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THE REPRODUCTIVE CYCLE OF YELLOW BASS, MORONE MISSISSIPPIENSIS, IN CLEAR LAKE, IOWA

by

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Signature was redacted for privacy.

Dean of Graduate College

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ABSTRACT

Gillnet collections of yellow bass, Morone mississippiensis, were made from April, 1967 to September, 1968 at Clear Lake, Iowa to determine the normal reproductive cycle and variations in fecundity which could be related to changes in food supply and water temperatures. A major mortality from Aeromonas infection occurred in May, 1968 which also allowed documentation of changes in body condition, fecundity and success of reproduction during the year preceding a mass mortality from disease.

Spawning was initiated during mid-May in 1967 and late April in 1968 when water temperatures approached 15°C after a rapid temperature rise of 3.5 to 4.5°C over several days. At spawning time ovaries of adult bass comprised up to 16 percent body weight and testes up to 8 percent body weight. Fish commenced spawning when maturing ova reached a mean diameter of 0.4 mm in the preserved state. Fresh ovulated ova averaged 0.8 $\pm$ 0.11 mm in diameter.

Wide variation in effective fecundity was apparent among mature females of similar length. Although 50 percent of the variation in fecundity could be attributed to body length in 1967, the relation was not significant in 1968 ($r = 0.32$). In 1967 mature females contained an average of 560 mature ova per mm total body length in contrast to 276 ova in 1968. In terms of body weight the average female produced 835 ova per gram body weight in 1967 but only 350 in 1968. The change in fecundity was attributed to poor body condition in 1968. Females measuring 200 mm total body length weighed approximately 137 grams in 1967 at spawning time but only 115 grams in 1968.

Atresia of developing ova was estimated at 20 percent during the period from December to May and was attributed to poor nutrition. Ova retention after spawning in 1967 was approximately 34 percent of total ova production. In 1968 most fish died shortly after initiation of spawning, with a minimum number of ova shed. Reproduction success in 1968 determined by standardized seining of young-of-the-year bass was 1 percent of the 1967 level (77 vs 7,015).

Young-of-the-year yellow bass were a major food item of adult bass during late summer and autumn when vitellogenesis was initiated. At other times of the year adult bass ate invertebrate food similar to that of young bass.

Mesenteric fat decreased steadily with gonadal development in both sexes from March to May, 1968 and reached zero levels at spawning time. Testicular moisture content remained constant at 81-82 percent from January to May, 1968; whereas, mean ovarian moisture decreased from 78 to 67 percent during the same period.

Insufficient food as reflected by poor body condition coupled with fluctuating spring water temperatures apparently allowed Aeromonas infection to reach epizootic proportions when spawning commenced in 1968. The yellow bass population was decimated by the disease but other species were not affected. Catch per gillnet hour decreased from 2.158 bass in mid-May to 0.025 in mid-June.

INTRODUCTION

For many years the yellow bass, Morone mississippiensis,[1] has been the dominant species of fish in Clear Lake, Iowa. Food habit studies have suggested that competition for food occurs between yellow bass and most other fishes in the lake at some time in their life cycle (Ridenhour, 1960; Buchholz, 1960; Welker, 1963). Yellow bass also serve as food for piscivorous species such as walleye and northern pike. Hence, the abundance of yellow bass in Clear Lake profoundly influences other species, some of which are highly desirable sport fish. Wide annual variations in abundance of young-of-the-year yellow bass occur in Clear Lake suggesting that reproduction success is determined either prior to or shortly after spawning. Information on the reproductive potential is needed as a basis for understanding the processes in the early life history which affect survival.

The current study initiated in April, 1967 was designed to obtain information on the normal reproductive cycle of male and female yellow bass and variations in fecundity and egg deposition which might be related to environmental factors such as water temperature and food supply. On a broader basis, the study sought insight into variations in reproduction potential in fish populations restricted in growth by limited food supply. Originally the study was designed for a three-year period, but in May, 1968 an Aeromonas infection decimated the adult population of yellow bass and forced termination of the project. Hence, in effect this

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[1]The yellow bass has been transferred from Roccus back to the genus Morone by recent authors (Wright, 1968).

report documents changes in condition, fecundity and reproduction success during the year preceding mass mortality from disease.

Clear Lake is the third largest natural lake in Iowa comprising 1,474 hectares (3,643 acres). It is located in north central Iowa in western Cerro Gordo County. The lake is shallow and eutrophic in nature, but due to a watershed that is smaller than the lake area itself, less sedimentation and artificial enrichment has occurred than in many other Iowa lakes. Bailey and Harrison (1945) described the lake and 23 species of fish present as well as management policies in effect in 1945. More recent publications have relied heavily on their description.

From 1941 to 1965 numerous studies were conducted on Clear Lake by students of the Iowa Cooperative Fisheries Research Unit. Research from 1965 to the present has been directed by personnel of the Iowa Cooperative Fishery Unit.

The yellow bass is not endemic to Clear Lake but made its first appearance in the catch about 1932 (Bailey and Harrison, 1945). The species was probably introduced into the lake from the Mississippi River where it is native. Helm (1964) concluded that many Wisconsin waters were also stocked with yellow bass in the 1930's and early 1940's as the result of fish salvage work from sloughs along the Mississippi River. Since 1939 the species has been dominant much of the time in Clear Lake even though wide fluctuations in year-class strength have occurred (Bailey and Harrison, 1945; Buchholz, 1960).

Food of Clear Lake yellow bass was studied by Bailey and Harrison (1945), Ridenhour (1960), Buchholz (1960), Welker (1963), Kraus (1963) and Atchison (1967). Yellow bass were highly piscivorous in early years

but later studies reported a predominance of chironomids, entomostracans and Hyalella in stomachs examined. In other populations of yellow bass, Helm (1958) and Collier (1963) also found immature insects and crustaceans as important food items; whereas, Kutkuhn (1955) reported that larger yellow bass fed heavily on forage fish in North Twin Lake, Iowa.

The transition from a fish to invertebrate diet was probably a major factor in the decrease in mean size of yellow bass which occurred in Clear Lake. Lewis and Carlander (1948) reported on the growth, year-class strength and condition of yellow bass collected from 1941 to 1943. Carlander, et al. (1952) published additional information on these subjects for the period from 1941 to 1951. Mean calculated total length at the end of 4 years of growth was 280 mm for the 1937 year class but only 213 mm for the 1947 year class. Buchholz and Carlander (1963) reported a further decrease in growth rate of Clear Lake yellow bass from 1951 to 1958 which they attributed to reduction of invertebrate food and increased competition. Growth was sufficiently low in certain years that annuli were not formed. By 1956 the size of yellow bass had decreased to the point where a 200 mm fish was considered large. Skillman (1965) found a slight increase in growth from 1959 to 1964 but the maximum mean total length he reported was 210 mm. In the present study the largest yellow bass of 1,975 measured was 223 mm in total length.

Since its introduction the yellow bass has contributed heavily to the angler catch in Clear Lake. In a four-year creel census, DiCostanzo and Ridenhour (1957) found that yellow bass were predominant

in the summer sport catch for 1953, 1954 and 1955 and were only surpassed by bullhead and bluegill in 1956. McCann (1960) estimated the standing crop of yellow bass over 6 inches total length as 7.8 pounds per acre for 1959, but it is thought to have been much higher in most years.

Ridenhour (1960) discussed the ecology and abundance of young-of-the-year yellow bass and other game fish in Clear Lake.

The diurnal activity of yellow bass in Clear Lake as indicated by gillnet catches has been documented (Sieh and Parsons, 1950; Carlander, 1953). Maximum feeding activity occurs shortly after sundown with a smaller peak in the early morning hours.

Atchison (1967) reviewed available information on the life history of the yellow bass in Clear Lake including mass mortalities which occurred in 1955, 1958, 1962, 1965 and 1966. He attributed the 1966 mortality to infection by bacteria of the genus Aeromonas and parasitism by species of the trematode Urocleidus. Yellow bass eggs were artificially fertilized and incubated in the laboratory. Hatching occurred in 48 to 66 hours at temperatures of 21.1 to 17.2°C (70° to 63°F).

Attempts have been made in other areas to artificially propagate yellow bass. Helm (1958) successfully fertilized yellow bass and white bass (Morone chrysops) although he had considerable difficulty obtaining ripe yellow bass females. In 1967 offspring of striped bass (Morone saxitalis) females and yellow bass males were successfully propagated and

released into a Kentucky lake.[2] The earliest and still most complete description on the spawning behavior and reproduction of yellow bass was made by Burnham (1909). He reported that yellow bass were being propagated by pond culture at the U.S. Fisheries Station, Tupelo, Mississippi in the early 1900's.

[2]Personal communication with Robert E. Stevens, North Carolina Cooperative Fishery Unit, N.C. State University, Raleigh, N.C. November 15, 1967.

METHODS

Two sites were selected in Clear Lake for sampling adult yellow bass. One site was located over the major spawning area and the other in deep water where yellow bass have been captured regularly in the annual gillnetting operations. Atchison (1967) reported that yellow bass apparently concentrate their spawning activity to three areas of Clear Lake with spawning occurring most consistently in recent years around the Island (Figure 1). The west shore of the Island is also the major walleye spawning area of the lake. The area is windswept and the bottom consists of coarse gravel and boulders. One collecting station was established at the Island spawning site in 1-2 meters of water. An additional station was located approximately 400 meters northeast of the Island in depths of 5-6 meters.

Yellow bass larger than young-of-the-year were collected with 125-foot experimental gillnets having the following mesh sizes: 3/4, 1, 1-1/4, 1-1/2 and 2-inches bar measure. Weekly gillnet samples were collected from April to June and monthly samples from July to March.

After young-of-the-year yellow bass moved into shallow water they were sampled weekly during the summer and monthly during the balance of the year when the lake was not frozen using a 25-foot bag seine (1/4-inch square mesh bag with 1/2-inch mesh wings).

Fish utilized for fecundity and fat measurements and for determining maturity indexes were preserved in 10-percent formalin upon capture and then measured. Total body length was measured to the nearest millimeter. Body weight and weight of mesenteric fat and gonads were measured to the

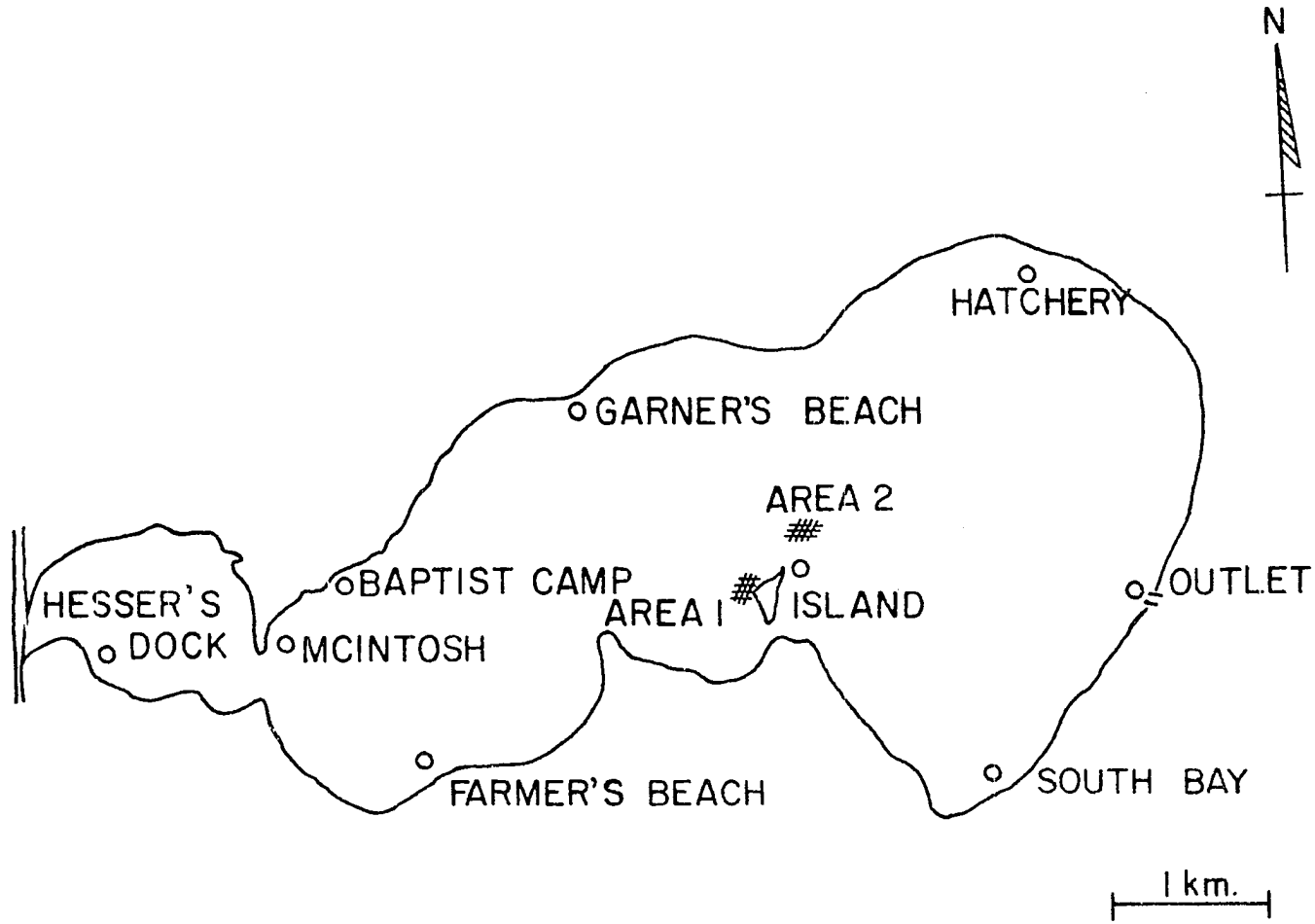


Figure 1. Map of Clear Lake, Iowa illustrating the two areas sampled for yellow bass reproductive studies 1967 and 1968. Open circles indicate standard summer gillnetting and seining sites

nearest 0.01 gram. The mesenteric fat was stripped from the digestive tract and internal organs with dissecting forceps for weighing. The fat separated from the internal organs with little difficulty. Gonads were stored in 85 percent alcohol after weighing. Stomachs were collected from all specimens when body measurements were completed and combined in the manner described by Borgeson (1963). The total volume of each major group of organisms within the combined sample was then determined using a 10-ml burette accurate to 0.05 ml. Results were presented by monthly intervals to indicate seasonal changes.

Examination of Clear Lake yellow bass during the 1967 spawning season indicated that all female fish larger than 180 mm total length had extensive gonadal development. Some females from 170 to 180 mm were mature but many were not. All male yellow bass larger than 170 mm total length were functionally mature during the spawning season. Thus, only female yellow bass 180 mm or longer and male fish 170 mm and longer were utilized in computing the maturity index to eliminate sub adults (LeCren, 1952). According to yellow bass age determination by Atchison (1967), males of the size used in the present study were three years of age or older; females were at least four years of age.

Fecundity terms used here are equivalent to the relative and total fecundity of Henderson (1963b) and Vladykov (1956). Potential fecundity is the number of maturing ova in the ovaries at any stage of secondary ova development. Effective fecundity refers to the number of mature or fully developed ova produced and spawned. The term functional maturity is defined as that stage of maturation when sex products can be expressed

from the fish by gentle hand massage of the abdomen. In the yellow bass functional maturity may or may not indicate that ova expressed are fully mature because abortion of ova is not uncommon.

Both ovaries were used in estimating potential and effective fecundity. Ovaries were removed from the preservative and the outer membrane was detached with forceps. The ova were placed in a plastic test tube containing alcohol and vigorously massaged with a pair of large forceps to separate individual ova with minimal damage. Ova collected earlier than December were firmly attached to the ovarian membrane and were not satisfactorily separated by the above method without considerable breakage of the ova. Ovaries from samples taken from September to November were separated by immersing an ultrasonic probe at low frequency into the test tube for 30-60 seconds. Ovaries collected in September were not entirely separated by either method because the alcohol excessively hardened the tissues. Bagenal (1966) found that Gilson's fluid was more satisfactory for breaking down the ovarian membrane and releasing ova of plaice.

After separation, the ova from a single fish were placed in a cylindrical museum jar and sufficient water was added to make a total volume of 400 cc. The jar was then inverted several times to evenly distribute the ova in the liquid. The lid was removed immediately and a 1.5 cc aliquot was extracted from the center of the jar. The aliquot was placed in a circular counting cell under a binocular microscope for determining number of ova present. Four aliquots were taken from each sample for estimating total ova present. Fecundity estimates were thus

based on counts of 1.5 percent of the total ova present. Differences in the four counts indicated the amount of variability inherent in the sampling method.

Only ova in which vitellogenesis was apparent were considered for fecundity estimates. Ova present in yellow bass ovaries were classified as

1. Primary oocytes: small transparent cells less than 5 microns in diameter and present throughout the year.
2. Maturing ova: those ova which had initiated yolk deposition (vitellogenesis) and were larger than 5 microns. Upon approaching maturity these ova increase rapidly in size and become transparent at ovulation similar to ova of striped bass (Stevens, 1966).
3. Atretic ova: ova of varying sizes with the chorion in different stages of deterioration. In advanced stages the cell was usually irregular in shape with the outer membrane ruptured. Cell contents were less opaque than normal ova.

Mean ova size at successive stages in the maturation cycle was determined from ova of 10 fish selected over the range in body length in each collection. A small sample of ova from the center of the ovary was placed upon a microscope slide and teased apart (MacGregor, 1957). The slide was then inserted in a microprojector and magnified 85 diameters. The projected image of 20 to 30 maturing ova selected at random was measured. In ova of normal shape, length of the long axis was considered to be the diameter. Slightly distorted ova were measured through both the long and short axis and the mean value used as the ova diameter.

Mean ova diameter for each sample was thus based on a minimum of 200 measurements.

The percent body weight consisting of gonads was used as an index of the stage of maturity (LeCren, 1952; Braekevelt and McMillan, 1967). The maturity index for each sample of fish was determined by averaging individual gonad-body weight ratios for all fish of a given sex in the sample. When possible, 30 fish of each sex were used to determine the mean maturation index for each collection date.

Gonadal moisture content was determined by the method employed by Clemens and Grant (1964). Fish used for measuring gonadal hydration were placed in plastic bags at capture and frozen. It is recognized that freezing might cause dehydration but as all samples were treated similarly, relative comparisons were considered valid. Small macerated portions (0.5-1.0 gram) of the gonad were placed on tared microscope cover slips, weighed on a balance accurate to $\pm$0.05 mg and dried for 12 hours at 65°C. The weight loss was considered as the moisture content of the sample.

Water temperature data were obtained from the City of Clear Lake water treatment plant. Water is withdrawn at a depth of approximately 3 meters at a point in the lake where maximum depth is approximately 4 meters. Temperature of the water is recorded at 1 pm daily.

Rainfall data were obtained from published U.S. Weather Bureau Climatological Records for Mason City airport located approximately 7 miles east of Clear Lake.

SEX DETERMINATION

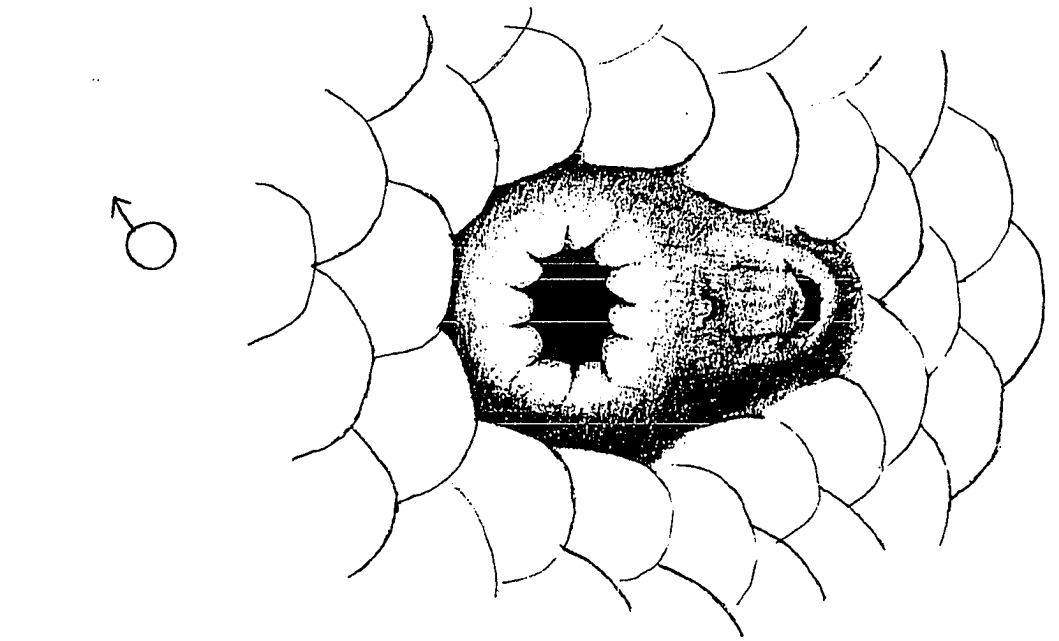
Sex identification was not a problem in the present study because all fish were examined internally as gonads were removed for weighing. However, Atchison (1967) had difficulty in distinguishing the sex of yellow bass after spawning was completed either externally or internally without the aid of a microscope.

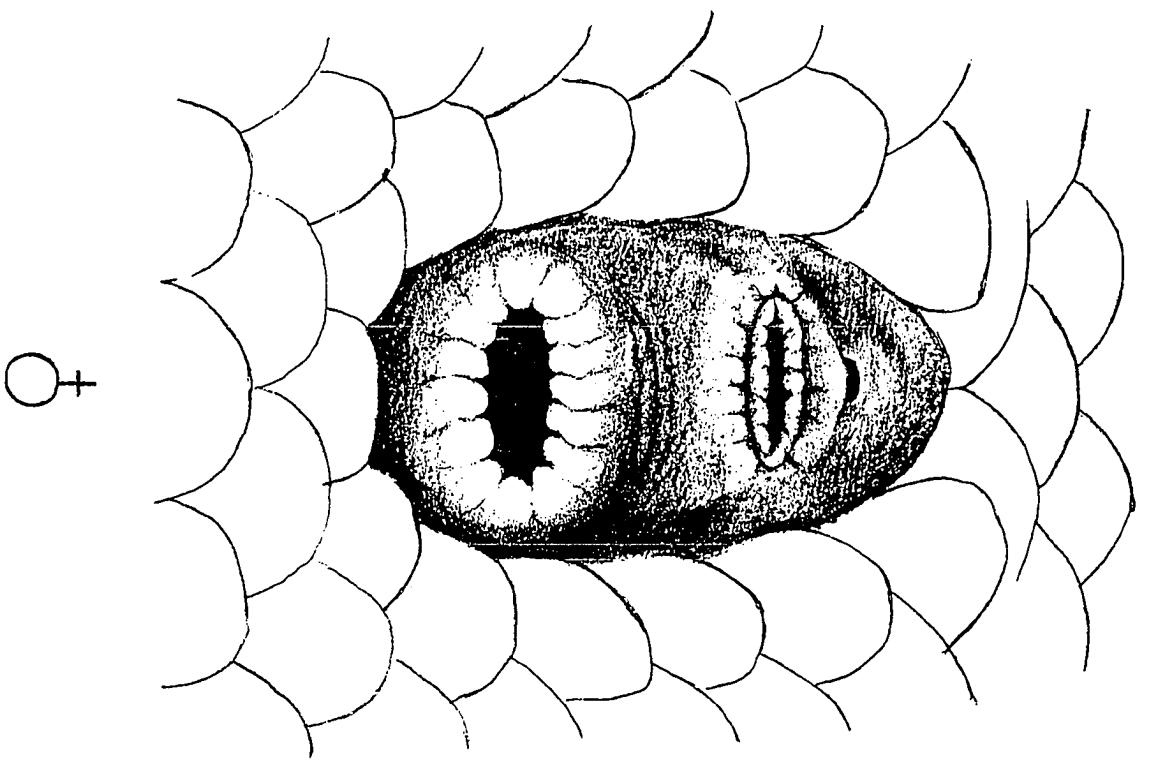
Sex of adult yellow bass can be readily determined externally during the spawning season and with reasonable accuracy during the balance of the year by examination of the urogenital and genital openings. Yellow bass of both sexes normally possess three body openings in the anal area (Figure 2). The anterior opening in males and females is the anus, which leads directly into the intestine. In the female, the central opening is the genital pore which leads up through the oviduct to the paired ovaries. The female genital opening is surrounded by a fringe of small papillae of varying development. The posterior pore leads into a well-developed urinary bladder. Papillae surrounding the genital pore frequently overlap the urinary pore making it somewhat inconspicuous.

In the male yellow bass the center opening leads into a blind sac of varying depth usually less than 3 mm in depth. In occasional specimens the pore is vestigial. The posterior opening is the urogenital pore through which both urine and milt are ejected. The sperm duct (vas deferens) unites with the urinary bladder just inside the urogenital opening. No papillae surround the male urogenital pore.

Thus, the central pore is the key to sex identification. If the pore is well developed and deep, the specimen is female. If the central

Figure 2. Diagrammatic illustration of genital and anal openings of adult Clear Lake yellow bass





opening is not present, or when present, if insertion of a dull probe into the central pore indicates a blind sac, the specimen is male. The criteria hold for sub-adult as well as mature specimens from Clear Lake.

Sigler (1948) found a similar number of openings in adult white bass although arrangement of the openings in the male fish was different. He reported that the male urogenital pore was centrally located. The posterior pore was a small pit similar to the central pore in the male yellow bass.

During the spawning season sexes of adult fish can be determined more rapidly, but also with more chance of error, by visual examination of the genital pore. In the female yellow bass, gonadal maturation, or more likely the spawning act itself, apparently ruptures the genital opening so that the red lining of the oviduct protrudes outward. McComish (1968) found a similar doughnut-shaped genital pore in the bluegill which was consistent enough to use for identifying female fish. The size and redness of the genital opening in the yellow bass varied widely among different fish but many females in the present study were readily detected throughout the year by the method. Checking the depth of the central pore with a probe confirmed the identification.

THE SPAWNING PERIOD

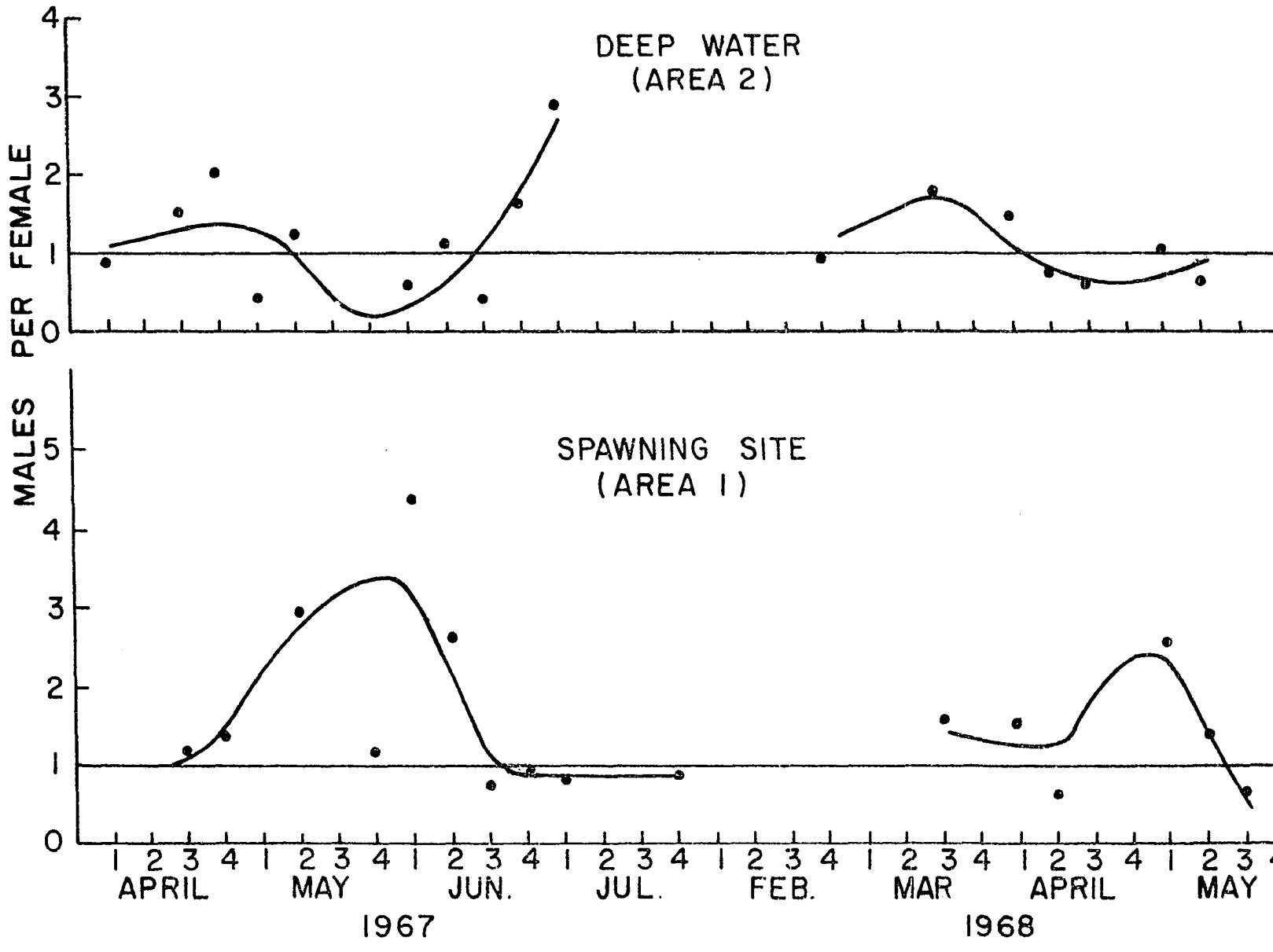
Sex Ratios

In 1967 and 1968, collections were made over the spawning area as well as in deeper water to determine if yellow bass form unisexual schools during the spawning period as reported for white bass. Male white bass mature and move to the spawning grounds earlier than the females. When ready to spawn the females travel to the spawning area, release their eggs and return promptly to the deeper water (Riggs, 1955; Horrall, 1961). Thus, the sex ratio during spawning favors males over the spawning area and female white bass in deep water.

Sex ratios of adult yellow bass in samples obtained from Clear Lake indicated a definite movement of male fish into the spawning area during April and May (Figure 3). Females became predominant in the deep water at this time. Hence, adult yellow bass are similar to the related white bass in forming somewhat unisexual schools during the spawning season. Fish in the schools sampled were never of a single sex, but males strongly predominated in the shallow spawning area; whereas, schools of predominantly female fish were found in deep water. Movement of males into the spawning area appeared to be later in 1967 than in 1968 by about two weeks. Males were most abundant in shallow-water samples the latter part of May, 1967 and in samples collected early May in 1968. The timing difference was attributed to temperature and will be discussed later.

The phenomenon of uneven sex distribution at certain times of year can easily lead to erroneous conclusions on the actual sex ratio of adult

Figure 3. Sex ratios of Clear Lake yellow bass in gillnet samples exceeding 15 fish during spawning season, 1967 and 1968. Line plotted by hand


DEEP WATER
(AREA 2)
MALES PER FEMALE
SPAWNING SITE
(AREA 1)
0
1
2
3
4
5
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
APRIL
MAY
JUN.
JUL.
FEB.
MAR
APRIL
MAY
1967
1968

fish in the population. Data in Figure 3 illustrate the danger of basing sex ratios on a single sample. In one collection over 4 males were captured for each female. Two weeks later in deep water 7.5 females were captured for each male. Pooling of samples collected in different areas of the lake and over a period of time provided a more accurate estimate of the actual sex ratio of the adult population. The ratio of male to female yellow bass in all samples from April 6 to June 29, 1967 was 1:1.112 (n = 1,093). The probability of a chi-square value larger than the computed value of 3.404 was greater than 0.05, supporting the conclusion that an equal sex ratio existed. For the period from February 27 to May 21, 1968, the ratio of males to females in combined samples was 1:0.997 (n = 631) also indicating that an equal number of fish of both sexes were present in the population (chi square = 0.002, p = 0.95). A total of 1,975 adult fish were examined during the study with a sex ratio of 1 male to 1.057 females (chi square = 1.532, p = 0.20).

The most biased sex ratio during the study was obtained from one of two collections made in midwinter by ice fishing. Of 69 adult bass captured by bait fishing at several places in the lake from January 30 to February 7, 1968, only 14 fish were males. The large excess of females in the sample suggested a differential feeding intensity between the sexes in early February. Gillnetting through the ice on February 27 produced 29 female and 26 male yellow bass indicating that the ice-fishing sample was not representative of the actual sex ratio of the population.

Time of Spawning

Yellow bass have been reported to spawn during April and May when water temperatures in the spawning area approach 68-72°F (20-22°C), usually from midmorning to noon on calm days (Burnham, 1909; Harlan and Speaker, 1951; Atchison, 1967). Spawning normally occurs in shallow water about 1 meter deep. Atchison failed to observe spawning of yellow bass at Clear Lake in 1966 but found schools of male fish over the spawning area on May 23 and captured two ripe females. He successfully fertilized and incubated ova from the two females indicating that spawning was occurring in the lake at that time.

Functional maturity in male yellow bass occurred prior to their movement inshore to the spawning area. Adult males were functionally mature in the earliest sample collected in 1967 (April 6). In a sample of 56 males collected May 19, 1968, 49 fish were functionally mature. All males collected April 2, 1968 were mature. The first appearance of a spent condition in male fish in 1967 was in the collection made June 8. Testes of most males in the sample were a greyish bloodshot coloration and were being resorbed. Testes of ripe males have a creamy-white coloration with free-flowing milt. In 1968 spent males were collected as early as May 7.

Functionally mature females were first collected on May 12 in 1967. Ovaries of 19 females from a sample of 27 collected on that date contained mature transparent ova. Fishermen reported schooling and surface agitation

by yellow bass presumably spawning at the Island on May 17.[3] Collections on May 24 contained 12 females with partly evacuated ovaries, 6 females with mature transparent ova and 5 smaller females that apparently had not spawned yet. The decision that partial spawning had occurred was based on a wrinkled flabby appearance of the ovary wall and a sharp ventral edge of the ovary in contrast to the well-rounded appearance earlier. Venation was closer together and the ovary itself was obviously shrinking. However, the ovaries were not much smaller on the average than those observed previously, indicating that only a small portion of the ova had been released. On June 2, only 2 fish among 57 females examined were functionally mature. Internal examination revealed that ovaries of the two fish contained transparent ova. Ovaries of the balance were still large but were in an obvious state of resorption. Hence, in 1967, major spawning occurred between May 12 and May 24 with spawning essentially over by June 2.

In 1968, ovaries of one female among 15 captured on April 30 contained mature ova. The collection of 38 females on May 7 contained two fish with many transparent ova and one with partly spent ovaries. Ovaries of three females had a few transparent ova in the lumen but showed no other evidence of having spawned. Ovaries of remaining fish in the May 7 sample were still developing. Several males of 31 captured on that date were in a spent condition. On May 14 a sample of 52 females contained 8 functionally mature specimens. Ovary examination revealed 17

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[3]Private communication with Robert Cooper, Fish Hatchery Superintendent, Iowa Conservation Commission, Clear Lake, Iowa. May 19, 1967.

females with small numbers of transparent ova. The remaining ovaries were being resorbed with complete atresia apparent. Ova were amalgamated into a gelatinous mass.

Two of the 30 males in the May 14, 1968 sample were still functionally mature. Testes of the remaining 28 males were in a state of resorption and appeared spent or partly spent. On May 21 one functionally mature female with transparent ova was captured. Ovaries of 20 other females appeared atretic. Milt of 4 males collected on May 21 was thickened and testes indicated a spent condition. Many yellow bass were observed swimming slowly on the surface in severe stress on this date. A large mortality occurred shortly thereafter forcing termination of adult collections. Cause and nature of the mortality will be discussed in a later section. Thus, spawning in 1968 apparently occurred from April 30 to May 14 but was very limited. Most fish retained their sex products and died prior to spawning.

Environmental Factors Associated With Spawning

Numerous environmental factors have been found to stimulate spawning behavior and ovulation in vertebrates. Light, temperature and rainfall have frequently been implicated as stimuli influencing teleost spawning. Pickford and Atz (1957) discussed more subtle environmental changes such as rate of stream flow, turbulence, turbidity and chemical conditions which are of critical importance in triggering fish spawning but are more difficult to isolate for examination. Many of these factors are obviously influenced by changes in temperature, rainfall and light, so that a complex

interaction is involved.

Data on temperature and rainfall at Clear Lake were analyzed to determine possible influence of these factors on yellow bass spawning (Figures 4 and 5). Little rainfall occurred in 1967 during the period when functionally mature female bass were collected. Maximum precipitation recorded was 9.4 mm on May 28. Precipitation was slightly higher during the 1968 spawning period (59.0 versus 14.0 mm in 1967), but was well distributed over the period in frequent light rains. Maximum precipitation on a single day was 16.5 mm received on May 15. Hence, precipitation did not stimulate spawning activity of yellow bass in 1967 and 1968. Rains which stimulate spawning in certain fishes are more of the torrential type occurring in the tropics (Pickford and Atz, 1957).

In 1967 the spawning activity reported on May 17 coincided with a sharp rise in Clear Lake water temperatures. From May 16 to May 18 water temperature increased from 10.5° to 14.5°C, a rise of 4°C. Another sharp rise from 13.4° to 17.8°C occurred from May 23 to May 27. As mentioned previously, spawning was completed prior to June 2 even though many ova were not ovulated and released. The rapid rise in water temperature (7.8 to 14.5°C) from April 25 to May 3, 1968, coincided with the period when females with mature ovulated ova were first captured. The May 14 collection contained the highest proportion of fish with ovulated ova which was shortly after another rapid rise in water temperature on May 11 to May 13 (10.5 to 13.9°C).

Atchison (1967) captured two free-flowing female yellow bass in Clear Lake on May 23, 1966, and successfully incubated their eggs. A check of

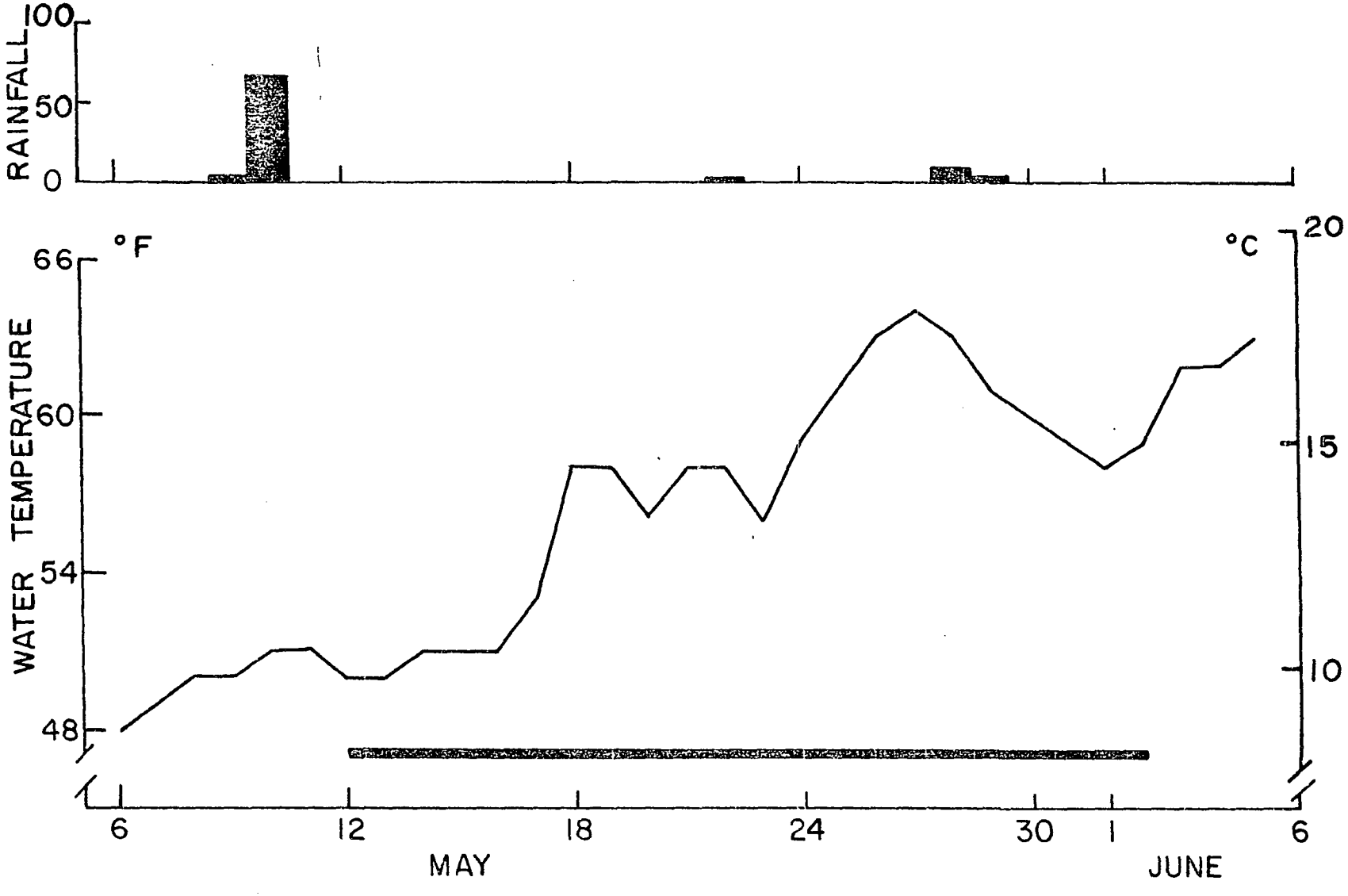

Figure 4. Spawning of yellow bass in relation to Clear Lake water temperature and rainfall (mm), 1967. Period of observed functional maturity is indicated by the broad horizontal line

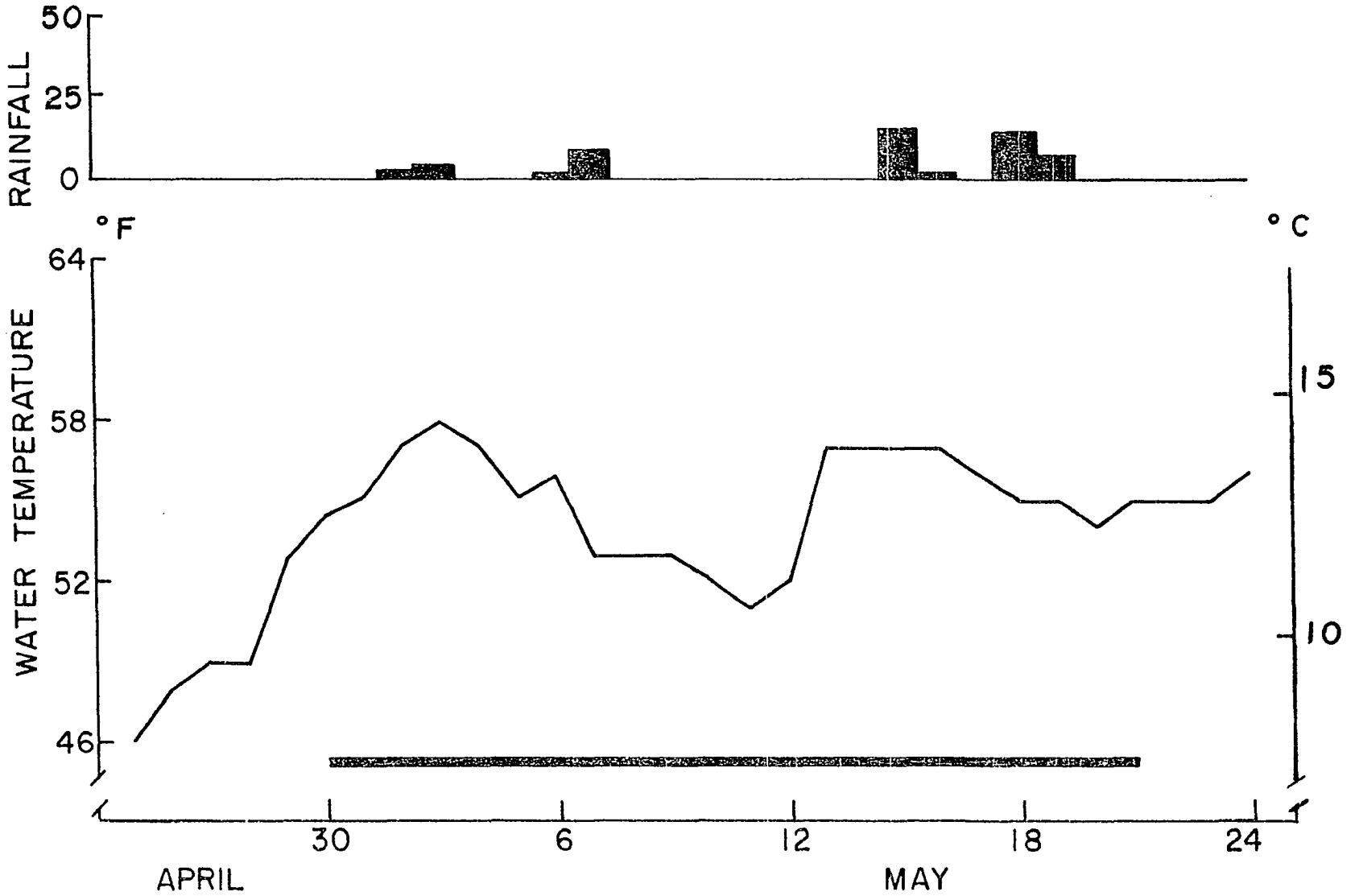

Figure 5. Spawning of yellow bass in relation to Clear Lake water temperature and rainfall (mm), 1968. Period of observed functional maturity is indicated by the broad horizontal line

Clear Lake water temperatures during May 1966 revealed a 3.3-degree rise in temperature from 12.8° on May 20 to 16.2°C on May 23. These data agree with findings in the current study. It appears on the basis of ovulation and female functional maturity that during May a rise in water temperature of 3.5 to 4.5°C over several days when the temperature is approaching 15°C is sufficient to stimulate yellow bass to spawn.

Temperatures of 14.5-15.5°C are 5.5 degrees lower than spawning temperatures reported for yellow bass by Burnham (1909). It might be thought that the temperature difference was due to using records of water temperature taken at the 3-meter depth in the open lake in the present study rather than in the shallow-water spawning area. However, surface temperatures in the spawning area were compared each collection day during April and May with water temperatures at the 3-meter depth recorded at the Clear Lake water treatment plant. Surface temperature over the spawning area averaged only 0.3°C warmer than treatment plant temperatures.

Other species in the genus Morone have been reported to spawn at temperatures around 15°C. Sheri and Power (1968) reported that white perch, Morone americanus, spawn when temperatures are between 11.1° and 15°C (52-59°F). A review of the literature by Albrecht (1964) indicated that striped bass will commence spawning on most areas at 14.5°C (58°F) and reach peak activity at 15.5-18.4°C (60-65°F). Eggs hatch in two days or less at these temperatures. Riggs (1955) stated that white bass separate into unisexual schools for spawning when water temperature approaches 12.8 to 15.5°C (55-60°F). Eggs hatch in 46 hours at 15.5°C (60°F). Yellow bass eggs require 2 to 2-3/4 days to hatch at temperatures from 17.2 to 21.1°C (63-70°F) (Atchison, 1967). Burnham (1909) reported

an incubation period of 4-6 days at 21.1°C (70°F).

Mean monthly water temperatures were lower during the spawning season in 1967 than in 1968. Mean temperatures for April and May were 9.0° versus 9.4° and 12.4° versus 13.1°C respectively. Temperature differences in the two years were more apparent during the first half of May (Figures 4 and 5). Average water temperature for the period from May 1 to May 15, 1967 was 9.8°C in contrast to 12.7° for the same period in 1968. Initial collection of functionally mature females reflected the temperature difference. Female fish functionally mature and containing mature transparent ova were first captured April 30 in 1968 and on May 12 in 1967. Hence, spawning commenced two weeks earlier in 1968 than in the previous year although differences in the time male fish moved into the spawning area were not as readily apparent (Figure 3).

Culture Possibilities

Large numbers of mature and near-mature female yellow bass were obtained from deep water during the spawning period in the present study. Helm (1958) and Atchison (1967) had considerable difficulty in capturing ripe females, presumably because they were collecting only over the spawning areas. Procurement of mature females was not a serious problem in Clear Lake if females were sought in deep water.

The present study was not designed to develop a successful method for artificial culture of yellow bass. Gillnets were left in place for sufficient time to obtain adequate samples of fish and were checked only frequently enough to prevent mortality of large walleye which were also netted. The delay of several hours in removing yellow bass with mature

ova from the nets and in transporting fish from the lake to the laboratory was apparently sufficient to cause loss of ova fertility. Stress induced by capture and long struggle in the gillnets presumably was sufficient to cause complete atresia. Ball (1960) reported that even minor environmental stress can cause atresia of developing fish ova.

Four functionally mature female yellow bass were transported to the laboratory on May 12, 1967 immediately after capture and hand spawned. The ova were fertilized and incubated. Hatching did not occur although various stages of cleavage were evident. Several workers have experienced difficulty in successfully incubating yellow bass eggs (Helm, 1958). The probable cause in many of these failures as well as in the current study was failure to fertilize the ova at the proper stage in their development. Stevens (1966) found that striped bass ova were fertile for 60 minutes or less after ovulation. Older ova and immature ova could be fertilized and cleavage would start, but no embryos would survive hatching. He indicated that striped bass ova gradually turn from an opaque to transparent color the last few hours of development. By following closely the increase in transparency, one can extract and fertilize the ova at the proper time. Observations on Clear Lake yellow bass indicate that ova of this species become transparent at maturity in a manner similar to the striped bass. Information now available suggests that culture of yellow bass for research purposes would not be excessively difficult. Females should be sought in deep water, removed from nets shortly after capture, and placed immediately in water under constant aeration to prevent death or atresia. Ova should be stripped and fertilized using the procedure developed by Stevens

(1966). Collecting gear such as midwater trawls would be more suitable than gillnets to reduce the trauma caused by capture.

Aeration of water containing captured yellow bass is important. Since Burnham's description (1909), the peculiar behavior of yellow bass upon capture has become well known. The fish arches the body into a semi-circle, becomes rigid and frequently dies, apparently from physiological shock. Even if the shock is not lethal, atresia of developing ova occurs shortly (Helm, 1958). Atchison (1967) also found that ovaries of mature female bass frequently became sticky homogenous masses of atretic ova shortly after capture. Adult bass were transported regularly in the present study with nominal mortality by placing fish in aerated containers immediately upon capture. Examination of ovaries one and two days after capture revealed no obvious atresia. However, whenever aeration was not provided during transport, ovaries near maturity became completely atretic overnight. Ova that could be extruded came out in gelatinous clumps in an obvious state of deterioration. Jernejcic[4] prevented the normally high mortality of captured young-of-the-year yellow bass by placing the fish immediately in plastic bags partly filled with water containing tricaine methanesulfonate (MS 222) and oxygen.

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[4]Private communication with Frank Jernejcic, Research Assistant, Iowa State University, Ames, Iowa. July 19, 1968.

SEASONAL GONADAL CHANGES

Maturation Cycle

Further insight may be gained into fish reproduction by following the cyclical development of gonads and sex products throughout the year. A method frequently utilized is to determine the ratio of gonad weight to total body weight (Braekevelt and McMillan, 1967). This ratio, expressed as a percentage, is considered an index to the stage of maturity and has been termed the gonosomatic index (GSI) by some workers (Pickford and Atz, 1957). Two weaknesses may be present when using percent body weight as an index of maturity. Varying fullness of the digestive tract causes body weight to fluctuate (LeCren, 1952). Fish with a full digestive tract have a lower gonad-body weight ratio than when the tract is empty. Evacuation of the entire digestive tract is not altogether practical for removing this variable. Hence, a minor portion of the sample variation was due to varying amount of food in the digestive tract. Seasonal variations in amount of stomach contents was not excessive in the present study except that fish collected in November and December had empty digestive tracts. However, mean weight of stomach contents did not exceed 1 percent of total body weight for any month sampled.

Another weakness in using percent body weight is that fish may gain body weight at the same time the gonads are growing rapidly so that increase in gonad size is not reflected in the gonad-body weight ratio. LeCren (1952) found a slight but regular increase in body-minus gonad weight of European perch (Perca fluviatilis) just before spawning. A similar situation in yellow bass will be discussed later.

Gonads of immature yellow bass comprise less than one percent body weight. In the current study gonads of mature fish also shrunk to less than one percent body weight shortly after spawning. Gonads of adult fish ready to spawn comprised up to 16 percent body weight in female bass and up to 8 percent in ripe males. Sample means reached peak values of 11.76 percent among females and 6.34 percent for male yellow bass (Table 1).

The maturity index of female yellow bass increased very rapidly during April and early May, 1967 (Figure 6) reaching a peak in the sample collected May 12. The wide range in maturity index during April and May was a reflection of differences in time of reaching full maturation by individual fish as well as individual variation in amount of body energies converted to sex products. After May 12 the index dropped rapidly so that by the end of June ovaries comprised less than one percent body weight. These data on changes in gonadal size agree with observations presented earlier on time of spawning.

From July to August, ovaries were in a quiescent state. In early August gonads of many adult females acquired a speckled appearance suggesting that oogenesis had commenced. Workers have not been in agreement as to whether oogenesis proper occurs after fish become mature but apparently there are differences among species. Franchi, et al. (1962) concluded that all definitive germ cells of fish are derived from primordial oocytes and that oogenesis continues into adult life in some species but not in others. Oogonial division does not take place in some elasmobranchs and certain teleosts after sexual maturity, but in most

Table 1. Mean body measurements and maturity indexes of Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Females				Males			
	Number of fish	Mean body length (mm)	Mean body weight (g)	Mean maturity index	Number of fish	Mean body length (mm)	Mean body weight (g)	Mean maturity index
1967								
4/6	33	204	136	4.76	29	196	116	2.89
4/20	44	203	143	6.86	41	190	112	4.34
4/27	9	203	146	6.29	20	183	92	3.45
5/4	16	201	148	8.82	8	194	124	5.72
5/12	27	201	147	11.76	66	193	122	6.34
5/24	23	201	139	8.18	25	190	111	5.34
6/2	30	202	142	6.36	42	197	124	4.81
6/8	29	196	122	5.00	33	194	121	4.37
6/14	46	195	121	3.76	21	195	120	4.17
6/22	28	196	119	1.26	33	194	119	2.54
6/29	29	196	121	0.66	29	197	124	0.96
8/3	21	193	115	0.51	10	193	108	0.12
8/28	14	200	119	0.76	14	195	108	0.20
9/25	8	199	115	0.94	12	191	100	0.33
10/23	35	202	121	1.70	34	193	104	1.38
11/22	19	196	112	1.71	23	200	113	1.41
12/18	29	202	122	1.82	17	198	120	1.25
1968								
1/30	37	200	109	2.10	14	194	101	1.40
2/26	29	199	124	2.38	26	193	111	1.70
3/18	38	196	108	2.38	32	191	97	1.60
4/1	35	197	112	3.01	29	194	106	2.42
4/15	17	194	105	4.19	21	191	98	3.45
4/29	16	196	113	5.12	15	193	108	4.69
5/6	25	193	104	6.38	30	191	97	4.62
5/10	8	192	105	7.03	18	193	105	4.91
5/13	30	195	109	8.36	30	191	96	4.81
5/20	20	196	108	6.07				

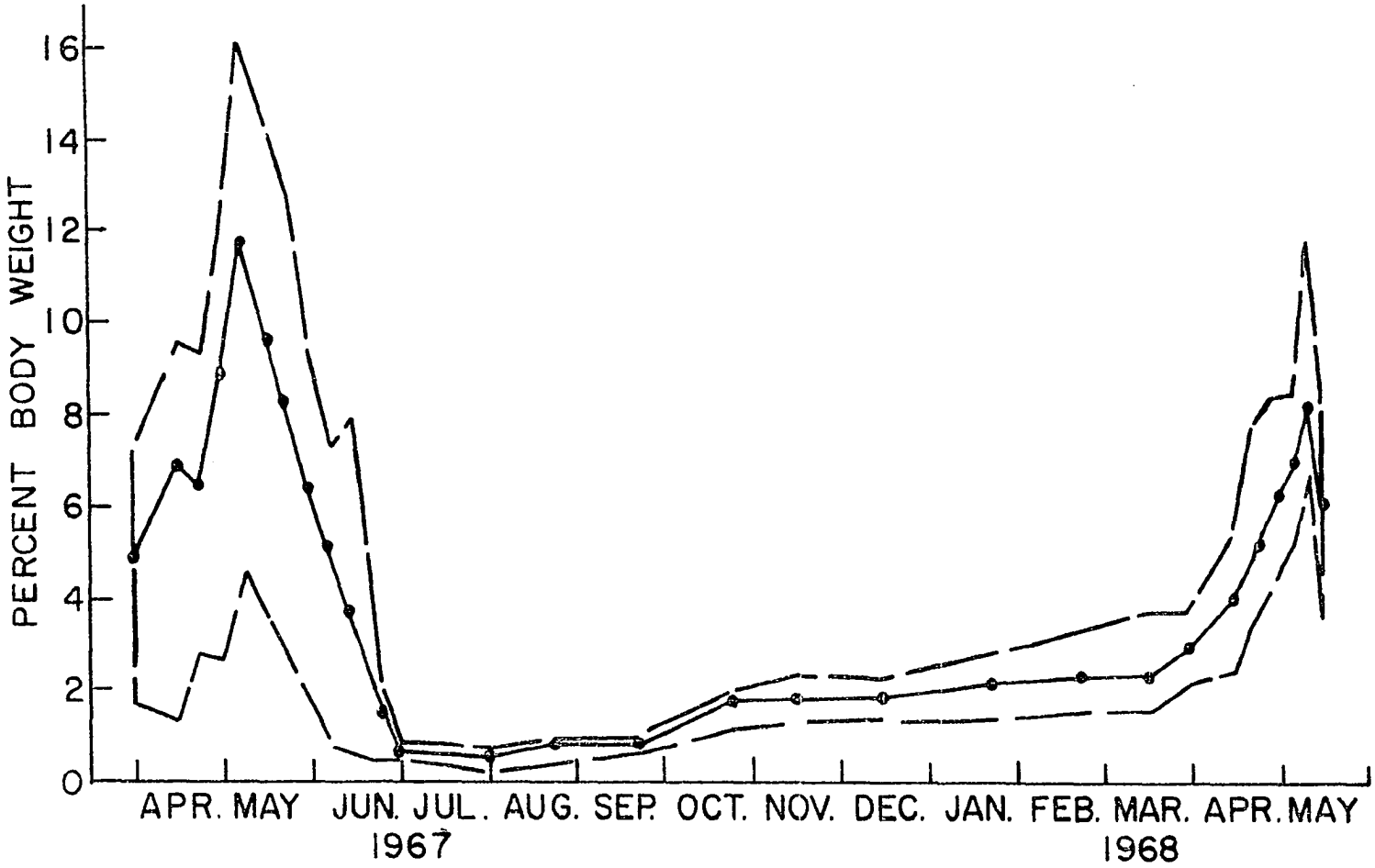


Figure 6. Maturity index of Clear Lake female yellow bass over 180 mm total length expressed as percentage of body weight consisting of ovaries, 1967-1968. Solid line connects sample means; broken lines enclose sample range

teleosts oogenesis occurs cyclically, with a peak after each spawning season. Craig-Bennett as quoted by Franchi (1962) reported that many oogonial divisions were apparent in the three-spined stickleback, Gasterosteus aculeatus, shortly after spawning. A small number of oogonia could be detected at other times of the year also. Stickleback oogonia grow into primary oocytes from July to September. Secondary yolk formation occurs between September and May when spawning takes place. Hann (1927) found oogonial division occurring in Cottus bairdii during May, shortly after spawning. Available information suggests that yellow bass commence oogenesis in August and September. In late September secondary yolk formation or vitellogenesis commences and by late October ovarian weight begins to reflect the increase in ova size. Ovaries of females collected October 24, 1967 had increased slightly above the one-percent body-weight resting level. Gonad growth from October to March proceeded at a slow pace. In early April ovarian weight increased very rapidly reaching a peak of 8.36 percent mean body weight on May 13, 1968. Some spawning apparently occurred shortly prior to this date, as suggested by the presence of functionally mature fish and ovulated ova, but was obviously of a very limited nature. The 1968 maturity index at spawning was 30 percent below that of the 1967 population. At functional maturity on May 12, 1967, ovaries of 27 females ranged from 4.3 to 16.0 percent body weight with a mean of 11.8 percent; whereas, 30 females collected May 13, 1968 had ovaries ranging from 6.9 to 11.9 percent body weight with a mean of 8.4 percent (Figure 6).

The maturation cycle of male yellow bass paralleled in general the

female cycle (Figure 7). A difference in size of fish in the samples was not the cause of the apparent low maturity index on April 26. As mentioned previously, the gonad-body-weight ratio was independent of body size within the range of fish used. Mean total length of female fish in the samples collected April 20, April 27 and May 4 were 203, 203, and 202 mm respectively. Obviously gonadal weight of individual fish did not drop during this period. The drop was attributed to sampling variation because the mean maturity indexes for samples collected April 20 and 27 were not statistically different at the 0.30 probability level ($t = 0.91$).

The male maturity index reached a peak in the May 12 sample similar to the female index but decreased more slowly. The mean maturation index for 65 male yellow bass on that date was 6.34 percent with a range of 1.13 to 8.02 percent body weight. Male gonads were smaller at maturity than female gonads. By mid-June the male index had decreased to 66 percent of its peak value but the female index was only 32 percent of the May 12 level. Male fish remaining ripe over a longer time assure proper fertilization of early as well as late deposited ova. By the end of June male gonads had also entered the quiescent state, weighing less than one percent body weight, and remained at that level until September. Coloration changes from transparent to creamy white in conjunction with increased growth rate suggested that spermatogenesis commenced the latter part of September. Harrington (1956) also found that the banded sunfish, Enneacanthus obesus, completed spermatogenesis in the autumn. By October 23 yellow bass males were functionally mature. Numerous spermatocytes and spermatids were present in the milt but no mature spermatazoa were observed. Microscopic examination of the milt in November revealed numerous motile spermatozoa.

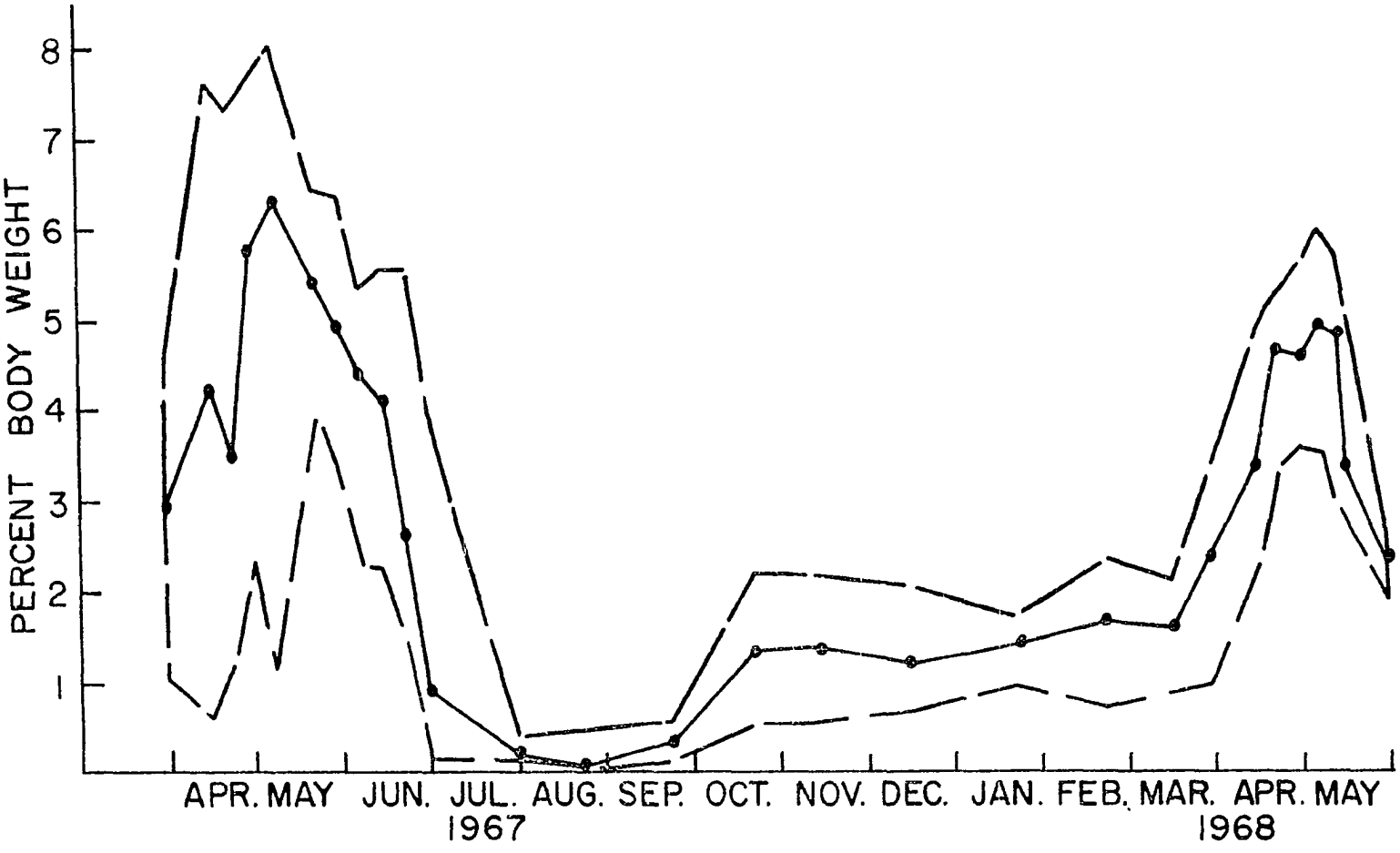


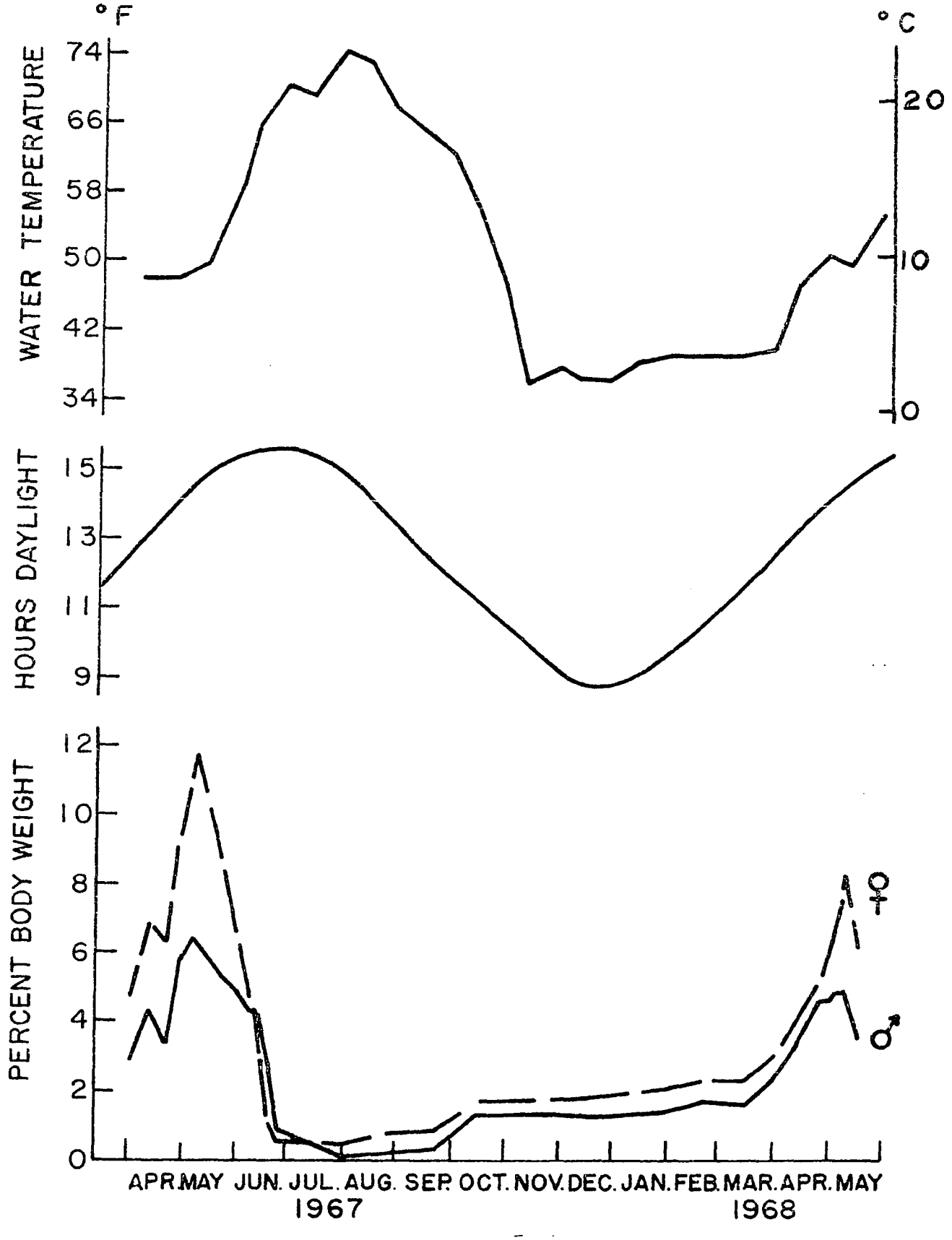
Figure 7. Maturity index of Clear Lake male yellow bass over 170 mm total length expressed as percentage of body weight consisting of gonads, 1967-1968. Solid line connects sample means; broken lines enclose sample range

Cooling water temperatures with resulting ice cover caused a slight regression in gonadal development by December. Testes were shrunken and no longer functionally mature. From October to March the male maturation index changed little but commenced a rapid rise the latter part of March coincident with spring turnover in the lake. Ice cover left the lake on March 17. Male yellow bass collected March 19 in 4°C water became functionally mature upon warming to room temperature. Spermatozoa were highly motile and numerous. The male maturity index peaked on May 10 in 1968 at a level 23 percent lower than the maximum measured in 1967.

With minor variations, the annual reproduction cycle agreed closely for both sexes. Gonadal development commenced in the autumn, went through a slow growth condition during the winter months, followed by a rapid growth in April and May. Upon spawning, gonads dropped quickly to a resting stage and appeared similar to immature gonads. Oogenesis was evident by midsummer and spermatogenesis by early fall.

Environmental factors regulating the annual cycle of gonadal development have been studied by numerous workers (Pickford and Atz, 1957). The annual cycle in day length working indirectly through the endocrine system has been proven in many instances to regulate the gonadal development cycle. Water temperature is also important. Both day length and water temperatures appeared to influence the yellow bass maturation cycle (Figure 8). Gonad weight commenced rising shortly after the autumnal equinox and continued gradually through the winter months. Colder temperatures apparently caused slight regression of testes in December as mentioned earlier. Pickford and Atz (1957) described the influence of temperature on

Figure 8. Relation of yellow bass maturity index to day length and Clear Lake water temperature, 1967 to 1968. Male yellow bass represented by solid line; females by dotted line. Water temperature presented as semi-monthly mean

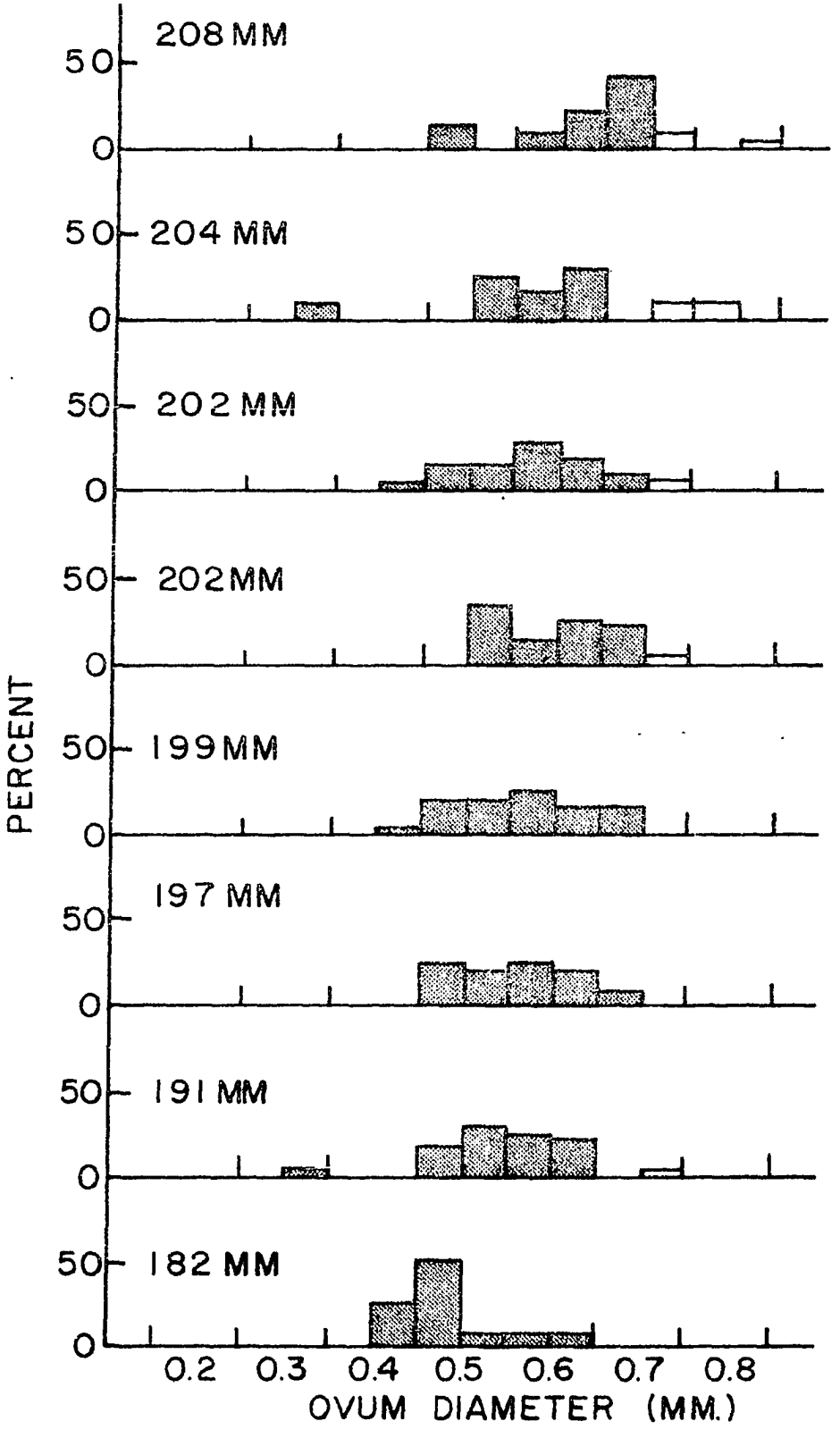

°F
°C
WATER TEMPERATURE
74
66
58
50
42
34
20
10
0
HOURS DAYLIGHT
15
13
11
9
PERCENT BODY WEIGHT
12
10
8
6
4
2
0
♀
♂
APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY
1967
1968

ripening and concluded that low temperatures halted maturation through inadequate production of gonadotropin. Whether low temperature influences the pituitary directly by lowering metabolism within the gland itself or by reducing secretion of releasing factors within the central nervous system is not certain. The rapid increase in gonadal development in the spring was attributed mainly to increasing water temperature. Day length was similar in 1967 and 1968 but female yellow bass were ready to spawn some two weeks earlier in 1968 than in 1967. As mentioned in the section on spawning time, mean April-May temperatures were higher in 1968 than in 1967.

Ovum Size and Development

Further indication of spawning habits and duration of spawning may be gained by measuring diameter of eggs in the ovaries (Brown, 1957). Fish that have an extended spawning period (fractional spawners) have ova of varying size within the ovary; whereas, fish that spawn only once contain developing ova of similar size. In 1967 and 1968 Clear Lake yellow bass contained ova in varying stages of development at spawning. Mature transparent ova along with opaque ova were readily visible in the ovary at maturity, giving it a mottled appearance. The size frequency of ova was determined by measuring 20 ova selected at random from ovaries of eight mature females collected May 14, 1967 (Figure 9). Total body length of the specimens ranged from 182 to 208 mm. Mean size of ovum was directly related to size of fish. Range in ovum diameter and standard deviation about the mean size was of similar magnitude for all fish except one (204 mm). The coefficient of variation about the mean ovum diameter (0.49 mm)

Figure 9. Size frequency of ova in samples from eight female yellow bass collected at Clear Lake, May 12, 1967. Total body length given for each fish. Clear portion of histogram represents mature transparent ova


208 MM
204 MM
202 MM
202MM
199MM
197 MM
191 MM
182 MM
50
0
PERCENT
0.2
0.3
0.4
0.5
0.6
0.7
0.8
OVUM DIAMETER (MM.)

for the combined sample was 5.5 percent. Thus, on the basis of range in ovum size, female yellow bass had the capacity to spawn more than once within the spawning season if all ova were brought to mature size and spawned. Whether females actually spawned several times within the season was not determined. Nikolsky (1963) cautioned against concluding that a species is a fractional spawner because of the presence of small and large ova in the ovary. In many fishes the smaller ova remain in the ovary after spawning and are gradually resorbed. Also, true fractional spawners usually have several distinct size groups of developing ova present in the ovaries which was not true of the yellow bass.

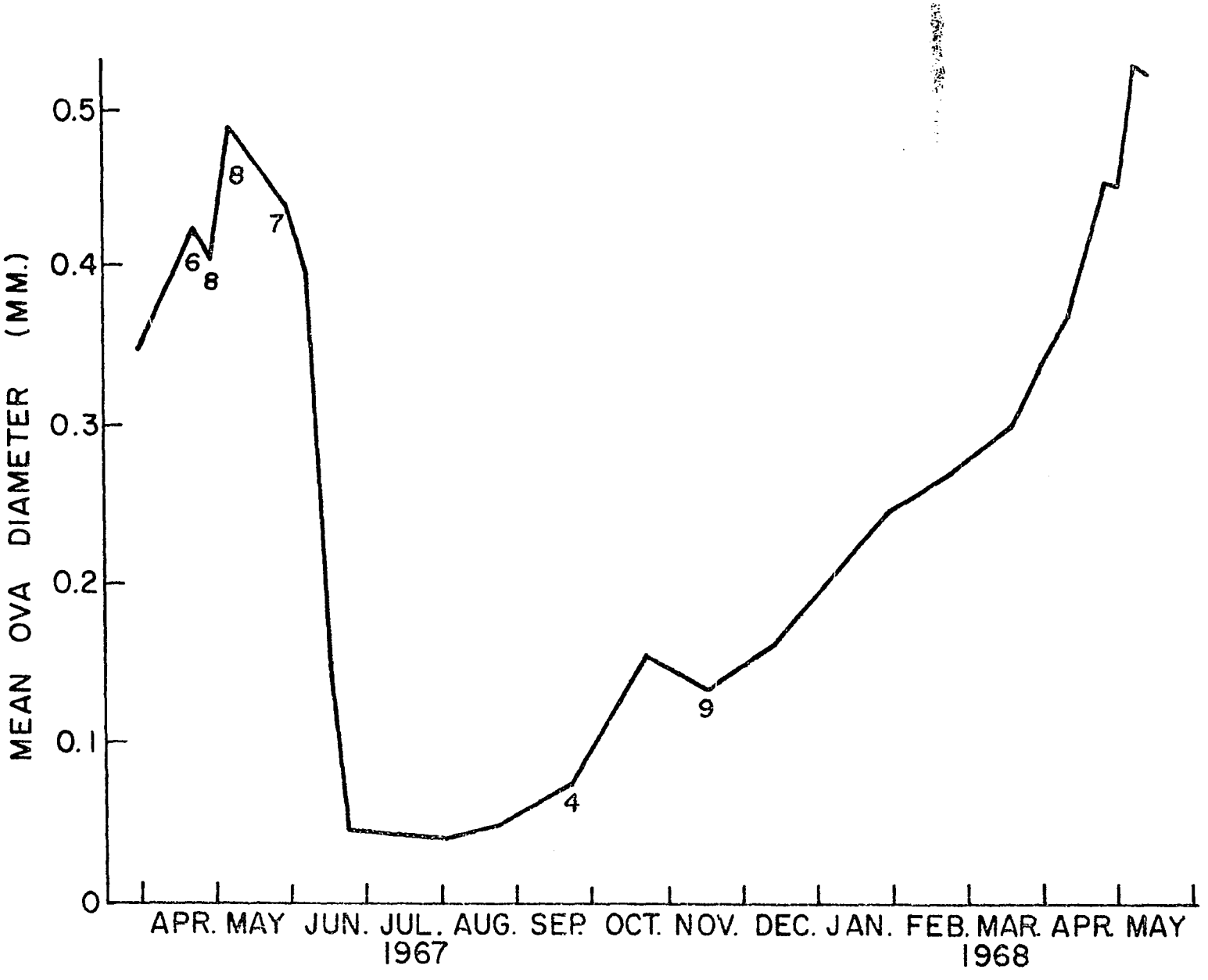
Variation in mean size of ova throughout the year was also determined from collected ovaries. Prior to measuring ovum diameter, the possibility that ovum size differed in the two ovaries was examined. Mean diameter of 30 ova each from the left and right ovaries of 27 females collected May 12, 1967 were compared. At the 0.50 level of probability ($t = 0.054$) the hypothesis could not be rejected that mean size of ova was similar in both ovaries of a given fish. Hence, center sections from either the left or right ovary were used for determining mean ovum size. Lewis and Bonner (1966) also found no difference in size of maturing ova among sections of the same ovary or between left and right ovaries of striped bass.

Henderson (1963a) used ovum diameter as an index of ovarian development in brook trout. She found that the secondary growth phase of ova began in July following the summer solstice, and was completed by mid-October soon after the autumnal equinox. Once secondary development of

brook trout ova was initiated, growth continued at a regular rate to maturity. In yellow bass an initial rapid growth in size of ova during October appeared to cease in November and December (Figure 10) although mean size of ova was not significantly different for October and November ($p = 0.05$; $t = 1.93$). If a pause in ovum growth did occur during early winter, temperature fluctuation was probably the factor involved. Water temperatures dropped rapidly during late November and reached a minimum for the year just before ice covered the lake in early December. Temperatures then increased slightly and were essentially unchanged during the period of winter ice cover (Figure 8). If the fish were affected by temperature, they had made adjustment by January 20 because ova were again increasing rapidly in size. Ensuing growth continued steadily until ovulation. Lewis and Bonner (1966) measured ovum diameter of striped bass collected periodically during the year in North Carolina and found that ova grew continually from September to the May spawning period. Ovum growth was very rapid during April and May. Available data on yellow bass suggest that gonadal development and ovum growth was relatively continuous from inception to maturity.

During the last few weeks of development, ova grew rapidly and appeared to reach a certain size before ovulation occurred. Mean size of ova decreased even more rapidly upon spawning indicating that the larger ova had been shed. Changes in mean ovum size (Figure 10) followed closely the maturation index based on gonad-body weight ratio (Figure 6) although mean ovum diameter was a better indication of time when spawning occurred in the two years. In the 1968 sample, peak female

Figure 10. Seasonal change in diameter of yellow bass ova from Clear Lake collected 1967 to 1968. Solid line connects sample means of 20 to 30 ova from 10 fish. Samples containing less than 10 fish are noted on the figure


MEAN OVA DIAMETER (MM.)
0.5
0.4
0.3
0.2
0.1
0
6
8
8
7
4
9
APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY
1967
1968

maturity index was several percent below the 1967 level when spawning took place (8.4 versus 11.8 percent). However, mean ovum diameter reached a similar peak in size in both years coincidentally with spawning. Whenever mean diameter of all maturing ova exceeded 0.4 mm, ovulation with ensuing spawning appeared to be imminent. It should be noted that the above measurements were taken from preserved ova and do not reflect the size of fresh mature ova. Most mature, ovulated ova in preserved condition measured 0.65 mm or larger. Atchison (1967) and Burnham (1909) reported that unpreserved mature ova at spawning averaged 0.75 to 0.77 mm. Measurement of 102 mature ova in fresh condition from four females collected in 1967 indicated a mean size of 0.80 mm with a standard deviation of 0.11 mm and a range from 0.66 to 1.18 mm.

Ovum Size Versus Body Length

Ovum size at maturity has frequently been found to correlate positively with fish body size (Rounsefell, 1957). Larger fish tend to produce eggs of a larger size. Egg size within a species is important because fry hatched from large eggs may have a better chance of survival than fry hatched from small eggs (Svärdson, 1949; Privolnev, 1960). Egg size is related to nutrition according to Nikolsky (1963) but Scott (1962) found that egg size in kamloops trout, Salmo gairdneri, was genetically controlled and that only egg number was affected by nutrition.

Correlation coefficients of body length versus ovum size were computed for most samples of yellow bass (Table 2). Significant relations were found in four samples. In the October 1967 sample, correlation between body length and mean ovum size was significant at the 0.05 level

Table 2. Correlation of mean ovum diameter with total body length of adult Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Number of fish	Mean body length (mm)	Standard deviation (mm)	Mean ovum diameter (mm x 85)	Standard deviation (mm x 85)	r value	Significance level
1967							
4/20	6	201	9.4	35.0	4.4	0.26	NS
5/4	8	201	9.9	33.4	4.4	0.74	0.05
5/12	8	198	8.2	40.4	4.1	0.90	0.01
5/24	10	199	10.7	37.6	4.2	0.49	NS
6/2	7	201	6.1	36.4	1.1	0.27	NS
6/8	10	200	11.1	32.8	2.7	0.03	NS
9/25	4	200	7.7	6.4	0.8	0.00	NS
10/24	10	199	8.6	13.3	2.6	0.76	0.05
11/22	9	198	10.2	11.3	1.9	0.33	NS
12/19	10	200	8.9	13.5	1.6	0.00	NS
1968							
1/30	10	199	9.9	20.5	2.6	0.10	NS
2/27	10	198	7.4	21.3	1.7	0.63	0.05
3/19	10	199	7.4	25.0	2.9	0.26	NS
4/2	10	197	7.1	28.4	1.0	0.45	NS
4/16	10	196	6.7	32.6	3.8	0.20	NS
4/30	10	195	7.2	37.6	4.8	0.08	NS
5/7	10	197	8.6	37.1	4.1	0.08	NS
5/14	10	195	8.6	43.9	7.8	0.24	NS
5/21	10	195	5.9	42.8	2.7	0.12	NS

($r = 0.76$). One explanation for the relation being significant at this time is that bigger fish, being repeat spawners, might start secondary ova development earlier than fish commencing ovarian development for the first time. A significant correlation ($p = 0.05$; $r = 0.63$) was found in the late February sample also. Collections on May 4 and May 12, 1967, were significant at the 0.05 ($r = 0.74$) and 0.01 ($r = 0.90$) levels respectively. Hence, 50 to 81 percent of the variation in ovum diameter at spawning time could be explained by difference in body size in 1967 but not 1968. It is not known whether small adults spawned smaller ova than large fish or were merely slower in reaching maturity. It appeared from observations that large fish were functionally mature and ready to spawn earlier than the small adults. There was also some indication that smaller fish in the samples failed to ovulate a significant portion of their ova as will be discussed later.

Hickling (1935) found that immature hake, Merluccius merluccius, had a seasonal variation in ovum diameter which coincided with the ovarian cycle of adult fish, but obviously no ova were brought to maturity. A similar condition was apparent in yellow bass. Numerous female fish under 180 mm total length possessed enlarged ovaries at spawning time but ova were obviously too small in diameter to reach maturity in that year. Some fish over 180 mm were also not fully mature in the sense that only a small portion of the developing ova reached full size.

Correlation between mean ovum size and body length was not significant in samples of mature fish in 1968 possibly because very few ova matured in that year. Based on conditions in 1967 when reproduction was

successful, positive correlation apparently exists between mean size of ova and body size in mature yellow bass. The significant relation is attributed to large fish bringing a greater portion of their ova to maturity rather than an inherent difference in mature ova size based on size of female.

Ovarian Weight

Ovarian weight has occasionally been used as an index of reproductive capability in the sense that gonad weight estimates the ability of the female to mobilize material for reproduction (McFadden, et al.; 1965). The use of ovarian weight as a measure of fecundity overcomes the influence of differences in ovum size which is possibly related to survival. Analysis of data collected in May, 1967 from yellow bass revealed that at maturity, gonad weight closely reflected mean size of ova present (Table 3). Even in 1968 when fewer ova reached maturity the correlation between mean ovum size and ovarian weight was significant at the 0.05 level.

The reason for the declining correlation as the spawning season passed was apparent upon plotting ovum size versus ovarian weight for each sample. At spawning, the fish with larger ovaries (usually the larger fish) had ova of greater mean size than fish with small ovaries. As the large fish spawned, they shed the large mature ova and retained ova that were undersize. Their ovaries then shrunk to the point where they were of similar weight to ovaries of small but still unspawned females. Thus, the correlation between mean ovum size and ovary weight decreased

Table 3. Correlation of mean ovum diameter[a] with ovarian weight of adult Clear Lake yellow bass collected 1967 and 1968

Date of collection	Number of fish	Ovarian weight (g)	Standard deviation (g)	r value	Significance level (p)
1967					
5/4	8	13.3	5.1	0.91	0.01
5/12	8	15.4	6.1	0.88	0.01
5/24	10	11.1	3.1	0.84	0.01
6/2	7	9.9	2.8	0.66	0.05
6/8	10	5.7	1.8	0.38	NS
1968					
5/7	10	6.7	1.1	0.66	0.05
5/14	10	10.3	2.2	0.42	NS
5/21	10	6.5	1.2	0.34	NS

[a]See Table 2 for values.

with time. In 1968 spawning was blocked so that ovarian weight did not change, but the correlation declined because ova within smaller ovaries increased in size instead of larger ovaries decreasing in weight as the result of spawning.

OVA PRODUCTION

Fecundity Determination

The most suitable method for estimating fecundity varies among species of fish depending upon number and size of ova produced. Fecundity is usually expressed in terms of the number of ova produced by a given organism because each ovum is potentially a new individual. In certain species which produce large ova such as some salmonids, total count of all ova present is not difficult (Henderson, 1963b; Bulkley, 1967). Other more fecund species such as the sardine (MacGregor, 1957), the plaice (Bagenal, 1966) and white bass (Riggs, 1955) require subsampling of the numerous ova unless automatic counting devices as used by Boyar and Clifford (1967) are available.

In the present study, total count of yellow bass ova was precluded by the large number of minute ova produced. The gravimetric method was suitable for mature ova which were loose within the ovary or could easily be parted from the ovarian membrane. A sample of the ovary was dried to constant weight, weighed, and the number of ova present in the sample determined. The method was unsuited for estimating yellow bass ova which were just starting development. The immature ova could not be separated from the membrane after drying. Weight changes during the weighing process made it impractical to weigh fresh material. Hence, the gravimetric method was used only as a check on the fecundity estimates presented here.

A volumetric method was more suited for measuring yellow bass

fecundity. Ova numbers based on the mean of four aliquots provided an acceptable estimate of fecundity although considerable sampling variation was present. Precision was not as high in some samples as is normally desired. Coefficients of variation ranged from 6.2 to 25.0 percent in the sample collected October 24, 1967 and from 4.0 to 11.5 percent in the sample collected February 27, 1968 (Table 4). The coefficient of variation in fecundity estimates for the average fish was approximately 8 percent.

Table 4. Coefficients of variation (percent) in estimates of Clear Lake yellow bass fecundity based on four aliquots for each fish collected from 1967 to 1968. Ten fish were sampled each date

Date of collection	Coefficient of variation	
	Mean	Range
1967		
5/12	11.5	4.4 - 17.5
6/4	7.1	3.3 - 16.7
10/24	10.4	6.2 - 25.0
12/19	8.7	3.8 - 16.0
1968		
2/27	7.0	4.0 - 11.5
4/30	7.7	3.1 - 18.1

Fecundity Versus Body Length

The numbers of ova produced within a species is usually related to body size. Large females produce more mature ova than do small females. In the samples of yellow bass considerable variation was evident in the

number of ova produced by similar-size fish (Table 5). Some fish with a total length of 195 mm contained more ova than fish with a length of 205-210 mm. Many of the largest fish contained smaller gonads and fewer ova than average. Although age of fish was not determined in the current study, the lower ova production in these large fish was attributed to senility or to poor body condition. Sheri and Power (1968) found a decrease in rate of egg production in the largest and oldest white perch. They also found considerable variability in fecundity among fish of similar length. The size range of fish selected for the present study (180-230 mm) also eliminated many small maturing females so that the fecundity body-length relationship was not as obvious as reported for other species. Justification for not including small females with enlarging gonads was based on the observation that many of these fish failed to contain ova of spawnable size. As mentioned earlier, cyclic gonadal development is not always an indication that the fish is maturing. Females smaller than 180 mm were not included in the samples to avoid biasing downward the gonad-body weight ratio used to follow the maturation cycle. Hence, several factors caused the correlation of fecundity to body length of Clear Lake yellow bass to be lower than expected.

In the sample of ripe females collected May 12, 1967, the relation between ova number and body length was significant at the 0.05 probability level, but only 50 percent of the variation in fecundity could be attributed to body length. After the 1967 spawning season, a negative correlation ($r = -0.22$) was apparent between ova numbers and body length, agreeing with the conclusion given earlier that the smaller females retained their eggs and did not spawn. Correlation was also not

Table 5. Potential fecundity of Clear Lake yellow bass collected 1967 to 1968 in relation to body total length. Number of fish in parenthesis

Date of collection	Mean body length (mm)	Mean fecundity	r value	Significance level	Mean fecundity at body length			
					180-189	190-199	200-209	210-219
1967								
5/12	199	203,800	0.72	0.05	51,300 (1)	221,000 (4)	213,300 (4)	249,200 (1)
6/14	198	72,200	-0.22	NS	94,600 (2)	49,800 (3)	79,900 (3)	80,900 (2)
10/24	203	112,600	0.26	NS	-	107,100 (5)	114,000 (3)	124,400 (2)
12/19	198	148,800	0.81	0.01	127,700 (2)	128,700 (3)	149,200 (5)	-
1968								
2/27	199	127,500	0.53	NS	-	119,300 (5)	135,700 (5)	-
4/30	195	113,600	0.32	NS	109,300 (2)	98,200 (4)	130,900 (4)	-

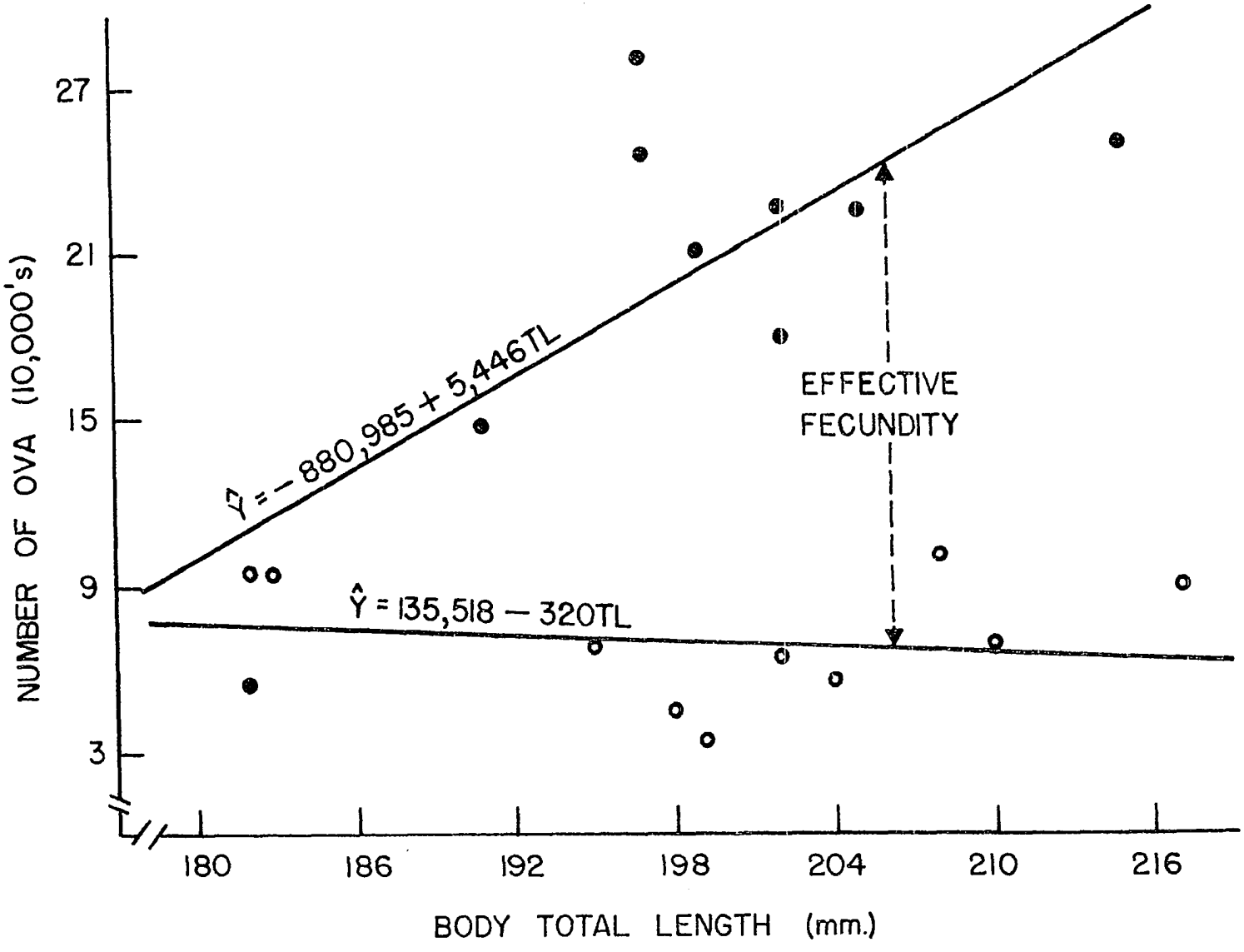
significant for mature fish in the sample collected April 30, 1968 when spawning was again impending.

Potential Fecundity

The average number of ova estimated to be present in yellow bass ovaries examined just prior to spawning time in 1967 (May 12) was 203,800 ova for a female measuring 199 mm total length and weighing 142 grams. Hence, in terms of unit measure, the average yellow bass produced 1,023 ova per millimeter of total body length or 1,439 ova per gram of body weight. Ova number varied within the sample from 51,300 for a fish measuring 182 mm and weighing 101 grams to 282,400 ova in a female 197 mm long and weighing 149 grams. The largest fish in the sample measured 215 mm in length and weighed 178 grams but contained only 249,200 ova.

All ova in advanced secondary development were included in the fecundity estimates, but only a portion actually reached maturity and were ovulated. Thus, the ova estimates represented potential fecundity rather than the number of ova shed. Differences between potential and effective fecundity were apparent upon comparing ovary contents before and after the spawning period. A comparison was made between ova numbers within the gonads when spawning was impending (May 12) in 1967 with the numbers of ova still present well after spawning activity had ceased (June 14). After spawning, ovaries of the average-size female still contained over 70,000 unspawned ova or approximately 34 percent of the total number present when spawning commenced (Figure 11). The body length-fecundity relationship for prespawners was expressed by the formula:

Figure 11. Estimated number of ova in female Clear Lake yellow bass collected May 12 (upper line) and June 14, 1967 (lower line). Difference between the two lines represents the estimated number of ova shed in spawning


27
21
15
9
3
NUMBER OF OVA (10,000's)
$\hat{Y} = -880{,}985 + 5{,}446TL$
$\hat{Y} = 135{,}518 - 320TL$
EFFECTIVE
FECUNDITY
180
186
192
198
204
210
216
BODY TOTAL LENGTH (mm.)

$$Y = -880,985 + 5,446TL$$

where Y refers to number of ova (potential fecundity) and TL is total body length in millimeters. In the post-spawning period the relationship assumed a negative slope:

$$Y = 135,518 - 320\ TL$$

Thus, fewer ova remained in the large fish than in the small fish.

The large proportion of unshed ova emphasizes the importance of differentiating between potential and effective fecundity when discussing yellow bass reproduction. The potential fecundity is much higher than the actual number of ova spawned. In Figure 11, potential fecundity is indicated by the top line, atresia by the bottom line, and effective fecundity by the difference between the two lines.

It is apparent that large females spawned a higher percentage of the ova present in their ovaries than did the small females. Weekly comparisons from May to June not shown here supported this observation. The large amount of ova retention agreed also with observations reported previously that gonads of the larger females soon shrank after spawning to a size equal to the ovaries of small fish, and remaining ova were of equal size to ova present in the smaller females.

Further examination of the size of unshed ova provided a separate estimate of effective fecundity in 1967. Size of secondary ova in 27 mature females collected May 12 was compared with ova remaining in gonads of 15 females collected June 14, 1967. A minimum of 60 ova selected at random was measured from each fish. It was apparent, as

mentioned earlier, that only the smaller ova remained in the ovaries after spawning. Few ova larger than 0.6 mm were present in the June 14 sample (Figure 12) whereas 49 percent of ova in the May sample were 0.6 mm or larger. Ova measuring from 0.6 to 0.7 mm were the largest size group in ovaries of fish ready for spawning. Hence, it appeared that essentially all ova larger than 0.6 mm were shed during the spawning period. The comparison is subject to error because a number of atretic ova could have been resorbed by June 4 and continued ova growth was not considered. Spawning was essentially completed by May 23 in 1967, several weeks prior to the June 14 collection. Atretic ova normally take from a few days to several weeks to be resorbed depending on the stage of development (Braekevelt and McMillan, 1967). Thus, the actual number of unspawned ova is unknown. Undoubtedly smaller ova were resorbed first and as many ova under 0.4 mm were still present in the post-spawning sample, most of the larger unshed ova were probably still present also. Possible shrinkage in size of unshed atretic ova was also not considered. In any event, ova still present on June 14 provided a minimal estimate of post-spawning atresia.

An estimate of the number of shed ova was made by determining the number of ova 0.6 mm in diameter and larger present in fish of various size just prior to spawning. Data presented in Figure 9 were used to determine the size frequency of ova for different body lengths (Table 6). Ovaries from a fish measuring 182 mm total length contained no ova 0.6 mm or larger; whereas, ovaries from a 208 mm female contained approximately 138,000 ova of this size. These estimates of effective fecundity were

Figure 12. Size frequency of ova in Clear Lake yellow bass ovaries collected in 1967 when spawning was imminent (May 12) and when spawning was completed for the year (June 14)

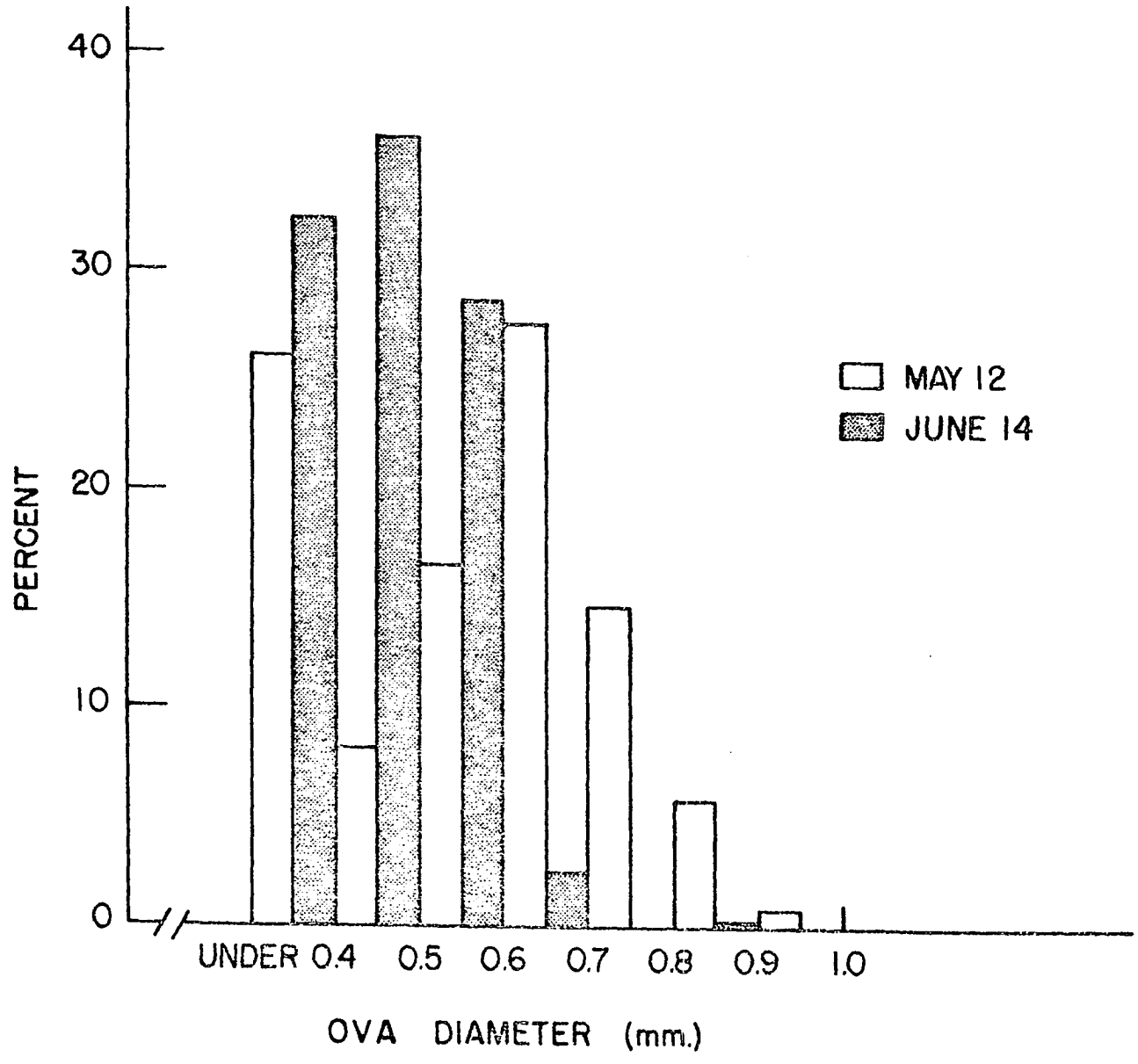

40
30
20
10
0
PERCENT
MAY 12
JUNE 14
UNDER 0.4
0.5
0.6
0.7
0.8
0.9
1.0
OVA DIAMETER (mm.)

Table 6. Data used for estimating effective fecundity of Clear Lake yellow bass based on number of ova larger than 0.5 and 0.6 mm present in ovaries collected May 12, 1967

Total length	Percent of ova larger than		Potential fecundity[a]	Number of ova larger than		Estimated effective fecundity[b]
	0.6mm	0.5mm		0.6mm	0.5mm	
182	0	16	111,200	0	17,680	32,900
191	5	50	159,200	8,000	79,600	81,900
197	10	55	191,900	19,200	105,500	119,400
199	15	55	202,800	30,400	111,500	130,900
202	17	65	219,100	43,800	142,400	148,400
204	20	65	230,000	46,000	149,500	159,800
208	55	85	251,800	138,500	214,000	182,800

[a]Computed from formula: $Y = -880,985 + 5446\ TL$.

[b]Difference between ova counts before and after spawning: $Y = (-880,985 + 5446TL) - (135,518 - 320TL)$.

considerably lower than estimates based on differences between ova numbers in the May and June samples. Factors such as ova growth during the spawning period obviously affected the estimates. Ova growth was very rapid just prior to spawning (Figure 10), and growth probably continued as long as factors stimulating gonadal development were present. Hence, many ova which were under 0.6 mm one week prior to spawning could easily have grown large enough to be ovulated before spawning ceased. The number of ova measuring 0.5 mm and larger in the May sample agreed closely with estimates of effective fecundity based on numbers of shed ova (Table

6). A common regression line fitted both sets of data ($p = 0.01$). Hence, based on number of ova 0.5 mm and larger, mean effective fecundity in terms of body length was approximately 560 ova per mm total length. In terms of body weight, effective fecundity was approximately 835 ova per gram body weight for the average-size fish (ca 199 mm).

Fractional Spawning

It is not uncommon for fish to spawn only a portion of secondary ova present and resorb the balance. Carp commonly exhibit this characteristic (Swee and McCrimmon, 1966), but under favorable circumstances become repetitive (fractional) spawners and eventually spawn all secondary ova present (Nikolsky as quoted by Woodhead, 1960). Fractional spawning has been suggested as one method of increasing individual fecundity (Nikolsky, 1963). The ovary cannot contain all of the ova present if they are of mature size, so only a portion of the ova mature at one time. After initial spawning, additional ova mature and are released. Fractional spawning has survival value because it allows a species to bridge short periods of unfavorable spawning conditions and still reproduce successfully.

The ability to spawn repeatedly is more common in tropical and sub-tropical fishes (Nikolsky, 1963). Frequently a single species will spawn repeatedly in the southern portion of its range and only once further north. It would be interesting to determine if yellow bass exhibit this quality particularly in view of the recently extended range of the species. Fractional spawning in conjunction with high fecundity might be one factor in the successful establishment of yellow bass

northward as reported by Helm (1964). However, it is highly probably that in Clear Lake, temperature and other environmental conditions suitable for spawning occur only briefly so that a large portion of the ova developed for fractional spawning become atretic in certain years.

Apparently fractional as well as complete spawning occurs in white bass. Bayliss (1967) observed mixed ova development in two of seven female white bass examined. The other five females contained ova in a similar stage of development. Riggs (1955) found residual ova in ovaries of all spent white bass examined. Striped bass tend to evacuate all secondary ova present in the gonads at a single spawning (Lewis and Bonner, 1966). Examination of striped bass used for artificial propagation revealed that at maturity the ova are of similar size and degree of transparency. In the normal female, ovulation occurs uniformly throughout the ovary in a very short period of time[5].

Fecundity of yellow bass in 1967 was somewhat higher than fecundity reported for other serranids in terms of body weight. Riggs (1955) found a potential fecundity of 565,000 ova in average-size white bass. The number of ova per gram of body weight ranged from approximately 814 to 1,138. The smallest female examined measured 254 mm (fork length) and contained 242,000 ova. Lewis and Bonner (1966) estimated average striped bass effective fecundity at approximately 176 ova per gram body weight (80,000 per pound) among fish weighing 2 to 16 pounds. Counts of near-mature white perch ova ranged from 143 to 786 per gram body weight

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[5]Personal communication with Robert E. Stevens, North Carolina Cooperative Fishery Unit, N.C. State University, Raleigh, N.C. November 15, 1967.

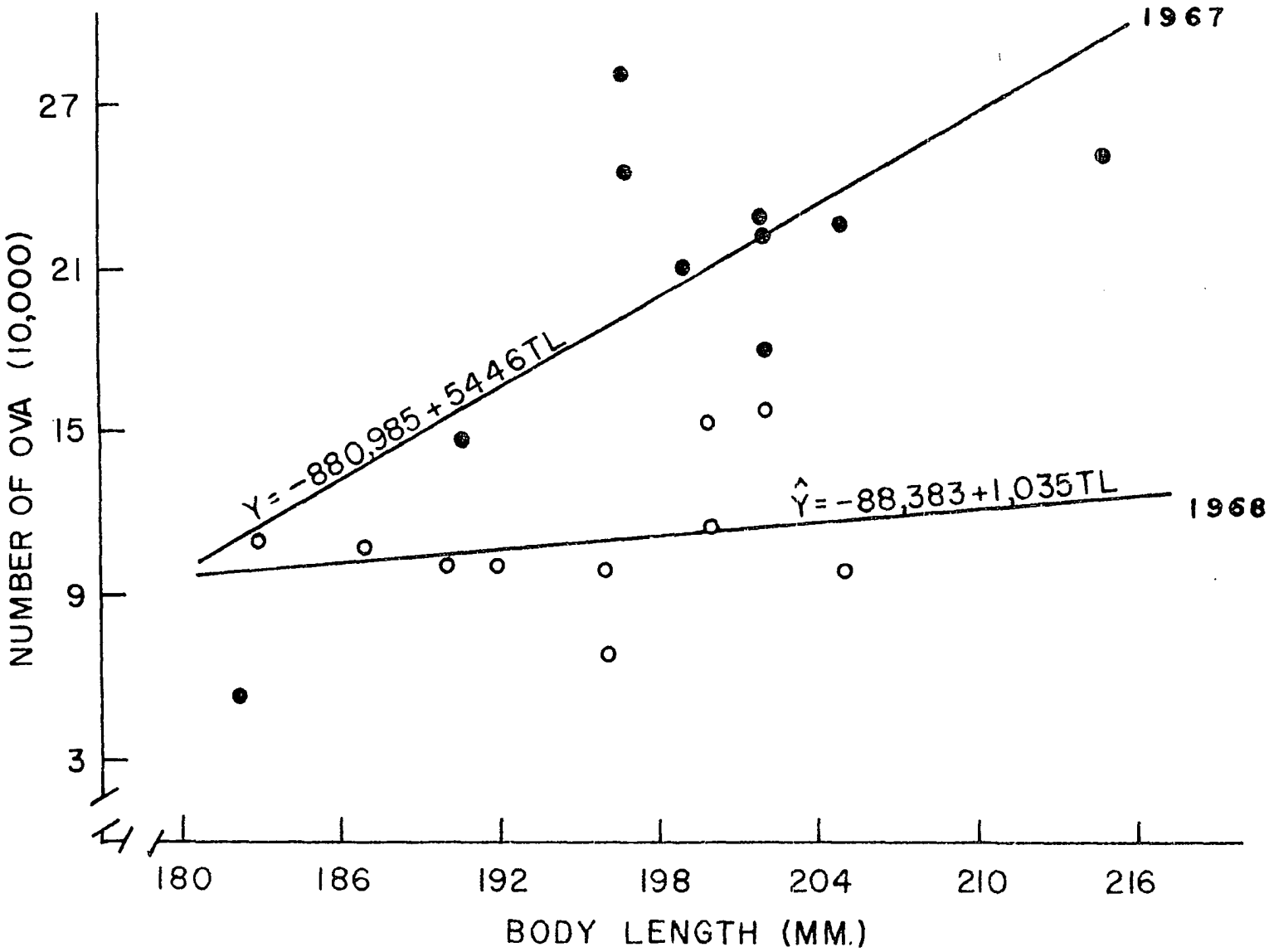
with 551 ova per gram in a female averaging 148.5 grams body weight (Sheri and Power, 1968).

Annual Differences in Fecundity

Potential fecundity was considerably lower in 1968 than in 1967. Ova estimates just prior to spawning in 1967 ranged from 51,300 in a 182 mm female to 282,400 ova in a fish 197 mm total length. The 1968 estimates ranged from 82,400 ova in a fish 196 mm long to 156,000 ova in a female measuring 202 mm in length (Figure 13). Potential fecundity in 1968 was expressed by the formula Y -88,383 + 1035TL in contrast to the 1967 formula Y = -880,985 + 5446TL. The hypothesis that a single regression line could describe potential fecundity in the two years was rejected at the 0.01 level of probability. Hence, fecundity for the two years could not be compared on the basis of adjusted mean fecundity. On the basis of ova production per unit of body length and weight, a yellow bass measuring 199 mm total length produced 1,023 secondary ova per mm body total length or 1,439 ova per gram body weight in 1967, in contrast to 591 ova per mm body length and 1,029 ova per gram body weight in 1968. Fecundity in terms of body length was more indicative of actual differences in the two years because fish were much lighter for their length in 1968. Mean weight for a fish measuring 199 mm in 1967 was 142 grams. In 1968 a female of similar length averaged 114 grams.

The decrease from 1967 to 1968 in estimated effective fecundity was similar to the 30 to 40 percent decrease in potential fecundity. Using the method of calculating effective fecundity based on the assumption

Figure 13. Potential fecundity of female Clear Lake yellow bass collected the week prior to spawning in 1967 (upper line) and 1968 (lower line)


1967
1968
Y = -880,985 + 5446TL
Ŷ = -88,383 + 1,035TL
NUMBER OF OVA (10,000)
27
21
15
9
3
180
186
192
198
204
210
216
BODY LENGTH (MM.)

that all ova 0.5 mm and larger will be spawned, effective fecundity was computed for 1968 (Table 7). There was no apparent relation between body size and the percentage of ova larger than 0.5 mm in diameter in the 1968 sample. Females near the mean length of fish in the sample (195 mm) contained most ova presumably large enough to be spawned.

Table 7. Data for estimating effective fecundity of Clear Lake yellow bass based on number of ova larger than 0.5 mm present in ovaries collected May 12, 1968

Total body length (mm)	Percent of ova larger than 0.5 mm	Potential fecundity[a]	Estimated effective fecundity
182	70	100,000	70,000
187	35	105,200	36,800
190	60	108,300	65,000
192	10	110,300	11,000
196	75	114,500	85,900
196	85	118,600	97,300
200	20	118,600	23,700
200	20	120,700	23,700
202	70	120,700	84,500
205	33	123,800	40,900

[a]Computed from formula Y = -88,383 + 1,035TL.

Mean effective fecundity was estimated at 53,900 ova for the average-size female. In terms of body size, effective fecundity in 1968 averaged approximately 276 ova per mm body length (versus 560 for 1967) or 350

ova per gram body weight (versus 835 for 1967). Hence, the number of secondary ova produced in 1968 as well as the proportion presumably large enough to be ovulated was 40 to 50 percent less than that of 1967. The reduction in ova numbers was related to poorer body condition of yellow bass which will be discussed later.

Based on the regression lines in Figure 13, females 180 mm long contained similar numbers of ova in both years, which would agree with the conclusion that few females around 180 mm actually spawned. Whatever factor influenced the larger fish to produce fewer ova in 1968 did not affect fish 180 mm in length. The probable explanation is that fish this size were immature even though considerable gonadal enlargement occurred. Gonadal enlargement even in a female 180 mm long could be a late adolescent extension of the immature gonadal cycling (Hickling, 1935).

FACTORS INFLUENCING OVA PRODUCTION

Source of Fecundity Variations

The large reduction in ova numbers and gonad size from 1967 to 1968 justified a review of factors regulating fecundity. Differences in fecundity among species is attributed frequently to differences in spawning habits and to the degree of protection afforded the developing egg and embryo. Fish that incubate the fertilized egg internally may produce one to several young at a time. In contrast are those species that produce and broadcast millions of pelagic eggs which float at the mercy of the environment until hatching. Within species, individual fecundity may be regulated by age, body size and growth rate plus factors such as nutrition. Increased fecundity by faster growing individuals reflects an adaptive response to environmental changes mainly to a change in food supply (Nikolsky, 1963). When food is abundant, more ova are brought to maturity and thus, more young are produced to utilize the extra food if still available. The role of nutrition in reproduction is being carefully considered by many workers. Scott (1962) found that fecundity of rainbow trout, Salmo gairdneri, could be altered by manipulating the food supply of maturing fish. McFadden, et al. (1965) related brown trout fecundity to fertility of the aquatic environment. Wydoski and Cooper (1966) found that an infertile stream environment could reduce brook trout fecundity up to 50 percent in females of similar size. Krumholz (1948) found that better feeding increased brood size of the mosquitofish, Gambusia affinis. Woodhead (1960) summarized the

relation between nutrition and the reprcductive capacity of fish and reported that feeding can alter the frequency of spawning as well as the number of eggs produced. Apparently when feeding conditions improve sufficiently carp, which normally resorb up to 35 percent of their eggs, will bring all ova to maturity and release them. Failure of yellow bass in the present study to spawn all secondary ova in 1967 and 1968 could well be related to limited food supply. As mentioned previously, the Clear Lake population has been stunted for some years as a result of overabundance and interspecific competition for food. Temperature fluctuations at spawning might also be related to the ova resorption.

Effective fecundity among individual fish may be regulated at two different stages of development: 1) at the commencement of vitellogenesis and 2) during secondary development. The number of oocytes commencing vitellogenesis is foremostly controlled by genetic factors. Under normal conditions the number of oocytes brought to maturity is affected by the environment during as well as prior to the maturation period. Nutrition is important at all stages of ova development. Either the fish must store sufficient food reserves in the form of fat, protein, etc. to supply energy for gonadal development as does the Pacific salmon or it must feed heavily during the maturation period. Stomach examination of yellow bass in the current study indicated that heavy feeding occurred in the fall at the time of vitellogenesis and also in the spring up to and during spawning. Feeding on forage fish occurred in late summer and autumn; whereas, invertebrates were utilized during the balance of the year. Some feeding during the winter period, particularly by females was

suggested by catches made by bait fishing from December to February although stomachs sampled in November and December were empty. Hence, yellow bass prepare for gonadal development through the storage of energy in the form of fat, etc. and by more or less continued feeding up to and during the spawning period.

Developmental Atresia

The number of developing ova present in yellow bass during the maturation period was checked at two-month intervals from October, 1967 to May, 1968. A common regression line of fecundity to body length fitted all samples at the 0.01 level of probability ($F = 1.95$). However, numbers of ova present in fish of similar size collected October, December, February and April were not equal ($p = 0.01$; $f = 7.56$). The October and December samples indicated differences at the 0.01 level, but no difference was suggested between the February and April samples ($p = 0.05$; $f = 0.61$).

Comparison of adjusted mean ova numbers (Figure 14) suggested that atresia of approximately 15 percent occurred from December to March and an additional 5 percent from March to April 30. In December ovaries of a female measuring 199 mm total length contained approximately 149,000 ova. By spawning time only 113,500 secondary ova were still present. Few atretic ova were detected in the samples but small immature ova are readily absorbed and are rarely seen (Braekevelt and McMillan, 1967). Also, a careful histological study necessary to detect atretic ova was outside the realm of the present study. The apparent increase in ova

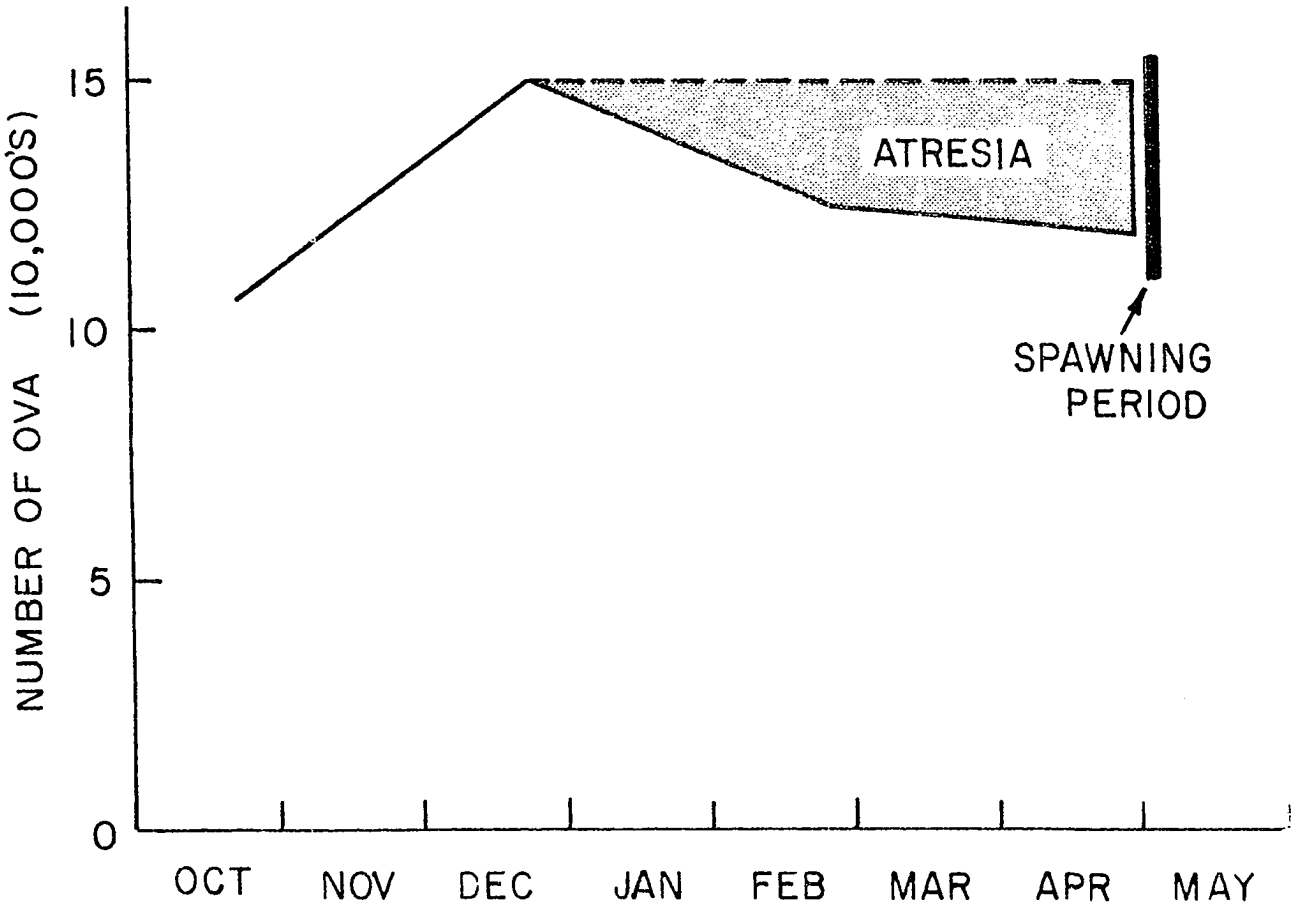


Figure 1. Adjusted mean numbers of ova from Clear Lake yellow bass with a mean body length of 199 mm by two-month intervals during the natural spawning period, 1967 to 1968

numbers from October to December suggested that additional ova commenced vitellogenesis after the October sample was taken.

Henderson (1963b) commented on the need to consider body growth when measuring developmental atresia in brook trout ova which Vladykov (1956) apparently failed to do. In contrast to brook trout which spawn in the fall, yellow bass body growth occurs at a different time of year than gonadal maturation. Also, adult yellow bass were growing very slowly in Clear Lake so that increase in body size during maturation could be completely disregarded when estimating developmental atresia.

Numerous studies have been conducted in recent years to determine factors causing reduction in ova numbers during maturation. Atresia of developing ova has been attributed to several factors besides nutrition which was discussed above. Ball (1960) stated that atresia can result from any form of stress induced by the environment such as cold, shock, etc. He feels that the ease with which atresia occurs suggests that the corpora atretica produced may be a normal source of estrogens to enhance development of remaining ova as is found in higher vertebrates. Ingram (1962) presented evidence that in higher vertebrates, oocytes particularly those having started development are very sensitive of ischemia, possibly as a result of oxygen or gonadotropin deprivation. Complete atresia in mature ovaries is easily induced in yellow bass by capture but apparently can be averted by increasing oxygen content of the holding water.

Thus, in light of the known sensitivity of yellow bass to environmental stimuli such as temperature changes and capture, it was surprising

that no atresia was detected between October and December. A possible reduction in mean ova diameter and a reduction in gonadal weight during November was mentioned earlier and attributed to thermal shock with the onset of ice cover. If atresia occurred in November it was apparently obscured by variation in fecundity estimates, or more likely by additional secondary ova commencing growth and thus compensating for ova that had become atretic.

Seasonal Food Selection

Although numerous studies on the food habits of Clear Lake yellow bass have been reported, most information is restricted to the summer months. The current study which was conducted over the full year provided new information on the diet of yellow bass during the colder months of the year. One disadvantage was that collections of yellow bass were made primarily for information on reproduction. When an adequate sample of fish was obtained for the reproduction study, the collecting was terminated regardless of the time of day. Hence, stomachs were not always collected during the same portion of a 24-hour period. Helm (1958) found that yellow bass had a diurnal variation in the type of food eaten. During the late evening when feeding was maximal, chironomids were the major item ingested; whereas, in the daylight hours zooplankton were selected for food. He postulated that either the chironomid larvae made prepupal emergences from their burrows at night and were thus more vulnerable or that zooplankton could not be seen by the fish in the dark. To the extent that Clear Lake yellow bass exhibit a diurnal variation in

food preference, conclusions based on data presented here may not be entirely accurate. However, a relatively large number of fish collected at different times of the day was examined each month so that any bias due to difference in time of feeding would appear to be negligible. Collections during July and August were made in a manner similar to earlier studies so are directly comparable. During this period gillnets were fished over a 24-hour period and were checked after each two hours of fishing.

Mean volume of stomach contents of all fish, both those with and without food, never exceeded 1 cc indicating that significant numbers of fish had little or no food in their stomachs (Table 8). The mean volume of food in stomachs collected in April, 1967 was higher than in any other month examined. Stomach contents were greater in both April and May, 1967 than in similar months in 1968. If stomach contents reflected food availability, a reduced amount of available food in 1968 agreed with findings on body condition of fish presented in the next section.

Stomach contents were grouped only into major taxonomic categories. Previous studies as reported in the introduction have identified many food items to genus or species. Two species of chironomids were present in most samples collected in 1967 and 1968. Chironomid larvae were present in all but one of the monthly samples containing food. Pupae and emerging adults were sporadically present during the warmer months. Planktonic crustacea were composed mostly of Daphnia in the spring and autumn, with Leptodora becoming more common in late spring and early summer. All fish remains which could be identified were young-of-the-year yellow bass.

Table 8. Number of stomachs examined and mean volume (cc) of major food items of 881 adult Clear Lake yellow bass collected 1967 to 1968

Month of capture	Number of stomachs	Stomachs with food	Mean volume of stomach contents			
			Chironomids	Fish	Zooplankton	Total[a]
1967						
April	89	83	0.28	0.00	0.42	0.74
May	82	69	0.39	0.00	0.05	0.44
June	140	117	0.19	0.001	0.04	0.24
July	30	10	0.18	0.15	0.06	0.39
Aug.	69	58	0.07	0.28	0.01	0.37
Sept.	26	19	0.02	0.31	0.01	0.37
Oct.	47	41	0.01	0.37	0.09	0.49
Nov.	42	0	0.00	0.00	0.00	0.00
Dec.	49	0	0.00	0.00	0.00	0.00
1968						
Jan.	50	-[b]	0.03	0.01	0.06	0.16
Feb.	55	-	0.00	0.00	0.18	0.18
March	32	23	0.01	0.00	0.02	0.03
April	90	-	0.07	0.00	0.28	0.43
May	80	-	0.10	0.00	0.17	0.30

[a]Total includes miscellaneous items and unidentified food remains.

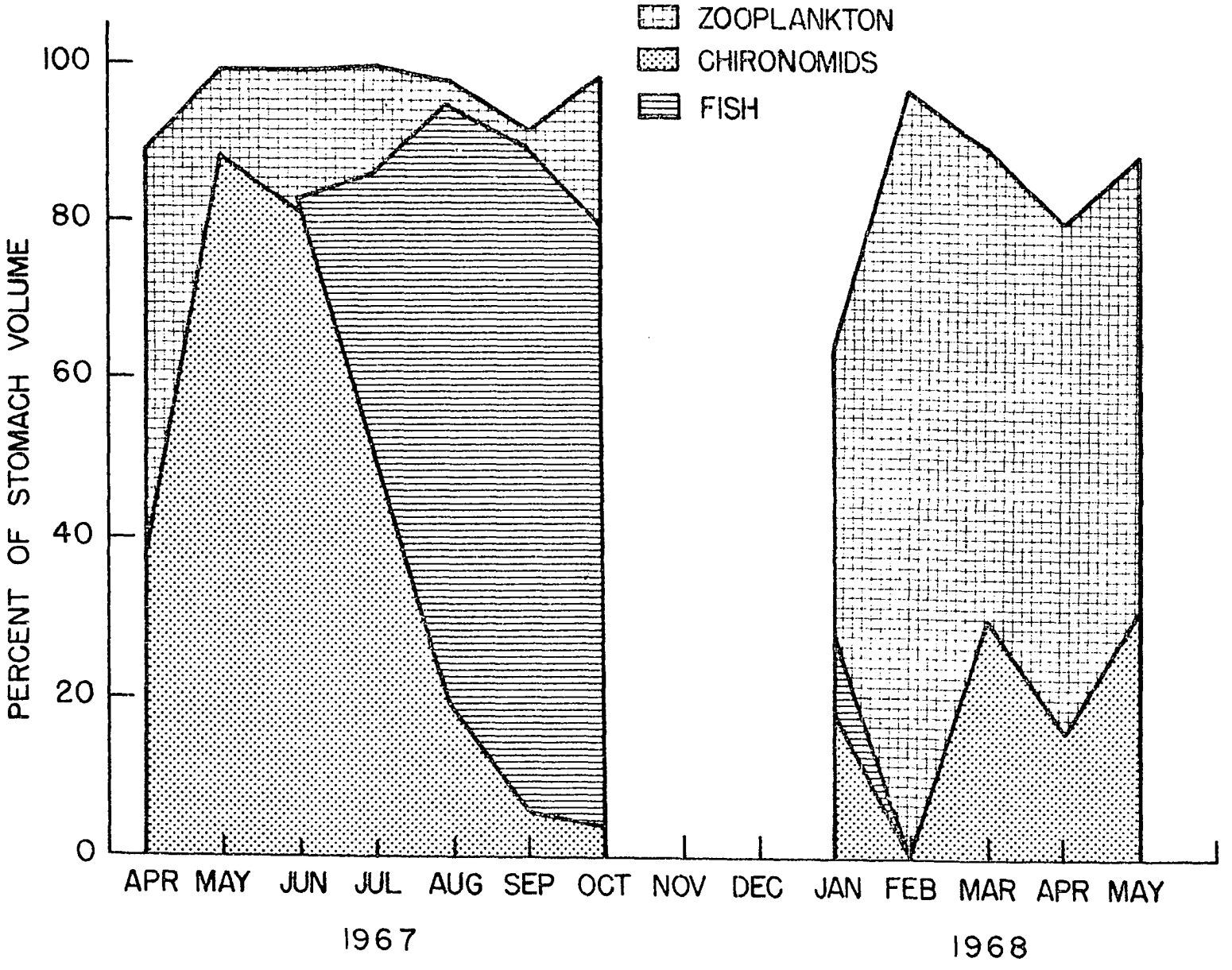
[b]Number not recorded.

In April and May, 1967 chironomid larvae were utilized heavily; whereas, in 1968 Daphnia comprised the major portion of the identified food in both months (Figure 15). Chironomids continued to be a major food item until midsummer in 1967 when replaced by young-of-the-year yellow bass. The volume of yellow bass in the average stomach increased steadily from July to October (Table 8), and from August to October, fish was the major food item found in adult bass stomachs. Average size of ingested yellow bass was consistently smaller than the mean size of fish in the Age 0 population as determined from seining samples indicating that the smaller fish were being selected. In August there were usually three to four yellow bass averaging 46 mm total length in each stomach containing fish. In September mean size of ingested bass was 57 mm. By October yellow bass in adult stomachs ranged from 48 to 76 mm in length and each stomach usually contained a single fish.

The large percentage of fish in the yellow bass diet during late summer and autumn in 1967 differed considerably from previous studies on food habits of Clear Lake yellow bass. Kraus (1963) summarized information on yellow bass feeding from 1957 to 1963 and reported that from one to five percent of stomachs examined contained fish. In 1967 the percent frequency of occurrence of fish in all stomachs, both empty and containing food, was 30 percent in August, 27 percent in September and 26 percent in October. Hence, young-of-the-year yellow bass were utilized for food by a significant percentage of the adult bass in that year.

An explanation for the apparently uncommon utilization of young yellow bass for food may lie in the large number of offspring produced

Figure 15. Major food items found in stomachs of 881 adult Clear Lake yellow bass collected April, 1967 to May, 1968 expressed as percent total volume of stomach contents


ZOOPLANKTON
CHIRONOMIDS
FISH
PERCENT OF STOMACH VOLUME
100
80
60
40
20
0
APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1967
1968

in 1967 which is reported later. Where young-of-the-year bass shortly after hatching commence eating similar invertebrate foods as the adults (Ridenhour, 1960; Kraus, 1963), the abundant 1967 year class undoubtedly utilized large amounts of food suitable for the adult bass. Hence, the adult fish presumably turned on their own offspring for sustenance when other food became more difficult to obtain. Another possibility was that limited food restricted growth of the young fish so that their small size exposed them to predation for a longer time.

The transition to a fish diet in late summer and autumn suggested that yellow bass exhibit the autumn feeding spree characteristic of several species of warm water fish. The actual volume of stomach contents did not increase from July to September (0.39 to 0.37 cc) but mean volume of stomach contents in October (0.49 cc) was only surpassed by the April sample. The high angling success for yellow bass in September and October reported by Harlan and Speaker (1951) is a reflection of this increased feeding intensity.

Maximum utilization of fish for food coincided with the period of the year when spermatogenesis and oogenesis was initiated. It is postulated that release of hormones for yellow bass gonadal development and vitellogenesis also resulted in appetite increase. In turn the hunger caused a transition to larger food items such as fish. Change in availability of forage fish in late summer was apparently not a major factor because fish were found in only one yellow bass stomach in June when young of the year were most abundant. Heavier feeding in autumn would allow storage of sufficient energy for continuation of gonadal develop-

ment through the winter period of semi-fasting. Investigation into the hormone production in domestic chickens provides a possible explanation for the appetite increase in yellow bass. As hens approach sexual maturity food intake increases (van Tienhoven, 1968). Estrogen secretions associated with ovarian maturation stimulates the appetite so that sufficient energy is ingested for deposition of the large amount of yolk material needed in the egg. In contrast, during the egg laying period, deprivation of food for a single day allows completion of ovulated ova but all unovulated follicles become atretic within 48 hours (Nalbandov, 1966). Apparently, when food intake is restricted, the pituitary ceases either to synthesize or release sufficient gonadotrophic hormones to maintain normal ovarian function. Hence, the hen has an endocrine mechanism for achieving maximum reproductive efficiency. By increasing food intake, egg production is maximized. Available information suggests that a similar mechanism might operate in yellow bass. Teleost production of estrogen needs additional documentation (Pickford and Atz, 1957), but appetite stimulation coincidentally with initiation of gonadal development would certainly be an effective mechanism for assuring successful reproduction in a species which must store much of the energy needed for gonadal maturation several months prior to spawning.

Body Condition

Adequate measurement of food supply available to maturing yellow bass is difficult to obtain. Competition for available food in Clear Lake exists not only between individual adult yellow bass but also

between adults and juveniles and with other species of fish in the lake. Black bullheads were particularly abundant and competed directly with yellow bass for food in 1967 and 1968. A fairly reliable index of food adequacy in the recent past may be obtained by examining body condition as reflected by the length-weight relationship. Within the same species, sex and stage of maturity, the heavier a fish is for a given length, generally the larger are its nutritional reserves. These nutritional reserves are indicative, in part, of the amount and quality of food ingested previously.

The length-weight relationship was computed by sex for each sample of yellow bass collected in 1967 and 1968 using the formula:

$$\text{Log } W = \text{Log } a + b \text{ Log } L$$

where W is body weight in grams, L is total body length in millimeters, a is a constant and b an exponent. Mean body weight and length and values of a and b for each sample are presented in Tables 9 and 10.

Fish tend to increase in body weight approximately in proportion to the cube of their length (i.e. b = 3). If values for the exponent b are larger than 3, the longer fish are proportionally heavier for their length than are the small fish. In the current study, it was apparent that during the 1967 prespawning period, the longer fish of both sexes were proportionally heavier for their length than were the small adults. One exception was the sample of female fish collected May 3 which had a b value which was not statistically different from 3 ($p = 0.01$).

Values of b during the 1968 prespawning period from April 1 to May 15 were much lower for both sexes than during the same period in 1967.

Table 9. Values of a and b in the length-weight relationship of female Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Number of fish	Mean length (mm)	Length range (mm)	Mean weight (g)	Log a	b value
1967						
4/5	33	204	182-221	136	-5.770	3.420
4/20	44	203	182-220	143	-5.980	3.526
4/27	9	203	196-208	146	-6.863	3.912
5/4	16	201	183-216	148	-4.863	3.037
5/12	27	201	182-215	147	-5.890	3.498
5/24	23	201	182-214	139	-5.115	3.152
6/2	30	202	181-213	142	-5.689	3.400
6/8	29	196	181-210	122	-4.928	3.058
6/14	46	195	180-217	121	-4.502	2.875
6/22	28	196	180-212	119	-5.001	3.088
6/28	29	196	182-217	121	-5.638	3.364
8/3	21	193	184-212	115	-4.711	2.963
8/28	14	200	181-214	119	-4.687	2.939
9/25	8	199	190-208	115	-4.719	2.948
10/23	35	202	188-218	121	-3.981	2.630
11/22	19	196	186-217	112	-4.055	2.663
12/19	29	202	188-207	122	-4.636	2.922
1968						
1/30	37	200	187-217	109	-3.866	2.566
2/26	29	199	184-207	124	-3.434	2.403
3/18	38	196	181-211	108	-3.573	2.446
4/1	36	197	186-210	112	-3.066	2.463
4/15	17	194	184-203	105	-4.717	2.943
4/30	16	196	182-205	113	-2.279	1.891
5/6	25	193	185-215	104	-4.384	2.800
5/10	8	192	185-200	105	-2.375	1.926
5/13	30	195	180-209	109	-3.113	2.249
5/20	20	196	185-219	108	-4.299	2.760

Table 10. Values of a and b in the length-weight relationship of male Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Number of fish	Mean length (mm)	Length range (mm)	Mean weight (g)	Log a	b value
1967						
4/5	29	196	171-211	116	-6.403	3.693
4/20	41	190	170-223	112	-5.883	3.483
4/27	20	183	170-203	92	-6.175	3.598
5/4	8	194	175-210	124	-6.051	3.559
5/12	66	193	171-211	122	-5.937	3.510
5/24	25	190	172-210	111	-5.127	3.149
6/2	42	197	175-211	124	-4.656	2.941
6/8	33	194	171-211	121	-4.848	3.028
6/14	21	195	172-211	120	-5.015	3.099
6/22	33	194	178-206	119	-5.388	3.260
6/29	29	197	179-223	124	-4.833	3.019
8/3	10	193	176-212	108	-4.837	3.005
8/28	14	195	178-208	108	-4.771	2.970
9/25	12	191	173-202	100	-4.622	2.904
10/23	34	193	177-207	104	-5.296	3.200
11/22	23	200	188-212	113	-4.327	2.774
12/19	20	197	182-207	116	-5.579	3.330
1968						
1/30	14	194	176-208	101	-5.392	3.229
2/26	26	193	176-210	111	-2.389	1.938
3/18	32	191	183-213	97	-4.238	2.729
4/1	29	194	183-214	106	-5.312	3.204
4/15	21	191	176-210	98	-4.667	2.916
4/30	15	193	178-209	108	-4.707	2.947
5/6	30	191	178-206	97	-5.526	3.292
5/10	18	193	179-210	105	-3.633	2.473
5/13	30	191	175-207	96	-4.984	3.052

The lower values were apparently not due to the inclusion of partially spent fish in the 1968 samples because the May 6 values were higher than those of the previous week. Thus larger females were proportionally lighter for their length than were small fish of the same sex ($p = 0.01$; $t = 1.18$). Males of all lengths were similarly shaped in 1968. During the summer of 1967 large and small adult bass of both sexes showed no change in plumpness with length. At this time of year the gonad-body weight ratio is similar in both mature and immature fish so that this possible source of variation was not present.

The above comparisons of length-weight differences within samples as indicated by the slopes for the length-weight formula provide some insight into growth conditions within the population. However, more information is gained by comparing weight of fish of similar length collected from the population at different times. Such comparisons are most valid if fish are collected by the same type of gear, are of similar stage of maturity, etc. The requirements were best met in comparisons of fish during the 1967 and 1968 prespawning period. There were no major shifts in length frequency of the samples in the two years and change in girth due to weight difference was not felt to seriously alter gillnet selectivity. Combined samples of yellow bass were compared by sex for the period from April 1 to May 15 for the two years (Table 11). A common regression line would not fit the length-weight relationship for both years ($p = 0.01$). Computed values of f were 21.43 for females; 205.05 for males. Values of b were also different at the 0.01 level (female f value = 113.18; male = 10.71). Hence, comparison of mean

Table 11. Length-weight data of adult Clear Lake yellow bass collected from April 1 to May 15 in 1967 and 1968

Sex	Year	Number of fish	Mean length (mm)	Length range (mm)	Mean weight (g)	Log a	b value
Female	1967	129	203	182-220	143	-5.240	3.205
	1968	132	195	180-215	108	-3.638	2.477
Male	1967	164	192	170-223	114	-6.048	3.552
	1968	143	192	175-214	99	-5.053	3.088

weights adjusted for length differences for the two years was not completely valid. However, since the size ranges and mean lengths are similar, adjusted mean weights near the overall mean length would be quite valid for comparison. The large difference in weight of females for a given length was apparent from plotted curves based on the calculated length-weight relationship (Figure 16). The average female measuring 200 millimeters weighed 137 grams in 1967 but only 115 grams in 1968, a 16-percent decrease in mean weight.

Males could be compared directly for 1967 and 1968 because mean body lengths were similar (Table 11). A sample of 164 males collected in 1967 from April 1 to May 15 measured 192 mm mean total length and 115 grams mean weight. In 1968 the sample of 143 adult males measured 192 mm total length but averaged only 99 grams in weight. Thus, the average spawning male was approximately 13 percent lighter in weight in 1968 than in the previous year.

The change in mean weight of adult bass between 1967 and 1968 was

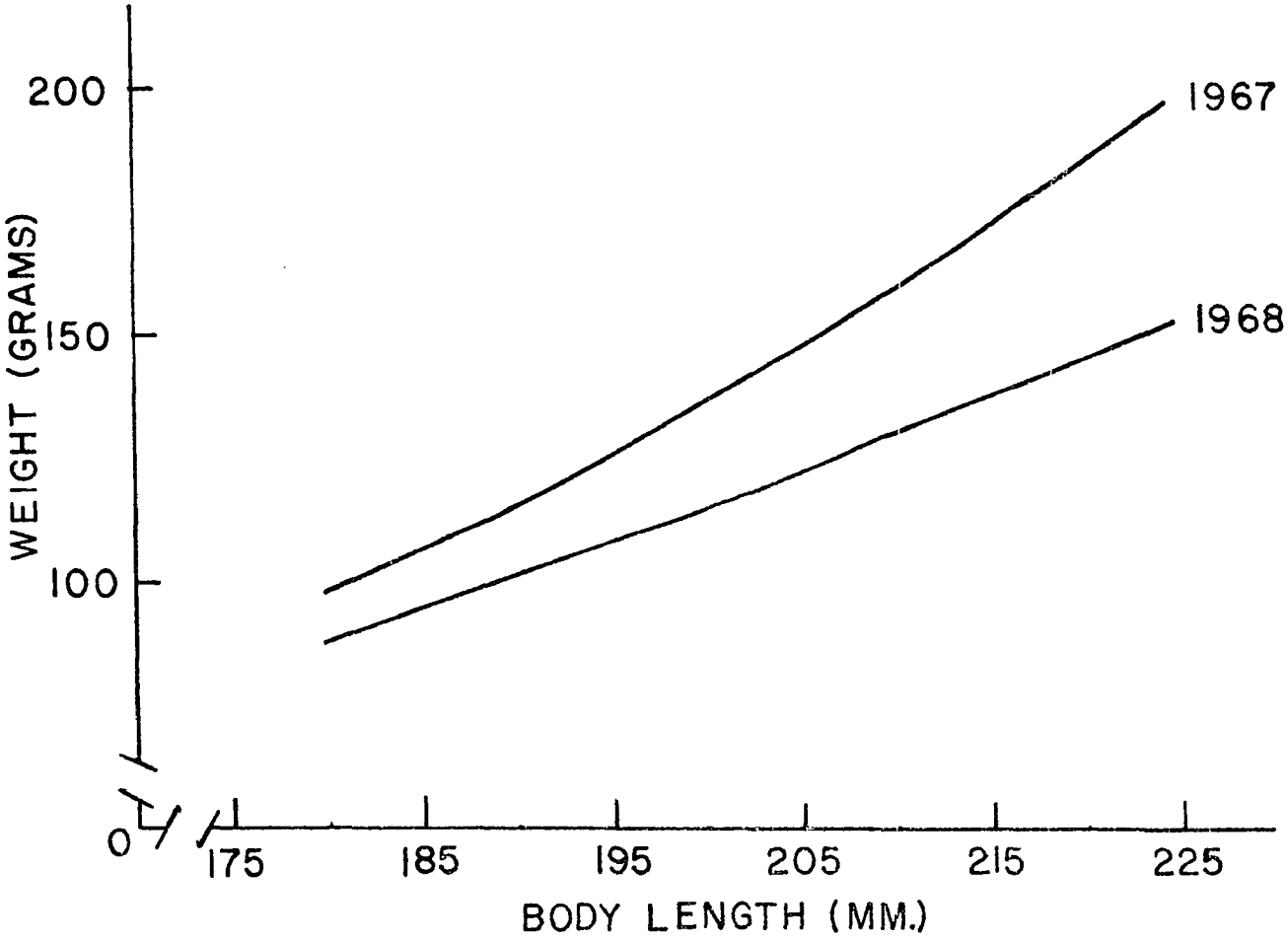


Figure 16. Length-weight relationship of adult female yellow bass collected in Clear Lake April 1 to May 15, 1967 and 1968

more evident by plotting computed weight of fish at a selected length (200 mm) for each collection date from the data presented in Tables 9 and 10. Ideally, weight comparisons should be on the basis of weight adjusted to a similar length for all samples through application of the analysis of covariance technic. However, if regression lines of length on weight are dissimilar, as in the present study, comparison on the basis of adjusted mean weights is not altogether valid. Fortunately, length distribution of fish within the various samples was fairly restricted so that no sample mean length varied more than 6 mm from the mean of all samples (3.4 percent for females; 5.4 percent for males). Considerable insight can thus be gained by examining the weight changes throughout the year of a fish near the mean length of the total sample even though certain weaknesses exist in the comparison.

In Figure 17 computed weights of 200-mm females have been plotted for the period from April, 1967 to May, 1968 which covered two spawning periods. The lower line in the figure represents body-minus gonad weight based on the mean maturity index for each sample. The index in effect is the percentage of body weight consisting of gonads. The figure is somewhat diagramatic in that the curves are plotted from the rolling average of three sample values. Figure 18 presents similar data for male yellow bass.

Several factors should be noted in the figures. Net body weight as well as total body weight and gonad weight increased in both sexes during the 1967 prespawning period. It appears unusual for body minus gonad weight to actually increase at a time when energy demands are at a peak for gonadal development. LeCren (1952) found a similar increase in body

Figure 17. Seasonal changes in computed body weight of a 200-mm female yellow bass with and without ovaries. The solid black represents total body weight and the lower edge the weight minus ovaries. The curves are based on rolling averages of three sample values

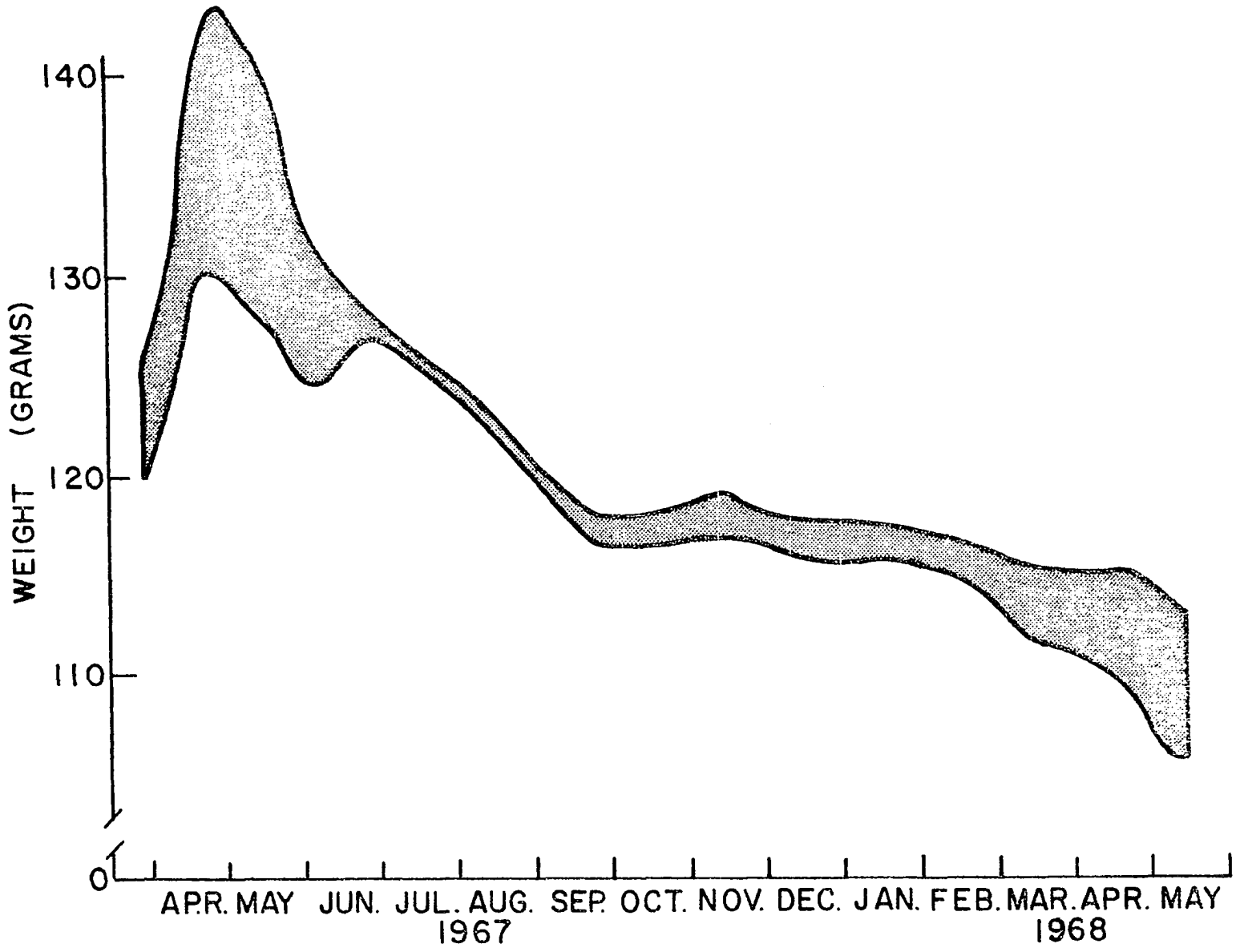
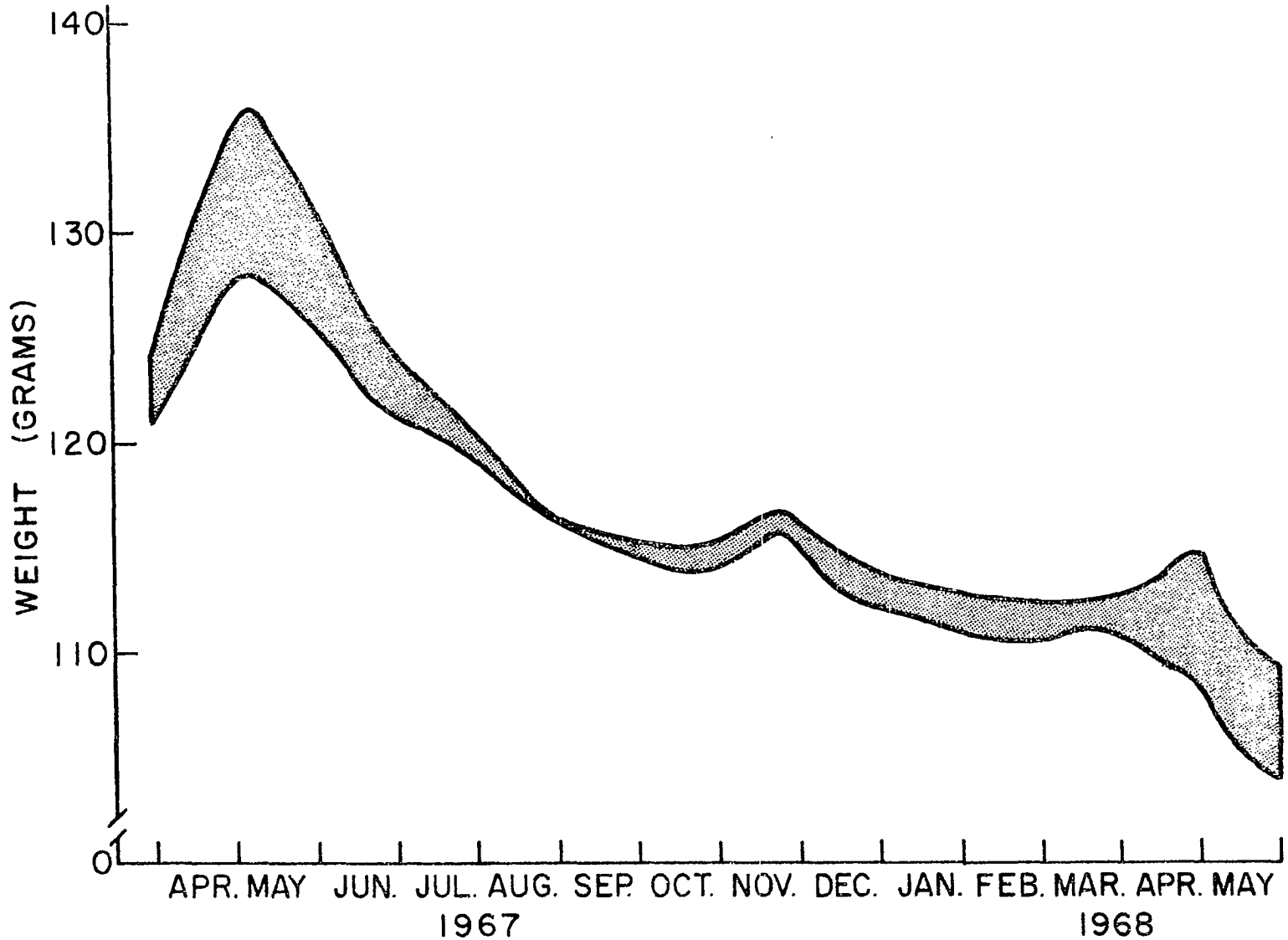

140
130
120
110
0
WEIGHT (GRAMS)
APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY
1967
1968

Figure 18. Seasonal changes in computed body weight of 200-mmm male yellow bass with and without testes. The solid black represents testes weight; upper edge of black represents total body weight and the lower edge the weight minus testes. The curves are based on rolling averages of three sample values


140
130
120
110
0
WEIGHT (GRAMS)
APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY
1967
1968

minus gonad weight for European perch from 1944 to 1947. Possible implications of this increased weight during the prespawning period will be discussed later along with gonadal hydration and body fat reserves. Hervey and Hervey (1966) in a series of studies reported that treatment of female rats with progesterone led to gains in lean tissue, fat and water similar to those gains occurring during pregnancy. Food intake also increased during hormone treatment but increased efficiency in energy conversion was involved along with increased food consumption (Hervey and Hervey, 1967). They concluded that the increased growth and fat accumulation were both consequences of a positive energy balance in a species which retains the capacity to grow throughout its life. A similar condition involving hormone regulation might exist in certain fishes such as yellow bass which although stunted still retain the capacity to grow whenever food becomes more available (Buchholz, 1960). Hormones produced during the late stages of maturation might increase efficiency of energy conversion and thus cause an increase in body weight.

In the current study no increase was noted in body minus gonad weight of bass during April, 1968 when gonads were again increasing in size. On the contrary, mean female weight decreased regularly from May, 1967 until termination of the study in May, 1968. Male bass showed a regular downward trend with only a slight swing upward in body weight during April, 1968, but mean values were well below April, 1967 values. Mean gonad weight was also less in 1968 as noted earlier.

Gonadal Moisture Content

The possibility existed that some of the weight changes noted during the prespawning period were related to variations in body and gonad moisture content. It is not uncommon among fishes for the gonadal moisture content to change as sexual maturity approaches. Brown (1957) discussed the decrease in specific gravity of eggs of marine teleosts caused by passage into the egg of a large volume of fluid from the granulosa cells. Clemens and Grant (1964) reported that ovarian water of goldfish decreases as the spawning season approaches, followed by a sudden increase at ovulation. They believe that the increased ovarian water at spawning is due to uptake of extracellular water. Pituitary injections caused a similar increase in gonadal water content. Garrod and Newell (1958) detected a decline in moisture content in ovaries of ripening Tilapia esculenta. They attributed the effect to a rapid build up of lipid material during maturation which increased the dry weight of the ovarian tissue. Clemens and Grant (1965) discussed the seminal thinning phenomenon which occurs among many male teleosts as they approach maturity. The semen changes from its viscuous condition common during much of the year to a more fluid consistency probably for ease in ejection. They were able to use this thinning response as an index to gonadotropin potency because the response is under hypophysial control.

Sufficient numbers of fish were present in certain samples collected in 1968 to determine the gonadal moisture content of adult yellow bass (Table 12) Testicular water content was relatively high from January to early May with little change detected. A slight decrease in moisture was

Table 12. Percent gonadal moisture content of adult Clear Lake yellow bass from selected samples collected in 1968

Sex	Date	Number of fish	Percent moisture content	
			Mean	Standard deviation
Male	1/30	13	82.47	1.36
"	4/29	12	81.86	3.00
"	5/10	18	81.44	0.57
Female	1/30	13	77.96	2.95
"	5/10	8	67.31	0.72

suggested as spawning time approached which was significant at the 0.05 level of probability ($t = 2.55$) but not at the 0.01 level. When one considers that male yellow bass were functionally mature the previous fall, a relatively high moisture content in the spring months is understandable because fish are already mature. However, any change in the early spring should be towards increased milt fluidity. Milt was observed to become more viscuous with the onset of cold temperatures in the autumn and males collected in March had to be warmed to room temperature before milt could be extruded. After the spawning season, milt of unspent males thickened noticeably and the increased viscosity was used as one indication that spawning had ceased.

Change in ovarian moisture content was more definite. Moisture decreased approximately 10 percent from January 30 to May 10. Variation in moisture content in the May sample was less than 2 percent, suggesting that none of the eight fish in the sample had ovulated. One would have expected a larger variation had some of the fish ovulated. Absence of

ovulated ova in the ovaries supported this conclusion. The noticeable increase in dry weight as the ovaries approached maturity agreed with reports on other species. Cellular water is apparently replaced with yolky material consisting of proteins, lipids, etc.

Mesenteric Fat

It was not the purpose of the present study to measure energy transfer in maturing yellow bass, but changes were noted in amount of mesenteric fat during late stages of maturation. Shul'man (1960) reviewed the complexities involved in determining the connection between dynamics of fat content and biology of the fish. He indicated that considerable caution is needed when generalizing on fat chemistry but agreed with Pearse (1925) that "fats play the chief role in the endogenous nourishment of fish during the wintering and spawning migratory fasts". He reported that fat metabolism is influenced by factors such as the time and nature of spawning, length of migration, duration of wintering, supply of food during maturation, water temperatures, etc.

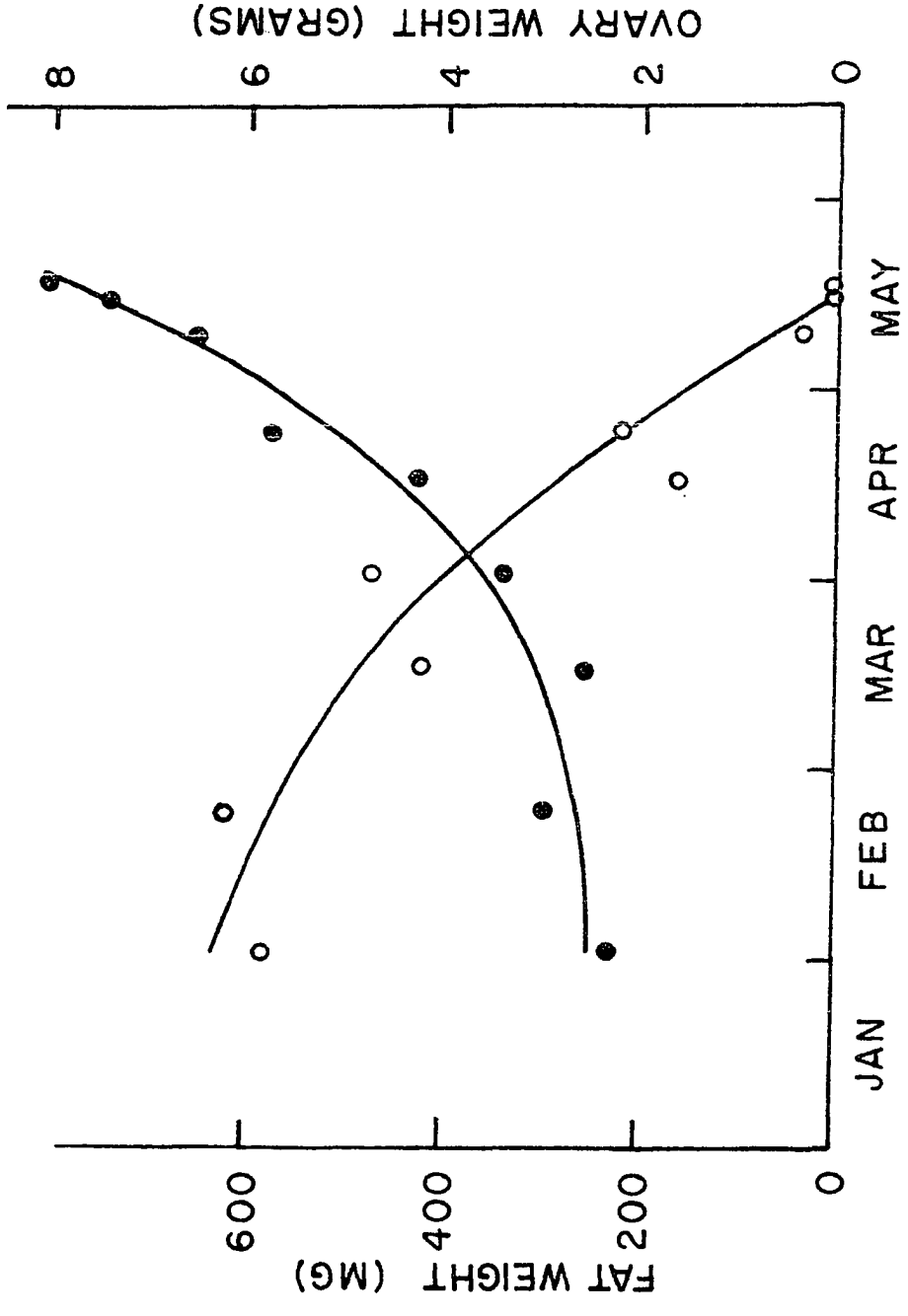
Because fats are the chief source of stored energy in fish, the fat content of many species drops during maturation of the gonads. Extent of fat utilization depends on intensity of gonadal development and conditions during the prespawning period. Other species which feed heavily during the prespawning period can actually increase fat storage levels. Thus, there are two types of fat metabolism in fish during sexual maturation. Yellow bass are similar to white bass (Riggs, 1955) in that they feed vigorously during the prespawning period. Thus, there is reason to

suppose that the species lies somewhere between the two types of fat metabolism mentioned above. That is, in years of abundant food, yellow bass rely little on energy stores during the spring prespawning period. Energy for gonadal development is obtained from food ingested during the period. In years of low food availability, body energy reserves are utilized for gonadal maturation. If reserves are inadequate, reproduction may be depressed either through lowered fecundity (Bekker, 1958), reduced frequency of spawning or increased egg mortality (Shul'man, 1960; Fontaine and Olivereau, 1962).

In both "fat" and "nonfat" fishes, the mesenteric fat is utilized first for maturation of the gonads (Shul'man, 1960). No measurements of mesenteric fat were made on yellow bass collected during the 1967 spawning season, but it was apparent after processing that part of the increased weight per length of the 1967 spawners over the 1968 fish was due to the amounts of fat present in the body cavity. Mesenteric fat was measured from fish collected during the 1968 prespawning period to determine its relation to gonadal maturation. Sample size ranged from 14 to 38 fish (mean = 26) except that the female sample collected May 10 contained only eight fish.

A negative correlation ($r = -0.92$), significant at the 0.01 level, existed between weight of mesenteric fat and ovarian weight from March to May (Figure 19). There was a suggestion that mesenteric fat actually increased from January to February, but by mid-May, fat reserves had dropped to negligible levels. It should be noted that the amount of fat lost during the period was much less than the gain in ovarian weight.

Figure 19. Relation of mean ovarian weight (solid circles) of female Clear Lake yellow bass to mean weight of mesenteric fat (open circles) during late stages of sexual maturation, 1968. Curves drawn in by eye

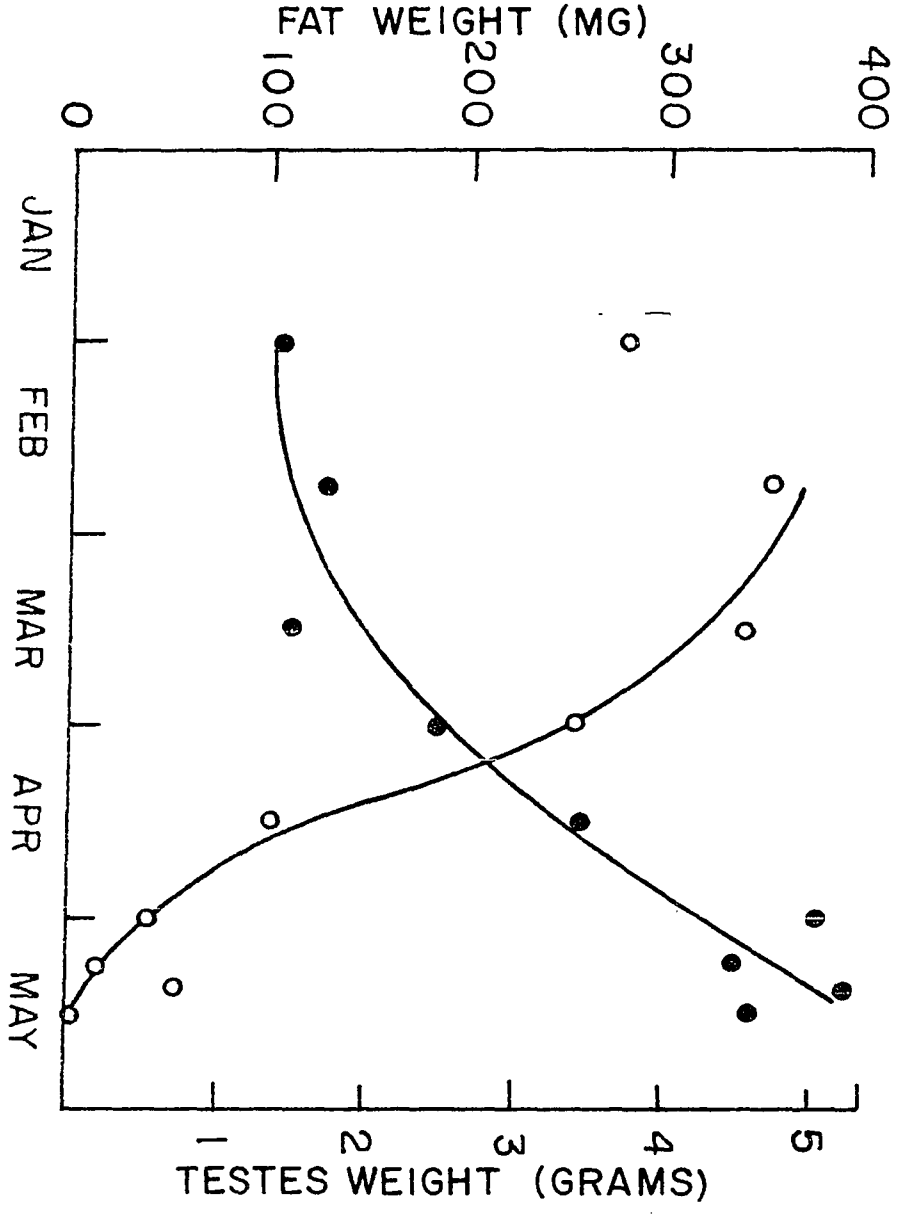

OVARY WEIGHT (GRAMS)
0
2
4
6
8
FAT WEIGHT (MG)
0
200
400
600
JAN
FEB
MAR
APR
MAY

Hence, energy other than that drawn from mesenteric fat was obtained either from other storage sites or through feeding. The continual decrease in body-minus gonad weight during the 1968 maturation period (Figure 17) suggested that much of the energy for gonadal development was obtained at the expense of other body tissue. Feeding apparently failed to provide adequate energy during the period. In 1967, however, body-minus gonad weight actually increased during late maturation. The increased body and gonad weight could not be attributed to additional hydration so it must have come from an external source through feeding. Hormonal influence during the period may also have increased efficiency of food conversion.

Males contained only half the amount of mesenteric fat found in females during January, February and March, 1968, but a similar rise in gonadal weight coincided with decrease in fat levels during the prespawning period (Figure 20). Negative correlation between fat level and gonad weight from March to May was significant at the 0.01 level ($r = -0.93$). As with females, more mesenteric fat was found in fish during March than in February. Mean weight of mesenteric fat of 358 milligrams dropped to 6 milligrams by May 14. Testicular weight almost tripled during the same period from 1.7 grams to 4.6 grams.

Additional information on the relationship between available food, mesenteric fat and gonadal development was sought by feeding adult female bass in the laboratory. Fish were obtained from Clear Lake on April 16, 1968 and maintained for 20 days in two 145-gallon aquaria. Ten fish were placed in each aquarium; all but three fish completed the experiment.

Figure 20. Relation of mean testicular weight (solid circles) of male Clear Lake yellow bass to mean weight of mesenteric fat (open circles) during late stages of sexual maturation, 1968. Curves drawn in by eye


FAT WEIGHT (MG)
0
100
200
300
400
JAN
FEB
MAR
APR
MAY
1
2
3
4
5
TESTES WEIGHT (GRAMS)

Water temperature was maintained at 16 ± 1°C. Light from cool white fluorescent lamps was provided equally to both groups for 15 hours per day, which approximated natural day length during the spawning period. Intensity of light at the water surface was 18 foot candles.

Fish were fed bluntnose minnows (Pimephales notatus) at two feeding levels. The low level group was fed approximately one percent body weight six days weekly. Live minnows were available to the second group at all times so they could feed to satiation. At termination of the experiment the latter group had consumed an average of 3.1 percent body weight (18.4 percent body weight per week). Daily food intake when forage minnows were always present varied from 0.6 to 5.2 percent body weight. Since feeding levels were computed on the basis of final body weight of the bass, the levels were not exactly as quoted above. Handling was kept at a minimum until termination of the experiment because previous tests indicated that yellow bass readily undergo atresia if stressed.

At the end of 20 days, fish fed to satiation contained mesenteric fat with a mean weight of 0.53 grams. Fish fed at the one-percent level had an average mesenteric fat content of 0.24 grams (Table 13). A common line fit the relation of body weight to mesenteric fat for both groups ($p = 0.01$; $f = 14.66$). Based on adjusted mean weight of mesenteric fat the fish fed to satiation had 135 percent more fat than the group fed at the lower level.

Amounts of mesenteric fat of laboratory-fed bass were also compared with other bass captured at the same date. Fish held in the laboratory, particularly those fed at a high level, increased in fat and body weight

Table 13. Measurements of Clear Lake yellow bass at beginning and end of feeding trials, April-May, 1968

Date	Source of sample	Number of fish	Mean body length (mm)	Mean weight (g)		
				Body	Ovaries	Mesenteric fat
4/16	Directly from lake	17	194.5	105.06	4.48	0.16
5/7	Low feeding level	7	196.7	109.86	3.43	0.24
5/7	High feeding level	10	194.3	108.60	4.33	0.53
5/7	Directly from lake	25	193.1	104.48	6.64	0.09

during the feeding trial. Fish in the lake remained essentially unchanged in body weight, but experienced a decrease in mesenteric fat as reported earlier.

Gonadal development appeared blocked in fish brought into the laboratory. Apparently certain stimuli necessary for continued ovarian maturation were lacking. Ovaries of fish fed at the one-percent level decreased in weight. Weight of ovaries of bass fed at the higher level remained unchanged; whereas, females of similar length in the wild increased gonadal weight by approximately 50 percent during the three-week period.

Hence, the additional food provided the laboratory fish decreased mobilization of mesenteric fat for ovarian development and actually increased lipid storage. However, the desired effect of increasing the number of ova brought to maturity was not realized.

CHANGES IN POPULATION ABUNDANCE

Mass Mortality

On May 21, 1968 numerous dead yellow bass were found in gillnets. Live fish appeared to be in a moribund condition with extensive growth of fungus over the body surface. Large schools of bass in severe stress were observed in shallow water along the lake shore. The epizootic reached a peak during the week of May 20 and mortality was essentially over by May 29. U.S. Fish and Wildlife Service biologists at the Genoa National Fish Hatchery identified the causative organism as a bacterium of the genus Aeromonas. Yellow bass of all age groups were affected but other fish species were not involved. A random sample of 23 dead yellow bass collected May 21 along the shoreline contained 7 fish of Age 1, 5 fish of Age 2, 4 fish of Age 4, 5 fish of Age 5 and 1 fish each of Age 6 and Age 8.

Hansen (1943) described a similar mortality of yellow bass at Lake Chautauqua, Illinois, but the causative organism was not identified. Periodic mass mortality of yellow bass is not uncommon in Clear Lake and has usually occurred in the autumn or early spring when temperatures were changing rapidly. Atchison (1967) summarized reports of mass mortality of yellow bass during the past two decades. A die off in 1966 was also attributed to an Aeromonas infection. The 1968 mortality was unique in that a major portion of the yellow bass population was removed from the lake (Table 14). Only one adult and two yearling yellow bass were caught from 119 hours of gillnetting effort on June 11. No bass were captured on July 29. Previous catches exceeded one fish per hour

Table 14. Catch of Clear Lake yellow bass per gillnet hour, April to July, 1968

Date	Hours of effort	Catch per gillnet hour
4/29	45	0.967
5/6	64	1.219
5/13	73	2.158
5/21	67	0.735
5/28	73	0.108
6/11	119	0.025
7/29	36	0.000

per 125-foot experimental gillnet.

The decrease in catch was not related to any change in distribution with the onset of warmer weather since no such change was indicated by summer gillnet catches from 1965 to 1968. Weekly gillnet sampling is conducted on a systematic basis at Clear Lake during July and August each year to obtain an index of relative fish abundance. Catch-per-gillnet hour of yellow bass during the four-year period was 1965, 2.633; 1966, 1.032; 1967, 2.009 and 1968, 0.029. With similar effort 703 yellow bass were netted in 1967 in contrast to 8 fish in 1968. Hence, the population was sufficiently depleted in 1968 to force termination of collections for studying reproduction.

Success of Reproduction

Young-of-the-year fish in Clear Lake have been seined annually by biologists of the Iowa Cooperative Fisheries Research Unit since 1946. Ridenhour (1960) introduced a standardized seining program in 1956 to provide acceptable estimates of growth rate during the first summer of life. Nine stations around the lake representing different habitat types are sampled at dusk once weekly during July and August. Counts are made of young-of-the-year fish in each seine haul to obtain estimates of relative year-class strength. Due to sampling variation the method reflects only gross differences of several-fold magnitude in the young-of-the-year population, but it does provide evidence of success or failure of reproduction in a given year.

During a six-week period prior to August 31, 1967, 7,015 young-of-the-year yellow bass were captured. In 1968 with a similar amount of seining effort, by the same personnel, 77 young-of-the-year yellow bass were captured. Thus, reproduction appeared to be almost one hundred fold greater in 1967 than in 1968. Average catch for the ten-year period prior to 1967 was 6,718 young-of-the-year bass (Table 15). Even considering the wide sampling variation inherent in seining, reproduction was much lower in 1968 than in any previous year of similar seining effort.

Table 15. Total catch of Clear Lake young-of-the-year yellow bass in weekly seine hauls during the six-week period prior to August 31 from 1956 to 1968

	Year												
Year	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
Catch	6,849	1,513	9,592	8,676	14,651	6,463	340	1,407	2,745	16,747	4,913	7,015	77

DISCUSSION

A fish population restricted in growth to the point of stunting by limited food supply offers an interesting study of the influence of environmental conditions such as food supply on reproduction. A commonly accepted hypothesis for bacteria as well as higher organisms including fish is that under certain conditions reproduction may be density dependent. Other factors being equal, the organism will respond to increased food supply with additional reproduction. In turn, an increase in population density to the point where food supply or some other factor is limited eventually has an adverse effect not only on reproduction but also on body growth. Bekker (1958) found that a sharp increase in population density of goldfish, Carassius auratus, with its attendant lack of food caused a suspension of vitellogenesis, resorption of oocytes close to maturity, and consequently, a disturbance in the intensity of spawning and reduction in number of offspring produced. All of these conditions could be caused by reduced pituitary output of gonadotrophic hormones as mentioned earlier. Clemens and Grant (1964) reported that goldfish showed weekly gains in body weight for seven months on a three-percent diet but lost weight as spawning time approached until the feeding level was increased. They concluded that fish such as the goldfish require more food during the spawning period for successful reproduction.

The yellow bass appears to have developed a sensitive response in Clear Lake to its food supply. It has a high fecundity and within a few weeks after hatching, young of the year feed on the same food as the adult fish. Even though food supply in the late summer and autumn allows

sufficient storage of energy reserves for successful reproduction, food available during the spring prespawning period also appears to influence the actual number of mature ova released. If adult bass enter winter in poor body condition with low energy reserves and additional food is not readily available during the prespawning period, low effective fecundity is almost assured. Hence, within limits, final determination of the number of offspring needed to utilize available food perhaps occurs shortly before the offspring are produced to utilize it.

A rapid response to increases in food supply would explain why the yellow bass is able to become the dominant species of fish in a lake. By responding rapidly it would have offspring utilizing the food before other species could respond. However, rapid response to increase in food supply of a temporary nature would be detrimental because more offspring would be produced than available food could support. The over-population and stunting frequently exhibited by yellow bass might well be related to their overly rapid response to short-term fluctuations in food supply.

The premise that yellow bass reproduction is controlled at times by its food supply does not preclude the influence of other factors on successful spawning. Nutrition appears to exert its main influence on the number of ova brought to maturity, but other factors probably have a major effect on the number of ova actually released. Rapid fluctuations in spring water temperature are common at Clear Lake and could easily cause sufficient physiological stress for mass atresia to occur and terminate further spawning. In both 1967 and 1968 a significant decrease in temperature occurred shortly after spawning was initiated (Figures 4 and

5). In 1967 the temperature dropped from 18 to 14.5°C over a five-day period and in 1968 a similar drop from 14.5 to 10.5°C occurred over an eight-day period. The physiological process by which temperature may inhibit gonadal maturation by controlling gonadotropin production or release was discussed in the section on the maturation cycle. In regards to mature ova, Butler as quoted by Pickford and Atz (1957) concluded that large mature ova of goldfish will remain intact only as long as temperature remains at a level where normal spawning and development are possible. Once the temperature drops and remains at a low level, atresia of the mature ova occurs. On the other hand, Faleeva (1966) observed ovarian atresia in fish kept at above spawning temperatures. Hypophysial hormones administered after the start of atresia apparently led to normal spawning.

Temperature influence in the present study appears highly probable because yellow bass are notably sensitive to environmental changes as indicated by the high mortality and atresia induced by capture. Stress from temperature fluctuations is also suggested by the frequency of mass mortality of yellow bass in Clear Lake during periods of the year (autumn and spring) when temperature is changing most rapidly. The additional stress presumably weakens the fish so that disease organisms can become established. However, nutrition cannot be ruled out as the cause of mature ova resorption as well as the cause of developmental atresia. Fish appeared to have adequate nutritional reserves in 1967 to ovulate more ova than were actually released but the 34-percent ova resorption was very close to that reported for carp when feeding was below optimum

(Woodhead, 1960).

It is unfortunate that mass mortality forced premature termination of the current project, but from another standpoint the population depletion provided information not otherwise available. The fecundity estimates for 1967 and 1968 must represent somewhat the extremes one could expect for yellow bass of the size and status found in Clear Lake. The 1967 spawners were in good body condition reflecting adequate food during the maturation period. Fecundity was high and a good year class was produced even with the high ova resorption that occurred. In 1968 reproduction was low, not only from the standpoint of low fecundity, but also from the number of ova shed and young of the year produced. As the Aeromonas organism was also present in 1967 when fecundity was high, the reduced 1968 potential fecundity was attributed to poor body condition from lack of food, not to disease. Morawa as quoted by Shul'man (1960) found that if the body energy stores (fats) of the sprat were reduced to a very low level before or during spawning, death from exhaustion frequently resulted. The low body condition of the yellow bass in Clear Lake and extensive utilization of fat stores during the 1968 prespawning period presumably weakened the fish to the point where conditions were ideal for disease outbreak. When fluctuating spring water temperatures stimulated spawning, the additional stress apparently triggered the Aeromonas outbreak. The disease probably exerted its influence on reproduction by aborting spawning activity, and mature ova were never released. In any event, reproduction was a failure in 1968 and the contributing factors appeared to be poor nutrition, adverse water temperatures and

disease. Further study is needed on the influence of nutrition and temperature fluctuations after the population becomes reestablished and when disease is not involved.

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