Abstract.—White sturgeon, *Acipenser transmontanus*, adults (n=855) were collected on their feeding grounds in San Francisco Bay, California, and their sex and stage of sexual maturity were evaluated histologically. They did not exhibit external sexual dimorphism, and the overall sex ratio did not differ from 1:1. Average fork length was 139 cm ±1.1 cm (mean ± standard error of the mean); females were longer (145 cm ±1.2 cm, n=443) than males (133 cm ±1.0 cm, n=412). In smaller size classes (≤115 cm), males were significantly (P<0.05) more numerous than females. The proportion of females, however, was significantly higher among larger fish (>155 cm). The sample of females consisted of 70% fish with "immature" (previtellogenic) ovaries, 12% with "maturing" (vitellogenic) ovaries, and 18% with "ripe" (large, pigmented eggs) ovaries. In contrast, most males were either "maturing" (meiosis, 56%) or "ripe" (spermatozoa, 39%). Ripe females represented only 9% of all fish sampled. Egg production by females, estimated by hatchery spawning, averaged 5,648 eggs/kg of body weight. The length at which white sturgeon in San Francisco Bay attain sexual maturity was estimated to be 95–135 cm in females and 75–105 cm in males. The duration of one ovarian cycle in iteroparous females was estimated to be longer than one year, with an apparent 2- to 4-year interval between spawning periods; the reproductive cycle of males was estimated to be 1–2 years. The low reproductive potential of white sturgeon in San Francisco Bay should be considered in fishery management of the species.

Manuscript accepted 24 June 1996.
Fishery Bulletin 94:628–634 (1996).

The reproductive condition of white sturgeon, *Acipenser transmontanus*, in San Francisco Bay, California

Frank A. Chapman
Department of Fisheries and Aquatic Sciences, University of Florida
7922 N.W. 71 Street, Gainesville, Florida 32653
e-mail address: FAA@GNV.IFAS.UFL.EDU

J. P. Van Eenennaam
S. I. Doroshov
Department of Animal Science, University of California
Davis, California 95616

White sturgeon, *Acipenser transmontanus*, have long been valued for their caviar and flesh for human consumption. Recently white sturgeon have become popular as a recreational fish (Galbreath, 1985; Kohlhorst et al., 1991) and are being raised by commercial aquaculturists (Logan et al., 1995). During the last four decades, researchers have gathered sufficient information on the biology of wild populations to improve management of the fishery. Information now exists on white sturgeon migratory patterns (Miller, 1972; Kohlhorst et al., 1991), feeding habits (Schreiber, 1962; Semakula and Larkin, 1968; McKechnie and Fenner, 1971; McCabe et al., 1993), age, growth, and population structure (Semakula and Larkin, 1968; Kohlhorst et al., 1980; Brennan and Cailliet, 1991; Kohlhorst et al., 1991; DeVore et al.[1]). Significant knowledge exists on their reproduction, including gonadal development (North et al.[2]; Welch and Beamesderfer[3]), natural spawning (Stevens and Miller, 1970; Kohlhorst, 1976; Parsley et al., 1993; McCabe and Tracy, 1994), gamete and fertilization biology (Cherr and Clark, 1985), and early development (Beer, 1981; Wang et al., 1987; Bolker, 1993).

White sturgeon are anadromous and endemic to Pacific estuaries and coastal rivers of North America. They are found from the Aleutian Islands of Alaska to Monterey Bay, California (Scott and Crossman, 1973). In the Pacific Northwest, they are most abundant in the Fraser, Columbia, and Sacramento–San Joaquin rivers. The San Fran-

[1] DeVore, J. D., B. W. James, C. A. Tracy, and D. H. Hale. 1993. Dynamics and potential production of white sturgeon in the Columbia River downstream from Bonneville Dam. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol. 1, report G, p. 137–174. Final Report (Project No. 86-50) to Bonneville Power Admin., Portland, Oregon.

[2] North, J. A., A. L. Ashenfelter, and R. C. Beamesderfer. 1993. Gonadal development of female white sturgeon in the lower Columbia River. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol. 2, report G, p. 109–121. Final Report (Project No. 86-50) to Bonneville Power Admin., Portland, Oregon.

[3] Welch, D. W., and R. C. Beamesderfer. 1993. Maturation of female white sturgeon in lower Columbia River impoundments. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol. 2, report F, p. 89–107. Final Report (Project No. 86-50) to Bonneville Power Admin., Portland, Oregon.

cisco Bay estuary has the largest population of white sturgeon in California. Adults spend most of their life in the bay and migrate into the Sacramento River in the late winter or early spring to spawn (Pycha, 1956; Stevens and Miller, 1970; Kohlhorst, 1976). White sturgeon are believed to reach sexual maturity at age 10 to 30 years, and iteroparous females spawn at intervals of two or more years (Pycha, 1956; Semakula and Larkin, 1968).

We focused our initial studies on the collection of wild broodstock for captive breeding in order to develop artificially induced spawning techniques and hatchery technology (Conte et al., 1988). Concomitantly, we sampled white sturgeon in San Francisco Bay in order to characterize the composition of the population in relation to sex and gonadal maturity.

Materials and methods

White sturgeon were collected in the San Francisco Bay estuary, California, from late October to February 1983–86. The fishing grounds included the area between Golden Gate Bridge, Angel Island, and San Francisco Bay Bridge. Miller (1972) observed that sturgeon congregate in this area to feed and that fish that were ripe migrated into the Sacramento River later in the season to spawn. Sturgeon aggregated while feeding on herring eggs and were seen frequently jumping out of the water. These aggregations of sturgeon were located with sonar. Fishing gear consisted of a short (167–214 cm) stiff pole (rated for 28 kg) equipped with reel (4/0), heavy monofilament line (18–28 kg strength), leader (45–55 kg strength), treble hook (4/0 or 5/0), and heavy sinker (142–227 g). The line was weighted with a sinker at the end of the leader, and the treble hook was attached approximately 30 cm above the sinker.

Sturgeon were usually encountered at water depths of 6 to 9 m and were snagged as they rubbed the line or hooked when they took a bait of herring fillet or eggs. Water temperatures and salinities during collection periods were 9–15°C and 24–32 ppt, respectively. Further details on fish-collection techniques are described and illustrated by Cuanang (1984). White sturgeon broodstock handling, sampling, and care followed procedures of Conte et al. (1988).

Sturgeon were examined for external structure and size, including morphometric and meristic characters. Measurements included fork and total length (±0.1 cm), head length (±0.1 cm), mouth width (including the lips, ±0.1 cm), and body weight (±0.1 kg). Meristic characters of the scutes in the dorsal, lateral, and ventral rows were recorded according to the methods of Vladykov and Greeley (1963). Proportional measurements (snout and head) were expressed as percentages of the head and fork length, respectively. Sturgeon were alive when sampled, and all fish, except for ripe broodstock, were released after capture. Samples of gonadal tissue and blood plasma were collected for histological analysis, but sections of fin rays were not collected for age determinations in order to avoid excessive trauma.

Sex and stages of sexual maturity in white sturgeon were examined by using histological slides of gonadal tissue and light microscopy (Chapman, 1989; Doroshov et al., 1991). Gonadal samples were collected from 300 females and 325 males. Ovarian stages in females were assigned a numerical score according to differentiation in the shape and size of the ovarian follicle (according to oocyte cytoplasm staining properties, nuclear and cytoplasmic inclusions, presence or absence of yolk platelets, differentiation of the vitelline envelope, and differentiation in the granulosa cells and thecal follicular layers). A numerical score was assigned to each male testis according to the proportion of cysts with different types of germ cells that were counted in several random fields on the slide (spermatogonia, spermatocytes, spermatids, and spermatozoa). Based on histological scores, the following classification was assigned for individual fish: (1) "immature," (2) "maturing," or (3) "ripe." Group-1 fish included females in the previtellogenic stage of ovarian development (in chromatin nucleolar stage and primary oocyte growth) and males in the gonial proliferation stage of testicular development. Group-2 fish included females with ovaries in early or intermediate phases of vitellogenesis (oocyte cytoplasm containing yolk bodies) and males with testes in the meiotic phase (spermatocytes and spermatids). Group-3 fish included females with ovaries containing large and darkly pigmented oocytes exhibiting yolk polarization and germinal vesicle migration and males in the postmeiotic testicular phase (spermiogenesis and differentiated spermatozoa).

Data on egg production (approximate individual relative fecundity) were collected from gravid females that had been captured in the Sacramento River from February to March 1991–94 in order that they might spawn in the hatchery. Estimation of egg production was based on the number of eggs collected surgically (a procedure routinely performed during artificial spawning of sturgeon [see Conte et al., 1988]) and represents 60–80% of actual individual fecundity.[4] The number of eggs removed from each female was

[4] The percentage of eggs collected was determined by comparing egg production at spawning of domestically raised sturgeon with a total fecundity estimate of domestic sturgeon (of equivalent size) processed for caviar production.

estimated volumetrically by using three 5-mL volume subsamples. Egg diameters were measured (±0.01 mm) along the animal-vegetal axis with a dissecting microscope and ocular micrometer.

Procedures described in Steel and Torrie (1986) were followed for statistical analyses. The Statistical Analyses System software (SAS, 1985) was used for data processing. The measure of variability is reported as standard error of the mean (±SEM), and the accepted level of statistical significance is $P<0.05$. All length measurements are given in fork length (FL).

Results

Body size, sex ratio, and sexual dimorphism

We sampled a total of 855 white sturgeon, ranging in fork length from 79 to 202 cm (mean=139 ±1.1 cm). Mean length of females (145 ±1.2 cm) was significantly greater than that of males (133 ±1.0 cm). The sex ratio was 1:1 (Table 1). The proportion of males, however, was significantly higher among fish ≤115 cm, whereas the proportion of females was higher among fish >155 cm (Table 1).

In most cases we could not determine by external examination the sex of white sturgeon, except for spermiating males and some ripe females (recognized by an enlarged abdomen). We found no significant differences between the sexes in numbers of dorsal and lateral scutes, relative lengths of the head and snout, and width of the mouth. Among all fish examined histologically, we found only one case of hermaphroditism, a maturing testis containing a few ovarian follicles with previtellogenic oocytes.

Table 1

Size classes and sex ratios of white sturgeon, *Acipenser transmontanus*, sampled in San Francisco Bay, California, from October to February, 1983–86. Significant deviations (chi-square) from the expected 1:1 sex ratio are marked by asterisks.

	Sample size			
Fork length (cm)	Total	No. of males	No. of females	Sex ratio
<95	14	9	5	0.64:0.36*
95.1–105	84	53	31	0.63:0.37*
105.1–115	119	79	40	0.66:0.34*
115.1–125	120	59	61	0.49:0.51
125.1–135	109	57	52	0.52:0.48
135.1–145	135	58	77	0.43:0.57
145.1–155	93	46	47	0.50:0.50
155.1–165	87	33	54	0.38:0.62*
165.1–175	56	12	44	0.21:0.79*
>175	38	6	32	0.16:0.84*
Total	855	412	443	0.48:0.52

Distribution of maturity stages in the population

The smallest ripe female and male were 104 cm and 100 cm, respectively. The female sample population comprised 70% group-1, 12% group-2, and 18% group-3 individuals (Table 2). Except for one large size class (175.1–185 cm), the proportion of immature females remained high (>62%) in each length class. Although females with vitellogenic or ripe ovaries (groups 2 and 3) appeared in length classes 95.1 to 125.1 cm, their proportions were small (average 3% for group 2 and 6% for group 3). In 135.1–195 cm sturgeon, the proportions of females with maturing and ripe

Table 2

Proportions of gonadal maturity stages in different size classes of white sturgeon females (n=300) and males (n=325) in San Francisco Bay, California.

Female size class (cm FL)	Number in sample	Female gonadal maturity stage (%)		
		Group-1	Group-2	Group-3
75.1–85	1	1.00	0.00	0.00
85.1–95	1	1.00	0.00	0.00
95.1–105	9	0.89	0.00	0.11
105.1–115	28	0.96	0.00	0.04
115.1–125	31	0.90	0.03	0.07
125.1–135	33	0.88	0.06	0.06
135.1–145	34	0.65	0.15	0.20
145.1–155	47	0.66	0.13	0.21
155.1–165	45	0.56	0.13	0.31
165.1–175	39	0.62	0.15	0.23
175.1–185	22	0.27	0.32	0.41
185.1–195	10	0.70	0.20	0.10
Male size class (cm FL)	**Number in sample**	**Male gonadal maturity stage (%)**		
		Group-1	Group-2	Group-3
75.1–85	2	0.50	0.50	0.00
85.1–95	1	0.00	1.00	0.00
95.1–105	18	0.33	0.50	0.17
105.1–115	52	0.10	0.59	0.31
115.1–125	59	0.04	0.64	0.32
125.1–135	54	0.04	0.54	0.42
135.1–145	51	0.02	0.63	0.35
145.1–155	37	0.00	0.49	0.51
155.1–165	33	0.00	0.45	0.55
165.1–175	12	0.00	0.42	0.58
175.1–185	3	0.00	0.67	0.33
185.1–195	3	0.00	0.67	0.33

ovaries (groups 2 and 3) increased and stabilized at an overall average of 16% (= 32/197) in group 2 and at a overall average of 25% (= 50/197) in group 3; the remaining 59% consisted of group-1 females. The average proportion of ripe females (group 3) in size groups less than 135.1 cm was statistically less than that observed in the combined size class of 135.1 to 195 cm (chi-square, $P<0.05$). A similar result holds for maturing (group-2) females (chi-square, $P<0.05$). Together, these data indicated that proportions of reproductively active females in the sturgeon population may be determined by a combination of two factors: 1) the recruitment of females into puberty (first vitellogenic cycle) occurs over a range of body sizes beginning at 95.1 cm; and 2) female white sturgeon require more than a one-year interval between consecutive spawnings. If one conjectures a predominant 4-year spawning period in iteroparous females (because of the percentage [25%] of ripe females), we could expect to see a ratio of immature to mature to ripe around 2:1:1 in size classes above 135 cm. Our data reject this ratio (chi-square, $P<0.005$). Unfortunately, we were not able to clearly distinguish between the first and second spawning cycles by histological examination of vitellogenic and ripe ovaries.

Male samples, in contrast to female samples, had overall low proportions of immature (premeiotic phase) individuals (5% in group 1), and recruitment into the meiotic phase of spermatogenesis (group 2) occurred at a smaller size, beginning at 75.1 cm (Table 2). Sampled fish from 105.1 to 195 cm were practically all (294 of 304) in group 2 (57%) or group 3 (40%). If one conjectures a predominant biennial spawning interval, we would expect the data to show a 1:1 ratio of meiotic and postmeiotic testicular stages. Our data reject this ratio (chi-square, $P<0.001$).

Relative fecundity (egg production)

Egg production from artificially spawned wild white sturgeon females ranged from 3,192 to 8,582 eggs/kg of body weight. The average size of ova was 3.7 mm ±0.02 mm. The average weight of these females was 36 ±2 kg and fork length was 153 ±4 cm (n=40). The estimated hatchery production was 203,328 ova for a female of average size; individual fish produced between 63,840 and 469,432 eggs. The relationship between the egg diameter and fork length was not statistically significant.

Discussion

We found that white sturgeon do not have external sexual dimorphism and, except for ripe fish on spawning grounds, there are no apparent morphological differences between the sexes. The 1:1 sex ratio (overall) of white sturgeon in San Francisco Bay is in agreement with data for the Columbia River system (Beamesderfer and Rien[5]) and Eurasian acipenserid species (Chugunov and Chugunova, 1964; Zubova, 1971; Persov, 1975). A greater proportion of males in smaller size classes and a predominance of females in larger size classes have also been observed in other species of sturgeon (e.g. *A. sinensis,* Xin et al., 1991). One possible explanation for this difference in sizes is that growth rates diverge between the sexes during the reproductive phase of life. Kohlhorst et al. (1980) found no difference in growth rates between sexes in white sturgeon of the San Francisco Bay; however, their study was limited to a narrow size and age range. An alternative explanation may be a higher rate of mortality in males and a resultant shorter life span in comparison with females. High rates of mortality for males may be associated with earlier puberty, more frequent breeding, and longer residence on the spawning grounds. Assuming that the population was sampled randomly, both differences in growth and mortality may have contributed to the substantial divergence in modal size classes between the males (105.1–115 cm FL) and females (135.1–145 cm FL). Although the predominance of females among larger fish may be explained by these factors, the predominance of males among smaller fish appears to contradict a chromosomally determined (gonochoristic) sex ratio and should be investigated further.

Although subject to high individual variation, the relative fecundity among sturgeon species appears to be generally similar. For example, for the large anadromous species *Huso huso,* Raspopov (1987) reported a relative fecundity of 2,750 to 10,500 eggs/kg of body weight. Smaller species such as shortnose sturgeon, *A. brevirostrum,* had an average relative fecundity of 11,568 eggs/kg of body weight (Dadswell, 1979). Although we could not directly estimate relative fecundity for white sturgeon females in San Francisco Bay, egg production from artificially spawned females averaged 5,648 eggs/kg of body weight and 203,328 eggs for an average length (153 cm) female. Relative fecundity for white sturgeon females in the Columbia River was not reported; however, the number of eggs produced was from

[5] Beamesderfer, R. C., and T. A. Rien. 1993. Dynamics and potential of white sturgeon populations in three Columbia River reservoirs. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol.1, report H, p. 175–204. Final Report (Project 86-50) to Bonneville Power Admin., Portland, Oregon.

98,200 to 699,000 eggs for fish 115 to 215 cm FL (DeVore et al.[1]). Comparisons of egg diameters in ripe females from the Sacramento and Columbia rivers revealed that female sturgeon from the Sacramento River had larger eggs (3.4–4.0 mm) than those found in females from the Columbia River (2.6–3.6 mm) (North et al.[2]). This difference may account for the apparent higher fecundity of white sturgeon females in the Columbia River. We found no relation between size of the female sturgeon and mature egg diameters. Lutes et al. (1987) also did not detect a relation between female body size and diameters of postvitellogenic oocytes in white sturgeon.

The size at which white sturgeon attain sexual maturity appears to vary between populations. Our observations indicate that female white sturgeon in San Francisco Bay mature at larger sizes (>95 cm) than males (>75 cm). Because the proportions of ripening individuals (groups 2 and 3) increased and stabilized above 135 cm in females and 105 cm in males, recruitment into puberty most likely occurs from 95 to 135 cm for females and from 75 to 105 cm for males. In the Columbia River, female white sturgeon did not mature until they were even larger (160–193 cm FL), revealing significant size variations in the river downstream from all dams and between different river reservoirs (DeVore et al.[1]; Welch and Beamesderfer[3]; Beamesderfer and Rien[5]). These differences in size at first sexual maturity were largely attributed to food availability and hydrologic conditions. Working with wild and domestic stocks, Chapman (1989) postulated that size and age at sexual maturity in white sturgeon were dependant on body size and nutrient composition. Size or age at sexual maturity, however, could be modified by growth, nutrition, and environmental factors.

Examination of the stage of gonadal development in different length classes of white sturgeon females in San Francisco Bay indicated a high fraction of group-1 (immature) individuals. The proportions of group-2 (maturing) and group-3 (ripe) females in the sampled population were low (12% and 18%, respectively); ripe females represented only 9% of all sturgeon sampled. Similar observations in the Columbia River system revealed even lower proportions, 6% maturing and 2% ripe (DeVore et al.[1]; North et al.[2]; Welch and Beamesderfer[3]). From histological analysis of oogenesis (Chapman, 1989) and from the proportions of different ovarian stages in the white sturgeon population of San Francisco Bay, we assume that iteroparous sturgeon females require longer than one year to complete an egg development cycle, including vitellogenic growth and prematurational polarization of the oocyte. Because the proportion of females with ripe ovaries (group 3, >135 cm) was on average 25% of all sampled individuals, the interval between two consecutive spawnings is most likely between 2 and 4 years. Our recent observations of domestically raised and continuously fed white sturgeon suggest predominantly biennial ovarian cycles. Because wild female sturgeon, compared with other fish including domestic sturgeon, lose a substantial percentage of weight and energy at spawning (Krivobok and Tarkovskaya, 1970), it is possible that they defer a new wave of ovarian vitellogenesis for some time after spawning, allowing recovery from spawning depletions (the high percentage [59%] of fish in group 1 strongly suggests this event). A final conclusion regarding spawning periodicity of white sturgeon cannot, however, be reached until fish that have been tagged are recaptured and sampled repeatedly or until the size and age interval of female recruitment to puberty is known. These are important considerations, because pubertal age of white sturgeon females may extend from 15 to 32 years (White Sturgeon Planning Committee[6]).

Considering the season of our sampling (late fall–early winter) and the potential overlap between meiotic and maturational phases of testicular development, the adult male white sturgeon may spawn annually (as in commercial hatcheries) or biennially. Existence of a biennial cycle in sturgeon males could be verified by continued sampling throughout spring and summer. Most spawning males accommodate the protracted spawning season (February–June) of females. This shorter reproductive cycle, which is associated with annual spawning migrations, may also result in a higher mortality for older and larger males.

A 2–4.5 year spawning period has been suggested for female white sturgeon in the Columbia River (Welch and Beamesderfer[3]). According to Trusov (1975), the refractory ovarian stages in iteroparous sevryuga, *A. stellatus*, last 2 to 5 years, whereas the ovarian vitellogenesis occurs within 1 to 2 years. Examining the sexual maturation of Russian sturgeon, *A. guldenstadti*, in the Sea of Azov, Kornienko et al. (1988) found that 72% of the sampled adult-size fish had either immature or refractory ovaries and that the remaining fish were approximately equally distributed between "maturing" and "ripe." In males, spermatogenesis was a continuous process.

We conclude that sexual maturation in white sturgeon is prolonged. Females mature slowly, and first maturation takes place over a wide range of body sizes. The average interval between spawnings by iteroparous females appears to range from 2 to 4

[6] White Sturgeon Planning Committee. 1992. White sturgeon management framework plan. 2501 S.W. First Avenue, Pacific States Marine Fisheries Commission, Gladstone, Oregon.

years. Males mature at a smaller body size and have shorter intervals between spawnings than do females. Sex differences in maturation rates of sturgeon create incredible combinations of individual matings from different generations that favor genetic diversity even with a small number of spawning females. Annual recruitment and genetic structure of a sturgeon population may be influenced by its sex ratio, the proportion of females spawning each year, and the number of eggs they produce. Monastyrski (1949) noted that the complex age-size structure of spawning populations and the iteroparity of sturgeons require a special approach for their management. Our data on the reproductive conditions of white sturgeon in the San Francisco Bay provide additional evidence for potential sensitivity of sturgeon populations to exploitation by either commercial or sport fisheries. The effect of prolonged sexual maturation may be compromised further by loss of spawning habitat, altered seasonal changes of temperature in rivers with controlled flow, and environmental pollutants that may affect sexual development and the reproductive cycle.

Acknowledgments

This work was supported by the National Oceanic and Atmospheric Administration through the California Sea Grant College Program project R/F-90 and, in part, by the California State Resource Agency. Data used for this investigation reflect the work by members of the Sturgeon Program at the University of California, Davis. We appreciate the assistance of those who participated in this work and are thankful to Abe and Angelo Cuanang, Eddie Tavasieff, and Dick Nelson for their help in collecting fish. We acknowledge personnel of two sturgeon farms, The Fishery and SeaFarms of California, for providing hatchery data for fecundity estimation.

Literature cited

Beer, K. E.
1981. Embryonic and larval development of white sturgeon (*Acipenser transmontanus*). M.S. thesis, Univ. California, Davis, CA, 93 p.

Bolker, J. A.
1993. The mechanism of gastrulation in the white sturgeon. J. Exp. Zoology 266:132–145.

Brennan, J. S., and G. M. Cailliet.
1991. Age determination and validation studies of white sturgeon, *Acipenser transmontanus*, in California. *In* P. Williot (ed.), *Acipenser*, Actes du premier colloque international sur l'esturgeon, p. 209–234. CEMAGREF-DICOVA, Bordeaux, France.

Chapman, F. A.
1989. Sexual maturation and reproductive parameters of wild and domestic stocks of white sturgeon, *Acipenser transmontanus*. Ph.D. diss., Univ. California, Davis, CA, 100 p.

Cherr, G. N., and W. H. Clark Jr.
1985. Gamete interaction in the white sturgeon *Acipenser transmontanus*: a morphological and physiological review. *In* F. P. Binkowski and S. I. Doroshov (eds.), North American sturgeons: biology and aquaculture potential, p. 11–22. Dr. W. Junk Publishers Dordrecht, Netherlands.

Chugunov, N. L., and N. I. Chugunova.
1964. Comparative study of fisheries and biology of acipenserids of the Azov Sea. Vses. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr., Trudy 52:87–182.

Conte, F. S., S. I. Doroshov, P. B. Lutes, and E. M. Strange.
1988. Hatchery manual for the white sturgeon *Acipenser transmontanus* Richardson with application to other North American Acipenseridae. Univ. California Publications Division of Agriculture and Natural Resources, Oakland, CA, 104 p.

Cuanang, A.
1984. San Francisco Bay sturgeon. Angler Publ., Oakland, CA, 9 p.

Dadswell, M. J.
1979. Biology and population characteristics of the shortnose sturgeon, *Acipenser brevirostrum* LeSueur 1818 (Osteichthyes:Acipenseridae), in the Saint John Estuary, New Brunswick, Canada. Can. J. Zool. 57:2186-2210.

Doroshov, J. N., J. P. Van Eenennaam, F. A. Chapman, and S. I. Doroshov.
1991. Histological study of the ovarian development in wild white sturgeon *Acipenser transmontanus*. *In* P. Williot (ed.), *Acipenser*, Actes du premier colloque international sur l'esturgeon, p. 129–135. CEMAGREF-DICOVA, Bordeaux, France.

Galbreath, J. L.
1985. Status, life history, and management of Columbia River white sturgeon, *Acipenser transmontanus*. *In* F. P. Binkowski and S. I. Doroshov (eds.), North American sturgeons: biology and aquaculture potential, p. 119–125. Dr. W. Junk Publishers, Dordrecht, Netherlands.

Kohlhorst, D. W.
1976. Sturgeon spawning in the Sacramento River in 1973, as determined by distribution of larvae. Calif. Fish Game 62:32–40.

Kohlhorst, D. W., L. W. Miller, and J. J. Orsi.
1980. Age and growth of white sturgeon collected in the Sacramento-San Joaquin Estuary, California: 1965–1970 and 1973–1976. Calif. Fish Game 66:83–95.

Kohlhorst, D. W., L. W. Botsford, J. S. Brennan, and G. M. Cailliet.
1991. Aspects of the structure and dynamics of an exploited Central California population of white sturgeon (*Acipenser transmontanus*). *In* P. Williot (ed.), *Acipenser*, Actes du premier colloque international sur l'esturgeon, p. 277–293. CEMAGREF-DICOVA, Bordeaux, France.

Kornienko, G. G., T. V. Lozichevskaya, and J. I. Rekov.
1988. Sexual maturation of the Azov Sea sturgeon. Rybn. Khoz. 3:38–40.

Krivobok, M. N., and O. I. Tarkovskaya.
1970. Lipid and protein metabolism during the sexual maturation in Russian sturgeon and sevryuga from the Volga River and Caspian Sea. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 69:109–132.

Logan, S. H., W. E. Johnston, and S. I. Doroshov.
1995. Economics of joint production of sturgeon (*Acipenser*

transmontanus Richardson) and roe for caviar. Aquaculture 130:299–316.
Lutes, P. B., S. I. Doroshov, F. Chapman, J. Harrah, R. Fitzgerald, and M. Fitzpatrick.
1987. Morpho-physiological predictors of ovulatory success in white sturgeon, *Acipenser transmontanus* Richardson. Aquaculture 66:43–52.
McCabe, G. T., Jr., R. L. Emmett, and S. A. Hinton.
1993. Feeding ecology of juvenile white sturgeon (*Acipenser transmontanus*) in the lower Columbia River. Northwest Sci. 67:170–180.
McCabe, G. T., Jr., and C. A. Tracy.
1994. Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River. Fish. Bull 92:760–772.
McKechnie, R. J., and R. B. Fenner.
1971. Food habits of white sturgeon, *Acipenser transmontanus*, in San Pablo and Suisun Bays, California. Calif. Fish Game 57:209–212.
Miller, L. W.
1972. Migrations of sturgeon tagged in the Sacramento-San Joaquin Estuary. Calif. Fish Game 58:102–106.
Monastyrski, G. N.
1949. Types of spawning populations in fish. J. Zoologichesky 28(6):535–544.
Parsley, M. J., L. G. Beckman, and G. T. McCabe Jr.
1993. Spawning and rearing habitat use by white sturgeon in the Columbia River downstream from McNary Dam. Trans. Am. Fish. Soc. 122:217–227.
Persov, G. M.
1975. Sex differentiation in fishes. Leningrad Univ. Publ. House, Leningrad, Russia, 147 p.
Pycha, R. L.
1956. Progress report on white sturgeon studies. Calif. Fish Game 42:23–35.
Raspopov, V. M.
1987. Fecundity of beluga sturgeon, *Huso huso*, of the Caspian Sea. J. Ichthyol. 27:141–140.
SAS, Inc.
1985. SAS/STAT guide for personal computers, version 6 ed. SAS Inst. Inc., Cary, NC, 378 p.
Schreiber, M. R.
1962. Observations on the food habits of juvenile white sturgeon. Calif. Fish Game 48:79–80.
Scott, W. B., and E. J. Crossman.
1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184, 966 p.
Semakula, S. N., and P. A. Larkin.
1968. Age, growth, food, and yield of the white sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. J. Fish. Res. Board Can. 25:2589–2602.
Steel, R. G. D., and J. H. Torrie.
1986. Principles and procedures of statistics: a biometrical approach. McGraw-Hill, New York, NY, 633 p.
Stevens, D. E., and L. W. Miller.
1970. Distribution of sturgeon larvae in the Sacramento-San Joaquin River system. Calif. Fish and Game 56: 80–86.
Trusov, V. Z.
1975. Maturation of the gonads in female sevryuga *Acipenser stellatus* during its life in the ocean. J. Ichthyol. 15:61–71.
Vladykov, V. D., and J. R. Greeley.
1963. Order Acipenseroidei. *In* Y. H. Olsen (ed.), Fishes of the western North Atlantic, p. 26–58. Mem. Sears Found. Mar. Res. Yale Univ. 1.
Wang, Y. L., R. K. Buddington, and S. I. Doroshov.
1987. Influence of temperature on yolk utilization by the white sturgeon, *Acipenser transmontanus*. J. Fish Biology 30:263–271.
Xin, D., D. Zonglin, and C. Mingyan.
1991. Spawning population characteristics of *Acipenser sinensis* in Yangtze River just below Gezhouba Dam. *In* P. Williot (ed.), *Acipenser*, Actes du premier colloque international sur l'esturgeon, p. 235–242. CEMAGREF-DICOVA, Bordeaux, France.
Zubova, S. E.
1971. The time of differentiation of the gonads and the sex ratio in the young of the Volga sterlet (*Acipenser ruthenus* L.). J. Ichthyol. 11:424–426.