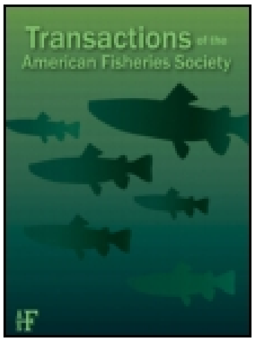

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[Article]

Reproductive Conditions of the Klamath River Green Sturgeon

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Abstract.—Reproductive characteristics of the adult Klamath River green sturgeon *Acipenser medirostris* were studied during the spawning migration. The locations of captures were from the mouth of the Klamath River upstream to river kilometer 72. A total of 82 females and 118 males were sampled for age, sex, body size, gonad weight, fecundity, egg size, and gonadal histology during April–July for five consecutive years (1999–2003). All fish sampled were considered mature adults, except for two immature males (body weight, 10 and 16 kg) captured close to the mouth of the river. The average body weight for males and females was 32 and 46 kg, respectively. The condition factor ranged from 0.60 to 0.92 for males and from 0.65 to 0.94 for females. The long tapered body conformation for both sexes made it difficult to sex individuals by external morphology, but in general, the females had a slightly more robust conformation. The fork length range was 139–199 cm in males and 151–223 cm in females. The majority (>90%) of males were 15–28 years old, and females were 19–34 years old. In all females the preovulatory condition was distinguished by the migration of the germinal vesicle to the animal pole, and the mean polarization index (distance of the germinal vesicle from the animal pole divided by oocyte diameter) was 0.042. The gonadosomatic index for females ranged from 7% to 17% and that for males from 2% to 8%. Individual and relative fecundity ranges were 59,000–242,000 and 2,000–4,000 eggs, respectively. The fully grown eggs were the largest recorded for North American sturgeon, averaging 4.33 mm in diameter. Although this study indicates that the Klamath River supports an important and potentially stable spawning migration, continued monitoring of the population and identification of spawning and nursery sites are critical for the long-term preservation of this species.

The green sturgeon *Acipenser medirostris* is an anadromous species inhabiting Asian and American shorelines of the northern Pacific Ocean (Moyle 2002; Antonenko et al. 2003). In North America, the green sturgeon range extends from the Bering Sea to Ensenada, Mexico, including the entire California coast. The migratory behavior of green sturgeon has been documented with tagged San Pablo Bay, California, fish being recovered as far north as Gray's Harbor, Washington, at the mouth of the Columbia River, and as far south as Santa Cruz, California (Chadwick 1959; Miller 1972). Despite the wide geographic distribution and occasional significant landings in the commercial fisheries of the West Coast (Houston 1988), the green sturgeon is considered a rare or vulnerable species in the United States and Canada (Birstein 1993; Moyle 2002; Campbell 1997), an endangered species in Russia (Artyukhin and Andronov 1990), and a candidate endangered species by the National Marine Fisheries Service (NMFS 2003) under the U.S. Endangered Species Act. The first status review of green sturgeon (Adams et al. 2002) was updated by the National Oceanic and Atmospheric Administration Biological Review Team (NOAA Biological Review Team 2005), and NOAA has recently proposed the listing of the southern population of North American green sturgeon as threatened (NOAA 2005). The southern distinct population segment encompasses the region south of the Eel River, California, and contains the Sacramento River, California, spawning population (Israel et al. 2004).

The currently known spawning populations of the green sturgeon in North America are in the Rogue River in Oregon and the Klamath and Sacramento rivers in California, all of which have flow regimes affected by water projects and intensive use of the watersheds (Moyle 2002). The largest spawning population of green sturgeon in California is in the Klamath River (Moyle 2002). There is currently no information on green sturgeon spawning in Canada, although some individual sturgeon have been caught in the Fraser and Skeena Rivers, British Columbia (Houston 1988). The closely related Asian form, Sakhalin sturgeon, is similar in morphology (North et al. 2002) but was recently considered a separate species *A. mikado*, based on molecular data on three

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mitochondrial genes (Birstein and DeSalle 1998). Sakhalin sturgeon are known to spawn in only the Tumnin River (Artyukhin and Andronov 1990).

The green sturgeon supports a subsistence tribal fishery in the Klamath River as well as a small commercial fishery and some sport fisheries along the Pacific Coast. The majority of harvest since 1985 has taken place in the lower Columbia River; however, this fishery has declined during recent years because of increasingly restrictive fishing regulations (Adams et al. 2002). The Klamath River green sturgeon have been central to the lives of Yurok people for thousands of years, and its fishery remains an integral part of the subsistence and culture of the Yurok Tribe (Van Eenennaam et al. 2001). From 1994 to 2003 the Yurok gill-net fishery harvested an average of 238 fish annually (D.C. Hillemeier, unpublished data); other mixed stock fisheries along the Pacific coast annually harvested an average of approximately 1,350 green sturgeon during 1994–2001 (Adams et al. 2002).

During the past few years there has been an increasing interest toward understanding the biology of the North American green sturgeon. Although the recent surge in research has provided new information on green sturgeon karyotype (Van Eenennaam et al. 1999), adult movement (Erikson et al. 2002), early life stages (Deng et al. 2002; Kynard et al. 2005), physiology (Gisbert et al. 2001; Gisbert and Doroshov 2003; Lankford et al. 2003; Van Eenennaam et al. 2005), bioenergetics (Mayfield and Cech 2004), and geographic patterns of genetic differentiation (Israel et al. 2004), many aspects of green sturgeon biology remain obscure. Among the eight members of North American Acipenseriformes, green sturgeon was only recently reproduced in captivity (Van Eenennaam et al. 2001), and only fragmentary information on reproductive characteristics of the species has been available (Nakamoto et al. 1995; Van Eenennaam et al. 2001; Adams et al. 2002; Deng et al. 2002; Moyle 2002). This paper provides a more recent and comprehensive summary of the current reproductive conditions of the Klamath River spawning population in relation to fish age and size.

Methods

Fish collection and sampling.—Green sturgeon were sampled from the Yurok Tribe gill-net fishery on the Klamath River. Fish were caught during March–July for five consecutive years (1999–2003) in the area from the mouth of the Klamath River to river kilometer (rkm) 72, just upstream from the confluence of the Klamath and Trinity Rivers, California. For management purposes, the Klamath River on the Yurok reservation is designated into three sections: lower river and estuary (rkm 0–6), mid-Klamath (rkm 6.1–32.3), and upper Klamath (rkm 32.4–72). The apparent upstream limit for spawning in the Klamath River is Ishi Pishi Falls (rkm 107.7); in the Trinity River, the largest tributary to the Klamath River, this limit is Grays Falls (rkm 139.5 from the mouth of the Klamath or rkm 70 from the confluence of the Klamath and the Trinity Rivers; Moyle 2002). The Yurok Tribe fishes only on its reservation (up to rkm 72). The fishers used anchored gill nets that were 10–15 m long and 7–9 m deep, with a stretch bar mesh of 17–19 cm. Nets were usually set along the shoreline in back eddies that were 3–6 m deep. Although fish collection and sampling were potentially affected by selectivity of fishing gear and fishing sites, and by variable fishing efforts between the three sections of river, the large number of green sturgeon sampled during five consecutive years provides representative data for characterization of the spawning population.

After capture, the green sturgeon were sampled on shore during cleaning and processing. Fork length (FL) and total length (TL) were measured ($\pm$0.1 cm) in all fish, except for three males. When possible, live weight W ($\pm$500 g) and gonad weight GW ($\pm$1.0 g) were also measured; however, not all fish could be so measured. Samples of the gonad tissue (20–30 g) were obtained from all fish, being excised from the mid-portion of the gonad and fixed in 10% buffered formalin for 4–8 weeks. These samples were processed in a vacuum infiltration processor (dehydrated, cleared, and infiltrated with paraffin), embedded into paraffin blocks, sectioned at 6 μm, and stained by periodic acid–Schiff (PAS) stain (Sheehan and Hrapchak 1980). Representative stages were photographed; the descriptions of gonad development we utilized were based on a study of Atlantic sturgeon (Van Eenennaam and Doroshov 1998).

Gonadal development.—A representative subsample ($n = 20$ from each individual) of all mature eggs collected for histological analyses were measured for egg diameter ($\pm$0.01 mm) by using a dark-field dissecting microscope with camera lucida, an image-analyzing tablet, and a microcomputer interface. An additional subsample of fixed eggs ($n = 15$ from each female) were bisected with a razor blade along the animal–vegetal axis and examined under a dissecting scope with a fiber optic illuminator. We used the distance of the germinal vesicle from the inner border of the egg chorion and the egg diameter to calculate polarization index (PI; this distance divided by the egg diameter), a morphologic criterion of egg ripeness (Dettlaff et al. 1993). Dettlaff et al. (1993) stated that a PI of less than 0.07 is an indication of spawning readiness.

Six subsamples of ovarian eggs (anterior, mid, and posterior portions of each ovary) from mature females were collected, weighed (±0.0001 g), and preserved in 10% buffered formalin for fecundity estimates. Fecundity was measured by a gravimetric method similar to that described by Bishai et al. (1974) and Keenlyne et al. (1992), with slight modifications (Van Eenennaam et al. 1996). Briefly, fully grown oocytes were counted in six subsamples (5–10 g wet weight) from the ovaries of each female. The subsamples were cut fragments of the whole ovary (somatic tissue and germ cells). The measurement was the mean number of oocytes per gram of ovary, and fecundity was determined by extrapolation from the gonad wet weight. Relative fecundity was calculated as the fecundity/body weight.

Age determination.—One pectoral fin ray was removed for age estimation. Cross- sections (0.2–0.6 mm) of base portions of air-dried pectoral fin rays were cut with a jeweler's saw. Sections polished with increasing grades of wet/dry sandpaper were mounted on slides and examined under a dissecting microscope with camera lucida and image analyzer (Van Eenennaam et al. 1996). In reading annuli, we followed guidelines of Cuerrier (1951), Probst and Cooper (1954), Semakula and Larkin (1968), Sokolov and Akimova (1976), and Brennan and Cailliet (1991). Aging was conducted by two readers who counted annuli on three replicate fin ray sections of each fish. Disagreement between the assigned age was resolved by the more experienced reader (the senior author). Although the fin ray method of aging has not been validated for green sturgeon, it has been validated for white sturgeon *A. transmontanus* (Rien and Beamesderfer 1994) and lake sturgeon *A. fulvescens* (Rossiter et al. 1995).

Data analysis.—The two immature males captured at the mouth of the river were not included in the data analyses. Data for seven postspawning females were used only in the analysis of age, FL, and TL of the spawning population. Fulton's condition factor was calculated as $K = 100 \times W(\text{g})/(\text{FL [cm]})^3$, the gonadosomatic index (GSI) was determined as $100 \times \text{GW}/W$. Tabulated data were analyzed by descriptive statistics and analysis of variance (ANOVA). The significant difference between sample means was examined by Student's *t*-test (two samples) or Fisher's protected least significant difference test (more than two samples). Correlations for length–age, oocyte diameter–length, and PI–sample date were analyzed by least-squares regressions; linear regressions were tested for the lack of fit. Weight–length, fecundity–length, and fecundity–age relationships were described by functional allometric regressions based on $\log_{10}$ transformed data (Ricker 1973). Differences were considered significant at $P \leq 0.05$. SAS software (SAS Institute, Cary, North Carolina) was used for computations. All percentage data were arcsine square root–transformed prior to analyses. All data presented in the text are mean ± SD, unless otherwise noted.

Results

Two hundred green sturgeon (82 females and 118 males) were sampled during the course of this study. The overall observed sex ratio was 1:1.38, significantly different from a 1:1 ratio (chi-square = 4.615, $P < 0.05$). Eighteen percent of the sturgeon were caught in the lower river, 30% in the mid-reaches, and 52% in the upper reaches of the reservation. Although the earliest capture was on March 21st and the latest on July 2nd, 88% of the fish in the spawning run were captured between April 1st and June 1st, when water temperatures range from 8°C to 15°C under normal precipitation years. The annual catch for the Yurok Tribe during the years 1999–2003 was 204, 162, 268, 273, and 287 fish, respectively. The mean percent of the total annual catch that was sampled each year was 17% (range, 13–23%).

Data on body size, condition factor, GSI, and age of sampled fish are summarized in Table 1. Females were larger and older than males. The mean TL for females was 196.7 cm; for males, 178.1 cm. Live weight ranged from 29 to 73 kg in females and from 19 to 56 kg in males. Mean age for female and male cohorts was 27 and 20 years, respectively.

Although the isometric condition factor was significantly higher for females, there was substantial overlap between the sexes, many males having body conformations similar to those of the females. What was initially considered to be a large female, on the basis of the external appearance of a relatively "full" abdomen and swollen vent, often turned out to be a large male. The allometric weight–length relationship for each sex is shown in Figure 1. The males and females have similar regression slopes but significantly different intercepts. The females, in general, are heavier at a given length than males.

The relative frequency distributions of length and age show different modal classes in males and females, although there was considerable overlap between the sexes, a number of larger and older fish being males and a number of smaller and younger fish being females (Figures 2, 3). The FL modal class for males and females was 149–156.9 cm and 173–188.9 cm, respectively; all fish with FL over 200 cm were females. The age of the Klamath River sturgeon ranged from 14 to 40 years, the modal classes for females and males being 27–28 and 17–18 years, respectively

TABLE 1.—Body size, condition factor (*K*), age, and reproductive traits of green sturgeon sampled in the Klamath River during 1999–2003. Data are means ± SDs, with sample size and range in parentheses. All means are significantly different between the sexes ($P < 0.05$).

Variable	Females	Males
Fork length (cm)	180.6 ± 13.7 (82; 151–223)	162.9 ± 12.9 (113; 139–199)
Total length (cm)	196.7 ± 14.9 (82; 162–242)	178.1 ± 14.7 (107; 152–216)
Weight (kg)	46.1 ± 8.6 (62; 29–73)	32.0 ± 8.0 (88; 19–56)
K (%)	0.78 ± 0.07 (62; 0.65–0.94)	0.74 ± 0.07 (85; 0.60–0.92)
Age (years)	27 ± 5 (80; 16–40)	20 ± 4 (113; 14–32)
Gonadosomatic index (%)	12.6 ± 2.5 (55; 7.1–17.2)	5.2 ± 1.4 (74; 1.7–8.2)
Fecundity (thousands of eggs)	142 ± 41 (60; 59–242)	
Relative fecundity (thousands of eggs/kg)	3.0 ± 0.5 (55; 1.9–4.2)	
Oocyte diameter (mm)	4.33 ± 0.14 (73; 4.04–4.66)	
Oocyte polarization index	0.042 ± 0.012 (73; 0.021–0.078)	

(Figure 3). The youngest age for a mature female and a mature male was 16 and 14 years, respectively; the oldest female and the oldest male in our sampled fish were age 40 and 32 years, respectively. Both sexes showed a proportional increase in FL with age. The FL–age regression equation for females was FL = 126.3 + 2.02age ($n = 80$, $r^2 = 0.51$, $P \leq 0.0001$); for males, FL = 114.4 + 2.37age ($n = 110$, $r^2 = 0.53$, $P \leq 0.0001$). The FL–TL regression equation for females and males pooled was TL = 1.083FL + 1.582; the reciprocal equation was FL = 0.9234TL – 1.479 ($n = 189$, $r^2 = 0.96$, $P \leq 0.0001$).

Except for the two caught at the mouth of the river, all males were mature, and many released milt during capture and handling. The smallest mature male (152 cm TL, 19 kg, age 14) appears to be a good estimate of size and age at first maturity for males; the two immature males were 129 cm TL, 10 kg, age 10 and 159 cm TL, 16 kg, age 15. The three smallest mature females were 162, 176, and 177 cm TL (ages 16, 21, and 23 years, respectively), but body weight (29 kg) was measured only for the oldest.

The gonadosomatic index was higher for females (range, 7–17%) than for males (range, 2–8%). The two immature males captured in the estuary (rkm 0–6) had low GSI values (<1%) and testes with spermatogonia enclosed in cysts (Figure 4a, inset). All remaining males were fully mature; the testicular cysts contained

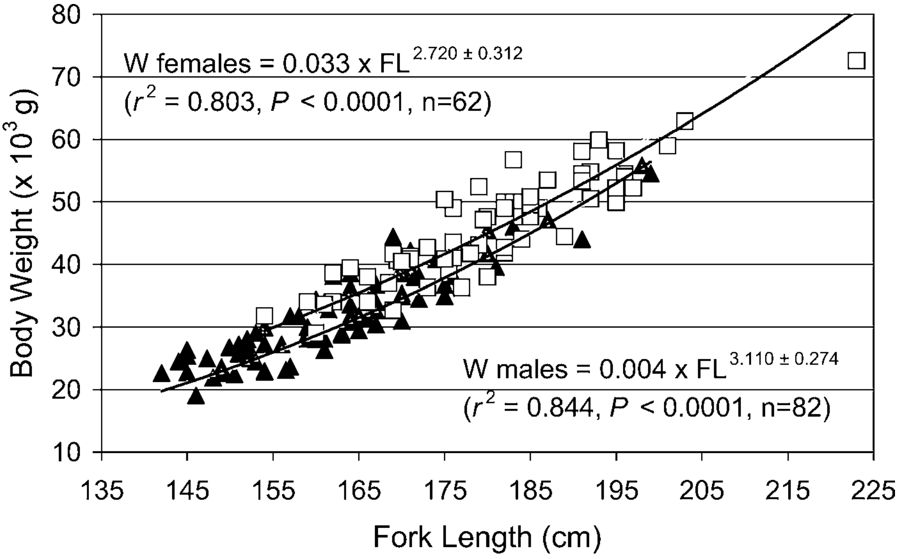

FIGURE 1.—The relationship between fork length and body weight for adult Klamath River males (triangles) and females (squares). The regression equation for the males (lower right) corresponds to the lower curve; that for females corresponds to the upper curve. Exponents are given with 95% confidence limits.

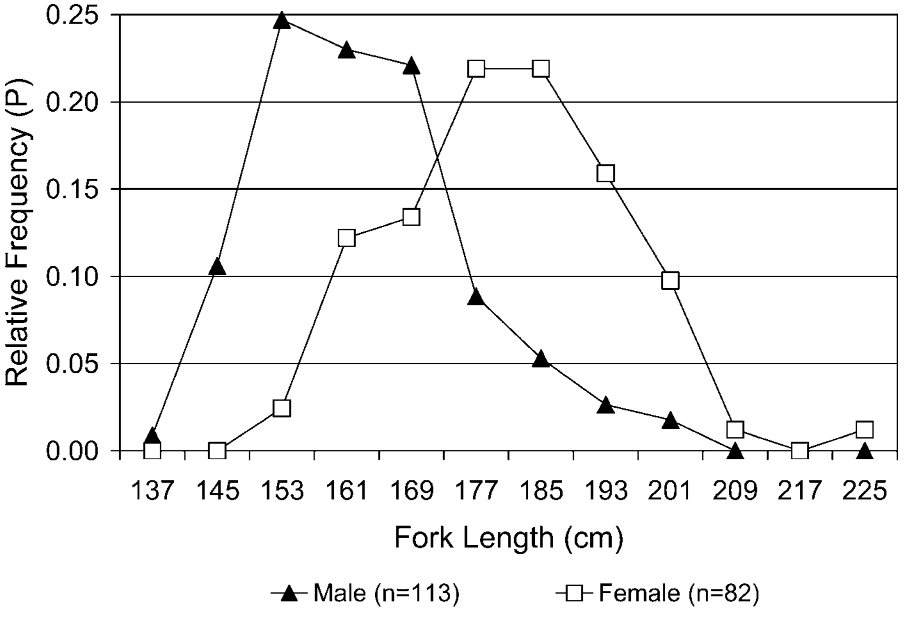

FIGURE 2.—Fork length frequency distributions of adult green sturgeon in the Klamath River, by sex. The *x*-axis values are the mid-points for size-class intervals of 8 cm (accuracy, 0.1 cm) from 133 to 229 cm (e.g., the 137 class ranges from 133 to 140.9 cm).

differentiated spermatozoa with no evidence of meiotic stages, suggesting spawning was imminent (Figure 4a). Two mature males were at the postspermiation stage, recognized by the regressed testis with residual spermatozoa in the cysts (Figure 4b). All females were in the preovulatory stage, except for seven that were postovulatory. The preovulatory stage females had large olive-green to light brownish colored oocytes with a three-layer egg envelope (Figure 4c). The germinal vesicle was displaced very close to the animal pole (Figure 4c insert), and the oocyte had a distinct polarized structure and a higher concentration of small yolk platelets in the animal hemisphere (Figure 4c and insert). The postovulatory females had ovaries containing numerous empty postovulatory follicles (POF), which made up approximately 10–15% of the histological sections (Figure 4d) and the next generation of previtellogenic oocytes in the primary growth phase. Some of these oocytes had a very thin PAS stain–positive glycoprotein egg envelope, but no obvious yolk globules were present in the cytoplasm. No intersex gonads were observed in any sturgeon sampled during this study. Seven females (FL 183 ± 9 cm, W 40 ± 6 kg) had spent ovaries; their condition factor and GSI decreased to 0.65 ± 0.02 and 1.9 ± 0.4%, respectively. No overripe females (ovulated but not having discharged the eggs) or females with preovulatory follicular atresia were found during this study

Seventy-five females were in the preovulatory state, their polarized oocytes being in an advanced stage of germinal vesicle migration. The average oocyte PI for the green sturgeon was 0.042 ± 0.012 (Table 1), a value indicating readiness of a sturgeon female for ovulation and spawning (Dettlaff et al. 1993). The regression analyses for individual PI and the distance of female capture from the river mouth (not shown) revealed no distinct trends ($r^2 = 0.002$, $P = 0.72$). The plot of mean individual PI and sample date showed some trend towards lower PIs later in the spawning season, but the relationship was not significant (Figure 5; $r^2 = 0.008$, $P = 0.44$). Thus, the green sturgeon enter the Klamath River in the advanced stage of germinal vesicle migration, ready to ovulate at any time. We examined the other reproductive characteristics (Table 1) of females and males in relation to time and location of capture but found no significant trends or differences.

The diameter of mature oocytes in green sturgeon females ranged from 4.04 to 4.66 mm (Table 1), and the linear relationship between oocyte diameter (Y) and fork length, $Y = 0.0054 \cdot \mathrm{FL} + 3.3542$ ($r^2 = 0.27$, $n = 73$, $P < 0.0001$), was significant (Figure 6).

Individual fecundity averaged 142,000 and ranged from 59,000 to 242,000 (Table 1). Fecundity also

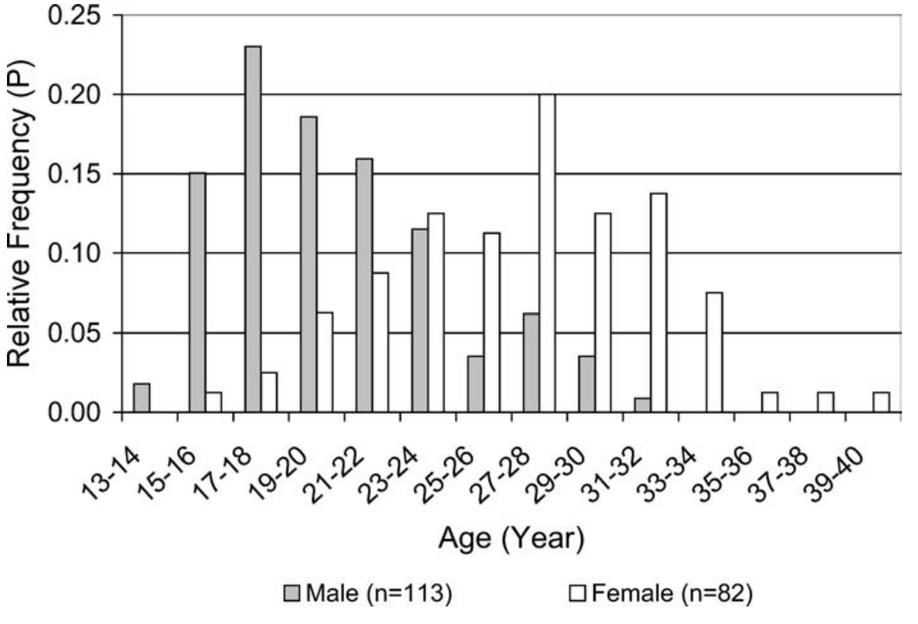

FIGURE 3.—Age frequency distributions of adult green sturgeons in the Klamath River, by sex.

exhibited an increase with fork length: $Y = 4.875 \times 10^{-5} \cdot FL^{4.188}$ ($r^2 = 0.55$, $n = 60$, $P < 0.0001$; see Figure 7). The fecundity–age relationship (not shown) was also significant but with a lower r^2 value: $Y = 483 \cdot age^{1.718}$ ($r^2 = 0.28$, $n = 58$, $P < 0.0001$). Relative fecundity averaged 3,000/kg, and ranged from 1,900 to 4,200 (Table 1).

We grouped the sampled females into three age groups to estimate the effect of age on reproductive conditions (Table 2). Fecundity and oocyte diameter increased with age, suggesting that females reach the peak of egg production when they are older than 32 years and can be assumed to spawn repeatedly. Oocyte PI was similar for all three age groups. Relative fecundity exhibited some increase in the older age groups but the differences were not significant (ANOVA: $P = 0.08$). Although the largest green sturgeon sampled was 242 cm TL, a number of larger (>250 cm TL) green sturgeon have been captured by some tribal members over the years, and released, to protect the largest and presumably oldest fish (A. A. Nova, unpublished data).

During this study, one large white sturgeon female in preovulatory condition was captured and sampled in the mid-Klamath region on April 30, 2000 (TL, 241 cm; weight, 104 kg; fecundity, 802,000; oocyte diameter, 3.55 mm; and PI, 0.06). Yurok Tribal members have reported other occasional white sturgeon sightings and captures during past years.

Discussion

Our observations on the time of annual spawning migration on the Klamath River are in general agreement with the previous report of Emmett et al. (1991), who stated the spawning period of green sturgeon as March–July, peaking from mid-April to mid-June. Our study found the peak spawning run to be from April to mid- May.

In general a predominance of males has been observed in any given sturgeon spawning run (Auer 1999; Bruch and Binkowski 2002). This probably reflects the different spawning periodicities between sturgeon sexes, as well as the smaller size and younger age at maturity for males (which may spawn with more than one female) than for females. However, several studies on different sturgeon species have found variations in the sex composition of a spawning population. The sex ratio of the spawning population of Chinese sturgeon *A. sinensis* approached 1:1 (Deng et al. 1985; cited by Deng et al. 1991). The Volga River *A. stellatus* had an average sex ratio of 1:1.1 (female:male) over a 21-year period, but during any given year the percent of females ranged from 19% to 77% (Veshchev 1991). Males dominated the spawning run of Russian sturgeon *A. gueldenstaedti*, ranging from 65% to 76% of the population (Veshchev and Novikova 1986). During the Hudson River Atlantic sturgeon spawning run, the female to male sex ratio was 1:2.3 (Van Eenennaam et al. 1996). The overall

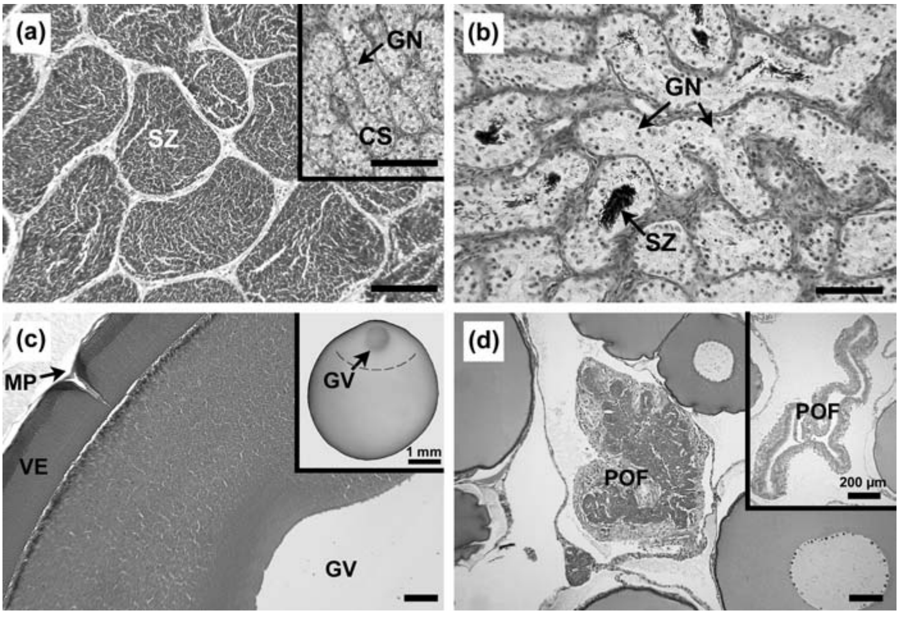

FIGURE 4.—Stages of gonadal development in Klamath River green sturgeon: **(a)** fully mature male caught in the river and (inset) an immature male caught near the river's mouth; **(b)** spent male with regressed testicular cysts, some containing residual spermatozoa; **(c)** portion of the fully grown ovarian follicle in a prespawning female, plus (inset) the whole bisected egg with the nucleus (germinal vesicle) in close proximity to the animal pole and fine yolk polarized into the animal hemisphere (above the dashed line); and **(d)** postovulatory stage (estimated to be 4–8 weeks after spawning) from a spent female in the river and (inset) an ovarian sample collected immediately after ovulation from a female that was induced to spawn at the University of California–Davis. All scale bars are 100 µm except where noted, and all sections were stained with PAS. Abbreviations are as follows: GN, spermatogonia; SZ, spermatozoa; CS, cysts; MP, micropyle; VE, vitelline envelope; GV, germinal vesicle; and POF, postovulatory follicle.

observed sex ratio for the sturgeon sampled in this study was 1:1.38. However, we cannot assume an entirely random sampling of the spawning run in any of these rivers, given potential effects of gear and site selectivity and the unknown spawning behavior of green sturgeon. Generally, the effective sex ratio in sturgeon (i.e., sex ratio in the spawning population) reflects the predominance of males, due to polyandry and longer residence time of males on the spawning grounds. Sex ratios (female : male) of adult lake sturgeon captured on the spawning grounds during the years with most natural water flow ranged from 1:1.25 to 1:2.7 (Auer 1999). Polyandry and estimated sex ratios of 1:5.7 during actual spawning events have been documented for lake sturgeon, which can be observed to spawn along the river shorelines (Bruch and Binkowski 2002).

The male and female green sturgeon cohorts differed in age and size composition. In the younger and smaller age- and size-classes, males dominated whereas females dominated in the older and larger classes. This is undoubtedly the result of the earlier maturity and the shorter life span of males. Similar data have been reported for other sturgeon species (shortnose sturgeon, Dadswell 1979; white sturgeon, Chapman et al. 1996; Atlantic sturgeon, Van Eenennaam et al. 1996; lake sturgeon, Bruch 1999). For the period of this study (1999–2003) the average size of adult females each year ranged from 189 to 206 cm TL. For the years 1990–1993 the average size was 187–205 cm TL (Nakamoto et al. 1995). Thus, there is no evidence that fisheries have resulted in a shift in the average size of the adult females since 1990. However, it does take approximately 16–20 years for a female to reach first sexual maturity, and a long-term effect of exploitation on recruitment cannot be assessed. Studies with lake (Bruch 1999) and Atlantic (Boreman 1997) sturgeon indicate high sensitivity of populations to fishing mortality.

The isometric condition factor *K* of green sturgeon was low compared with that of other species, supporting our field observations on the slender tapering body shape in both sexes of mature adults. In comparison, the more robust mature female and male Hudson River Atlantic sturgeon had higher condition factors (0.94 for females, 0.83 for males;

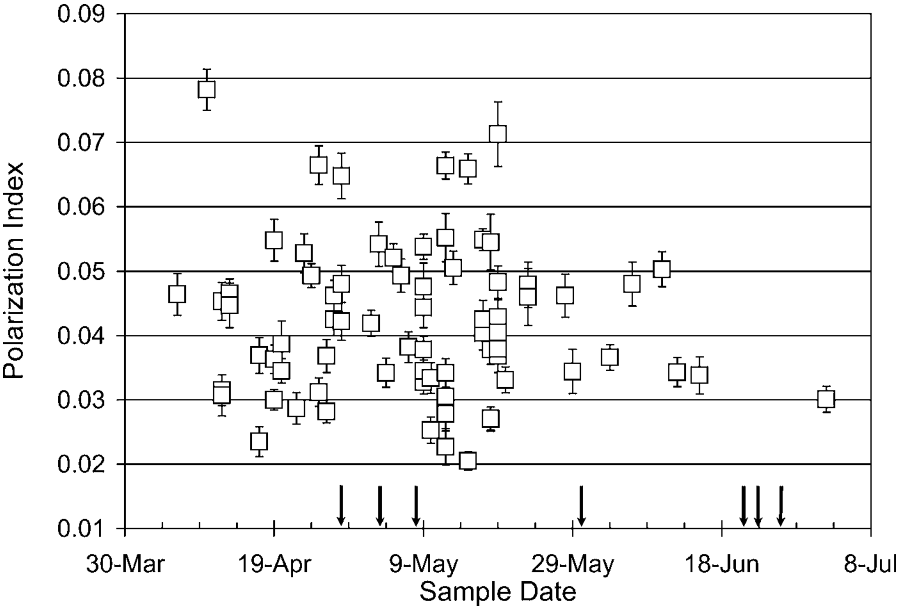

FIGURE 5.—The individual oocyte polarization index (mean ± SE) and capture date for green sturgeon females in the Klamath River. Boxes depict mean values and vertical lines depict SEs. Overlapping means create seemingly interior lines in some boxes. The arrows indicate the times when postovulatory females were captured.

Van Eenennaam et al. 1996). The analysis of allometric growth in green sturgeon revealed no difference between sexes in the rate of weight increase (exponent) but showed a significant difference in increases associated with higher GSI in females.

All the gravid females captured in the river were in the preovulatory state, as shown by the low oocyte PIs. This synchronous ovarian maturation and advanced stage of oocyte development suggests a single spring spawning run of green sturgeon on the Klamath River. The low oocyte PIs could also indicate that there are a number of spawning locations throughout the river and that the females are able to hold eggs at this advanced stage of maturation until they reach the desired spawning grounds. Because water temperatures typically range from 8°C to 15°C during the peak spawning run (Van Eenennaam et al. 2005), females may have the ability to hold the eggs at this preovulatory state for several weeks. The sampling of several postovulatory females and the apparent absence of females undergoing atresia indicate that successful ovulations and spawnings were occurring in the river.

The very small, darkly pigmented atretic bodies present in the ovaries of other sturgeon species were not seen in the green sturgeon sampled in this study. This indication of a previous completed maturation cycle, seen as distinct "salt-and-pepper" ovaries, were observed in white and Atlantic sturgeon (Van Eenennaam et al. 1996; Webb et al. 1999; Linares-Casenave et al. 2002). Apparently the olive-green to brownish pigment of the green sturgeon oocytes breaks down more quickly or completely, or possibly the large oocytes are more readily ovulated and released from the follicle, in comparison with species with smaller eggs. Although there were no occurrences of intersexes in the sampled green sturgeon gonads, rudimentary and pathological hemaphroditism has been reported for a number of other sturgeon species (shovelnose: Harshbarger et al. 2000; Atlantic: Atz and Smith 1976, Van Eenennaam et al. 1998; white: Chapman et al. 1996). Because the intersexes have all come from polluted habitats, some have hypothesized that their occurrence indicate contaminant-related effects (Harshbarger et al. 2000).

Only fragmentary information has been available on the fecundity and egg size of green sturgeon. Moyle (2002) reported females producing 60,000–140,000 eggs about 3.8 mm in diameter. Artyukhin and Andronov (1990) reported the fecundity (60,000 and 160,000 eggs) for two female Sakhalin sturgeon spawned on the Tumnin River and stated that the large size of the oocytes and the body conformation contributed to their low fecundity in comparison with other anadromous sturgeon species. In this study, fecundity ranged from 59,000 to 242,000, and both oocyte diameter and fecundity increased with body

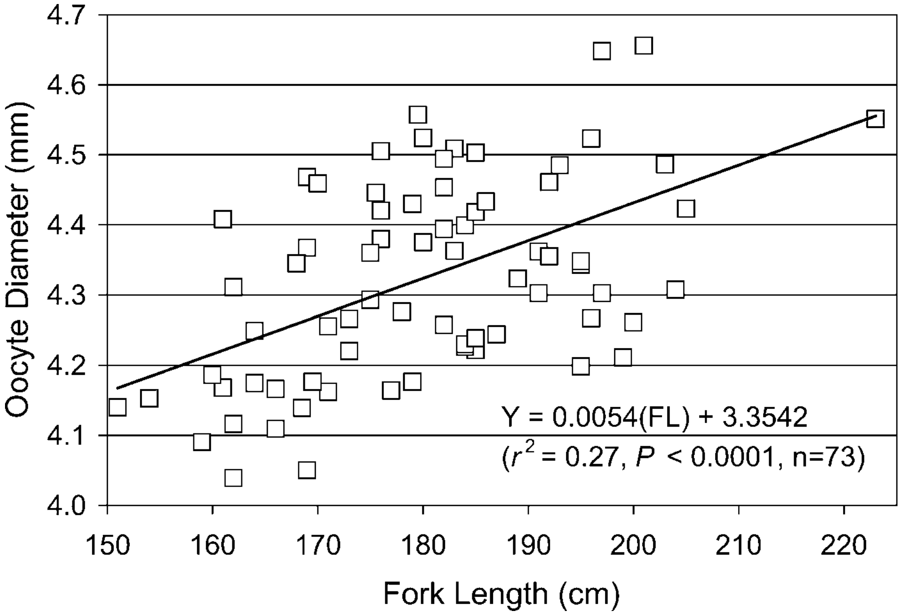

FIGURE 6.—Relationship between mean oocyte diameter and female fork length for the Klamath River green sturgeon.

size. The Atlantic sturgeon fecundity ranged from 4×10^5 to 2×10^6, with an egg diameter of 2.4–2.9 mm (Van Eenennaam et al. 1996), and both of these parameters also increased with fish size. Similar observations of increasing fecundity with fish size have been reported for shortnose sturgeon *A. brevirostrum* (Dadswell 1979) and several European species (Holčík 1989). A number of biotic, genetic, and environmental factors have been shown to influence fecundity and egg size, one of the most important

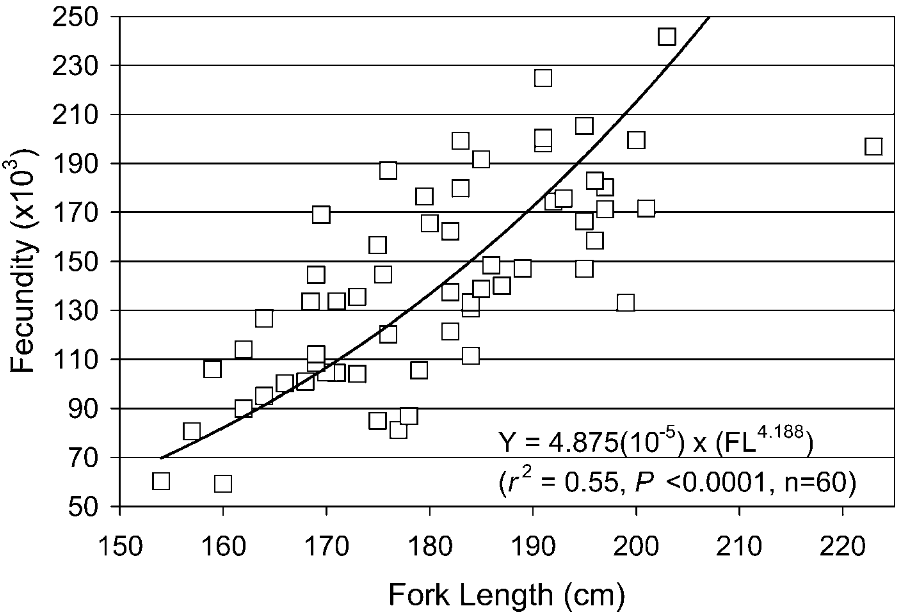

FIGURE 7.—Relationship between individual fecundity and female fork length in the Klamath River green sturgeon.

TABLE 2.—Body size and reproductive traits of green sturgeon females in different age-groups. Different letters denote significant differences between the means ($P < 0.05$); n = sample size.

Variable	17–24 years		25–32 years		33–40 years	
	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n
Fork length (cm)	180 ± 10 x	24	184 ± 11 y	46	195 ± 13 z	9
Body weight (kg)	39 ± 6 x	18	48 ± 7 y	36	58 ± 9 z	6
Oocyte diameter (mm)	4.20 ± 0.12 x	19	4.36 ± 0.11 y	44	4.51 ± 0.11 z	7
Oocyte polarization index	0.045 ± 0.012 x	19	0.041 ± 0.012 x	44	0.044 ± 0.013 x	7
Fecundity (thousands of eggs)	114 ± 34 x	18	147 ± 35 y	35	194 ± 34 z	7
Relative fecundity (thousands of eggs/kg)	2.9 ± 0.6 x	18	3.1 ± 0.7 x	30	3.4 ± 0.6 x	6

factors being body size (Wootton 1998). Generally, as fish size increases, so does fecundity and egg size. The optimal egg size is that which maximizes the number of offspring surviving to become reproductively active, so it is the size at which the product of fecundity and juvenile survival is a maximum (Wootton 1998). An increase in egg size is likely to increase juvenile survival because bigger eggs tend to produce bigger larvae. Larger larvae will be able to take a wider range of prey sizes, survive periods of food shortage better, and have fewer predators (Wootton 1998).

The fully grown oocytes in the Klamath River green sturgeon ranged from 4.0 to 4.7 mm in diameter, the largest recorded oocytes in North American acipenserids. Worldwide, Chinese sturgeon have the largest oocytes, ranging in size from 4.2 to 5.0 mm (Wei et al. 1997). In comparison, the beluga *Huso huso* from the Caspian Sea has ova ranging in diameter from 3.6 to 4.3 mm (Pirogovskii et al. 1989). Compared with white sturgeon, green sturgeon produce eggs that are two times larger in volume and thus invest a greater amount of maternal yolk for nourishment of the embryo, resulting in larger larvae and juveniles (Deng et al. 2002). Green sturgeon juveniles grow fast and have, probably, shorter residence time in the river. This reproductive strategy is in great contrast with other anadromous sturgeon species, such as the Atlantic sturgeon *A. oxyrinchus* and European sturgeon *A. sturio*, which have a very high fecundity but small eggs and larvae (Holčík et al. 1989; Van Eenennaam et al. 1996).

White sturgeon occasionally have been sighted or captured in the Klamath River (Snyder 1908; USFWS 1980–1991, cited by USFWS 1995); historically, there may have been small runs of white sturgeon (Moyle 2002). The white sturgeon female captured in the mid-Klamath region during this study had a low oocyte PI, was in the preovulatory stage, and thus theoretically could have spawned. However, data from domestic white sturgeon indicate that females with low oocyte PIs can maintain their oocytes at the preovulatory stage for 4–6 weeks, if held in water colder than 12°C (J. P. Van Eenennaam, unpublished data). Thus it is possible that the white sturgeon could have entered the Klamath River for foraging or some other reason, in the process of migrating to another river on the west coast. The potential spawning of white sturgeon in the Klamath River and documented spawning of green and white sturgeon in the Sacramento River during the same season raises an interesting question regarding the mechanisms of reproductive isolation in these two sympatric species (Van Eenennaam et al. 2005).

Green sturgeon adults were generally similar in age and size to the white sturgeon in the San Francisco Bay–Delta (Kohlhorst et al. 1980; Chapman et al. 1996). There was, however, a 50-cm overlap in FL and an 18-year overlap in age between the two green sturgeon sexes. In contrast, a similar study on the spawning run of Atlantic sturgeon found only a 2- cm overlap in size and an 8-year overlap in age (Van Eenennaam et al. 1996), and a study on a spawning stock of lake sturgeon also found only a 25-cm overlap in size between the sexes (Auer 1999). In this study, we saw a number of small and young mature females and a number of old and large (>200 cm TL) males that produced this overlapping effect. During the years 1990 through 1993, Nakamoto et al. (1995) also reported the capture of several large males (>200 cm TL) and observed a similar multi-age and size-class population, with a large overlap between sexes. In addition, the average annual Yurok Tribe harvest (266 fish) on the river has shown no apparent trend in quantity captured since 1985 (Adams et al. 2002), and little change in catch per unit effort since 1994, the time period for which catch per unit effort data are readily available (D.C. Hillemeier, unpublished data). In summation, these data could be an indication of the relative strength and current sustainability of the Klamath River green sturgeon spawning run, although such a conclusion would be based on the relatively short time frame of this study, relative to their life history.

In conclusion, we found no indications of abnormalities in individual fish (ovarian atresia, intersexes) or in the size and age composition of the spawning population of green sturgeon in the Klamath River. Although the presence of spermiating males and postovulatory females indicates successful spawning of green sturgeon in the Klamath River, these are not the only factors determining the reproductive success of a population. Regulation of river flow, pollution, and climate fluctuations could affect the annual recruitment. For example, recent laboratory studies indicated limited tolerance of green sturgeon embryos to the fluctuations of the thermal regime of the Klamath River (Van Eenennaam et al. 2005), high oxygen requirements of green sturgeon larvae (Gisbert et al. 2001), and sensitivity of the larvae to starvation at the onset of exogenous feeding (Gisbert and Doroshov 2003). Survival rates of eggs, larvae, and juveniles in their natural habitats are unknown at this time. Identification, protection, and improvement of spawning and nursery habitats of green sturgeon in the Klamath River are critical for the long-term well-being of this valuable species.

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