A review of the age structure of the Yellowstone-Sakakawea stock of paddlefish, 1963-1993 and its relation to the ecology of Lake Sakakawea.

Dennis L. Scarnecchia

Department of Fish and Wildlife Resources

University of Idaho

Moscow, ID 83843

Phillip A. Stewart

Montana Department of Fish, Wildlife and Parks

RR1 Box 2004

Miles City, MT 59301

and

Greg Power

North Dakota Game and Fish Department

100 North Bismarck Expressway

Bismarck, ND 58501

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Abstract

This paper reviews current and historical age structure information on the Yellowstone-Sakakawea stock of paddlefish *Polyodon spathula* in relation to the completion (in 1953) of Garrison Dam and subsequent filling of Lake Sakakawea, a large (156,000 Ha) impoundment on the Missouri River. Commercial and recreational catches indicate that paddlefish abundance increased greatly after the closure of Garrison Dam, and the first large group of nearly all-male paddlefish migrated up the Yellowstone to Intake, MT in 1962-63. By the mid-1970s, after the gradual filling of the reservoir (1954-65), both females and males paddlefish had fully recruited to the fishery, so that by 1974, for the first time, female paddlefish outnumbered males in the harvest at Intake. By the 1980s, older females predominated in the harvest, although reproduction was occurring, as evidenced by the presence of young males in the harvest. Extensive efforts at age determination over the period 1991-1993, in which more than 4,400 paddlefish from Intake and North Dakota were aged with dentary bones, indicated that the Yellowstone-Sakakawea stock of paddlefish has continued to age, from a mean of 10.3 years in 1964-65 to 14.8 in 1974 to 20.3 in 1985 to 23.5 in 1992. Mean age of both male and female paddlefish at Intake dropped in 1993. In 1991 and 1992, males from Intake were characterized by bimodal age distributions with ages ranging from 7 to 40 (means 18.4 and 17.8, respectively); females demonstrated unimodal age distributions and ranged in age from 10

to 42 (means 25.5 and 26.1). Males commonly matured for the first time at age 9, but females almost never matured before age 15. The oldest paddlefish encountered was a 14-kg male caught in 1985 and estimated to be 55 years old. Although relationships between length and age, as well as between weight and age, were highly significant for both males and females, none of the relationships were so close that aging by dentaries is not preferable where possible. Although substantial recruitment has occurred within the past decade (as indicated by recruitment of young males to the fishery in 1991-1993), and reproduction appears to have occurred in 1991 and 1993 based upon counts of young-of-the-year in Lake Sakakawea, the age structure suggests that recruitment may be less than during those years soon after the reservoir was closed and filled. Caution in harvest is called for until it is clear that reproduction is adequate to sustain harvest well into the future.

Introduction

The Yellowstone-Sakakawea stock of paddlefish, *Polyodon spathula* supports important recreational snag fisheries in eastern Montana and western North Dakota (Scarnecchia et al. 1994). Fish of this stock rear in Lake Sakakawea, a mainstem impoundment on the Missouri river, and mature fish become vulnerable to harvest when they undertake spawning migrations up the Missouri River to the tailwaters of Fort Peck Dam, and up the Yellowstone River as far as Intake, a low-head diversion dam 27 km northeast (downriver) of Glendive, MT (Figure 1). In high water years, paddlefish may ascend even farther up the Yellowstone, to the Cartersville diversion near Forsyth, MT. In the Missouri River, some fish also evidently remain year-round in the Dredge Cuts below Fort Peck Dam.

This stock, in contrast with most other paddlefish stocks throughout the species' range (Carlson and Bonislawsky 1981; Gengerke 1986) has evidently increased significantly in numbers in the past 40 years. Although paddlefish are documented from photographs to have been captured since the early 1900s in the Yellowstone River of Montana and the then-unimpounded Missouri river of western North Dakota, a significant fishery for the stock first developed at the Intake site in 1962 (Robinson 1966), nine years after the closure of Garrison Dam resulted in the creation, in 1953, of Lake Sakakawea. Since 1962, the harvest of paddlefish at Intake, typically between 2,000 and 5,000 fish annually, has been sampled regularly by biologists for length, weight, and sex information (Stewart 1992). Only occasionally, however, has the age structure of the stock been monitored through collection and interpretation of dentaries (lower jaw bones), the most commonly used method of age determination for this species (Adams 1931; 1942). In addition, no attempt has been made to relate age structure changes over time to the changing habitat features in the Upper Missouri River, and in particular to the creation of Lake Sakakawea. Robinson (1966) estimated ages of 343 paddlefish caught at Intake, and also sampled dentaries from 109 fish caught at the Dredge cuts below Fort Peck Dam. Van Eeckhout (1980) reported ages of 52 paddlefish caught by a commercial fisherman in Lake Sakakawea. Rehwinkel (1978) estimated the ages of 55 female and 44 male paddlefish snagged at Intake in 1973 and 478 female and 503 male paddlefish snagged at Intake in 1974. Stewart (1987) estimated the age of 221 paddlefish sampled by snagging at Intake in 1985. Beginning in 1991, a comprehensive assessment of the stock of paddlefish was begun, and as part of that assessment, large numbers of dentaries were sampled, mainly from the snag fishery at or near Intake, but also from fishing sites in North Dakota downriver of Intake including the area near the confluence of the Missouri and Yellowstone Rivers ("the Confluence"). The objectives of this paper are to 1) review past efforts at age determination, 2) report on studies of the age structure of the stock over the period 1991-1993, 3) investigate the relations among sex-specific age and length and weight for this stock, and 4) to relate the changes in age and size structure over time to what is known about the ecology and habitat of the stock in its riverine and reservoir habitats.

The Lower Yellowstone River and Lake Sakakawea

The lower Yellowstone river extends approximately 630 km from the mouth of the Bighorn River to its confluence with the Missouri river approximately 40 km southwest of Williston, ND (Figure 1). Haddix and Estes (1976) and Graham et al. (1979) reviewed the physical, chemical and biological attributes of the lower Yellowstone, which has a mean gradient of 0.53 m/km and supports a warm water fish community of 46 different fish species in 12 families. The Yellowstone River mainstem is unregulated, but two low-head irrigation diversion dams, Cartersville (near Forsyth) and Intake (near Glendive), impede fish migrations. From these and other diversions, the discharge of the Lower Yellowstone has on average decreased 24% from historic discharges (Power et al. 1994). After its confluence with the Missouri River, the Missouri River then flows freely until empties into Lake Sakakawea, a distance of from 24 to 80 km depending on Lake Sakakwea's level. Lake Sakakawea, the largest of the Missouri River mainstem reservoirs, is 320 km long, has a maximum surface elevation of 565.4 m above sea level, an area of 156,000 Ha, and a storage capacity of more than 30 billion cubic meters. High rates of sediment deposition (an average of 32 million cubic meters per year), mainly from the unregulated Yellowstone river, result in shallow, turbid water in the upper portion of the reservoir (Power et al. 1994). Although young of the year paddlefish have been found in many locations throughout the reservoir, by far the greatest concentrations documented have been found in the upper portion of the reservoir during August and September (Fredericks 1994). Adult paddlefish have been reported to occupy much of the reservoir, with most of the sightings in the western-most half of the reservoir, as well as in the Missouri River immediately upriver of the reservoir. After closure of the Dam in 1953, the reservoir filled gradually over the period 1954-1966, and reached full pool in 1967, where it remained until 1976. In 1977, the reservoir level began periodic fluctuations downward, followed by rises, until about 1988, when it dropped well below full pool until mid-1993. Heavy precipitation throughout the Great Plains in 1993 and retention of water in the reservoirs to avoid flooding downriver resulted in a rapid rise in the reservoir level in mid-1993 (Figure 2).

Review of past studies (1963-1989)

Stock expansion and reservoir filling in the 1950s-1960s - Robinson (1966) sampled paddlefish at Intake during the May-June fishing seasons of 1964 and 1965, soon after the first large run of paddlefish up the Yellowstone River in 1962. Ages were determined for 343 paddlefish from interpretation of thin sections of dentaries according to methods described by Adams (1931, 1942). Although ages of these fish ranged from 4 to 25 years, more than 90% were less than 15 years old (Figure 3). As of 1994, young paddlefish aged 4-5 have not been documented since found by Robinson (1966). The three most common ages were 9-11, which is consistent with the idea of an increase in year class strengths of paddlefish 9-11 years earlier (about 1954-56), immediately after the closure of Garrison Dam, when the reservoir was initially filling (Figure 2). Of 1,403 fish for which sex was determined, more than 97% were found to be males, so nearly all of the 343 fish that were aged were undoubtedly males. Of the estimated 38 females aged by Robinson, 71% were older than age 16, and were thus born before Garrison dam was closed. Robinson was uncertain of the cause of this high ratio of males to females (36:1), but suggested that "the greater preponderance of males at this place may have resulted from males migrating farther upstream than females during the spawning season, or it may be due to a difference in time of migration between the sexes." A more likely explanation is that males of these strong year classes matured earlier than the females, and that the first females from these strong year classes had not yet matured nor recruited to the fishery. The hypothesis of population expansion is consistent with paddlefish commercial catch statistics from Lake Sakakawea. Power et al. (1994) reported that 21 paddlefish caught in the reservoir in 1954 weighed an average of only 65 grams, and that 13 paddlefish caught in 1955 averaged only 87 grams. These fish would have been young of-the-year. The first significant catches occurred in 1961, when 779 paddlefish averaged 3.5 kg (7.7 lb) in weight. As of the mid 1960s, therefore, the paddlefish fishery at Intake was evidently in a strong expansion phase as a result of the stock increases that began about a decade earlier. The fishery was dominated by several year classes of young male recruits, with many later-maturing females of those same year classes to be recruited 6-10 years later.

The mean age was much higher, in contrast, for 109 paddlefish sampled at that time by Robinson (1966) from the Dredge Cuts below Fort Peck Dam. Ages ranged from 8 to 28, and only 2 in 10 were less than 15 years old. The three most common ages were 17, 19 and 20. The sex ratio was also more balanced than at Intake. Of 75 fish sampled in 1963 for which sex was determined, 77% were males; of 45 fish sampled in 1965, 69% were males. Of 12 females sampled at the Dredge Cuts in 1965 for which eggs were counted, 11 had immature eggs and 1 had mature eggs. These results suggest to us that the paddlefish inhabiting the Dredge Cuts at that time were not predominantly mature migrants from the strong year classes in Lake Sakakawea, but were instead part of a river-resident group of fish consisting of older mature and immature fish. Although subsequent tagging studies (Needham and Gilge 1986) of adult fish have indicated that fish tagged in the Dredge Cuts are caught at Intake, and vice-versa, the Dredge Cuts evidently harbor some resident fish as well. There is no evidence that numbers of these resident fish were expanding in the 1950s and 1960s as were the migratory fish caught at Intake. In addition, the degree of genetic separation of the resident fish from the migratory fish was and remains unknown.

Full recruitment of both sexes and a full reservoir in the 1970s - A decade after Robinson's study, Rehwinkel (1978) again aged paddlefish from Intake with dentaries, according to methods described by Adams (1942), and reported that 44 male paddlefish snagged in 1973 ranged in age from 9 to 18 and averaged 12. Ages 11 and 12 were the most common ages (Figure 4a). Fifty-five females ranged in age from 15 to 19 (average = 17), with ages 16 and 17 the most common (Figure 4b). The resulting age distribution was bimodal, with the first peak nearly all males and the second peak both males and females, mainly the latter (Figure 4c). In 1974, a larger sample of 503 male paddlefish ranged in age from 9 to 26, and averaged 13, with ages 11 and 12 the most common (Figure 4d). A sample of 478 female paddlefish averaged 18, and ranged in age from 15 to 20, with ages 17 and 18 the most common (Figure 4e). This age distribution (Figures 4e,f) indicates to us that the females sampled by Rehwinkel (1978) first recruited to the fishery at 15, and did not fully recruit until perhaps age 17 or 18, again consistent with the idea that these were the first female recruits produced from the large post-impoundment year classes 15 to 20 years earlier (1954-1958). Young males aged 9-14 were abundant and constituted 87% of the males. No males evidently recruited before about age 9, and only one male was sufficiently old (26) to have been born before the closure of Garrison Dam. The high fraction of males in younger age classes (9-14) also indicated that substantial reproduction of paddlefish continued to occur at least in some years during the period 1960-65, as the reservoir was still filling. Substantial recruitment of female paddlefish from these year classes could also be expected 6-10 years afterward (in the late 1970s and early 1980s. Whereas more than 9 of 10 fish creeled in 1964-65 were males, only 52% of the fish creeled in 1972 and 56% of the fish creeled in 1973 were males. Although the sex ratio was approaching 1:1, the selective harvest (high-grading) of females, which was permitted at that time, and their higher vulnerability to harvest (P. Stewart, Unpublished tagging data) indicted that as of 1973, males were still strongly recruiting to the stock, and many female recruits had not yet migrated upriver for the first time. By 1974, females began to outnumber males harvested at Intake, and the predominance of females persisted until 1993 (Stewart 1994; Figure 5).

Van Eeckhout (1980) reported ages of 52 paddlefish of unknown sex collected in 1977 from a commercial fisherman. These fish ranged in age from 4 to 18 years old (Figure 6), which is consistent with the idea that the fish were post-impoundment recruits.

Predominance of large, older females and a dropping reservoir level in the 1980s - Although age determination of paddlefish was attempted only once in the 1980s (1985), sex ratios and weight distributions of paddlefish indicted that large, older females were the predominant sex contributing to the catch at Intake throughout the decade. Sex ratios always favored large females in the catch (Figure 5), and mean weight of female paddlefish at Intake rose slowly but consistently throughout the decade (Figure 7). For example, female paddlefish less than 28.6 kg (63 lbs) constituted 82% of the females during 1981-83 but constituted only 77% during the period 1987-89. Ages of 221 paddlefish were assessed from dentaries in 1985, and Stewart (1987) reported that 94 males ranged from 7 to 30 years and averaged 15; the most common ages were 10, 11, 15 and 17. Females (127) ranged in age from 15 to 28 years and averaged 20.4, with the most common ages 19 and 21 (Figures 8a-c). These dentaries, unlike Robinson's (1966) and Rehwinkel's (1978) samples, are as of 1994 still in existence, and were subsequently (1992) re-cut and re-aged with more advanced sectioning and reading equipment (described below) at the University of Idaho. Upon re-reading, 94 males ranged from 9 to 29 (with one fish aged 55) and averaged 17; the most common ages were 9, 11, 21 and 25. Females (127) ranged in age from 15 to 30 (with one fish at 37) and averaged 22.7; the most common ages were 21 and 22 (Table 1; Figures 8d-f). Ages reported by Stewart (1986) as well as those of the re-cut sections support the idea of an aging paddlefish population consisting of females commonly exceeding 20, and even 25 years, with very few fish (2) of either sex old (age>32) enough for them to have been born before Garrison Dam was closed. These female-predominated catches occurred at a time when reservoir levels were generally slightly below full pool in the mid-1980s, and considerably below full pool in the late 1980s (Figure 2).

Investigations from 1991 to 1993

Materials and Methods

Intake - In 1991, dentaries were collected from 1,696 paddlefish (721 males and 975 females). Lengths were also obtained from 637 of the 721 males, and 840 of the 975 females, for which dentaries were available. Weights were obtained from 717 of the 721 males, and 963 of the 975 females. In 1992, dentaries were collected from 690 paddlefish (219 males and 471 females), or 91% of the estimated catch in this poor-fishing year. Lengths were obtained from 183 of 219 males, and 384 of 419 females. Weights were obtained from all 219 males and 384 females. In 1993, dentaries were collected from 1,749 paddlefish (1144 males and 672 females). Lengths were obtained from 995 of 1265 males and 534 of 672 females. Weights were obtained from 1143 males and 605 females.

North Dakota - Ages were determined from dentaries from 131 paddlefish (74 males, 54 females, 3 unknown sex) in 1991, 61 paddlefish (19 males, 22 females, 20 unknown sex) in 1992, and 121 paddlefish (48 males, 72 females) in 1993. Most of these fish came from the Confluence, but some samples also were obtained from the Fairview Bridge area, and from the Pumphouse area near Williston.

Based upon observations of maturation state of fish as observed at the cleaning stations, essentially all of these samples were from fish that had migrated up from the reservoir in preparation for spawning. Nearly all females had mature, black eggs. Maturation state of males was not immediately discernable, but they were believed to be mature and capable of spawning.

Dentary preparation - In most cases, both left and right dentary sections were removed from each fish. Dentaries were removed with diagonal pliers by cutting at the anterior point of the whole dentary, dividing the dentary into mirror image left and right halves. A second cut was then made about 7 cm posteriorly from the first cut. The cut section included the more rounded, curved anterior portion, as well as some of the flatter, less curved posterior portion. Excess skin was removed from the dentary sections, and the sections were then stored in small, individually-numbered (by state (MT or ND) paddlefish tag) manila envelopes for at least a month prior to further processing. The left dentary was sectioned; the right dentary was saved and only processed further if later interpretation of the left dentary proved difficult.

Processing of dentaries followed, with few changes, procedures used by other investigators (Reed 1989). Left dentaries were immersed individually in a solution of 5% detergent (Ajax) and warmed to 41-43 C for 14-16 hours. After this time, dentaries were removed from the solution and cleaned gently with a soft-bristled toothbrushes to remove any remaining soft tissue. Particular care was taken to not abrade the mesial arm of the dentary, used for age determination. Clean dentaries were then immersed in a 50% ammonia and water solution for 5-6 hours, at which time the ammonia was poured out, and bottles were refilled with a 50% ethanol and water solution. Samples were kept in this solution for 24 hours, and then allowed to dry for a week before sectioning. Left dentaries were sectioned with a diamond-edged blade on a Buehler Isomet Low Speed saw. Two sections of 0.635 mm (25/1000 inch) thickness were obtained at about 10 mm posterior to the point of greatest curvature, as described by Reed et al. (1992). Sections were stored in small glassine envelopes with their larger manila envelopes. Sections to be aged were immersed in glycerine and interpreted for age by counting annual bands with the aid of a Biosonics Optical Pattern Recognition System (OPRS). Inasmuch as samples were identified only by state paddlefish tag number, samples were always interpreted without knowledge of the size or sex of the fish from which the sample was taken, except insofar as smaller fish tended to have smaller diameter sections. Annuli were counted along the long axis of the mesial arm. Some dentaries had "halo bands" within the first 10 annuli. These halo bands were false annuli characterized by somewhat more diffuse contrast than annual bands, and usually showed a lower luminosity than adjacent annual bands on the OPRS. All dentary interpretation was done by one person, but one of three other persons periodically worked with the person on interpretation, and checks were repeatedly made for consistency of interpretation. Each dentary was rated for readability by the reader as 1 (good), 2 (acceptable), and 3 (poor). Dentaries rated as good had annuli that were distinct to the edge of the section. Dentaries rated acceptable were interpretable with little difficulty, but typically had some distortion or significant crowding of annuli, usually near the edge. Dentaries rated poor were typically either distorted or had a badly "washed out" appearance so that repeatable enumeration of individual annuli was difficult. The great majority of samples were good or acceptable; poor samples constituted less than 10% of the samples, and for those samples, the right dentary section was usually cut and interpreted before a final age was assigned. All samples, regardless of quality, were interpreted for age, because it was found that, overall, sections from very old fish tended to be of poorer quality and more difficult to interpret than those of young fish. It was common for annuli on very old fish to be crowded closely together, so that underestimates of age for these fish might occur. A specific protocol was also developed for interpreting dentaries using a sequence of different magnifications. In an evaluation of the consistency of interpretation among observers, it was found that observers tended to disagree much less on ages of good and acceptable specimens than on ages of poor specimens. Inasmuch as there were no paddlefish of known age, age validation was not possible.

The relation between length and age, and between weight and age, were determined by a two dimensional plot and a line fitted to the relation by linear regression analysis. Inasmuch as the relation between length and age, as well as between weight and age, are often described effectively by a von Bertalanffy equation (Sparre et al. 1989), length and weight-converted von Bertalanffy curves were also fitted to the data. In this process, the time parameter, t_0 was set equal to 0, i.e., forced through the origin.

Results

Intake -- In 1991, male paddlefish ranged in age from 7 to 40, and averaged 18.4 years old. Female paddlefish ranged from 14 to 42 and averaged 25.5. Although 205 (28%) of the 721 male paddlefish sampled at Intake were between 7 and 13 years old, the youngest females were 14 years old, which indicated a considerably older age at maturity (and hence delayed migration pattern and delayed vulnerability to harvest) for the females. Age-frequency distributions for the sexes also differed: males had a bimodal distribution with a minor peak at about 9 and the higher peak at about age 21, whereas females had a unimodal distribution with the peak at about 26 (Figure 9a,b).

Age distributions in 1992 were remarkably similar to those in 1991. Males ranged in age from 7 to 33 years and averaged 17.8, or 0.6 yr younger than in 1991. Females ranged from 10 to 40 years and averaged 26.1, or 0.6 yr older than in 1991. Although 79 of the 219 males (36%) were aged 7-13, only one of the 471 females was under age 14. As in 1991, males had a bimodal distribution with the highest peak at about 21, whereas females had a unimodal peak at about 27 (Figure 10a,b).

In 1993, for the first time in nearly 20 years, the paddlefish harvest at Intake was predominantly males. The age structure also differed from those in 1991 and 1992. Males ranged in age from 6 to 35, and averaged 15.8, a full 2 years younger than in 1992. Females ranged in age from 9 to 38, and averaged 22.8, or 3.3 years younger than in 1992. Mean weight of aged males was the same in 1992 (11.5) as in 1993 (11.5), but mean weights of aged females dropped by 0.7 kg in 1993 (26.5) from 1992 (27.2; Figures 11a,b).

Age of female paddlefish was not very closely related to fish length (Spearman $r = 0.31$; $p<0.0001$) or weight (Spearman $r = 0.32$; $p<0.0001$). For males, the relations of age to length (Spearman $r = 0.69$, $p<0.0001$) and weight (Spearman $r = 0.64$; $p<0.0001$) were closer than for females, although less than half of the variation in age was explained by either length or weight with a linear model. Because of the non-linear relation between fish length and age, as well as between fish weight and age, we fit a von Bertalanffy growth model to data for males and females, one for length and one for weight. The von Bertalanffy curves improved the fit (Figures 12, 13), but considerable variation remained.

In 1992, as in 1991, ages of male paddlefish were more closely related to length (Spearman r = 0.76; $p<0.0001$) and weight (Spearman r = 0.74; $p<0.0001$) than were ages of females related to length (Spearman r = 0.43;$p<0.0001$) and weight (Spearman r = 0.42;$p<0.0001$). Overall, however, the age of neither sex was very closely related to either length or weight, even when fitted with von Bertalanffy growth functions.

Results in 1993 for relations between length, weight and age were similar to previous years. As before, the relations between male length and age (Spearman r = 0.74; $p<0.0001$) and male weight and age (Spearman r = 0.70; $p<0.0001$) were closer than for female length and age (Spearman r = 0.49; $p<0.0001$) and female weight and age (r = 0.46; $p<0.01$). In all three years, males and females showed distinctly different age specific length and weight, which indicated distinctly different growth rates.

North Dakota - Although samples from North Dakota were much fewer in number than from Intake, results from their analysis are in general agreement (except for 1993) with results from Intake. In 1991, 74 males ranged in age from 9 to 37, and averaged 21. Only one of the males (a 37 year old) was older than Lake Sakakawea; the next oldest male was age 32. Fifty-four females ranged in age from 17 to 33 and averaged 24. In 1992, 19 males ranged in age from 9 to 33 and averaged 22; 22 females ranged from 19 to 34 and averaged 24. In 1993, 48 males ranged from 9 to 29 and averaged 18; 72

females ranged from 16 to 35 and averaged 25. Mean age of both males and females in North Dakota in 1993 was 2.2 years higher than at Intake, and similar to results from Intake in 1991 and 1992. As with the Intake samples, females did not recruit until 6 to 10 years after males, and few paddlefish were older than Lake Sakakawea. Also as with the Intake samples, the relation between age and length, as well as between age and weight, were not close, and von Bertalanffy growth curves indicated distinctly different growth rates for males and females.

Discussion

Age structure relative to other localities - The Yellowstone-Sakakawea paddlefish stock consists of older (commonly 25-35 years) and later maturing (at least 9 for males, 15 for females) fish than reported in most other locations. Gengerke (1978) reported that only one of 787 paddlefish in Iowa's portion of the Mississippi river was older than 20; male fish of that stock matured as young as age 4, and females as young as age 6. In the Osage river, Missouri, Purkett (1963) and Russell (1986) reported paddlefish as old as 30, and commonly reaching 25. In more southerly and more heavily exploited populations, maximum age observed is evidently lower. Reed et al. (1994) found paddlefish only up to age 14 in Lake Ponchartrain, Louisiana. None of the above stocks exhibit the old age of the Yellowstone-Sakakawea stock, where fish exceeding 25 years of age are abundant and fish exceeding 30 are not uncommon.

The oldest fish found thus far, a 14 kg male caught in 1985 and estimated to be 55 years old, is to our knowledge the oldest reported paddlefish anywhere. Although few paddlefish in our stock exceed 40 years of age (based on our age determination), it is evident that even in the presence of fishing, fish of this stock can and do live well into their thirties or forties. Old paddlefish fish are also found in the Fort Peck Stock above Fort Peck Dam (Russell 1986; D. L. Scarnecchia and K. Gilge, Unpublished data). If ages of old fish are underestimated, as occurs for old sturgeon (Rien and Beamesderfer 1994) 40 year old fish may be more common than it appears based on our aging technique.

Sex specific length, weight, and age distributions - The sex-specific differences in length, weight, age-at-maturity and adult size (sexual size dimorphism; Shine 1990) underscore the necessity of performing stock assessments on paddlefish with knowledge of the sex of individual fish. These sex-specific differences have been reported by other investigators (Reed et al. 1992; Brown and Murphy 1993), and the differences have been attributed to different optimal reproductive strategies for each sex (Scarnecchia et al. 1989). Based on the extrapolated von Bertalanffy growth curves for males and females from this stock (Figure 12), males and females are the same length at age 4, and it is not until ages 6 or 7 that females begin to be substantially larger than males. This age (6-7) is about when males begin maturation and diversion of energy into gonadal development, an action which the females delay for several more years. Once both males and females are mature and have spawned (e.g., after age 20), differences in growth rates between males and females are much less than between ages 6 and 20 (Figures 12,13), suggesting to us that sexual size dimorphism in paddlefish is mainly determined by sex-specific optimization of maturation and the process of reproduction (Kozlowski 1989; Shine 1990). If egg number, as indicated by total roe weight, is related to fitness, eggs of female paddlefish at Intake commonly weigh 15 to 20% of the total fish weight (Unpublished), and egg number and total weight of eggs in general increases with the weight of a female paddlefish (Scarnecchia et al. 1989). Males, in contrast, obtain no such fitness advantage from later maturation and larger size, since even small males would have abundant sperm. Male paddlefish probably gain little courtship advantage from a large size, as long as they are sufficiently large to avoid predation. They thus spawn earlier in life, and at shorter yearly intervals (Russell 1986).

This sexual size dimorphism in paddlefish creates some difficulties in managing fisheries, because females, which are the largest fish in the stock, are generally most desired by anglers. At all fishing sites for this stock except on the Missouri river below Fort Peck Dam, mandatory retention of snagged paddlefish is required. Anglers often dislike the mandatory retention of smaller fish, and suggest that they be allowed to release the small fish so that those released may grow to a larger size. Unfortunately, nearly all of the small fish are males, and will never attain the large size of the females. Despite visible and conscientious enforcement, high-grading, or illegal release of small fish (typically males) in favor of large fish (typically females), occurs to some degree at all fishing sites (e.g. at the Confluence, Figure 14).

Age estimation from length and weight - Because length, weight, and sex data are available continuously for this paddlefish stock from 1972 onward, but age information is sporadic, a close relation between length and age, or weight and age, would provide a useful method for estimating age structure of the population for past years when dentaries were unavailable. A close relation would also eliminate the need for the collection and processing of numerous dentaries. Based on study results, however, age could be predicted from length or weight with only moderate to low accuracy. Linear models for weight versus age typically explained less than half the observed variation for males, and less than 25% of the variation for females. Even though a von Bertalanffy growth curve provides a closer and more appropriate fit biologically (Figures 12, 13), considerable unexplained variation remained.

At least two causes probably contribute to the high variation. The first cause is errors in age determination. Although annuli are widely spaced on all paddlefishes during the first 7-9 years, the outer annuli on fish 20 years and older are commonly spaced very closely, nearly on top of one another. After fish reach maturity for the first time, available tagging data (P. Stewart, Unpublished) and growth data (Figures 12, 13) indicate that a high fraction of an individual fish's production goes toward gonadal development, and little toward increased length and weight associated with elaboration of somatic tissue. In addition, paddlefish growth is mainly in girth rather than length once they reach maturity, and the contribution of such growth to the incremental growth on dentaries may be slight. So even though it is not difficult to distinguish by dentaries a 10 year old fish from a 30 year old fish, it is not always clear if the 30 year old fish is actually that age, or somewhat younger or, more likely, older. Although age validation is a clear need for this species, it will only be possible in the near term (from tagging and stocking studies) for only younger fish. It will take much longer to validate ages on the oldest fish. For this reason, and because ages of older Chondrosteans are commonly underestimated (Rien and Beamesderfer 1994), these ages have error associated with them, and should probably be considered a minimum for the older specimens. Most of the error in the length-age and weight-age relations is probably in age determination; length and weight are measurable with accuracy and precision, and the relations between body length and weight were close (e.g., 1991 Intake samples: $r = 0.89$).

Secondly, much of the variation in length-age and weight-age relations may be biological, related to the length, weight, and age at first maturation. As paddlefish begin to mature and energy is diverted into sexual products, growth slows, so that fish of a given length or weight may have a wide range of ages, depending on their approximate length and weight at which they first matured.

Although males were more accurately aged by length and weight than were females, neither sex was aged accurately by length or weight. Aging of dentaries remains the best way to assess age structure in future years, at least until other methods are developed, or until ages can be validated through tagging studies. In years where historical dentary samples are not available, however, the von Bertalanffy growth equations may be useful in reconstructing age structure. The large samples of aged dentaries in this study may result in growth equations that, on average, accurately indicate age, especially in situations where no systematic over- or underestimation of ages occurs. More analysis is planned to ascertain if we can approximate the age with acceptable success by using a given length or weight group.

Age structure and stock status - Based upon the dentary samples taken during the period 1991-1993 and on the steady increase in weight of paddlefish since 1981 (Figure 7), the Yellowstone-Sakakawea paddlefish stock has continued to age over the past 35 years. Since 1953, when the population first expanded after the closure of Garrison Dam created Lake Sakakawea, mean age of paddlefish caught at Intake has increased from 10.3 years in 1964-65 to 14.8 in 1974 to 20.3 in 1985 to about 23.5 in 1992. Year to year variations are not large in relation to the overall trend depicting a paddlefish stock where an increasing fraction of the harvest consists of old, repeat spawners. From a recruitment perspective for a species with a recent history of inadequate reproduction and recruitment in many areas of its range, it would be preferable to have more young recruits in relation to the older fish. The existing age structure argues for caution in harvest until it is clear that reproduction and recruitment are adequate to sustain the stock and some level of harvest well into the future.

Age structure in relation to stage of reservoir - In relating paddlefish age structure from the Intake samples to the age and water level of Lake Sakakawea (Table 1), we find that nearly 60% of the females in 1991 and 1992 were born in years when the reservoir was initially filling (1954-66). In 1993, in contrast, lower mean ages and mean weights of females resulted in only about 24% of the fish having come from these years. A high percentage of males in all three years came from the years when the reservoir was full (1967-76), and by 1993, young males from the year classes 1977-88 constituted half of all males aged. Inasmuch as 1993 was a very unusual year at Intake in that it was the first year in nearly 20 years that males outnumbered females harvested (Stewart 1994), it would be unwise to draw strong conclusions about the stock status based on that year's data. We can conclude, however, that 1) female paddlefish of this stock do not fully recruit to the fishery until about age 18; 2) the mean age of the stock in 1991-1993 is higher than available earlier estimates had indicated (Rehwinkel 1978; Stewart 1986); 3) nearly 60% of females in 1991 and 1992 were from year classes when the reservoir was filling, and 4) any underestimation of ages of either males or females would result in even higher percentages of older males and females, that is, of fish born during the earlier years' of Lake Sakakawea's existence.

Although reproduction and some recruitment are occurring, as evidenced by documented young-of-the-year in Lake Sakakawea in 1991-1993 (Fredericks 1994), and presence of 7-14 year old males in the catch in 1993 (Figure 11), the age structure suggests to us that recruitment may be less than during the years soon after the reservoir was closed and filled. Despite years of harvest, older fish still constitute a significant fraction of the catch. The positive effects of trophic upsurge on fish stock are well documented (Baranov 1966; Poddubny 1976; Ostrofsky and Duthie 1978; Kimmel and Groeger 1986). In Lake Francis Case (South Dakota), another Missouri River Reservoir, Gasaway (1970) reported (but did not statistically show) that post-impoundment growth of 13 species of fish initially increased after impoundment, but later decreased. Neel (1967) reported that phytoplankton density in Lake Sakakawea over the period 1954-58 peaked in 1956, the second summer after dam closure, and declined greatly in 1957 and 1958. Unfortunately, no comparable later data are available, and the evidence is lacking on the intensity and duration of trophic upsurge in Lake Sakakawea. For paddlefish, which recruit to the fishery many years after birth, any such upsurge effects would not be evident for years after the initial strong year classes resulted, and a decade or more after its effects would have dissipated for shorter lived fishes. In addition, the gradual, 13-14 year filling of Lake Sakakawea would perhaps have resulted in more gradual trophic changes than if it had filled over a much shorter period. For this reason, the entire filling period (1954-66) and perhaps some years afterward could be viewed as the upsurge phase of the reservoir. From this perspective, most of the large females constituting the mainstay of the paddlefish fishery in 1991-93 may have been born during conditions of productivity not sustainable over the long term.

Little direct information exists, however, on the ecological conditions in Lake Sakakawea during the early years as they would relate to survival of young-of-the-year paddlefish. It is known that during the latter part of the period of filling (i.e., the early to mid 1960s), a strong northern pike *Esox lucius* fishery developed amid excellent spawning conditions created by recently flooded vegetation. The northern pike fishery remained strong until the early 1970s. After the reservoir had filled, a more stable water level and significant shore erosion resulted, by 1979-80, in strong year classes of walleye *Stizostedion vitreum vitreum* and saugers *Stizostedion canadense* and a nationally-renowned fishery in the mid 1980s (Power et al. 1994). Natural reproduction of walleye waned with reservoir water levels after the mid-1980s, precipitating significant stocking of walleye by the North Dakota Game and Fish Department. Although walleye and sauger are known predators on paddlefish in Lake Sakakawea (Mero 1992), the effects of these changes in predator abundance on paddlefish are unknown. More information is needed on factors affecting annual year class strength and its relation to reservoir conditions and resulting abundance of coinhabiting species. We are also unsure of the importance of the upper end of Lake Sakakawea, as well as the Missouri river near the Confluence, on the reproduction and recruitment of paddlefish. The rapid refilling of Lake Sakakawea in 1993 may provide us with information on the effects of reservoir aging and water levels on paddlefish reproduction and recruitment. Until then, harvest should be managed with the possibility of reduced reservoir productivity in future years.

Literature Cited

Adams, L. A. 1931. Determination of age in fishes. Transactions of the Illinois State Academy of Science 23:219-226.

Adams, L. A. 1942. Age determination and rate of growth in *Polyodon spathula*, by means of the growth rings of the otoliths and dentary bone. American Midlands Naturalist 28:617-630.

Baranov, I. V. 1966. Biohydrochemical classification of the reservoirs in the European U.S.S.R. Pages 139-183 *in* P. V. Tyurin, editor. The storage lakes of the U.S.S.R. and their importance for fishery. Bulletin of the State Scientific Research Institute of Lake and River Fisheries Volume 50. Israel Program for Scientific Translations, Jerusalem.

Brown, M. L., and B. R. Murphy. 1993. Management evaluation of body condition and population size structure for paddlefish: a unique case. Prairie Naturalist 25(2):93-108.

Carlson, D. M., and P. S. Bonislawsky. 1981. The paddlefish (*Polyodon spathula*) fisheries of the midwestern United States. Fisheries (Bethesda) 6(2):17-22, 26-27.

Fredericks, J. 1994. Distribution, abundance, and feeding ecology of young-of-the-year paddlefish in Upper Lake sakakawea, north Dakota. Master's Thesis, University of Idaho, Moscow, ID.

Gasaway, C. R. 1970. Changes in the fish population in Lake Francis Case in South Dakota in the first 16 years of impoundment. United States Fish and Wildlife Service, Bureau of Sport fisheries and Wildlife Technical Paper 56., Washington, D. C.

Gengerke, T. W. 1978. Paddlefish investigations. Iowa Conservation Commission. National Marine Fisheries Service Project 2-225-R, Segment 1-3. Final Report. Des Moines, IA.

Graham, P. J., R. F. Penkal, and L. Peterman. 1979. Aquatic studies of the Yellowstone river. Submitted to the Bureau of Reclamation, Upper Missouri Region, Billings, MT. REC-ERC-79-8.

Haddix, M. H., and C. C. Estes. 1976. Lower Yellowstone River fishery study. Final Report. Montana Department of Fish and Game, Helena, MT.

Kimmel, B. L., and A. W. Groeger. 1986. Limnological and ecological changes associated with reservoir aging. Pages

103-109 *in:* G. E. Hall and M. J. Van Den Avyle, editors. Reservoir Fisheries Management: strategies for the 80s. Reservoir Committee, southern Division American Fisheries Society, Bethesda, MD.

Kozlowski, J. 1989. Sexual size dimorphism: a life history perspective. Oikos 54:253-255.

Mero, S. W. 1992. Food habits of walleye, sauger, and their hybrids in Lake Sakakawea, North Dakota. North Dakota Game and Fish Department, Federal Aid Project F-2-R-38, Job VI. Bismarck, ND.

Needham, R. G., and K. W. Gilge. 1986. Paddlefish investigations. Montana Department of Fish, Wildlife and Parks. Project No. F-11-R-34, Job II-a. Helena, MT.

Ostrofsky, M. L., and H. C. Duthie. 1978. An approach to modelling productivity in reservoirs. Verh. Internat. Verein. Limnol. 20:1562-1567.

Power, G. J., J. C. Hendrickson, J. D. Lee, and F. Ryckman. 1994. Missouri river system fishery reference and operational management document. North Dakota Game and Fish Department Report 10. Bismarck.

Purkett, C. A., Jr. 1963. The paddlefish fishery of the Osage river and the Lake of the Ozarks, Missouri. Transactions of the American Fisheries Society. 92:239-244.

Reed, B. C. 1989. Paddlefish investigations. Louisiana Department of Wildlife and Fisheries Project Number F-60(03). Baton Rouge, LA.

Reed, B. C., W. E. Kelso, and D. Allen Rutherford. 1992. Growth, fecundity, and mortality of paddlefish in Louisiana. Transactions of the American Fisheries Society 121:378-384.

Rehwinkel, B. J. 1978. The fishery for paddlefish at Intake, Montana during 1973 and 1974. Transactions of the American Fisheries Society. 107(2): 263-268.

Rien, T. A., and R. C. Beamesderfer. 1994. Accuracy and precision of white sturgeon age estimates from pectoral fin rays. Transactions of the American Fisheries Society 123:255-265.

Robinson, J. W. 1966. Observations on the life history, movement, and harvest of the paddlefish, *Polyodon spathula*, in Montana. Proceedings of the Montana Academy of Sciences 26:33-44.

Russell, T. R. 1986. Biology and life history of the paddlefish --a review. Pages 2-20 *in*: J. G. Dillard, L. K. Graham, and T.

R. Russell. 1986. The paddlefish: status, management and propagation. American Fisheries Society, North Central Division Special Publication 7.

Scarnecchia, D. L., T. W. Gengerke, and C. T. Moen. 1989. Rationale for a harvest slot limit for paddlefish in the Upper Mississippi River. North American Journal of Fisheries Management 9:477-487.

Scarnecchia, D. L., P. A. Stewart, and G. J. Power. 1994. Management plan for the paddlefish stocks in the Yellowstone River, Upper Missouri River, and Lake Sakakawea. Montana Department of Fish, Wildlife and Parks and North Dakota Game and Fish Department, Helena, MT and Bismarck, ND.

Shine, R. 1990. Proximate determinants of sexual differences in adult body size. The American Naturalist 135:278-283.

Sparre, P., E. Ursin, and S. C. Venema. 1989. Introduction to tropical fish assessment. Part 1 -- Manual. FAO Fisheries Technical Paper 306/1, Rome, Italy.

Stewart, P. A. 1987. Yellowstone River paddlefish investigations. Montana Department of Fish, Wildlife, and Parks. Fisheries Division Job Progress Report F-30-R-23, Job IIa. Helena, MT.

Stewart, P. A. 1991. Yellowstone River paddlefish investigations. Montana Department of Fish, Wildlife, and Parks, Fisheries Division, Job Progress Report Project F-46-R-4, Job III-c. Helena, MT.

Stewart, P. A. 1994. Yellowstone River paddlefish investigations. Montana Department of Fish, Wildlife and Parks, Fisheries Division, Job Progress Report Project F-46-R-7, Job III-c. Helena, MT.

Van Eeckhout, G. 1980. Investigations of selected fish populations by the mark-recapture method. North Dakota Game and Fish Department, Dingell-Johnson Project F-2-R-27. Bismarck, ND.

List of Figures

36 kg.

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10. Age distribution of a) 219 male and b) 471 female paddlefish sampled at Intake, 1992.

11. Age distribution of a) 1144 males and b) 672 female paddlefish sampled at Intake, 1993.

12. Sex-specific von Bertalanffy growth curves for male and female paddlefish sampled at Intake, 1991.

13. Sex-specific, weight-converted von Bertalanffy growth curves for a) male and b) female paddlefish sampled at Intake, 1991.

14. Length frequencies for gill-netted, tagged, and released paddlefish near the Confluence in April, 1993 (solid line) and distribution of lengths harvested and landed at the Confluence in May and June, 1993. High-grading is suspected because of the higher than expected frequency of longer fish landed.

Table 1. Percentages of paddlefish caught at Intake from 1991 to 1993 according to their year class and relation to reservoir water levels. Period 1 = Pre-1954 (before reservoir); Period 2 = 1954-66 (reservoir filling); Period 3 = 1967-76 (full); Period 4 = 1977-88 (reservoir variable, full or slightly below full).

	Year class							
Year of catch	Pre-1954		1954-66		1967-76		1977-88	
	M	F	M	F	M	F	M	F
1991	<1	<1	18	59	51	40	31	<1
1992	0	<1	15	58	46	41	39	<1
1993	0	0	3	24	46	66	50	10

Figure 1.

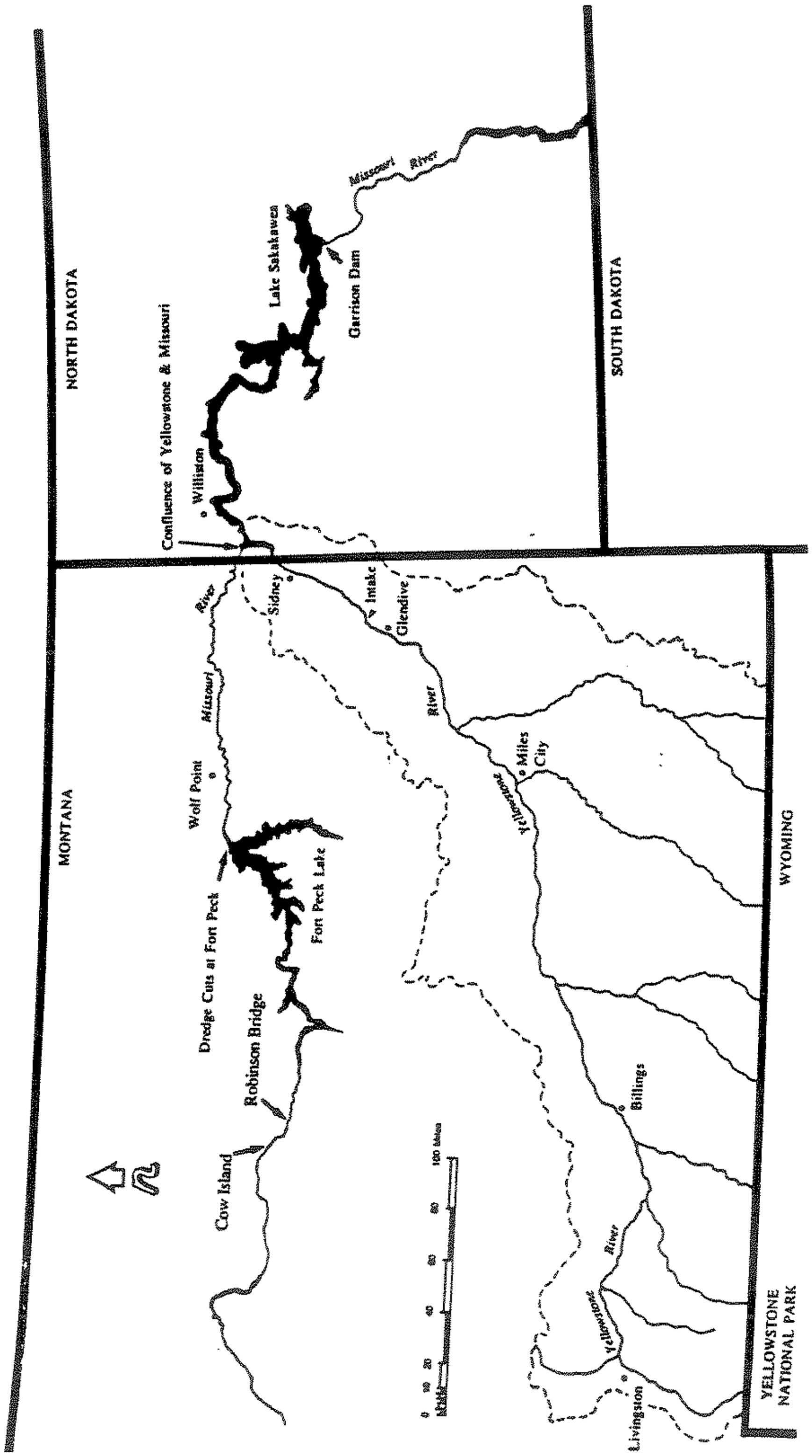

NORTH DAKOTA
SOUTH DAKOTA
MONTANA
WYOMING
YELLOWSTONE NATIONAL PARK
Missouri River
Lake Sakakawea
Garrison Dam
Confluence of Yellowstone & Missouri
Williston
Sidney
Intake
Glendive
Yellowstone River
Miles City
Wolf Point
Missouri River
Fort Peck Lake
Dredge Cuts at Fort Peck
Robinson Bridge
Cow Island
Billings
Yellowstone River
Livingston
0 10 20 40 60 80 100 Miles

Figure 2

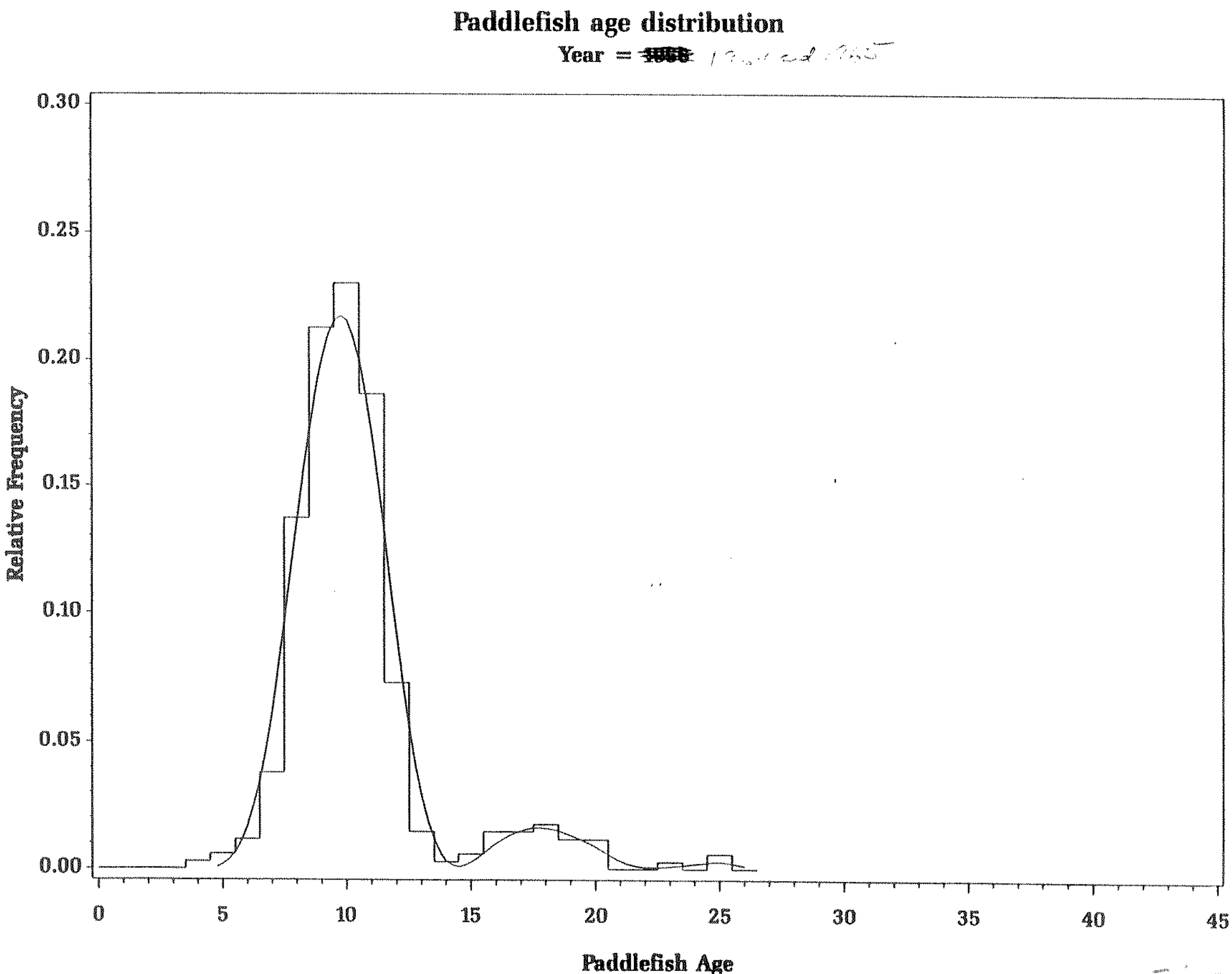


Fig 2

Fig 3

Daily elevation above sea level of Garrison Reservoir from December 1, 1953 to February 28,1994

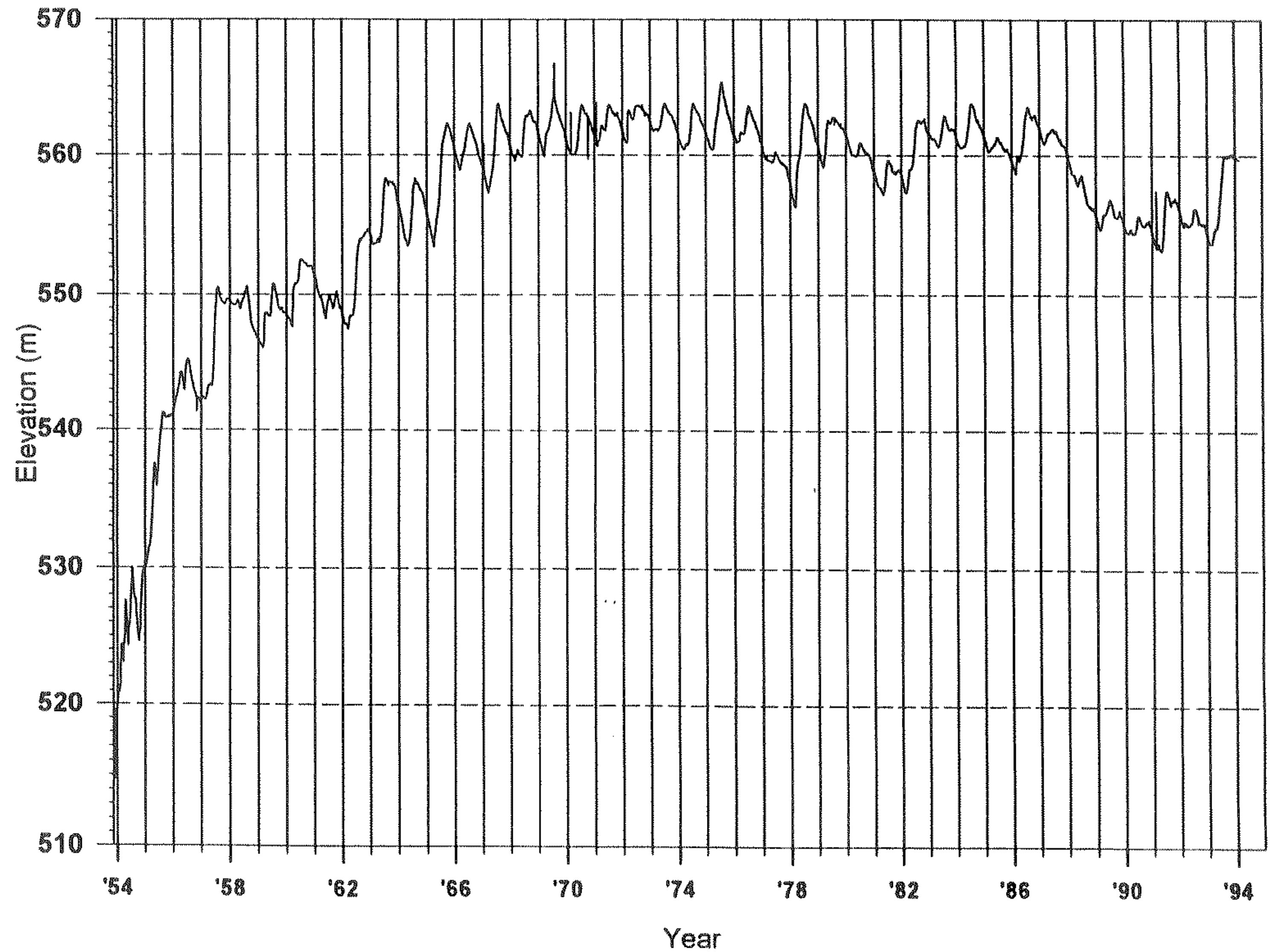
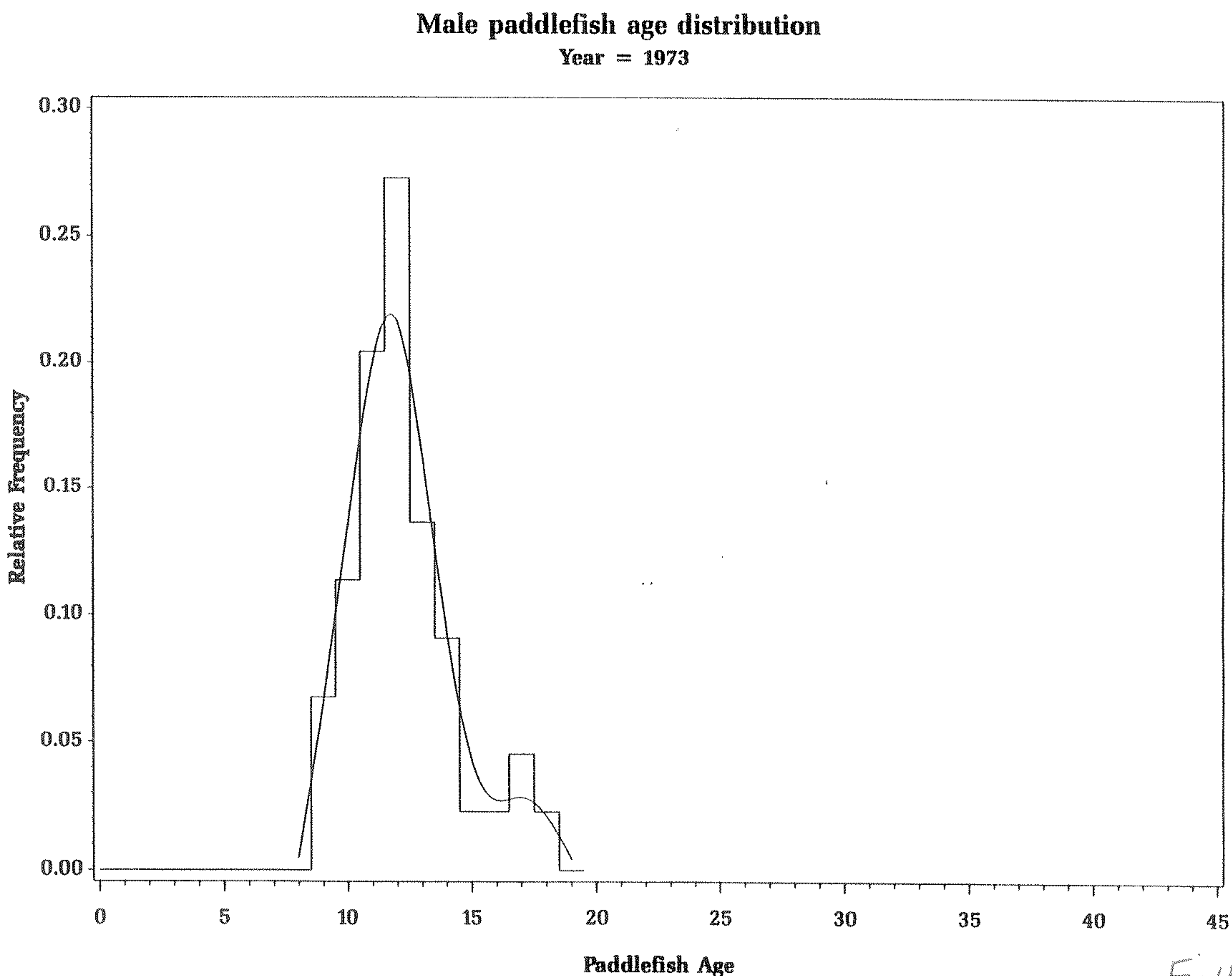


Fig 3

Fig 4A


Male paddlefish age distribution
Year = 1973
Relative Frequency
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0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
30
35
40
45
Paddlefish Age

Fig 4a

Female paddlefish age distribution

Year = 1973

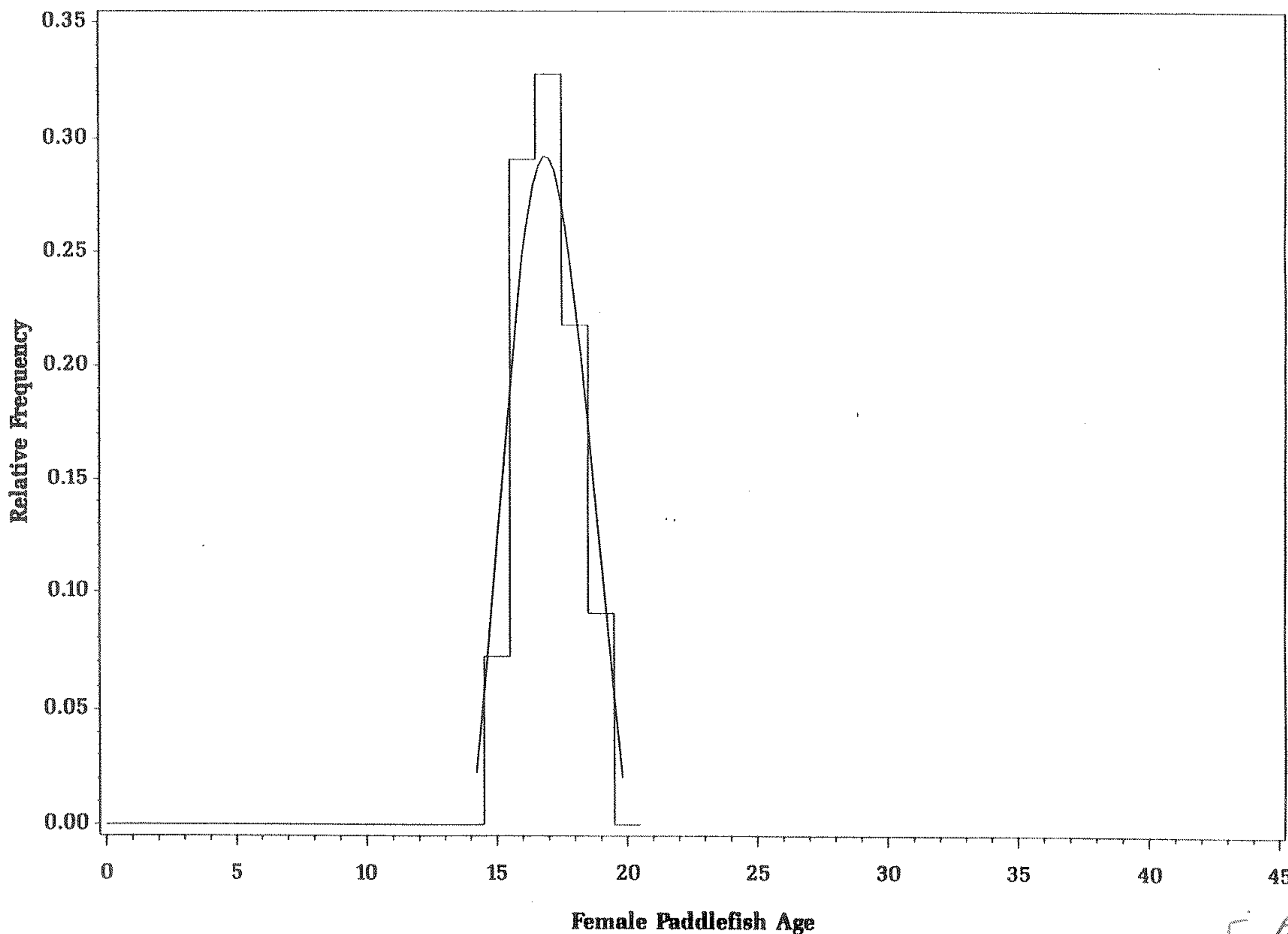

Fig ~~4~~6

Fig 4c

Paddlefish age distribution

Year = 1973

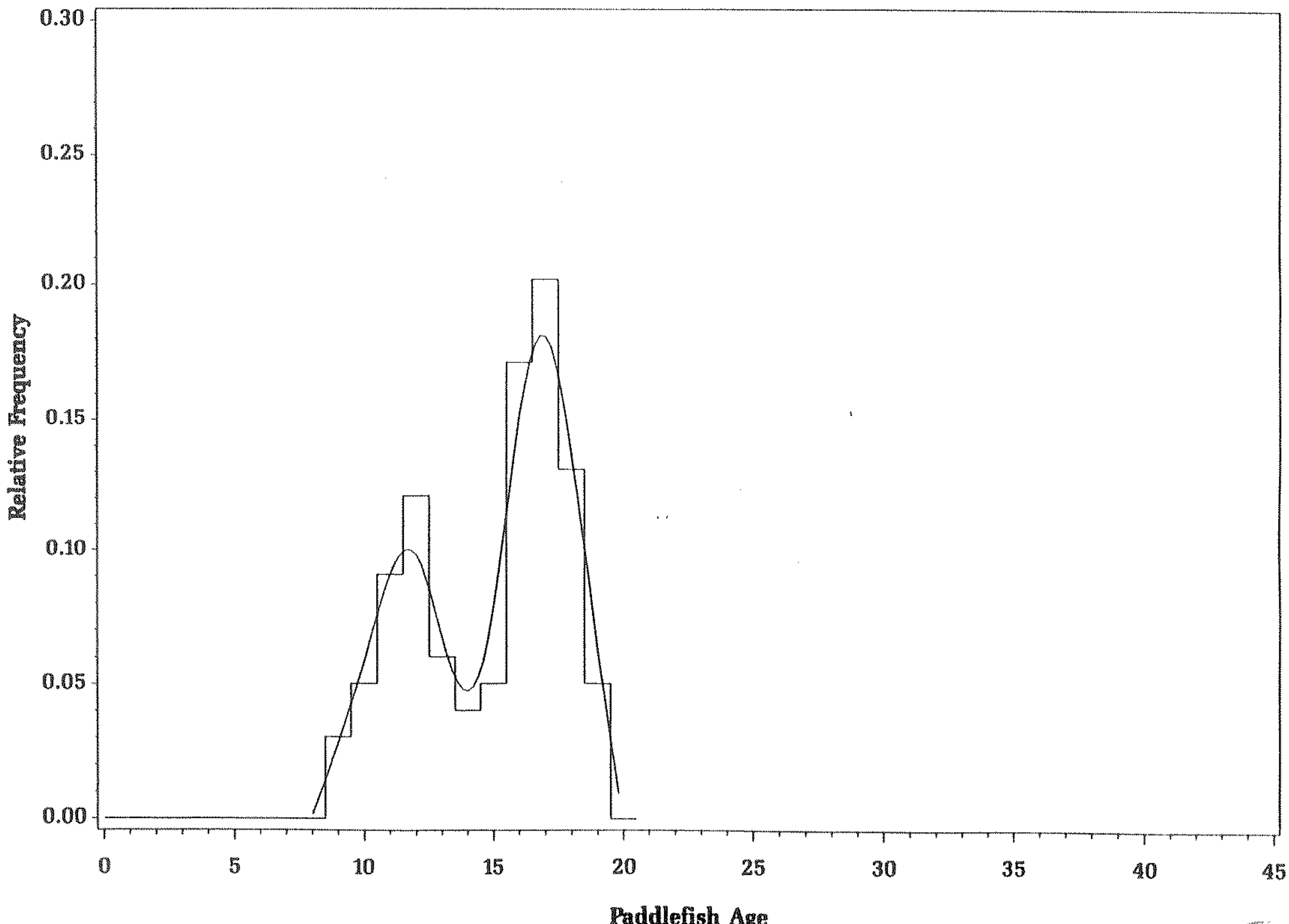

Fig 4c

Male paddlefish age distribution

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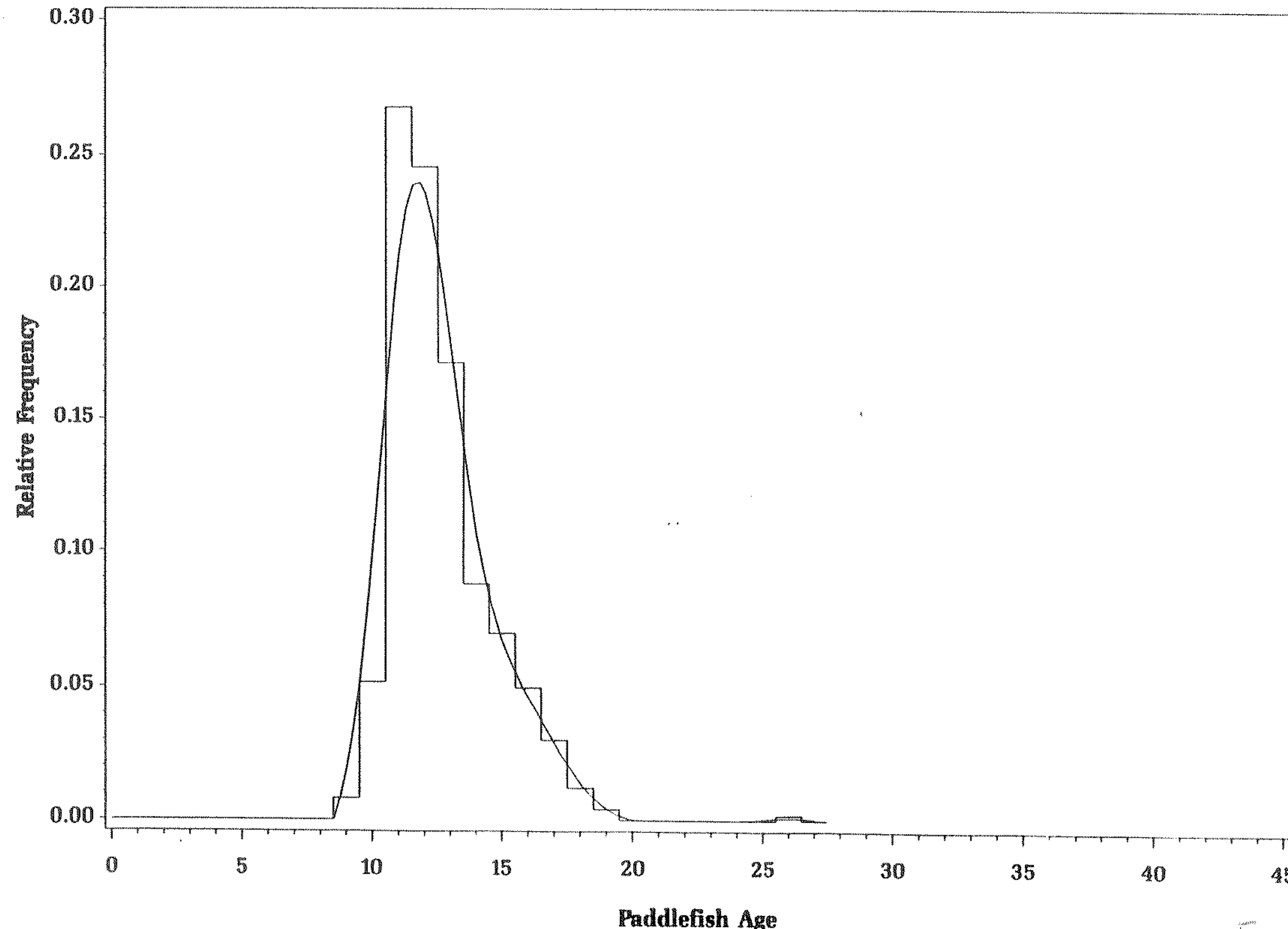
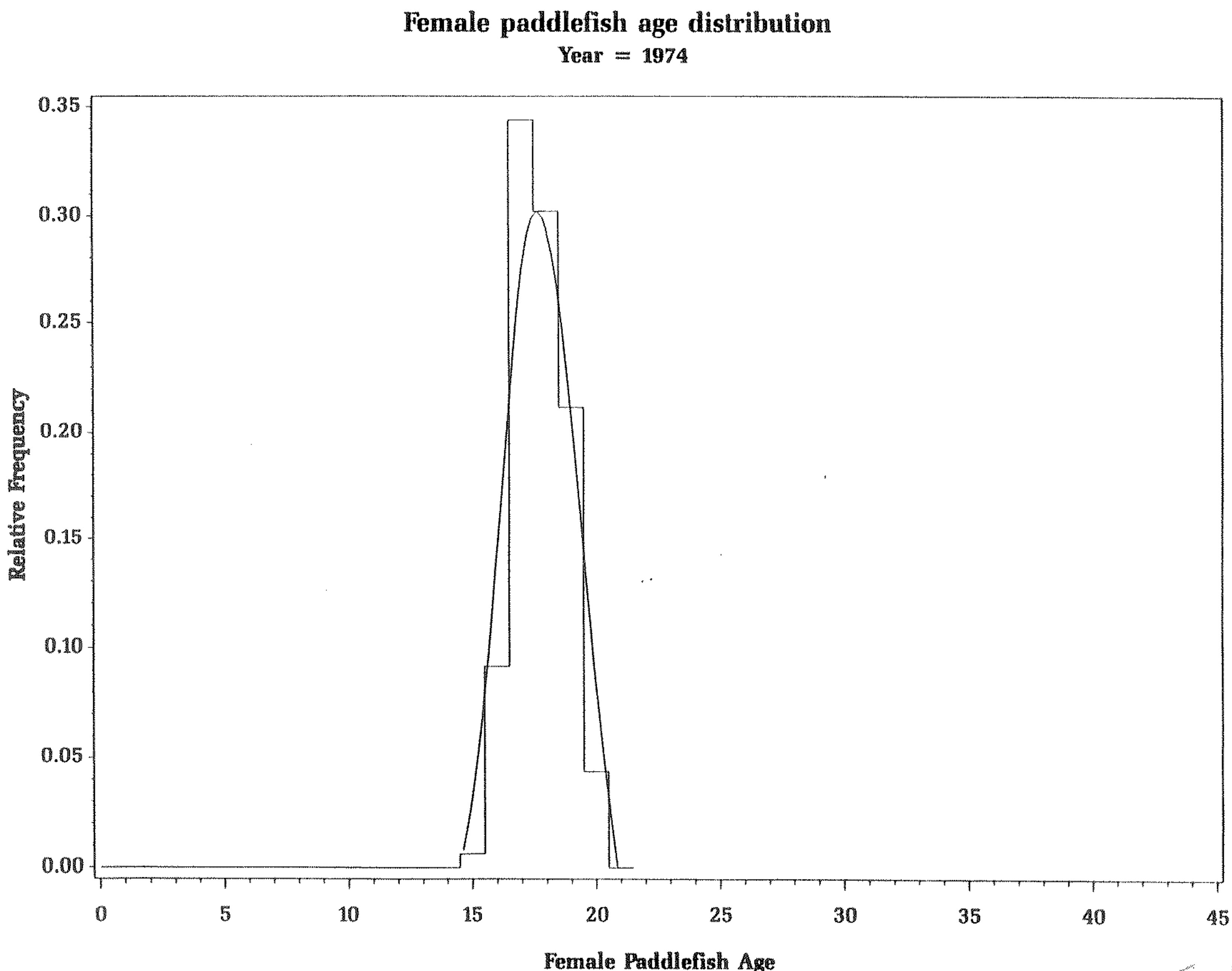


Fig 4F


Female paddlefish age distribution
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Relative Frequency
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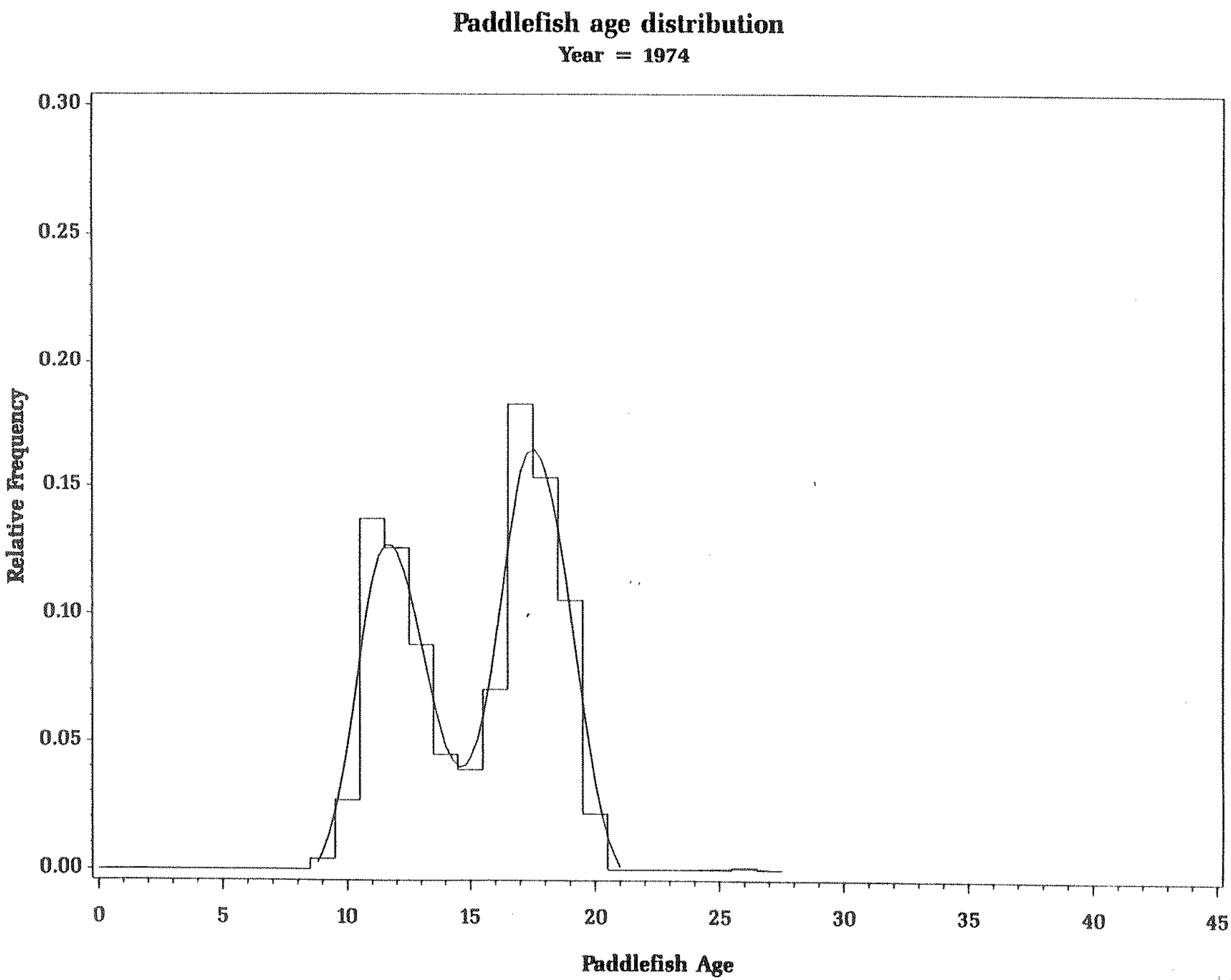
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
30
35
40
45
Female Paddlefish Age

Fig 4e

1974.



Paddlefish age distribution
Year = 1974
Relative Frequency
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0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
30
35
40
45
Paddlefish Age

Fig 4f.

Percentage of female paddlefish in Intake catch

1963-1993

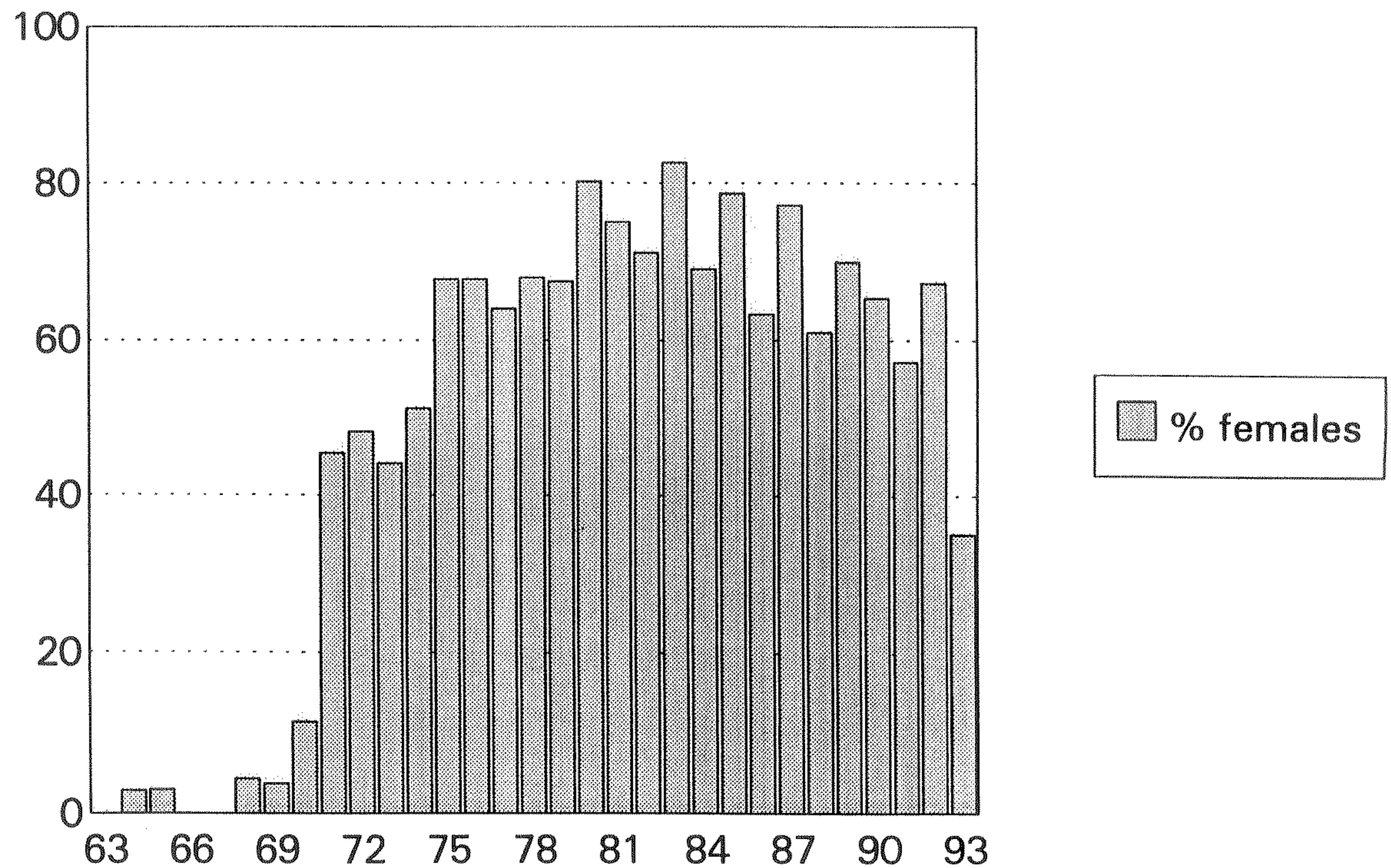
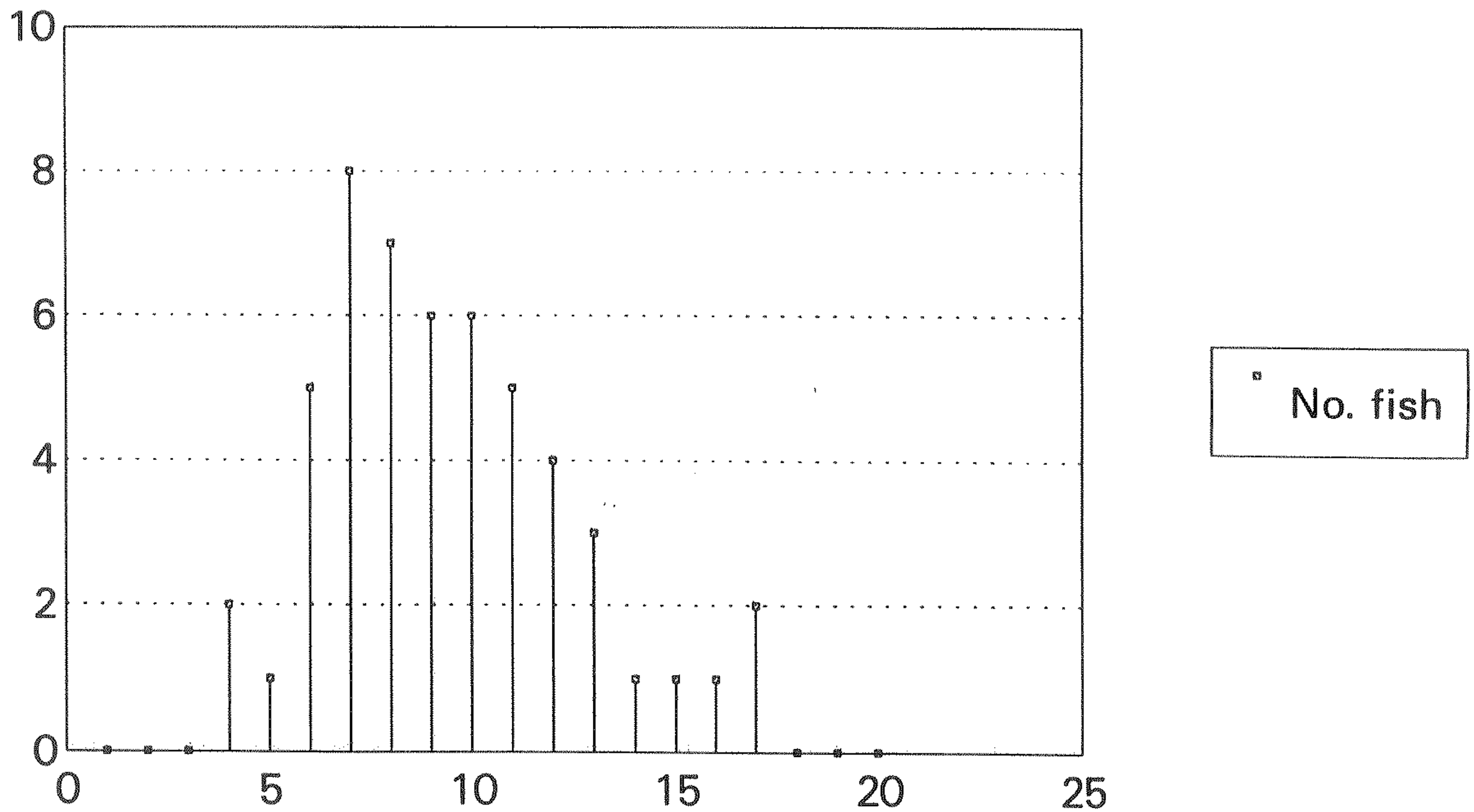


Fig 5

Paddlefish age

Lake Sakakawea, 1977



Data from Van Eeckout (1980).

Fig 6

Approximated weight distribution:

Female paddlefish (1981–83, 1984–86, 1987–89, 1990–92)

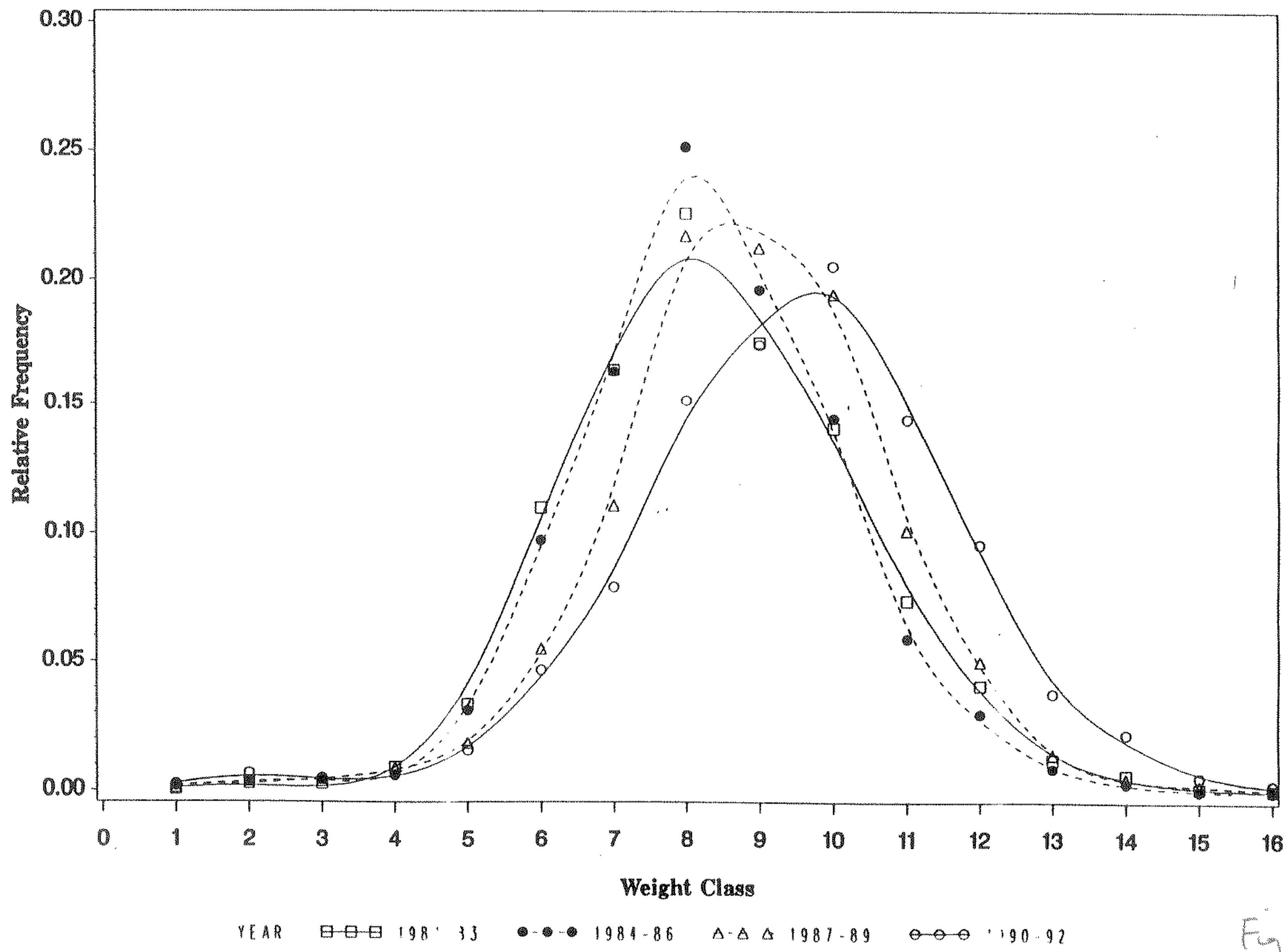


Fig 7

Fig 8a

Male paddlefish age distribution

Year = 1985 M

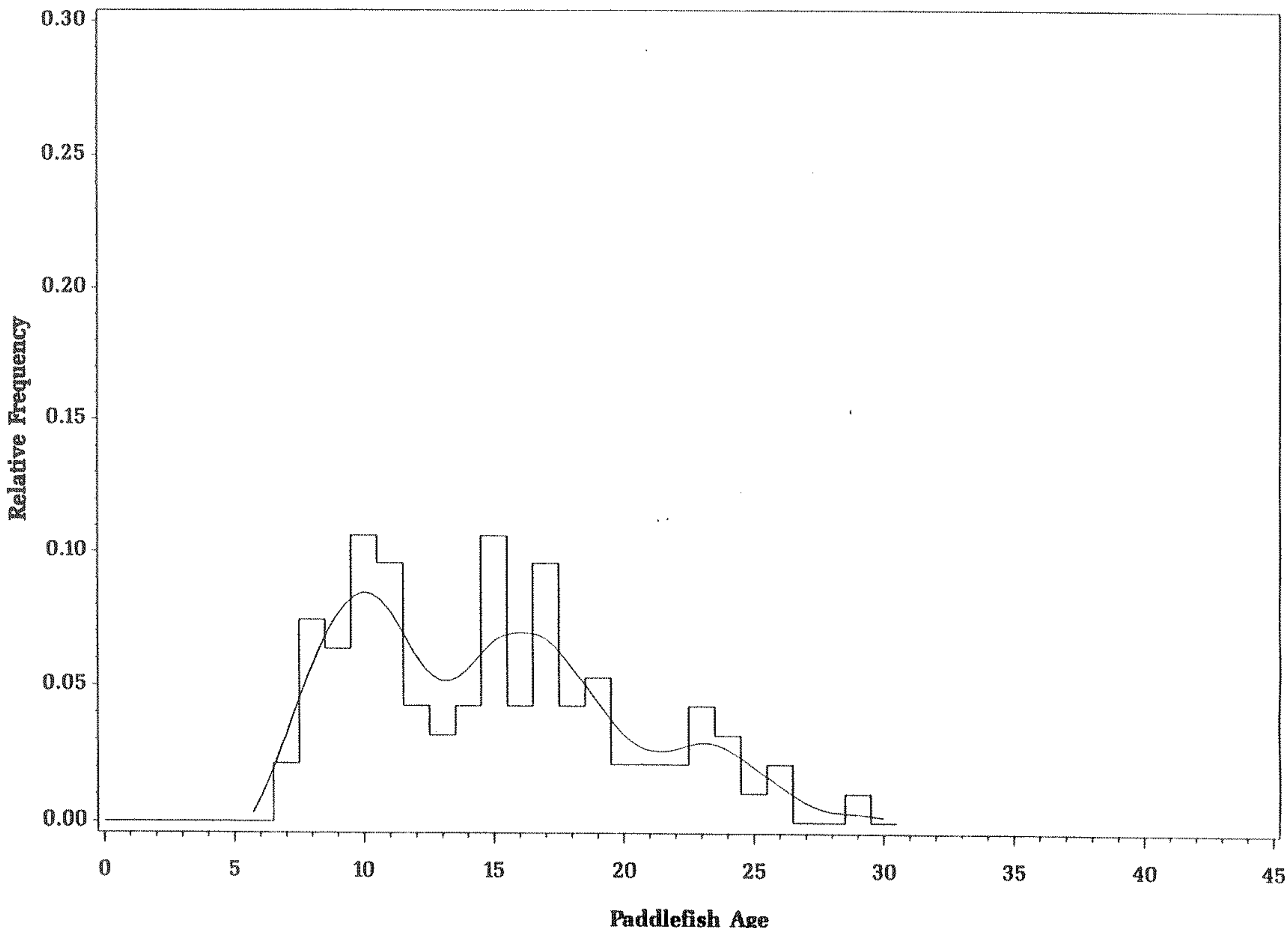
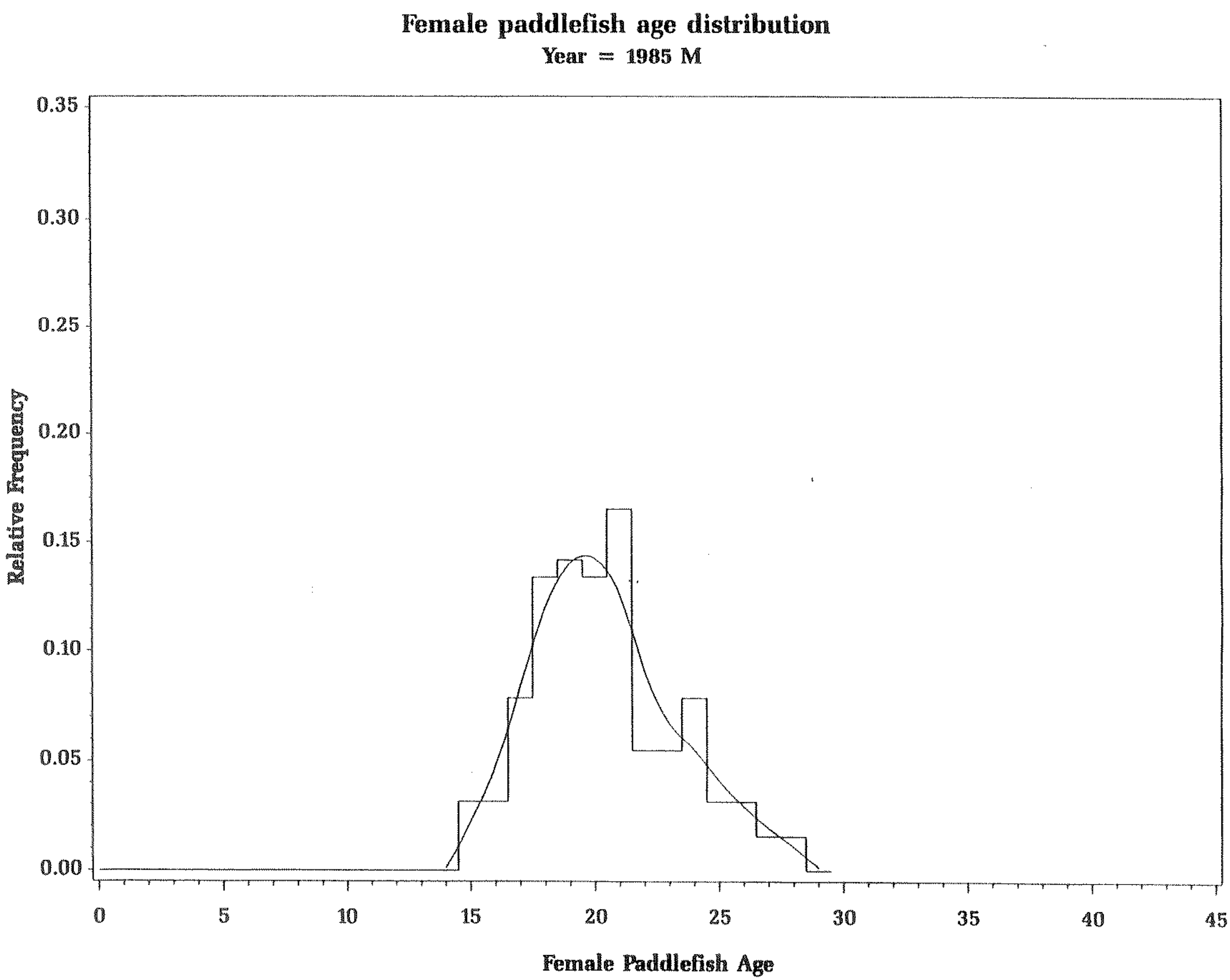


Fig 8a

Fig. 8b


Female paddlefish age distribution
Year = 1985 M
Relative Frequency
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0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
30
35
40
45
Female Paddlefish Age

Fig 8b

Montana age
Fig 8c

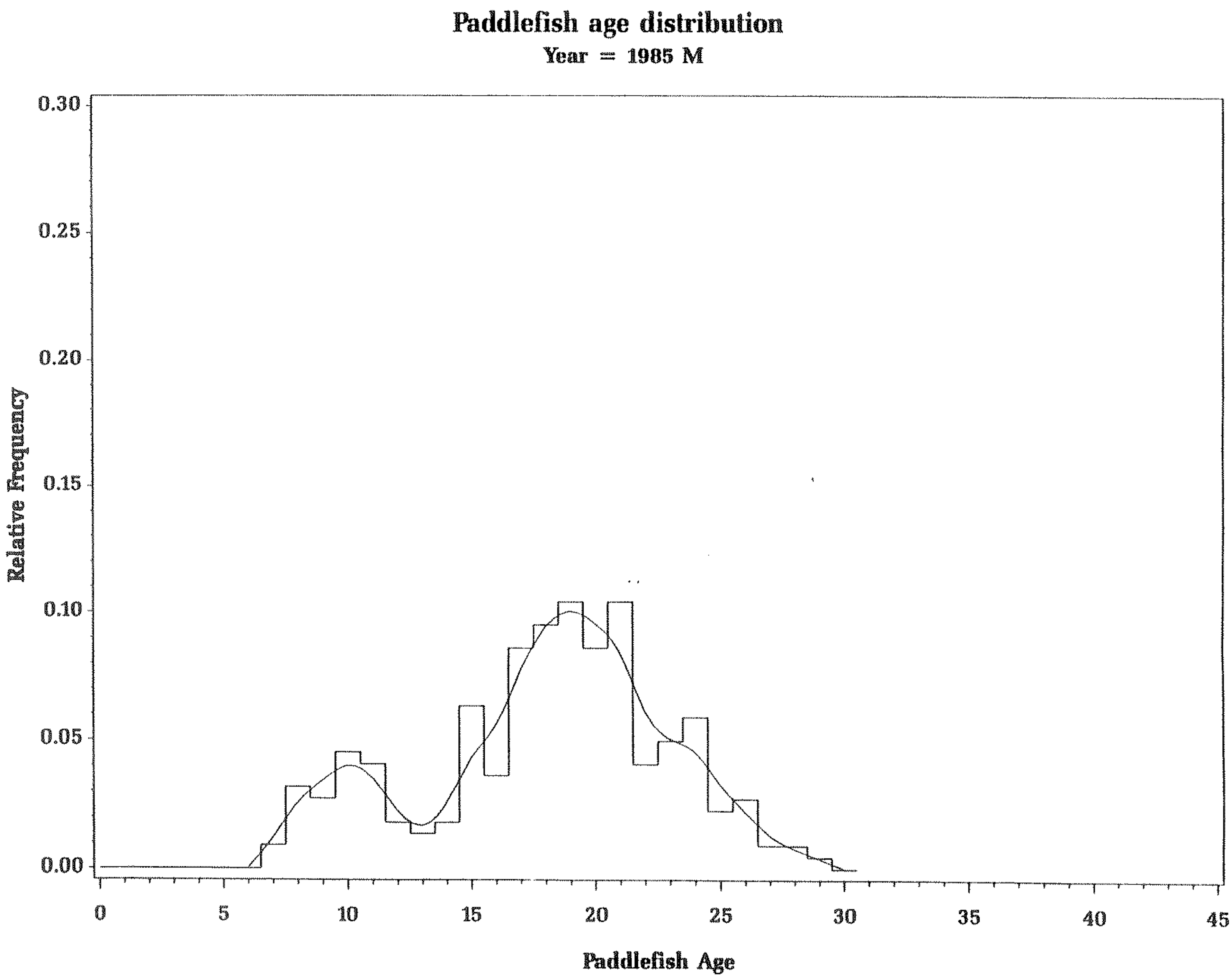
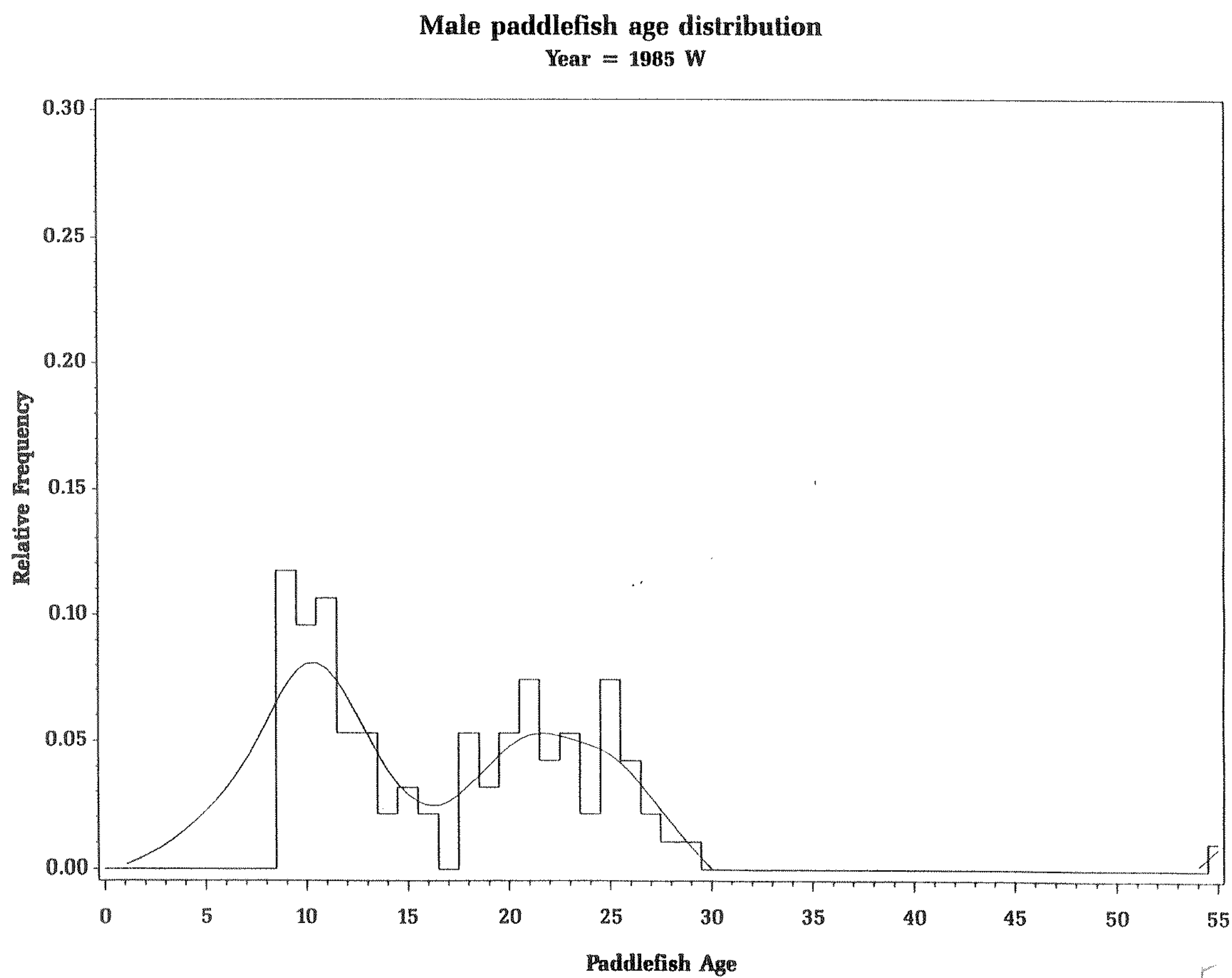


Fig 8c

Fig 8d


Male paddlefish age distribution
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0.30
0.25
0.20
0.15
0.10
0.05
0.00
Relative Frequency
0
5
10
15
20
25
30
35
40
45
50
55
Paddlefish Age

Fig 8d

Fig 8e

Female paddlefish age distribution

Year = 1985 W

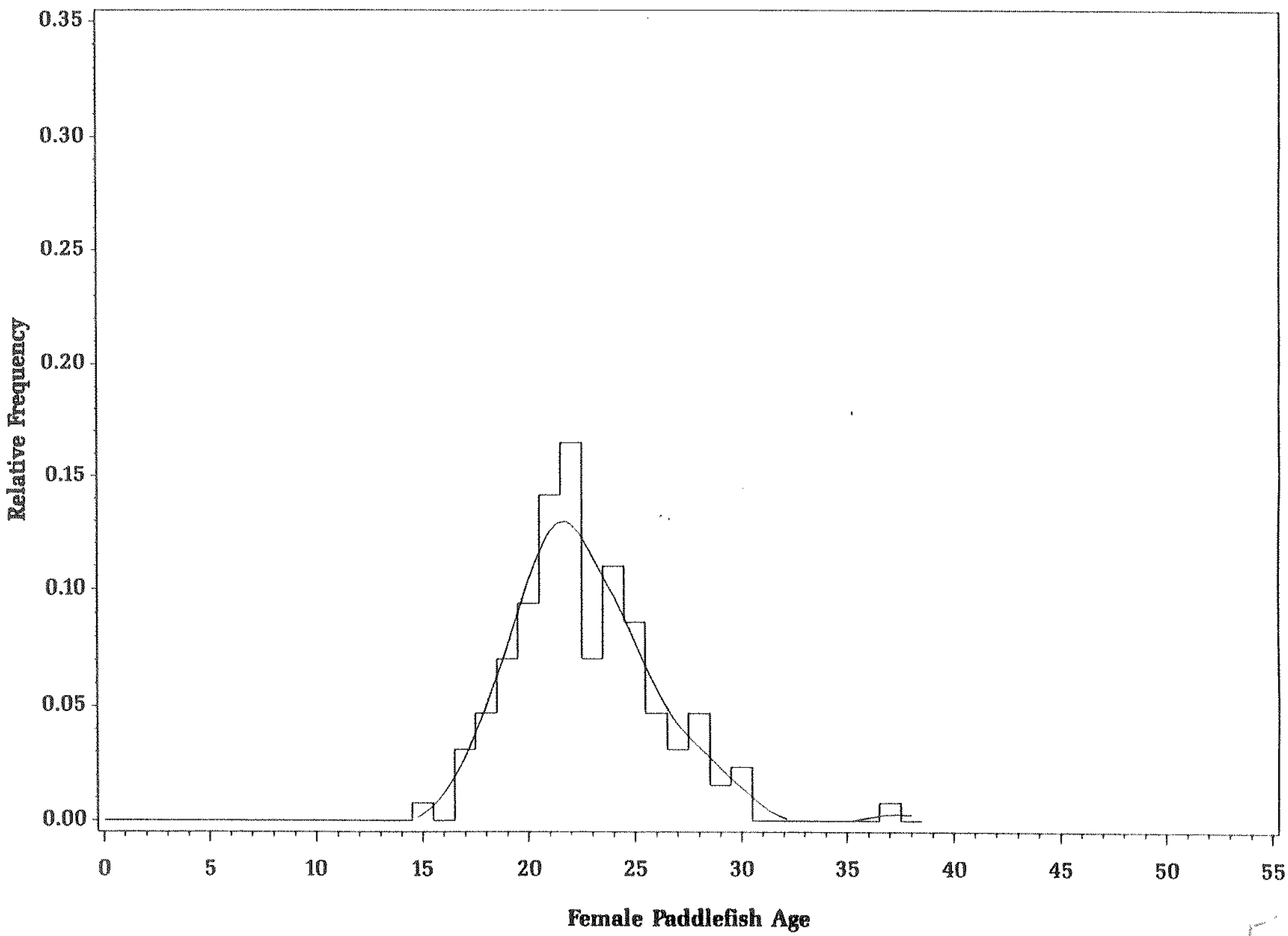
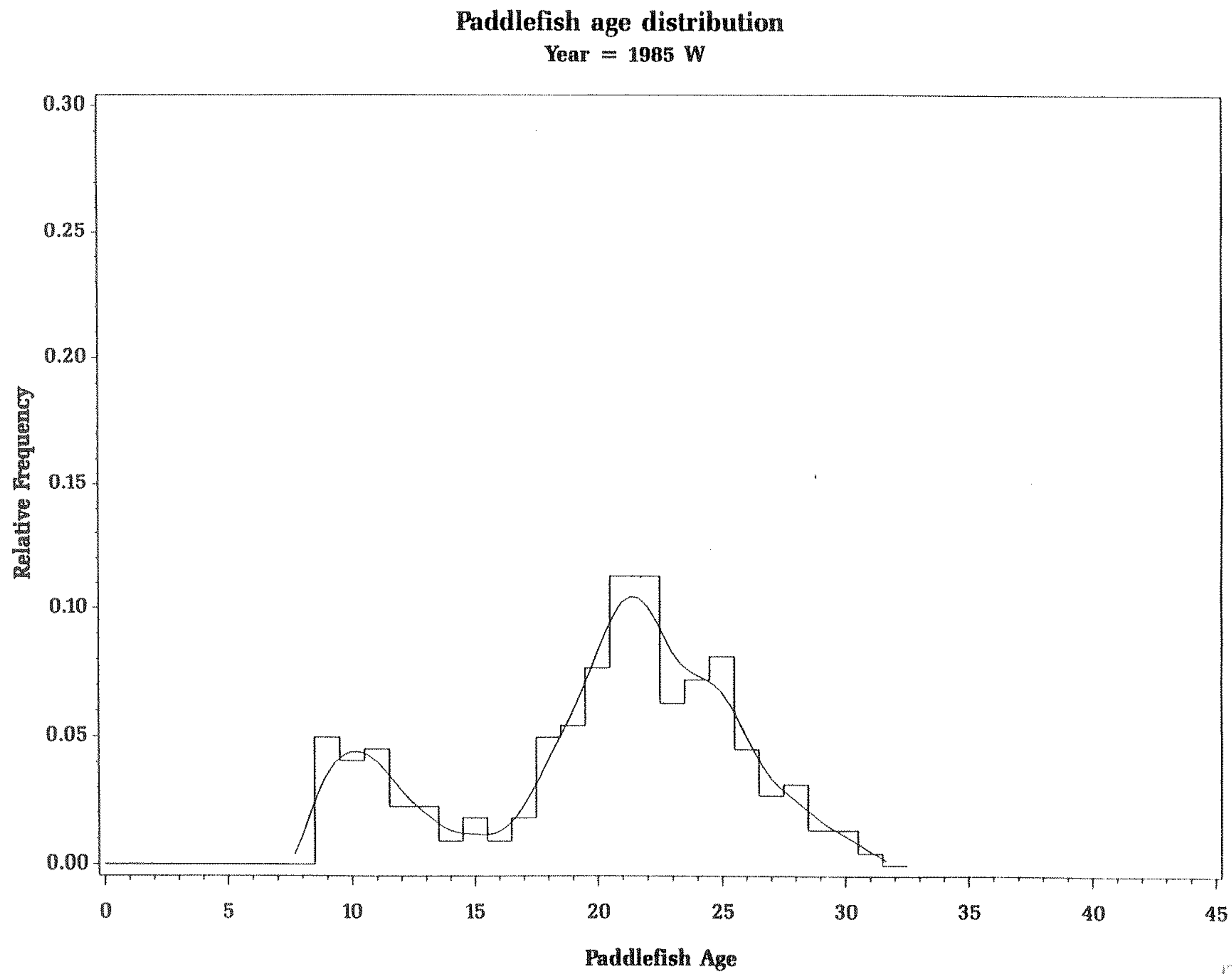


Fig 8e


Paddlefish age distribution
Year = 1985 W
Relative Frequency
0.30
0.25
0.20
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25
30
35
40
45
Paddlefish Age

Fig 8f

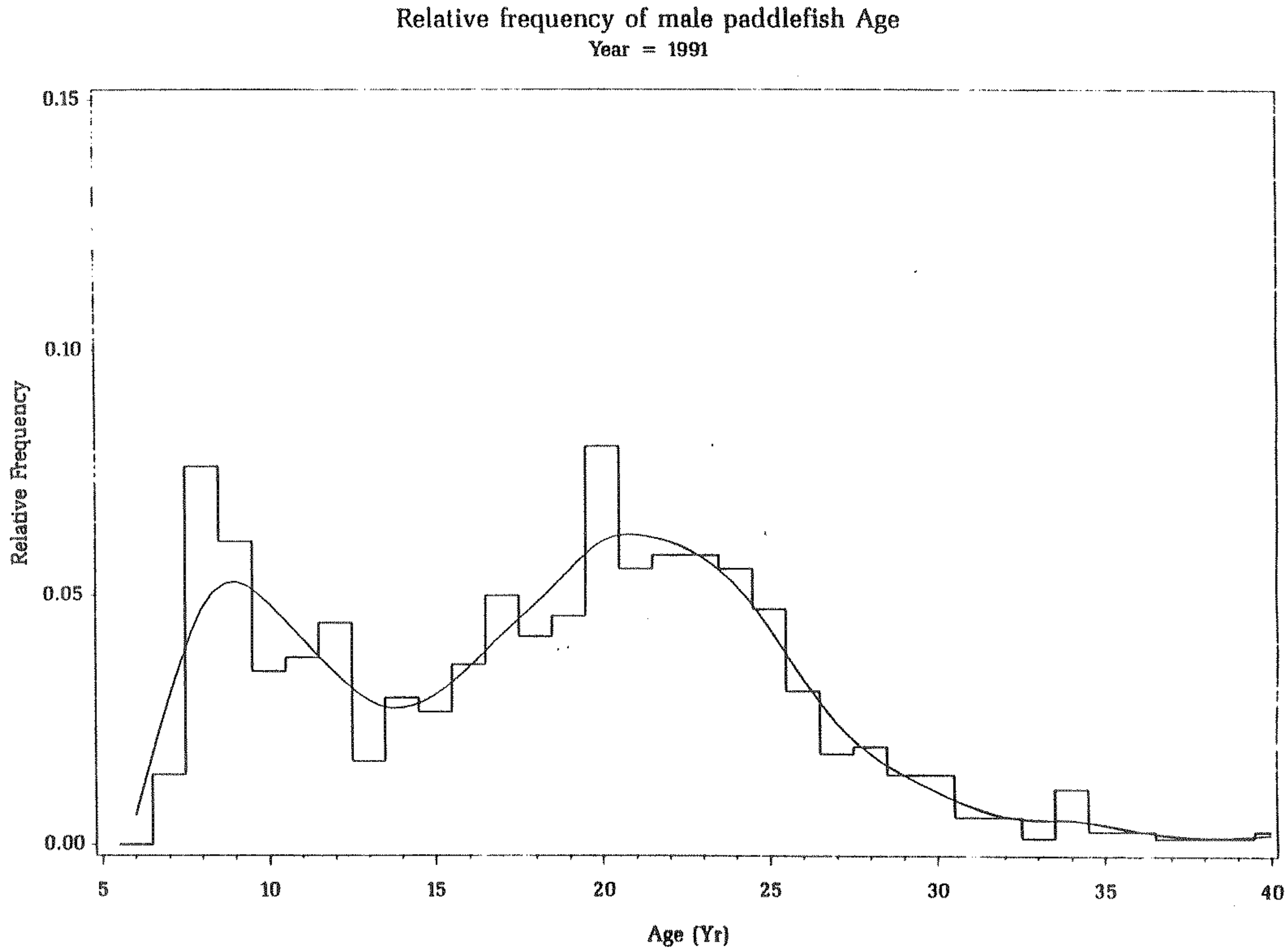

Figure 9a Age distribution of 721 male paddlefish sampled at Intake, 1991.

Fig. 9a

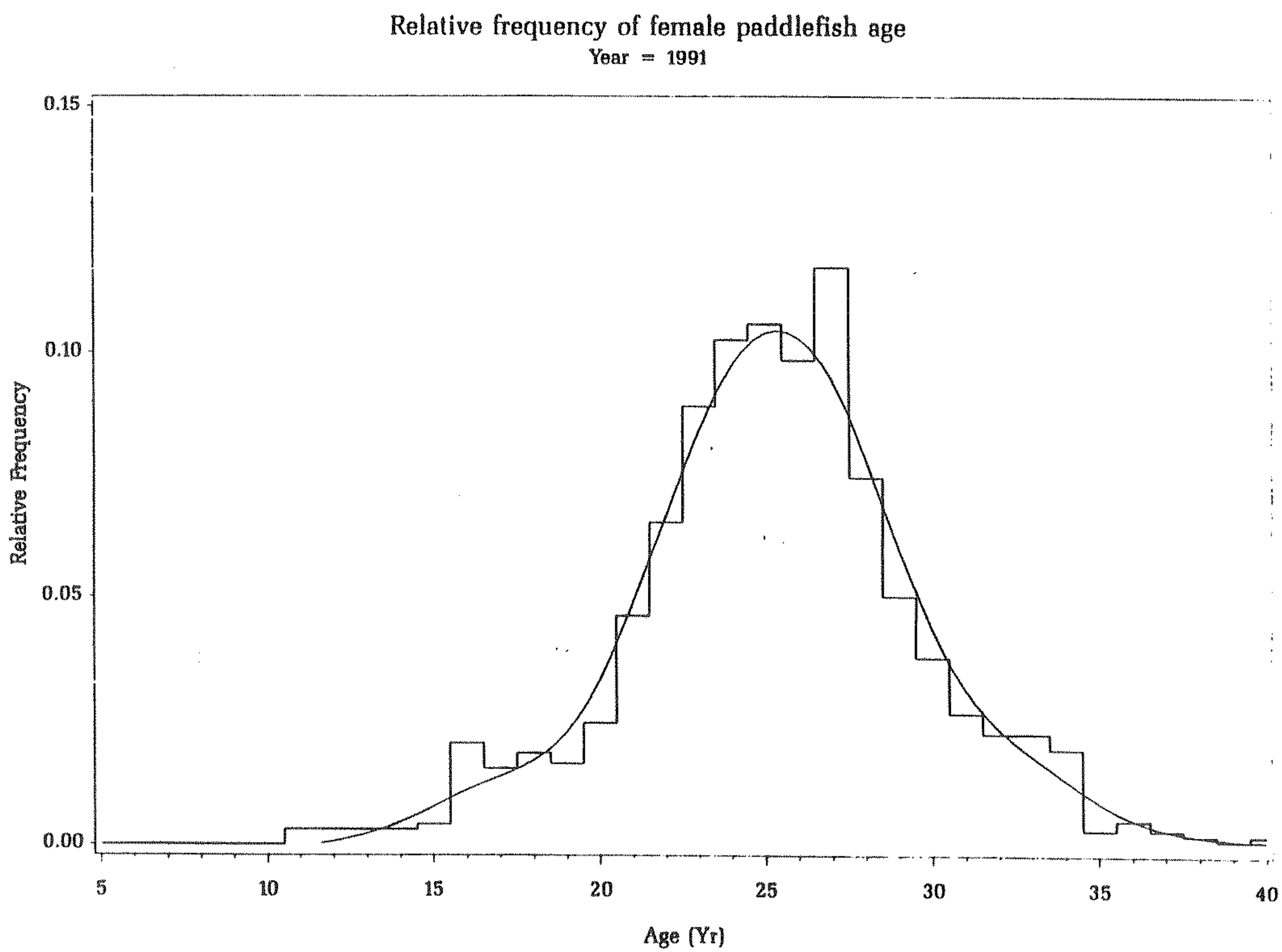

Figure 9b. Age distribution of 975 female paddlefish sampled at Intake, 1991.

Fig 9b

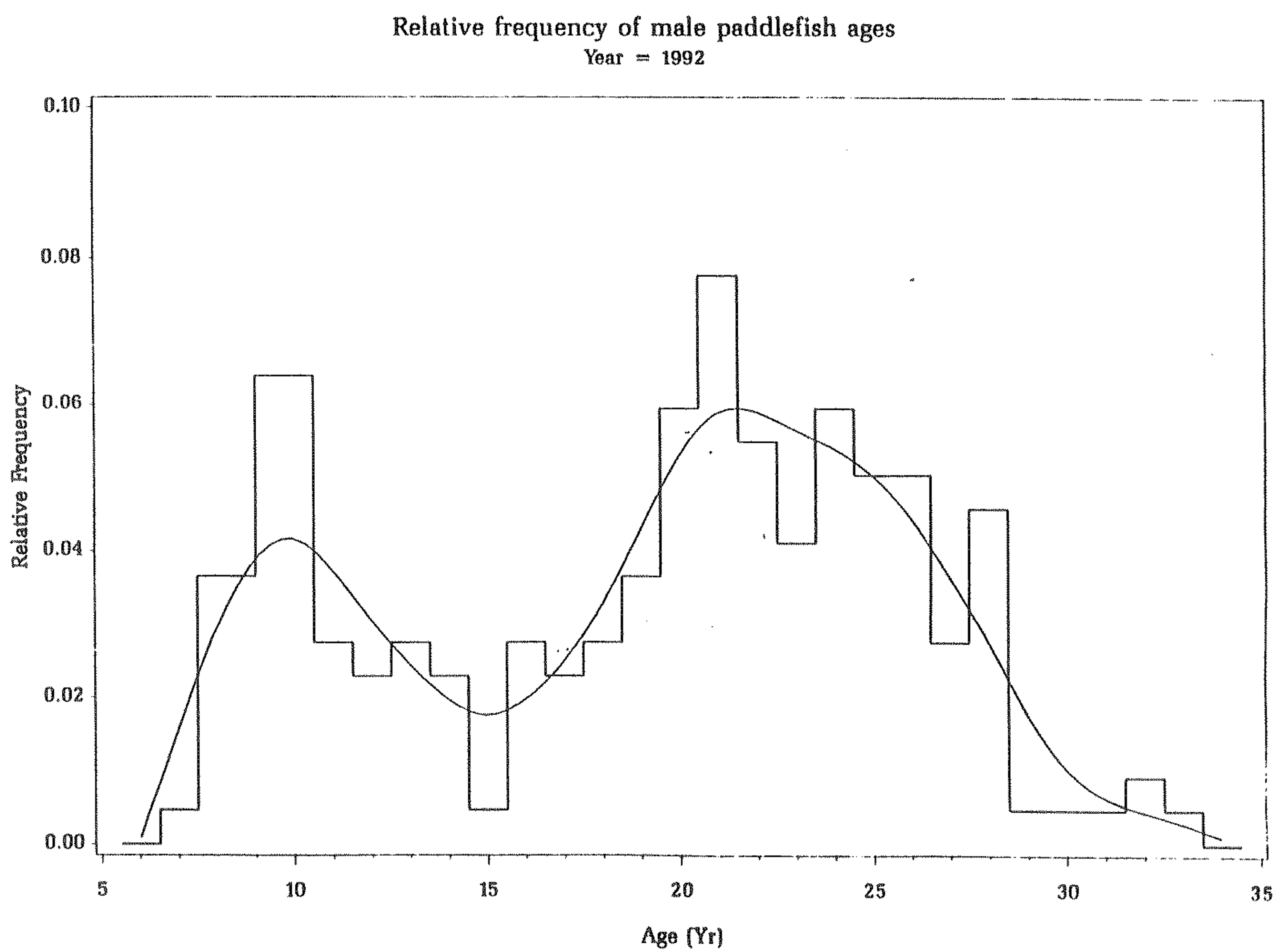

Figure 10a Age distribution of 219 male paddlefish sampled at Intake, 1992.

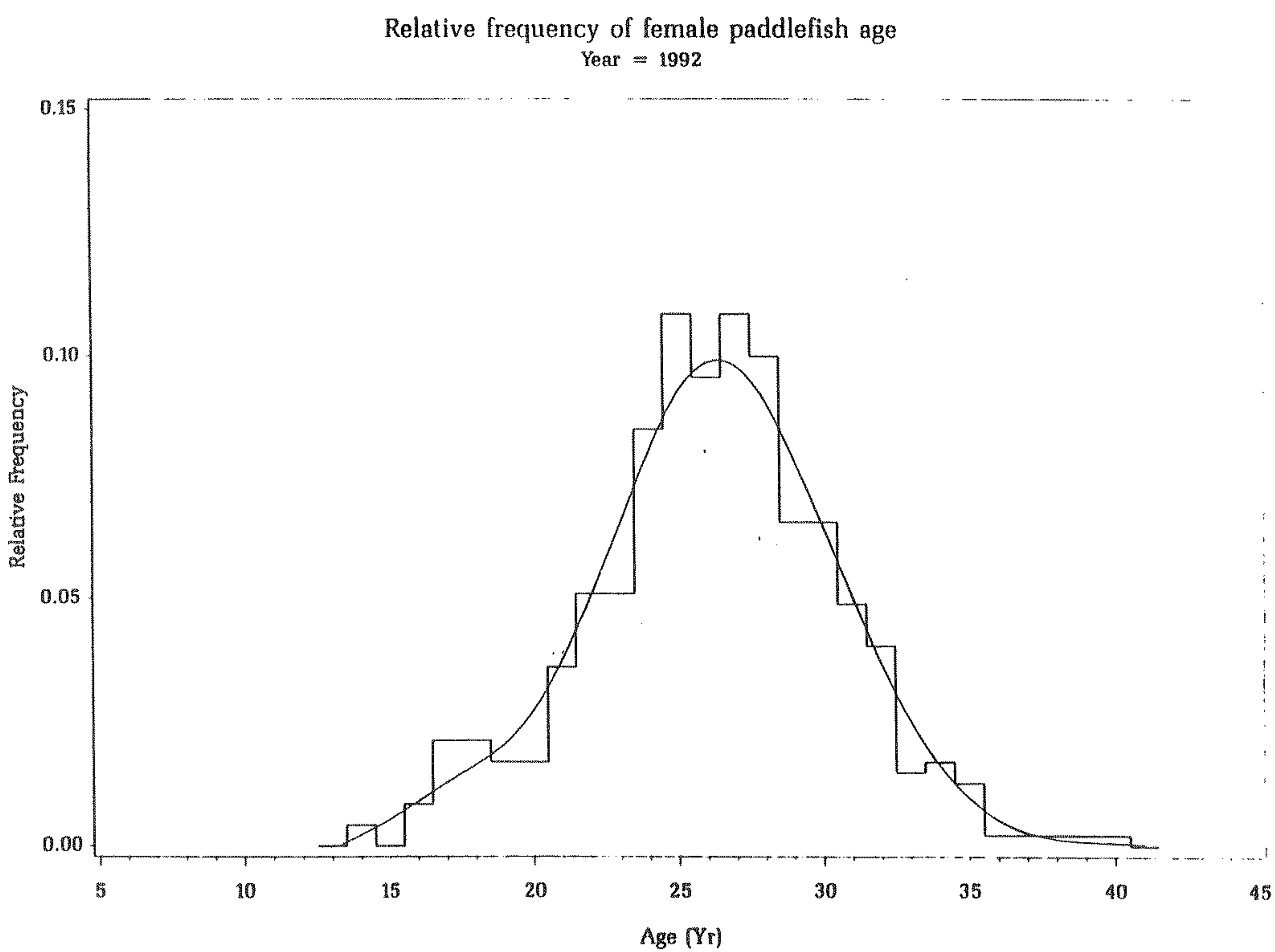

Figure 10b Age distribution of 471 female paddlefish sampled at Intake, 1992.

Fig 10b

Relative frequency of male paddlefish age
Year = 1993

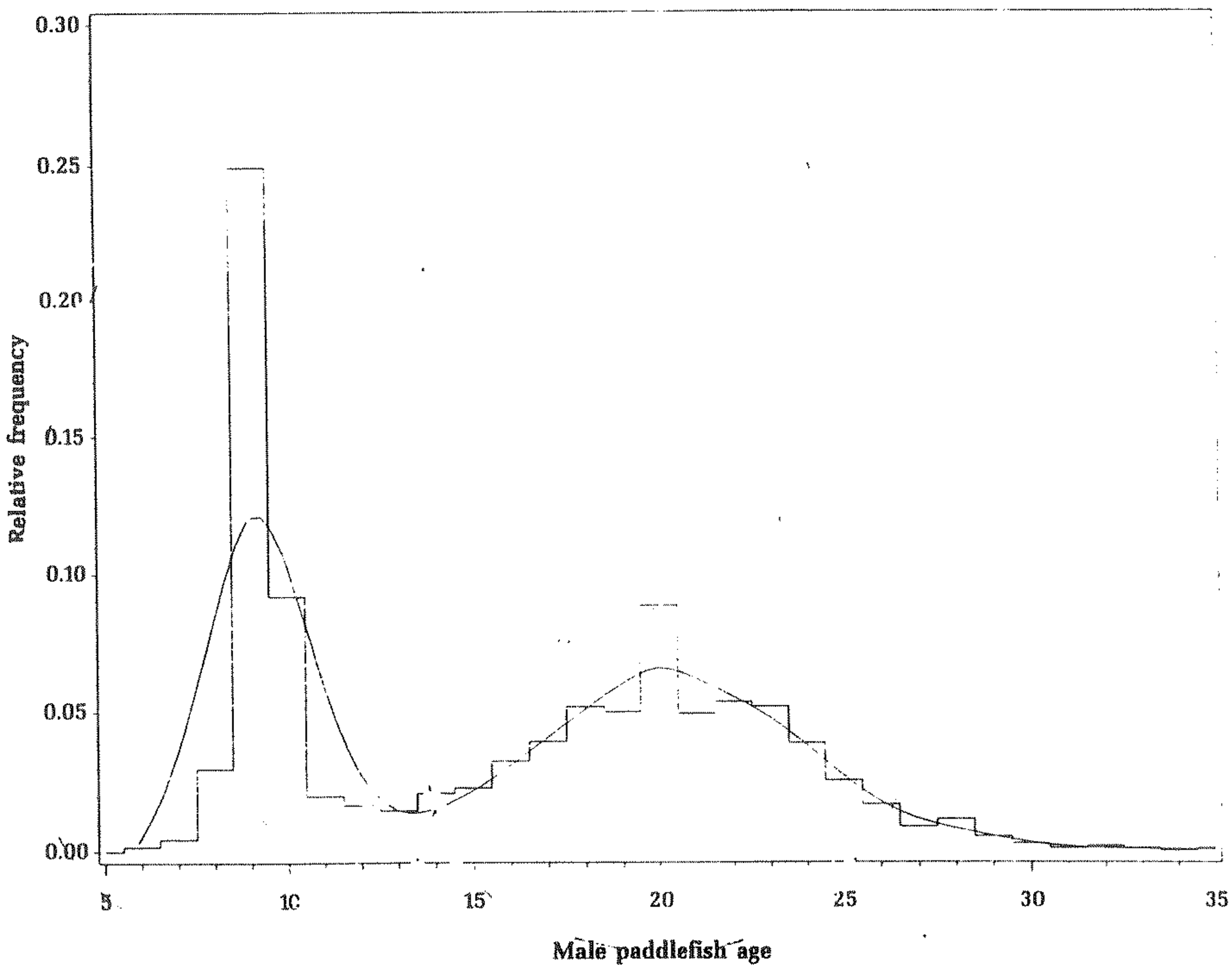

Fig 11a

Relative frequency of female paddlefish age

Year = 1993

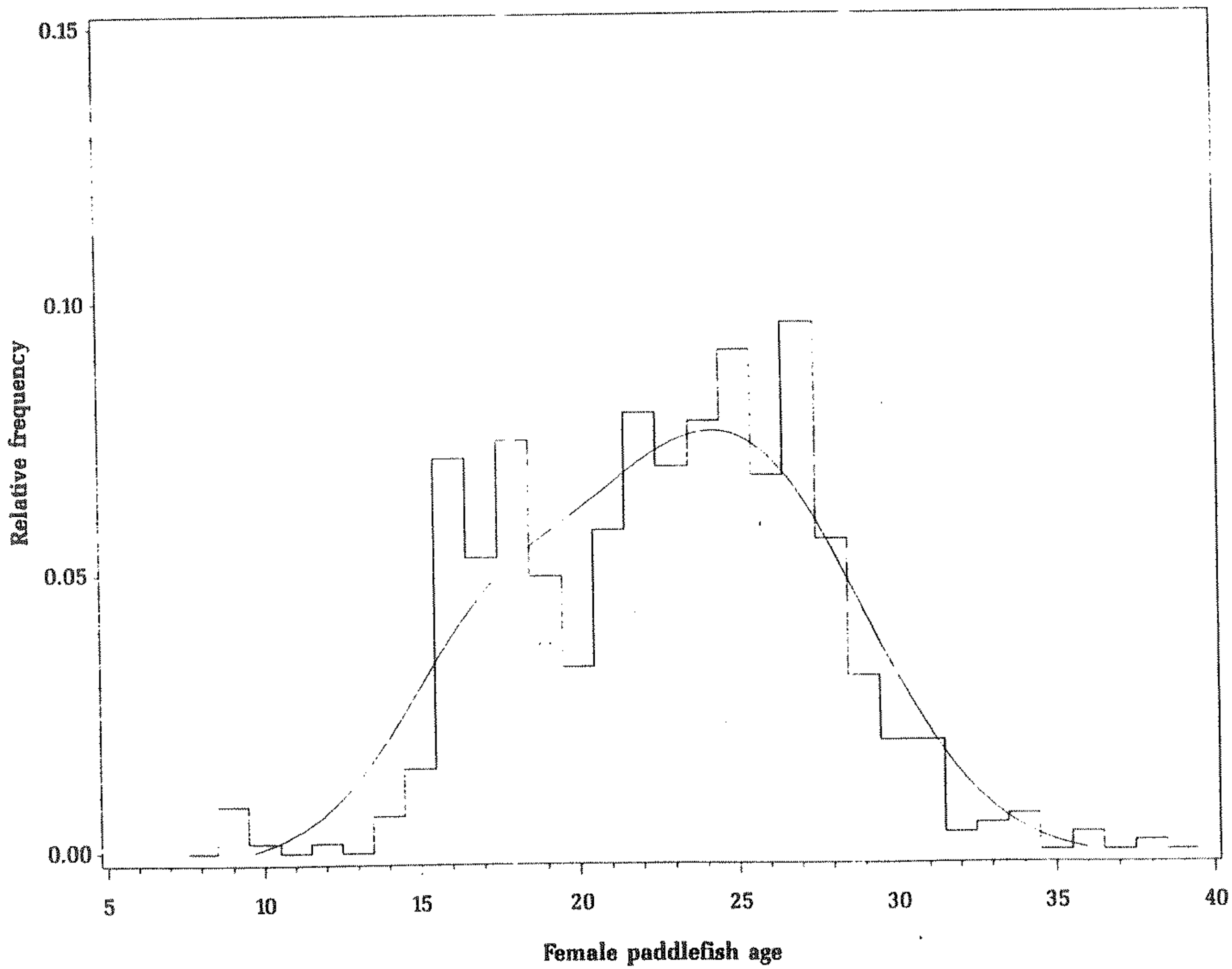

Fig 11b

Fig 12

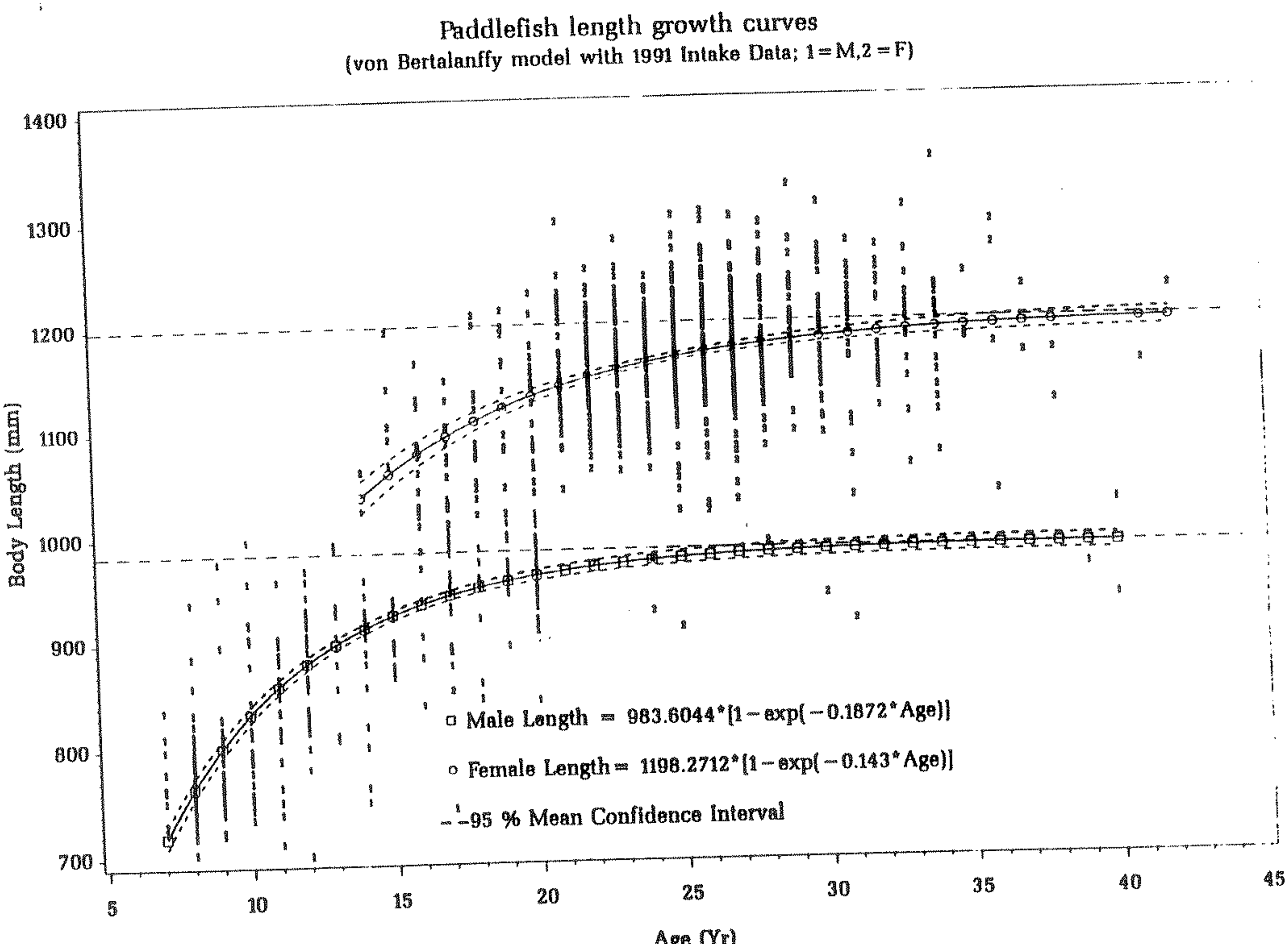

Figure 12. Sex-specific von Bertalanffy growth curves for male and female paddlefish sampled at Intake, 1991.

Fig 12

Fig 13a

Male paddlefish weight growth curves with 1991 data

(von Bertalanffy eqn. with no initial condition parameter)

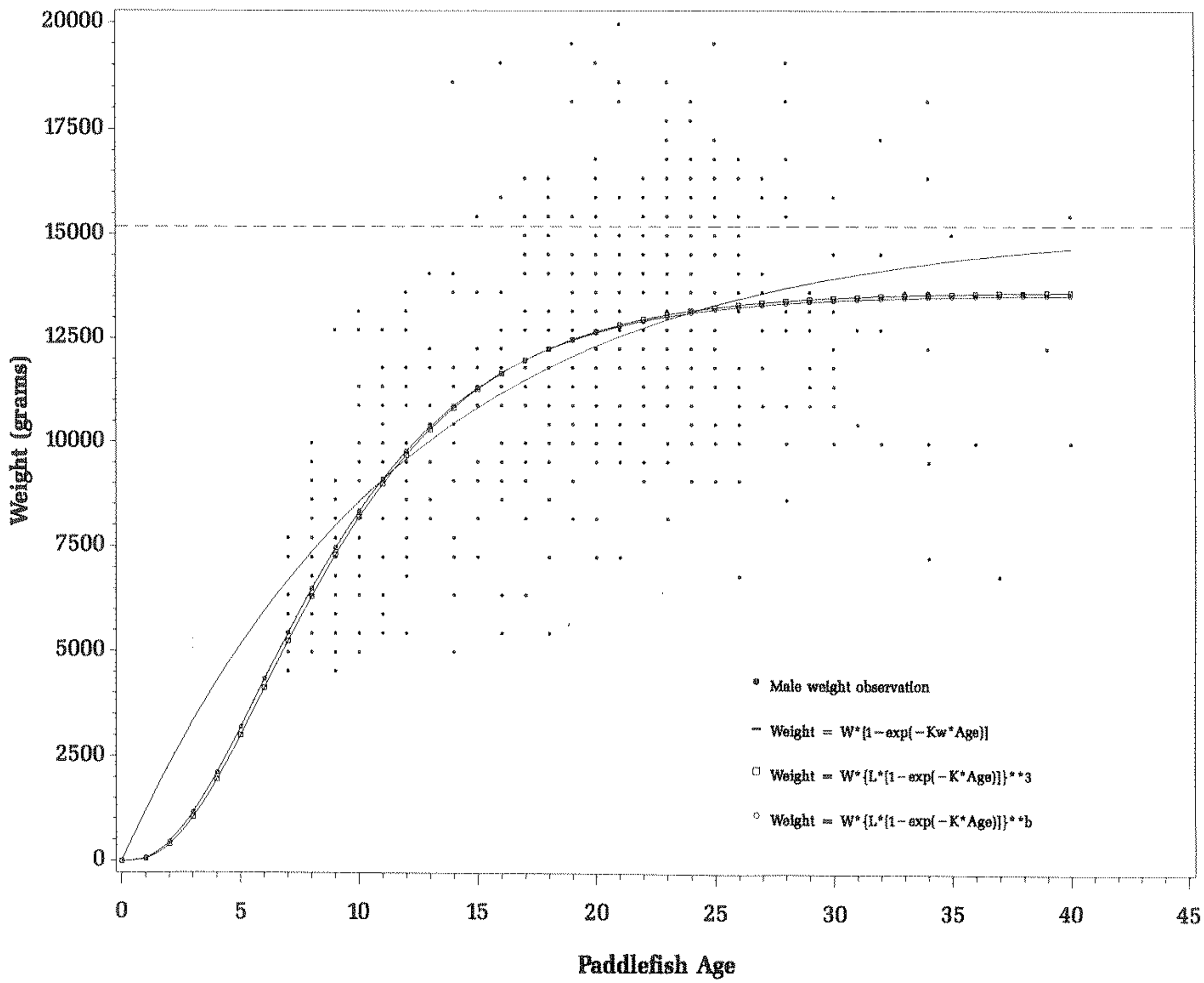

Fig 13a

Female paddlefish weight growth curves with 1991 data
(von Bertalanffy eqn. with no initial condition parameter)

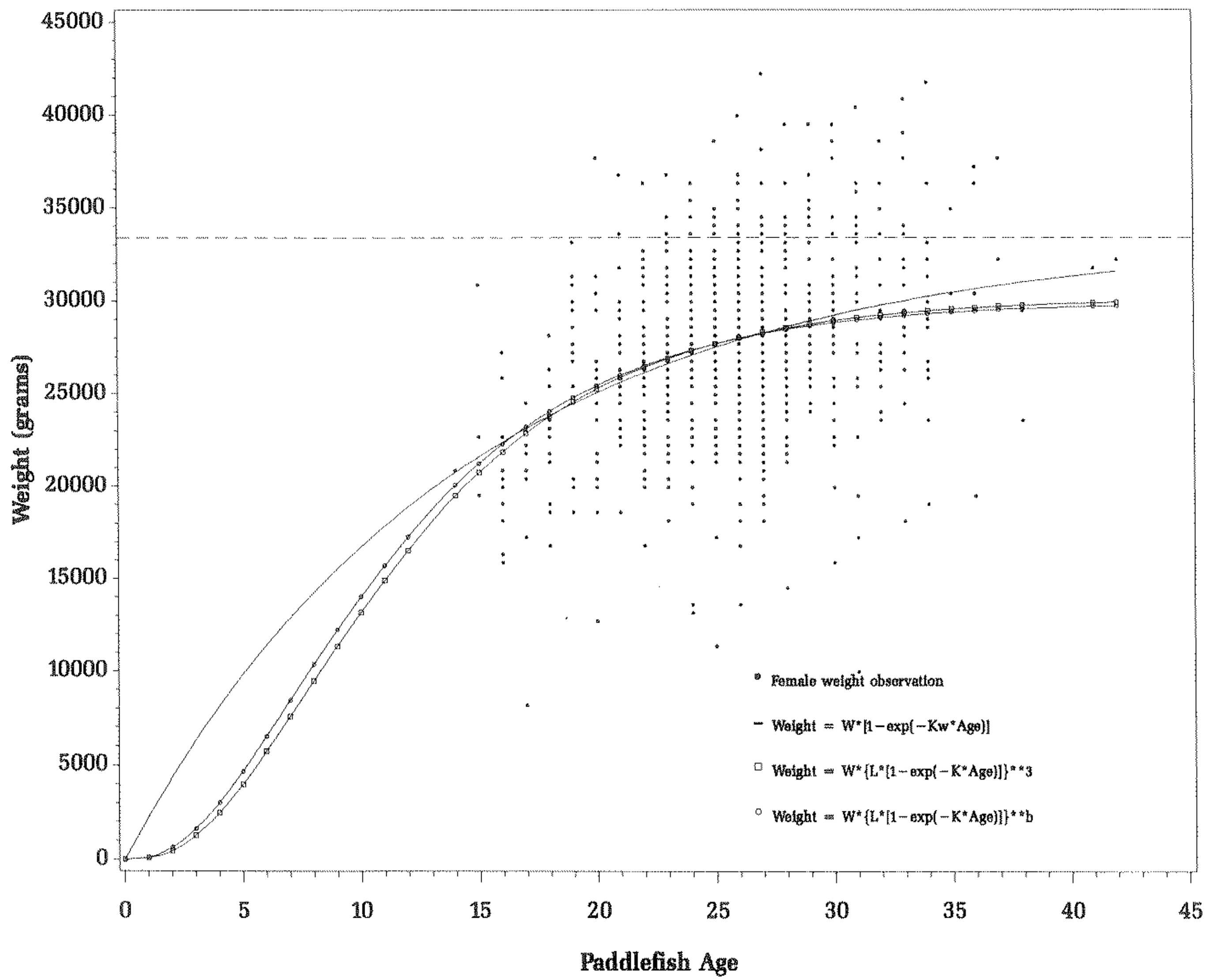

Fig 13b

PADDLEFISH LENGTH FREQUENCIES

(Tagged fish vs. Harvested fish)

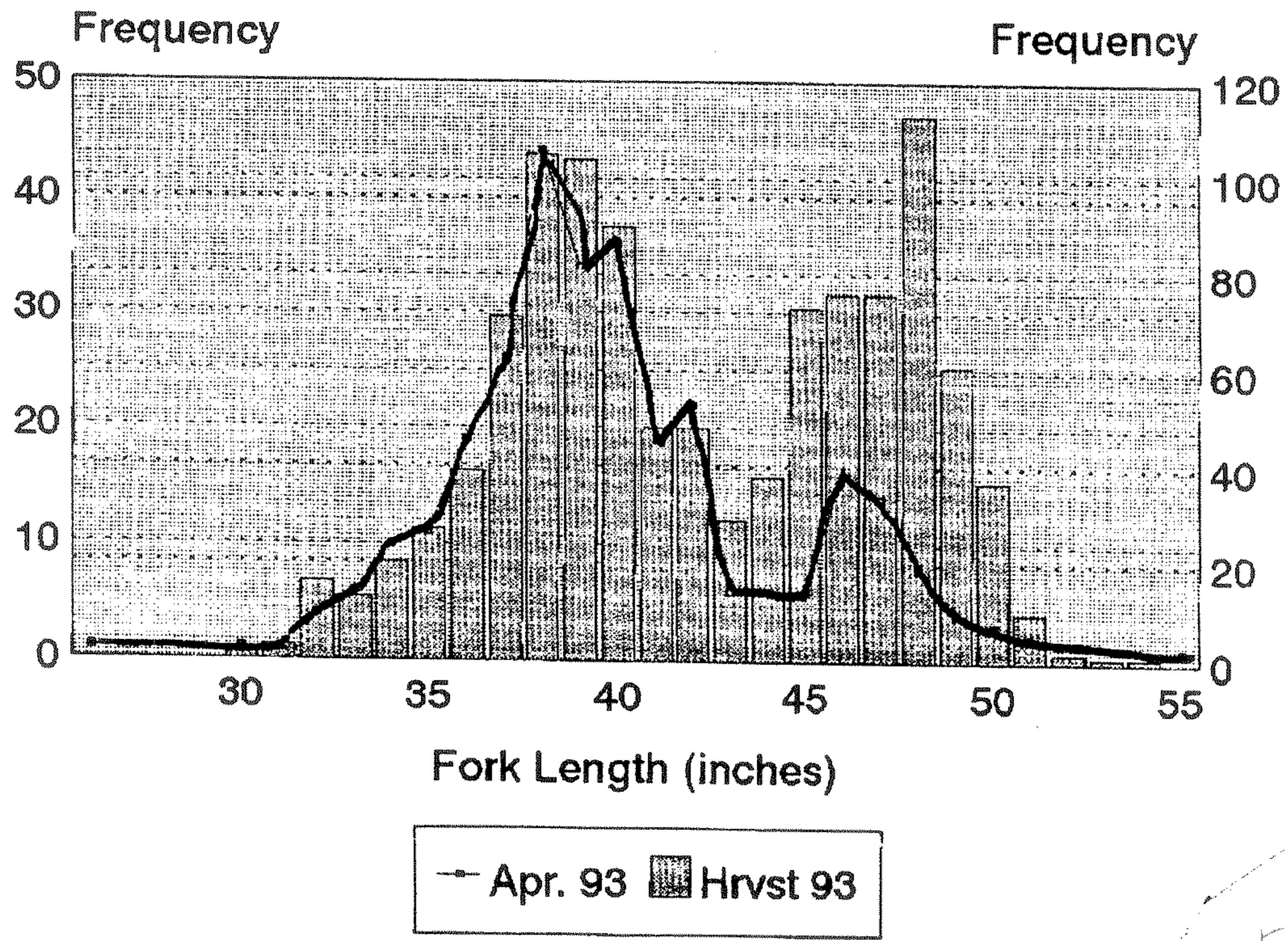

Fig 14