0/ 0	0/ 0
4	0/0	0/0	0/0	0/0	0/0	0/ 0	0/ 0	0/ 0
5	0/0	0/0	0/0	0/0	0/0	0/ 0	0/ 0	0/ 0
6	0/0	0/0	0/0	0/0	1/0	0/ 4	0/ 0	1/ 4
7	0/0	0/0	0/0	0/0	0/0	0/ 0	0/ 0	0/ 0
8	0/0	0/0	0/0	0/0	8/0	0/ 0	0/16	8/16
B.B.[1]	0/0	0/0	0/0	0/0	1/0	0/ 0	0/ 0	1/ 0
B.C.M.[2]	0/0	0/0	0/0	0/0	0/0	0/ 0	0/ 0	0/ 0
B.C.[3]	0/0	0/0	221/0	0/0	0/0	0/ 0	0/ 0	221/ 0
	0/0	0/0	221/0	2/0	10/0	0/10	0/16	233/26

[1] Beaver Bay

[2] Buncombe Creek mouth

[3] Buncombe Creek