Distribution, life history, and population characteristics of green sturgeon <u>Acipenser medirostris</u> in California's Central Valley

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Synopsis

We review the limited and widely scattered information on green sturgeon to evaluate status of the Sacramento-San Joaquin River population. Status is inferred from information on distribution, life history, and population characteristics. Life history characteristics from other populations also provide the basis for a simple deterministic life table model useful for predicting the how population characteristics may contribute to population vulnerability. The Sacramento River population of green sturgeon is the southernmost of five known or suspected green sturgeon populations. Green sturgeon from all spawning areas range widely in the nearshore Pacific Ocean from Mexico to southeast Alaska. The species is widely distributed in the Sacramento-San Joaquin Delta and spawning in the Sacramento River mainstem has been well documented over the last 15 years. Green sturgeon occasionally range into the Feather and Yuba rivers but numbers are low and no data have been collected to document the use of these rivers by green sturgeon for spawning, now or in the past. No adult or juvenile green sturgeon have been documented in the San Joaquin River upstream from the Delta and historical occurrence remains speculative. Fish spawn during late winter and early spring, larvae migrate downstream following a brief hiding phase, and juveniles rear in freshwater and estuarine areas for 1-3 years before dispersing into the ocean. Like all sturgeons, green sturgeon are large, long lived, late-maturing, and fecund. Abundance data is limited but other evidence suggests that the Sacramento River and estuary may number in the thousands or tens of thousands. Available time series are not adequate for evaluating abundance trends, particularly of the Sacramento population. Adults comprise a relatively small portion of the population which primarily consists of subadults that are widely distributed in the ocean. Population parameters indicate that green sturgeon may be well-adapted to take advantage of variable spawning conditions but also sensitive to increases in mortality over their life cycle. Small sample sizes, intermittent reporting, problems with fishery dependent data, limitations in directed sampling efforts, and potential confusion with white sturgeon make assessments of green sturgeon status highly uncertain. Accurate assessments of green sturgeon status will require consideration of the unique features of their life history strategy and population characteristics.

Introduction

Green sturgeon are among the most elusive and poorly studied species in this unique and ancient order of fishes. Unlike other sturgeon species, green sturgeon provide little fishery value (McDonald 1894, Galbreath 1985) and this has resulted in a historic lack of attention. Until recently, several spawning populations were known only from anecdotal accounts (Moyle 2002). This anadromous species spends most of its life in Pacific coastal marine and estuarine waters from Mexico to Alaska, returning to large river mainstems to spawn, and rearing in freshwater for only a few years before migrating back to the ocean (Fry 1973, Hart 1973, Moyle 1976). The large, turbulent, and often remote river systems favored by green sturgeon are difficult to sample, particularly during high, turbid, spring runoff periods when spawning occurs. The poorly adhesive nature of eggs (Van Eenennaam et. al 2001), apparent lack of a larval dispersal stage (Deng et al. 2002), larval hiding behavior (Deng et al. 2002), nocturnal habitats (Cech et al. 2000), and benthic habitat preferences (Kynard et al. 2005) make eggs, larvae, and juveniles particularly reclusive.

A life history strategy involving a long lifespan, large size, delayed maturation, high fecundity, and high mobility has proven to be tremendously successful since sturgeon first evolved over 200 million years ago (Bemis et al. 1997). One or more sturgeon species occur in most major temperate river systems throughout the northern hemisphere (Birstein 1993). However, the same life history strategy that contributed to sturgeon success through the ages has made most species vulnerable to widespread habitat destruction and overfishing (Rieman & Beamesderfer 1990, Beamesderfer & Farr 1997, Boreman 1997). Sturgeon are presently depleted, threatened, or extinct almost everywhere they historically occurred (Rochard et al. 1990, Birstein 1993, Musick et al. 2000).

Concerns for the apparent rarity of green sturgeon and the widespread depletion of other sturgeon species led to a 2001 petition for listing under the U.S. Endangered Species Act. This petition stimulated a formal review of the available information and new research on green sturgeon status (Adams et al. 2002, NOAA 2005). This assessment was hampered by the lack of specific studies and basic information on green sturgeon distribution, biology, and status. This lack of information was particularly acute for central California's Sacramento-San Joaquin river system, which is considered one of the most significant of the historic populations and where aquatic habitat changes have been widespread.

In this paper, we review the available information on the Sacramento-San Joaquin green sturgeon. Although no comprehensive survey of biology and status has ever been undertaken for any green sturgeon population, significant information exists from limited and often unpublished studies, results of other fish sampling activities, anecdotal information, information from other green sturgeon populations, and inferences from sympatric white sturgeon Acipenser transmontanus populations. Organized in a simple population model, the available information provides useful insight into the biology and characteristics of green sturgeon populations in California's Central Valley and throughout their range.

Approach

Distribution

Changes in green sturgeon distribution have been of particular interest in assessments of current status and threats to continued existence (EPIC et al. 2001, Adams et al. 2002). Current and historical distribution of green sturgeon in California's Central Valley is from a review of published records of occurrence. Areas of interest in California's Central Valley include the Sacramento-San Joaquin delta, the Sacramento River, the Feather River, and the San Joaquin River (Figure 1). Records include scientific publications, unpublished agency reports, and newspaper articles. Because of a general lack of published information, anecdotal accounts are also identified where applicable.

Life History

An understanding of the life history of green sturgeon provides a critical context for interpretation of the available information on status. Information on the life history of green sturgeon in California's Central Valley is extremely limited, and so green sturgeon life history was described based on a review of information from all populations. Life history descriptions include spawning, early life history, the freshwater juvenile rearing period, and ocean residence.

Population Characteristics

Population characteristics including age, growth, maturation, fecundity, recruitment, mortality, abundance, and trends were described based on a review of information from all green sturgeon populations. Maximum reported ages, lengths, and weights were summarized based on catches in stock assessment samples. Growth was based on von Bertalanffy length-age (Table 1, Eqn. 3) and female exponential length-weight (Table 1, Eqn. 4) functions reported for Klamath River samples that encompassed the greatest reported range of fish sizes. Maturation was described using a cumulative normal probability function (Table 1, Eqn. 6 and 7) calibrated to match the reported size range at maturation. Fecundity-length relationships (Table 1, Eqn. 8) were as reported for the Klamath population. Approximate total annual mortality rates were estimated based on a catch curve analysis of age-frequency data (Ricker 1975) of mature fish in the Klamath River and subadults in Columbia River estuary samples. Fishing mortality of the Klamath population was estimated from the difference between Klamath and Columbia River estimates of total mortality based an assumption that Columbia River samples were representative of the unexploited segment of the population. Male and female rates were averaged for life table analyses. Estimates of green sturgeon mortality reflect fishing levels prior to implementation of recent fishery reductions and are uncertain due to untested assumptions of the catch curve estimation method (e.g. constant recruitment and mortality). No direct estimates of green sturgeon abundance are available but relative size of the Sacramento population was inferred from genetic data in mixed stock samples from the Columbia River, and estimated harvest numbers and mortality rates from the Klamath population. Population trend analysis considered the available data time series of green sturgeon samples.

Life Table Model

Despite our many unknowns about green sturgeon in California, life history parameters from the Klamath and Columbia can provide us with a basic model to predict how population characteristics may contribute to vulnerability of green sturgeon populations in the Central Valley. A deterministic life table model was used to describe what a green sturgeon population might look like under conditions of constant recruitment and mortality, and resulting stability in numbers and age structure (Table 2). Although equilibrium assumptions are rarely met, the model still provides an accurate picture of the average features of a population over time. Values were expressed per recruit because we lack information on the direct relationship between spawning stock and number of recruits.

A representative green sturgeon population structure was inferred from population statistics summarized in Table 3. Hypothetical age-specific numbers for the Sacramento River population were inferred from annual 8% natural and 5% fishing mortality rates, an average maturation age of 20 years, and an average spawning periodicity of three years. Sensitivity analysis evaluated the effects of mortality at various life stages on fish numbers, reproductive potential, and fishery yield. For the purposes of this analysis, "additional mortality" was defined as that in addition to normal natural mortality and may refer to fishing or other human-caused mortality factors.

Reproductive potential was evaluated based on lifetime fecundity of one age 1 female (EPR or egg production per recruit) (Boreman 1997). EPR provides a useful index of potential population sustainability in the face of human-imposed mortality and alternative management strategies, particularly in the absence of data on the relationship between the spawning stock and numbers of recruits produced (Prager et al. 1987, Goodyear 1993). EPRs of 20-50% the inherent value in the absence of additional mortality are typically used to identify levels needed to preserve adequate population reproductive potential. Relationships between EPR and fishing rates can be used to identify sustainable fishing levels. Appropriate fishing rates depend on the sizes of fish vulnerable to the fishery. These inferences assume that spawning and rearing habitat is adequate for effective reproduction.

Yield per recruit provided an index of productivity related to potential fishery value and the effects of fishing on different size ranges. Yield refers to the weight of fish harvested at any given fishing rate. Estimates of yield per recruit generally highlight fishing strategies that maximize the biomass of sturgeon harvested from any given cohort through an optimal balance of growth and mortality. Estimates of yield per recruit assume recruitment that is independent of fishing effects. As a result, fisheries based solely on simple maximum sustained yield models have often lead to overexploitation and more precautionary management strategies are appropriate in the face of uncertain population productivity. Sustainable fishing strategies must thus consider effects of fishing on both egg production and yield per recruit.

Distribution

The Sacramento River population of green sturgeon is the southernmost of five known or suspected populations (NOAA 2005). Spawning has also been documented in the Klamath and Rogue rivers and is suspected in the Umpqua and Eel Rivers (NOAA 2005). Southern (Sacramento) and Northern (Klamath, Rogue, and Umpqua) populations are genetically distinct and mixed stock samples appear to indicate that not all spawning populations have been identified (Israel et al. 2004).

Green sturgeon from all spawning areas appear to range widely in nearshore waters up and down the Pacific coast from Mexico to southeast Alaska (Houston 1988, Moyle et al. 1995). Green sturgeon are commonly observed in Pacific coastal bays and estuaries with large concentrations in the Columbia River estuary and Washington's Grays Harbor and Willapa Bay during summer (Galbreath 1985, Rien et al. 2001, Moser & Lindley 2005). No spawning occurs in the Columbia River, Coastal Washington rivers, or the Fraser River British Columbia (ODFW & WDFW 2004, Houston 1988). Genetic samples from green sturgeon captured in the Columbia River estuary include a mixture of fish originating from northern and southern populations (Israel et al. 2004).

Sacramento-San Joaquin Delta

The occurrence and wide distribution of green sturgeon in the Sacramento-San Joaquin delta has been well documented since the late 1800s (Table 4). The most consistent records are of juveniles salvaged from south delta water pumping facilities and subadults captured in San Pablo Bay during semi-annual white sturgeon assessment (Figure 3). Returns of fish in San Pablo Bay and recaptured in California, Oregon, and Washington marine and estuary commercial fisheries provided the first indication of the widespread anadromous distribution of green sturgeon from the system (Miller 1972, Moyle 1976, Langness 2005).

Sacramento River

Anglers commonly report catching adult green sturgeon in the Sacramento River from the Delta as far upstream as Bonnyview Bridge (Rkm 471) (Moyle et al. 1992, Brown 2002). Spawning in the upper Sacramento River mainstem was undetected until recently but has been well documented over the last 15 years (Table 4). Green sturgeon spawn upstream from Hamilton City to above Red Bluff Diversion Dam (Rkm 391) and possibly as far upstream as Keswick Dam (Rkm 486) (CDFG 2002). Significant numbers of larvae and post-larval green sturgeon are collected in rotary screw traps operated since 1991 at the Glenn-Colusa Irrigation District pumping plant (Rkm 339) and the Red Bluff Diversion Dam.

The upstream extent of historical spawning by green sturgeon in the Sacramento River is unknown. Access of anadromous fish into the upper Sacramento River basin was blocked by construction of Shasta Dam at Rkm 505 in 1944 (USFWS 1995). There is no information that green sturgeon spawned in the three Sacramento River tributaries upstream from Shasta Dam or that this distribution represented significant spatial population structure. Only white sturgeon were historically reported from areas upstream of Shasta Dam, primarily in the PIT River system (USFWS 1995). If green sturgeon historically spawned in areas now blocked by Keswick and

Shasta dams (a fact not shown by the data), loss of that area has apparently been offset by creation of favorable spawning habitats downstream where discharge of cool water from Shasta Dam has reduced temperature to a range suitable for green sturgeon spawning and incubation. Brown (2002) observed that temperature and flow are suitable for green sturgeon both upstream and downstream of Red Bluff Diversion Dam.

Feather River

Green sturgeon occasionally range into the Feather River but numbers are low and there is no data to document that spawning occurs now or occurred in the historical time frame (Table 4). Unspecific reports of green sturgeon spawning (Wang 1986, USFWS 1995, CDFG 2002) have not been corroborated by observations of young fish or significant numbers of adults (Seesholtz 2003, Beamesderfer et al. 2004). Most reports of sturgeon have been incidental to other activities and sampling efforts focused specifically on sturgeon have frequently failed to observe or collect sturgeon (Schaffter & Kohlhorst 2002, Niggemeyer & Duster 2003, Beamesderfer et al. 2004).

Sturgeon (unknown species) also regularly occur in the Yuba and Bear rivers (Feather River tributaries) particularly during wet years (Beamesderfer et al. 2004). Potential confusion of green and white sturgeon often confounds interpretation of historical records. Many historical reports of sturgeon in the Feather River system were white sturgeon (Anonymous 1918, Talbitzer 1959, USFWS 1995). White sturgeon have been documented in the Feather River system on numerous occasions (Miller 1972, Schaffter 1997, Schaffter & Kohlhorst 2002, Schaffter 2002, Beamesderfer et al. 2004).

It remains unclear whether suitable spawning habitat for green sturgeon is available or has ever been available, development and water use has made conditions unsuitable for spawning, or conditions were always marginal. Recent sampling in the Feather River system occurred during drought years and it is possible that spawning occurs only during high flow conditions in wet years (Schaffter & Kohlhorst 2002, CDFG 2002). Elevated temperatures during low flow years might exceed preferred ranges (Schaffter & Kohlhorst 2002). Several references also suggest that natural and man-made barriers in the Feather River might limit upstream movements during low flow years (Schaffter & Kohlhorst 2002, Niggemeyer & Duster 2003).

San Joaquin River

It is unclear whether green sturgeon were historically present, are currently present, or were historically present and have been extirpated from the San Joaquin River (NMFS 2005). Moyle et al. (1992) surmised that some spawning by green sturgeon may take place or once did in the lower San Joaquin River. Sturgeon remains (unidentified species) in deposits at Tulare Lake illustrate that anadromous species were historically capable of reaching the south San Joaquin Valley (Gobalet et al. 2004). However, no green or white sturgeon appear to have been trapped behind Friant Dam on the San Joaquin River when it was constructed in the 1940s (CDFG 2002). No adult or juvenile green sturgeon have been documented in the San Joaquin River upstream from the Delta (CDFG 2002), but no directed sturgeon studies have ever been undertaken in the San Joaquin River (USFWS 1995, CDFG 2002, Adams et al. 2002, Beamesderfer et al. 2004, NOAA 2005). Given difficulties in effective sampling of green sturgeon in their large river habitats, limited use of or periodic straying into the San Joaquin River is possible. Significant current use would probably have been detected by sampling activities for other fish throughout the San Joaquin River system.

Anecdotal information indicates that small numbers of adult sturgeon are regularly observed in the San Joaquin River upstream from the Delta (Beamesderfer et al 2004). All of these identified to date have been white sturgeon. Spawning is suspected to occur in wet years (Shaffter, CDFG retired, 2004 personal communication). Catches of two juvenile white sturgeon in a rotary screw trap on the Mokelumne River at Woodbridge (Rkm 63) in 2003 were the first documentation of sturgeon spawning the San Joaquin system. No juvenile sturgeon have been collected or observed in other San Joaquin fish sampling activities including annual trawl sampling at Mossdale and seining at several sites between Mossdale and the Tuolumne River (Tim Heyne CDFG, personal communication 2004).

Small fisheries for sturgeon occur in late winter and spring between Mossdale and the Merced River (Kohlhorst 1976). White sturgeon tagged in San Pablo Bay have been caught by anglers in the San Joaquin River (Kohlhorst et al. 1991). A series of local newspaper articles during the 1990s noted that spawning by sturgeon (species unspecific) is thought to occur in two spots in the lower San Joaquin River near Sturgeon Bend (Rkm 120 just downstream from Stanislaus River) and Laird County Park (Rkm 145 just upstream from the Tuolumne River), poaching can be a problem especially in years of low flows, significant legal harvest of sturgeon also occurs, and harvest numbers were thought to have declined over the last two decades (Scott 1993, Lewis 1995, Palomares 1995, Keo 1996, Jardine 1998).

Every observation of green sturgeon juveniles or unidentified sturgeon larvae in the San Joaquin River has occurred in the Delta downstream from Old River (Rkm 86) in the tidally-influenced portion of the south delta downstream from free flowing sections of the San Joaquin. Larval sturgeon of unidentified species were collected from Delta reaches of the San Joaquin River in 1966 and 1967 but were not considered evidence of spawning in the San Joaquin system (Stevens and Miller 1970). Significant numbers of juvenile green and white sturgeon are periodically collected from the lower San Joaquin River at south delta water diversion facilities (Tracy Fish Collection Facility and J. E. Skinner Delta Fish Protective Facility) and other sites but is unclear whether these originated from the San Joaquin or Sacramento rivers (Radke 1966, Moyle et al. 1995, Moyle 2002). CDFG (2002) concluded 'based on movement of other fishes in the Delta, young green sturgeon found in the lower San Joaquin could easily, and most likely, come from the known spawning population in the Sacramento River.' However, NMFS (2005) has suggested that the high percentage of San Joaquin River flows at the Tracy Collection Facility could mean that some entrained green sturgeon originated in the San Joaquin.

Life History

Spawning

Spawning migrations from the ocean into freshwater generally occur from February through June based on observations in the Klamath (Moyle et al. 1995, Belchik 2005, Hillemeier 2005), Rogue (Erickson et al. 2002, Erickson & Webb 2005), and Sacramento rivers (Brown 2002, CH2M Hill 2002). Spawning generally occurs from March through July with peak activity from April to June (Moyle et al. 1995, Van Eenennaam et al. 2004). Sacramento River spawning is estimated to occur from late April through July with a peak in May based on back-calculations from larvae captured in rotary screw traps below Red Bluff Diversion Dam (Gaines and Martin 2002) and development periods determined in the laboratory (Deng et al. 2002). In other systems, adults may emigrate soon after spawning or may remain in freshwater through summer before returning to the ocean in the fall (Belchik 2005). Large, deep pools are key resting habitats for adult sturgeon during upstream migration and post-spawn periods.

Spawning occurs in large, turbulent river mainstems (Moyle et al. 1995). Specific spawning habitat preferences are unclear, but eggs are likely broadcast over large cobble where they settle into the cracks (Moyle et al. 1995). Eggs and larvae have been collected in the upper Sacramento River in areas of gravel, cobble, and bedrock (Brown 2002). Appropriate substrate may be critical for green sturgeon because adhesiveness of eggs is poor compared to white sturgeon (Van Eenennaam et al. 2001, Deng et al. 2001).

Temperatures of 17-18ºC appear optimal for green sturgeon embryos and temperatures exceeding 20-22ºC were lethal in laboratory experiments (Cech et al. 2000, Van Eenennaam et al. 2004). Water temperature may vary from 8 to 21°C during green sturgeon spawning in the Klamath River (Van Eenennaam et al. 2004). Upper Sacramento River temperature is typically between 11 and 15°C during the spawning period (Brown 2002) as a result of cold water releases from Shasta Dam since 1988.

Optimum velocity and flow requirements for spawning and incubation are unclear, but spawning success in most sturgeons appears related to flow (Kohlhorst et al. 1991, Beamesderfer and Farr 1997). Variable depths in turbulent, high velocity areas near lower velocity resting areas are a common denominator of spawning sites among other sturgeon species (Parsley et al. 2002). Very specific combinations of conditions are selected by other sturgeon species because many sites of apparently suitable substrate, velocity and depth are not utilized.

Early Life History

In laboratory studies at 16ºC, eggs hatch in 6-8 days, exogenous feeding begins in 10-15 days post hatch at 23-25 mm in length, and larval metamorphosis is typically completed within 45 days at 60-80 mm in length (Deng et al. 2002). Green sturgeon larvae are distinguished from other sturgeon by the absence of a pelagic swim-up stage within the first few days after hatching (Deng et al. 2002). Larvae began to display to display a nocturnal swim-up behavior at 6 d post hatch, hiding during the day from the onset of exogenous feeding to metamorphosis (Cech et al. 2000, Deng et al. 2001). Around the onset of exogenous feeding, larvae initiated a downstream nocturnal migration (Kynard et al. 2004). Downstream dispersal of larval green sturgeon in the upper Sacramento River occurs from May through August at sizes of 20 to 60 mm based on trap samples at Red Bluff Diversion Dam (Gaines & Martin 2002) and the Glenn Colusa Irrigation District (CDFG 2002).

Post migrant larvae and juveniles forage diurnally with a nocturnal activity peak (Kynard et al. 2004). Additional downstream movements at 110 to 181 days of age until water temperatures decreased to about 8ºC indicate that juveniles migrate downstream to wintering habitat (Kynard et al. 2004). Behavior of 9-10 month old juveniles suggests a wintering preference for deep pools with low light and some rock structure (Kynard et al. 2004).

Freshwater Juvenile Rearing

Juvenile green sturgeon are widely distributed throughout the Sacramento-San Joaquin delta (Radke 1966). Juveniles may spend one to four years in freshwater and estuarine environments before entering saltwater habitats based on observations in the Klamath River (Nakamoto et al. 1995). Laboratory tests indicate that juvenile sturgeon less than six months of age are sensitive to salinity (Allen & Cech 2005). Bioenergetic performance of age 0 and 1 green sturgeon is optimal between 15ºC and 19ºC (Mayfield & Cech 2004).

Ocean Residence

Green sturgeon spend most of their lives in the ocean but their distribution and activities are little understood. Green sturgeon are benthic feeders on invertebrates including shrimp and amphipods, small fish, and possibly mollusks (Houston 1988). Recent analyses from archival tags, acoustic tags, and Oregon bottom trawl logbook records indicate that green sturgeon are widely distributed in the nearshore ocean at depths up to 110 m with most use occurring between depths of 40-70 m (Erickson & Hightower 2004). Summer concentrations in coastal estuaries might represent feeding aggregations or thermal refugia. In the Sacramento-San Joaquin River system, significant numbers of subadult green sturgeon are found in San Pablo Bay.

Population Characteristics

Age and Growth

The largest confirmed green sturgeon in the Sacramento River was a 239 cm total length fish captured at Rkm 330 for Glenn-Colusa Irrigation District passage evaluations (Vogel 2005). Green sturgeon reach total lengths of up to 270 cm and weights of up to 175 kg in the Klamath River (Moyle 2002). No ages have been estimated from Sacramento system green sturgeon but ages as great as 53 were reported in Columbia River estuary samples based on pectoral fin ray samples (Farr et al. 2001). Green sturgeon grow 30 cm in their first year and 7 to 10 cm per year from ages 1 through 10 based on age-length relationships reported from Klamath River and

Columbia estuary samples (Table 3). Total lengths average 100 cm at age 9 and 200 cm at age 33. Rapid growth and large size likely confers a survival advantage for green sturgeon by reducing vulnerability to predators.

Maturation and Fecundity

Males mature at about 8-18 years and 120-185 m TL, whereas females mature at 13-27 years and 144-202 cm TL based on observations in other areas (Table 3). Fecundity ranges from 59,000 to 242,000 eggs per female and increases with body size (Van Eenennaam et al. 2004). Egg size also increases with body size (Van Eenennaam et al. 2004). Eggs and larvae of green sturgeon are substantially larger and fecundity is less than in other sturgeon species (Van Eenennaam et al. 2001).

Recruitment

Recruitment data are almost nonexistent but some inferences can be made from incidental catches of juveniles in several areas. Both Sacramento and Klamath River populations appear to be characterized by variable year class strengths that subsequently drive fluctuations in population size and age composition. Incidental catches of postlarval green sturgeon in Red Bluff Diversion Dam traps, Glenn Colusa Irrigation District traps, and delta pumping facilities vary substantially from year to year although it is unclear if patterns are an artifact of low sampling efficiencies for sturgeon. Juvenile green sturgeon are consistently observed in the Klamath system (Adair et al. 1983, Rueth et al. 1992, Craig & Fletcher 1994, USFWS 2000) but Nakamoto & Kisanuki (1995) describe changes in size frequencies of juveniles among years. These ebbs and flows illustrate the need for extreme caution in attempting to identify long term trends in green sturgeon status from short time series of data.

Mortality

The longevity of sturgeon is clearly associated with low natural mortality rates beyond the first few years of age. Approximate total annual mortality rates estimated from catch curves for the Klamath River and Columbia River estuary ranged from 8 – 28% per year (Table 3). Total annual rates include both natural and fishing mortalities. The lower rate for Columbia River subadults (8%) than for Klamath River adults (19-28%) may be due in part to additional fishing mortality during Klamath River spawning migrations although subadults are also subjected to fishing mortality in the Columbia River. These estimates might suggest a natural annual mortality rate of 8% or less and fishing mortality rates of 10-20% or less on Klamath River adults.

Fishing mortality rates of Sacramento River green sturgeon are likely to be less than in the Klamath River because there is no terminal fishery on spawners in the Sacramento River. Sturgeon harvest in the Sacramento River and delta has been limited by a protective slot regulation since 1990 (current slot limits 117 to 183 cm). Exploitation rates on green sturgeon within the Sacramento system are likely to be less than the 1-4% per year estimated for white sturgeon (Schaffter & Kohlhorst 1999), because green sturgeon are less preferred by anglers. Green sturgeon are also subject to incidental fishing mortality in coastal and estuary fisheries of Oregon and Washington.

Abundance

Empirical abundance information is not available for the Sacramento River population. Low catches of green sturgeon preclude estimates or indices of green sturgeon abundance from a white sturgeon sampling program in San Pablo Bay (Schaffter & Kohlhorst 1999, Gingras 2005). Green sturgeon estimates based on freshwater and estuary samples will also drastically underestimate population size because most of the population is comprised of subadults that are widely distributed in the ocean. Corresponding low local densities of green sturgeon may have contributed to perceptions of rarity.

Although direct estimates of abundance do not exist, approximate estimates might be inferred from other information. Genetic samples from the Columbia River suggest that the Sacramento population may be as large as or larger than all other green sturgeon populations combined. Columbia River samples, which represent a mixed sample from all populations, cluster more closely with San Pablo Bay samples than with Klamath or Rogue samples (Israel et al. 2004). If fish from all populations are equally likely to enter the Columbia River, then samples should cluster more closely with the larger population groups.

Based on these assumptions, the Sacramento population might be at least as large as the Klamath population which represents one of several northern populations. Order-of-magnitude abundance estimates can be inferred from Klamath River harvest and harvest rate information. Harvest in Klamath River tribal fisheries has averaged 279 green sturgeon per year from 1985-2003 (Hillemeier 2005) and we estimated annual harvest rates of 10-20% based on estimated total and assumed natural fishing rates. Thus, the adult population of Klamath River green sturgeon would average about 1,900 fish (279/0.15). Effective population size (Waples 1990) is obviously substantially greater than average annual spawner numbers. If adults typically comprise 10% of the total population at equilibrium rates of recruitment and mortality, then the total population would number approximately 19,000 and annual recruitment of age 1 fish would average about 1,800 based on estimated annual mortality rates. Klamath fisheries would be harvesting almost half of the annual spawning run to produce a 15% net harvest rate if only one third of the adult population spawns per year as suggested by Erickson and Webb (2005). Most harvest occurs on spent fish during spring salmon seasons (Hillemeier 2005).

Significant population sizes of green sturgeon are corroborated by large season concentrations and historic harvest numbers in coastal areas and estuaries of Oregon and Washington. Annual harvests as great as 4,000 to 8,000 were reported prior to fishery reductions during the 1990s. Green sturgeon abundance must be significant if fish are widely distributed, large numbers can be caught in many areas at different times, and sampling efficiency (percent of available fish that are caught) is low.

Trends

Available time series are not adequate to evaluate abundance trends of the green sturgeon, particularly of the Sacramento population (Heppell & Hofmann 2002, Adams et al. 2002). Limitations include small sample sizes, intermittent reporting, fishery dependent data, lack of directed sampling, and potential confusion with white sturgeon. Most data is from incidental catches in fisheries or other fish samples that are not designed specifically to index green sturgeon abundance. Catches in fisheries are confounded by changes in fishing effort and regulations enacted over time to protect green sturgeon. Catches while sampling other fish are confounded by a low incidence of green sturgeon and inherent variability in effort and catchability. Time series are too short to effectively distinguish short term patterns from normal population cycles of a long-lived species like the green sturgeon. Variable sampling effort and uncertain patterns in catchability confound interpretation of formal statistical analyses.

Annual catches of juvenile green sturgeon in Sacramento-San Joaquin River delta water diversion facilities illustrate the problems of attempting to infer trends from incidental capture information. Two large diversion facilities, the State Water Project (SWP) and the Central Valley Project (CVP) export water from the south delta for urban and agricultural use. Since

1957 (CVP) and 1968 (SWP), fish were collected at diversion facilities and released back into the river (CDFG 2004). Based on subsamples, from 0 to juvenile 7,313 green sturgeon were estimated to have been salvaged per year from 1974 to present with the greatest numbers observed prior to 1986 (Figure 4). However, salvage is not designed to index annual abundance and patterns can be confounded by variable sturgeon dispersal patterns and collection vulnerability due to changes in delta flow dynamics, changes in configuration and operation over time, difficulties of sturgeon species identification, and expansions from small sample sizes (Moyle et al. 1996, Puckett et al. 1996, Hiebert 1995, CDFG 2002). A lack of significant correlation between annual counts of green sturgeon from these state and federal projects highlights problems of interpretation. Incidental catches of juvenile green sturgeon in other sampling in the Sacramento River also indicate that significant green sturgeon reproduction continues to occur in most years even when salvage numbers are low.

Length distributions from semi-annual San Pablo Bay sturgeon sampling vary substantially among sample periods (Figure 5). No long term trend in size distribution was apparent. Peak numbers at size reflect fish availability and trammel net selectivity. Green sturgeon appear to be fully recruited to this sample gear at approximately 80 to 100 cm TL and 6 to 9 years of age. It is unclear whether the apparent variation in size structure results from variable recruitment or is an artifact of small sample sizes, pooling of sample years, or variable distribution patterns between freshwater and ocean portions of the population.

Green sturgeon are widely counted in the sport, commercial, and tribal fishery harvests, particularly in Oregon and Washington commercial fisheries (ODFW & WDFW 2004, Hillemeier 2005). With the except of a Klamath River fishery on the Klamath population, green sturgeon are not targeted by fisheries but are taken incidental to harvest of white sturgeon and salmon. Harvest of mixed green sturgeon populations in Oregon and Washington fisheries has steadily declined from a peak of over 8,000 per year in 1986 to less than 1,000 fish per year since 2001 (Figure 6). This change reflects a series of regulations enacted for green sturgeon protection rather than a decline in abundance. Corresponding fishing effort is not available. Green sturgeon abundance will have increased in response to reduced fishing over the last 10 years if recruitment was consistent.

In the absence of solid abundance data or indices, green sturgeon trends must be inferred from trends in limiting factors. The longevity of sturgeon means that historical factors can have long term effects on sturgeon numbers. For instance, historical trends in green sturgeon abundance might be at least partly inferred from white sturgeon harvest records (Figure 7). Large commercial fisheries developed in San Francisco Bay, the Columbia River, and the Fraser River during the late 1800s for previously-unexploited white sturgeon populations. Green sturgeon were not targeted by fisheries (McDonald 1894) but both species are vulnerable to the same fishing gear and green sturgeon populations were likely depleted as a result of bycatch. Fisheries collapsed within a few years as sturgeon were rapidly mined at rates far in excess of sustainability (Skinner 1962, Semakula & Larkin 1968, Galbreath 1985). Protective regulations were enacted following the fishery collapse but populations did not begin to recover for almost 50 years because of the white sturgeon's late age of maturation. Modern harvests have never approached historic levels as harvest is more strictly regulated. Green sturgeon were probably partially protected from excessive early fisheries by their marine distribution but spawning runs were probably heavily exploited. We speculate that green sturgeon, like the white sturgeon, probably recovered slowly during the 1900s until significant numbers were again seen in Columbia River harvests (Figure 7).

Life Table Model

Population Structure

Life table model analyses based on representative population parameters show that subadults rearing in the ocean would comprise the majority (64%) of a population at equilibrium (Figure 8). Juveniles in the approximately 3-year freshwater rearing stage would represent 26% of total population numbers. Adults would comprise only 10% of a hypothetical green sturgeon population on average. Only a very small fraction of the total population is represented by mature sturgeon that spawn in any given year. The annual spawning population may represent only 3% of the total green sturgeon population based on the observed spawning periodicity. Population biomass is similarly heavily weighted to the subadult life history stage. Population fecundity, which is the total number of eggs based on female number, size, and individual fecundity, peaks around age 24 when all females have matured.

Population Size

The sensitivity of sturgeon to increasing mortality is demonstrated by the abrupt decline in numbers in hypothetical life table analyses (Figure 9A). The model suggests that additional mortality of just 10% over the life span of this long-lived species would reduce total numbers by over 50% and numbers of adults by over 90%. Additional mortality of 20% over the life span would result in virtually no green sturgeon surviving to adulthood.

Reproductive Potential

Egg production per recruit of green sturgeon is high (49,000) in an unexploited hypothetical population. The inherent reproductive potential suggests that green sturgeon have a high capacity for replacement under the proper conditions. Reproductive potential declines rapidly with increasing mortality concurrent with the decline in survival to adulthood (Figure 9B). Additional rates of only 2-5% throughout the life cycle reduce EPR to less than the 20-50% thought to be critical for long term sustainability (Figure 9B). Reproductive potential is much less sensitive to added mortality that is limited to a small portion of the life cycle. Additional mortality of 30-60% is required to reduce EPR to 20-50% when applied to only the first 3 years of age when green sturgeon rear in freshwater prior to seaward migration.

The high sensitivity of reproductive potential to increasing mortality explains why sturgeon can be extremely susceptible to overfishing. EPRs of 20-50% occur at fishing rates of 5-10% on fish 117 to 183 cm in length as prescribed by California's current sport fishery regulations (e.g. Sacramento River population). Fishing rates of 17-25% produce EPRs of 20-50% where the additional mortality occurs on fish greater than 165 cm as would occur if fishing was primarily on adult spawners (e.g. Klamath River).

Yield Potential

Because green sturgeon grow to large sizes and natural mortality rates are low, potential yield per recruit generally increases when fishing is focused on larger fish (Figure 9A). Maximum yields are achieved in slot limit (117-183 cm) and adult (>165 cm) fisheries at fishing rates of 15-20% (Figure 9A). Our yield per recruit estimates assumed no relationship between spawning stock biomass or status and recruitment when recruitment may in fact be highly correlated with spawner numbers. However, rates that maximize yield per recruit when fishing is limited to adults are similar to rates that appear to provide for sustainable reproductive potential based on EPR. Rates that maximize yield per recruit appear to exceed rates needed for sustainable reproductive potential for a subadult fishery slot limit. Effective use of subadult slot limits will require careful regulation of exploitation to ensure that adequate numbers of fish survive to spawning ages. Slot limit fisheries for sturgeon will provide for greater catch rates and harvestable numbers than a strictly yield-based fishery focused on adults. The tradeoff is between more smaller fish and fewer larger fish. Higher catch numbers are generally preferred in sport fisheries whereas higher yields are typically the target in commercial fisheries.

Conclusions

Our knowledge of green sturgeon has improved several fold in just the last five years as a result of work stimulated by consideration of listing under the U.S. Endangered Species Act. This new information has substantially improved our understanding of green sturgeon distribution, life history, and population characteristics. Much of this new information suggests that green sturgeon status is more robust than initially feared. For instance, more populations exist than initially suspected, it is unclear whether other populations thought to have been lost ever existed, and apparent low densities in estuaries and rivers result from the fact that most juveniles and a fraction of adults remain in the marine environment.

Status of green sturgeon remains highly uncertain, particularly in the Sacramento-San Joaquin River system. This review of the available information on distribution, life history, and population characteristics highlights significant research needs for green sturgeon. These include historical distribution, the significance of any portions of the range that have been lost, critical habitats and habitat requirements in freshwater, historical changes in the amount and distribution of suitable habitat, limiting factors, relative population sizes, migration patterns, and effective sampling methods. It is particularly unclear whether threats to long term persistence are significant, existing habitat and fishery improvements for a variety of species provide adequate protection for green sturgeon, or additional actions are warranted. These uncertainties may ultimately pose the greatest risk to the protection of this unique species. The most critical information needs for reducing uncertainty in status and risks include population-specific estimates of spawner abundance, strength and consistency of juvenile recruitment, and sources of significant human-caused mortality.

Accurate assessments of status, productivity, and risk require consideration of the unique features of the sturgeon life history strategy and population characteristics. Green sturgeon have evolved a life history strategy including a long life span, delayed maturation, spawning by only a portion of the adult population in each year, multiple spawning over their lifespan, and anadromy. The sturgeon's long life span and repeat spawning in multiple years allows them to outlast periodic droughts and environmental catastrophes. The high fecundity that comes with large size allows them to produce large numbers of offspring when suitable spawning conditions occur and potentially make up for years of poor conditions. Adult green sturgeon do not spawn every year and only a fraction of the population enters freshwater where they might be at risk of a catastrophic events such as floods, landslides, volcanic eruptions, or contaminant spills. The widespread ocean distribution of green sturgeon ensures that most of the population at any given time is dispersed among areas where they are not vulnerable to catastrophic losses in freshwater. Two-hundred million years of existence in the face of tremendous upheavals over geological time have demonstrated the success of the sturgeon life history strategy. It remains to be seen whether these same attributes will continue to be successful in our changing world.

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Table 1. Equations, definitions, and values of variables and parameters used in life table model. All values are derived from data presented in this paper.

Term	Definition	Value	Equation
$N_{x,}$	Age-specific number of fish in population		
	$= (N_{x-1})(S_x)$		[1]
x	Age		
N_1	Annual recruitment	10,000	
S_x	Age-specific annual rate of survival		
	$= 1 - [n_x + m_x - n_x\ m_x]$		[2]
n_x	Natural mortality rate	0.08	
m_x	Exploitation (harvest mortality rate)	0.05	
	Sizes vulnerable to exploitation	117-183 cm	
L_x	Total length at age (cm)		
	$= L_\infty \{1 - \exp[-k (x - t_0)]\}$		[3]
L_∞	Von Bertalanffy equation length at infinity	238 cm	
k	Von Bertalanffy equation slope parameter	0.053	
T_0	Von Bertalanffy equation intercept parameter	-2.0	
W_x	Weight at age (kg)		
	$= (a_w)(L_x)^{bw}$		[4]
a_w	Length-weight equation coefficient	4.0E-06	
b_w	Length-weight equation exponent	3.11	
B_x	Biomass at age		
	$= N_x\ W_x$		[5]
pf	Proportion of the population that is female	0.5	
ps_x	Proportion of the population of females of each age class that spawn in any year		
	$= 1 - [1/(1 + \theta / C_\infty)]$ for $L_x \le \mu$		[6a]
	$= 1 - \{1/[1 + (1 - \theta) / C_\infty]\}$ for $Lx > \mu$		[6b]
C_∞	Female spawning periodicity at maturity	3 years	
θ	Cumulative normal distribution function dependent variable		
	$= 1/(2\pi)^{0.5}\ \exp[-(L_x - \mu)^2/ \sigma^2]\ \sum_{i=1}^{5} bi\ \{1 + p\ \|((L_x - \mu)/ \sigma\ \|\}^{1-i}$		[7]
M	Mean length of female sexual maturity	165	
Σ^2	Variance about mean length of female sexual maturity	10	
b1,..,b5	Constants (0.31938153, -0.356563782, 1.781477937, -1.821255978, 1.330274429)		
P	Constant (0.2316419)		
F_x	Fecundity (eggs)		
	$= (a_f)[0.92\ L_x]^{bf}$		[8]
a_f	Length-fecundity equation coefficient	5.3E-05	
b_f	Length-fecundity equation exponent	4.19	
P_x	Reproductive potential at age (population fecundity)		
	$= N_x\ pf\ ps_x\ F_x$		[9]
EPR	Egg production per recruit		
	$= \sum P_x / N_1$		[10]
H_x	Harvest at age (number of fish)		
	$= N_x\ m_x$		[11]
Y_x	Yield at age to fisheries (kg)		
	$= H_x\ W_x$		[12]
YPR	Yield per recruit		
	$= \sum Y_x / N_1$		[13]

Table 2. Life table for green sturgeon based on a simple equilibrium model and population parameters reported for various populations. Terms are as defined in Table 1.

x yrs	L_x cm	W_x kg	n_x	m_x	S_x	N_x	Bx kg	pf	ps	F_x x1,000	P_x x1,000	H_x	Y_x kg
1	35	0.2	0.08	0.00	0.920	10,000	1,927	0.5	0.000	0		0	0
2	45	0.4	0.08	0.00	0.920	9,200	4,010	0.5	0.000	0		0	0
3	55	0.8	0.08	0.00	0.920	8,464	6,829	0.5	0.000	0		0	0
4	65	1.3	0.08	0.00	0.920	7,787	10,246	0.5	0.000	0		0	0
5	74	2.0	0.08	0.00	0.920	7,164	14,093	0.5	0.000	0		0	0
6	82	2.8	0.08	0.00	0.920	6,591	18,191	0.5	0.000	0		0	0
7	90	3.7	0.08	0.00	0.920	6,064	22,373	0.5	0.000	0		0	0
8	98	4.7	0.08	0.00	0.920	5,578	26,491	0.5	0.000	0		0	0
9	105	5.9	0.08	0.00	0.920	5,132	30,422	0.5	0.000	0		0	0
10	112	7.2	0.08	0.00	0.920	4,722	34,071	0.5	0.000	0		0	0
11	118	8.6	0.08	0.05	0.874	4,344	37,364	0.5	0.000	0		217	1,868
12	125	10.1	0.08	0.05	0.874	3,797	38,242	0.5	0.000	0		190	1,912
13	130	11.6	0.08	0.05	0.874	3,318	38,550	0.5	0.000	0		166	1,927
14	136	13.2	0.08	0.05	0.874	2,900	38,352	0.5	0.000	0		145	1,918
15	141	14.9	0.08	0.05	0.874	2,535	37,720	0.5	0.000	0		127	1,886
16	146	16.6	0.08	0.05	0.874	2,215	36,725	0.5	0.022	39.7	948	111	1,836
17	151	18.3	0.08	0.05	0.874	1,936	35,440	0.5	0.051	45.4	2,242	97	1,772
18	156	20.0	0.08	0.05	0.874	1,692	33,929	0.5	0.095	51.3	4,113	85	1,696
19	160	21.8	0.08	0.05	0.874	1,479	32,252	0.5	0.144	57.5	6,131	74	1,613
20	164	23.6	0.08	0.05	0.874	1,293	30,463	0.5	0.189	63.8	7,784	65	1,523
21	168	25.3	0.08	0.05	0.874	1,130	28,609	0.5	0.225	70.3	8,928	56	1,430
22	171	27.1	0.08	0.05	0.874	987	26,728	0.5	0.258	76.9	9,805	49	1,336
23	175	28.8	0.08	0.05	0.874	863	24,852	0.5	0.285	83.6	10,280	43	1,243
24	178	30.5	0.08	0.05	0.874	754	23,009	0.5	0.304	90.3	10,358	38	1,150
25	181	32.2	0.08	0.05	0.874	659	21,218	0.5	0.316	97.1	10,130	33	1,061
26	184	33.8	0.08	0.00	0.920	576	19,497	0.5	0.324	103.9	9,697	0	0
27	187	35.5	0.08	0.00	0.920	530	18,795	0.5	0.328	110.6	9,629	0	0
28	189	37.0	0.08	0.00	0.920	488	18,064	0.5	0.331	117.3	9,464	0	0
29	192	38.6	0.08	0.00	0.920	449	17,312	0.5	0.332	124.0	9,234	0	0
30	194	40.1	0.08	0.00	0.920	413	16,548	0.5	0.333	130.5	8,962	0	0
31	197	41.6	0.08	0.00	0.920	380	15,780	0.5	0.333	137.0	8,661	0	0
32	199	43.0	0.08	0.00	0.920	349	15,014	0.5	0.333	143.3	8,342	0	0
33	201	44.4	0.08	0.00	0.920	321	14,256	0.5	0.333	149.5	8,009	0	0
34	203	45.7	0.08	0.00	0.920	296	13,510	0.5	0.333	155.6	7,670	0	0
35	204	47.0	0.08	0.00	0.920	272	12,781	0.5	0.333	161.6	7,326	0	0
36	206	48.2	0.08	0.00	0.920	250	12,070	0.5	0.333	167.4	6,982	0	0
37	208	49.4	0.08	0.00	0.920	230	11,382	0.5	0.333	173.0	6,640	0	0
38	209	50.6	0.08	0.00	0.920	212	10,717	0.5	0.333	178.5	6,303	0	0
39	211	51.7	0.08	0.00	0.920	195	10,077	0.5	0.333	183.8	5,972	0	0
40	212	52.8	0.08	0.00	0.920	179	9,463	0.5	0.333	189.0	5,648	0	0
41	214	53.8	0.08	0.00	0.920	165	8,877	0.5	0.333	194.0	5,334	0	0
42	215	54.8	0.08	0.00	0.920	152	8,317	0.5	0.333	198.8	5,029	0	0
43	216	55.8	0.08	0.00	0.920	140	7,785	0.5	0.333	203.5	4,735	0	0
44	217	56.7	0.08	0.00	0.920	128	7,279	0.5	0.333	208.0	4,453	0	0
45	218	57.5	0.08	0.00	0.920	118	6,800	0.5	0.333	212.3	4,182	0	0
46	219	58.4	0.08	0.00	0.920	109	6,347	0.5	0.333	216.5	3,923	0	0
47	220	59.2	0.08	0.00	0.920	100	5,920	0.5	0.333	220.5	3,676	0	0
48	221	60.0	0.08	0.00	0.920	92	5,517	0.5	0.333	224.4	3,442	0	0
49	222	60.7	0.08	0.00	0.920	85	5,138	0.5	0.333	228.1	3,219	0	0
50	223	61.4	0.08	0.00	0.920	78	4,782	0.5	0.333	231.7	3,007	0	0

Table 3. Green sturgeon vital statistics reported in the scientific literature.

Statistic	Value	Source
Maximum size	225 cm TL (204 cm FL)	Rogue River (Rien et al. 2001)
	260 cm TL (233 cm FL)	Klamath River (Nakamoto et al. 1995)
	females 242 cm TL (223 cm FL) males 216 cm TL (199 cm FL)	Klamath River (Van Eenennaam et al. 2004)
	202 cm TL	San Pablo Bay (CDFG unpublished)
	239 cm TL	Sacramento River (Vogel 2005)
	270 cm TL	Klamath River (Moyle 2002)
Maximum weight	73 kg (females), 56 kg (males)	Klamath River (Van Eenennaam et al. 2004)
	148 kg (females), 112 kg (males)	Klamath River (Nakamoto et al. 1995)
	175 kg	(Moyle 2002)
Maximum age	53	Misc. Oregon locations (Farr et al. 2002)
	45	Klamath River (Nakamoto et al. 1995)
	40 (females), 32 (males)	Klamath River (Van Eenennaam et al. 2004)
Length-Weight	$KG = (1.84E\text{-}6)\ FL^{3.26}$	Columbia River estuary (Rien et al. 2001) N = 2,377 (100-180 cm)
	$KG = -27.99 + 0.0039\ FL^{2}$	Klamath River (Nakamoto et al. 1995) N = 90 (length in cm)
	$KG = (3.3e\text{-}5)\ FL^{2.72}$ (males) $KG = (4.0e\text{-}6)\ FL^{3.11}$ (females)	Klamath River (Van Eenennaam et al. 2004) N = 62 (males), N = 82 (females) [1]
Age-Length	$FL = 176[1 - e^{-0.081\ (AGE + 2.377)}]$	Misc. Oregon locations (Farr et al. 2001) N = 258 (Ages 0 – 53)
	$TL = 238[1 - e^{-0.053\ (AGE + 1.9943)}]$	Klamath River (USFWS 1983, Nakamoto et al. 1995) (Ages 0 – 40) [1]
Size at maturity	120 – 165cm TL (males) 145 – 185 cm TL (females)	Klamath River (Nakamoto et al. 1995)
	152 – 185 cm TL (males) 165 – 202cm TL (females)	Klamath River (Van Eenennaam et al. 2004) [1]
	146 – 180cm TL (males) 144 – 180 cm TL (females)	Columbia River Estuary (Rien et al. 2001)
Age at maturity	13-18 (males), 16 – 27 (females)	Klamath River (Van Eenennaam et al. 2004)
	8+ (males), 13+ (females)	Klamath River (Nakamoto et al. 1995)
Spawning periodicity	2-4 years	Erickson & Webb 2005 [1]
Fecundity	59,000 – 242,000	Klamath River (Van Eenennaam et al. 2004)
Length-Fecundity	$Eggs = 4.875E\text{-}5FL^{4.188}$	Klamath River (Van Eenennaam et al. 2004) [1] N = 60
Length -oocyte diameter	$MM = 4.875e\text{-}5\ FL + 3.354$	Klamath River (Van Eenennaam et al. 2004)
Annual mortality	0.19 (males), 0.28 (females)	Klamath River (Van Eenennaam et al. 2004) [1,2]
	0.08	Columbia River Estuary (Rien et al. 2001) [1,2]
Total – Fork Length	$TL = 1.09\ FL$	Columbia River estuary (Rien et al. 2001) N = 1,244 (Fork length 100-180 cm)
	$TL = 1.1374\ FL - 4.6131$	Klamath River (Nakamoto et al. 1995) N = 91 (length in cm)
	$TL = 1.083\ FL + 1.1582$	Klamath River (Van Eenennaam et al. 2004)

[1]*Values used in life table model.*
[2]*Catch curve estimates based on reference data.*

Table 4. Historical observations of green sturgeon in the Sacramento River system.

Year	Observation
Sacramento-San Joaquin Delta	
1879	The earliest available record of green sturgeon in the Sacramento-San Joaquin system noted this species as being 'abundant in the bay and the rivers and creeks flowing into it' (Lockington 1879).
Late 1800s-present	Green sturgeon are widely observed in delta and bay commercial and sport fisheries although it is often difficult to distinguish green sturgeon from white sturgeon species in historical records (Skinner 1962, Fry 1973).
1948	California Department of Fish and Game began tagged green sturgeon during other fish studies in San Pablo Bay during 1948 and 1949 (Schaffter & Kohlhorst 1999).
1954-2001	Five to 110 green sturgeon have been captured during each Fall in San Pablo Bay as part of a semi-annual white sturgeon assessment from (Gingras 2005).
Early 1960s	Trawl net and gillnet catches confirmed wide distribution of juveniles in the Delta and estuary (Ganssle 1966, Radke 1966).
1965	The first documentation of sturgeon spawning in the system with two sturgeon larvae (species unidentified) collected in the Sacramento River during a striped bass spawning survey (Stevens & Miller 1970).
1968	Juvenile green sturgeon identified in fish samples at south Delta water pumping facilities (Adams et al. 2002, CDFG 2004).
1967-1970	Green sturgeon tagged in the delta are reported in California, Oregon, and Washington commercial fishery catches (Miller 1972).
Sacramento River	
1966	Local newspaper accounts of several large green sturgeon caught near Red Bluff (EPIC et al. 2002).
1973	First formal report of green sturgeon spawning in the Sacramento River upstream from the delta (Kohlhorst 1976). A total of 257 larvae and nine sturgeon eggs was collected between the mouth of the Feather River and Colusa from March 5 to June 17, 1973. Species was unidentified but one larva was thought to be a green sturgeon based on its different size and coloration.
1974	Spawning confirmed with the capture of 12 juvenile green sturgeon (25-60 mm) at the Glenn-Colusa canal intake near Hamilton City and a 60 mm juvenile taken at Hamilton City (Kohlhorst 1976).
1989-2002	Adult sturgeon regularly observed in the vicinity of Red Bluff Diversion Dam by USFWS personnel (CDFG 2002, Brown 2002).
1991	Young green sturgeon first observed at the Red Bluff Diversion Dam in October 1991 (Moyle et al. 1992).
1991-2001	Young-of-the-year green sturgeon regularly observed in rotary screw trap fish samplers at the Glenn-Colusa canal. Catches have ranged from 23 in 1994 to over 700 in 1993 (CDFG 2002).
1994-2000	A total of 2,608 larval and post larval green sturgeon were caught in a rotary screw trap at the Red Bluff Diversion Dam from 1994-2000 (Johnson & Martin 1997, Gaines & Martin 2002). All sturgeon grown to identifiable size were green sturgeon (Gaines & Martin 2001).

1990-1991	Adult sturgeon radiotagged between Hood and Freeport including one 183 cm green sturgeon in March of 1991 (Schaffter 1997). This fish was located once, 7 days after tagging at which time it had moved upstream above the mouth of the American River.
2000-2001	Artificial substrate mats and drift nets used to sample green sturgeon eggs and larvae from above and below the Red Bluff Diversion Dam with limited success (Brown 2002). One green sturgeon larvae was captured by a drift net on July 13, at Bend Bridge (above the Red Bluff Diversion Dam) and two green sturgeon eggs were collected with artificial substrates below the dam on June 14, 2001.
2001-2002	Green sturgeon were tagged with sonic and radio transmitters in San Pablo Bay, and signal detectors were placed throughout the Sacramento River but tagged fish have not yet matured and undertaken upstream spawning migrations (Kelly et al. 2005).
2003	Anglers captured 14 adult green sturgeon from July through November in 2003 near RKm 324 for use in telemetry studies of passage at the Glenn Colusa Irrigation Facility (Vogel 2005).
<u>Feather River</u>	
1975-1988	Fishing guide reports that green sturgeon were frequently caught with most catches between March and May, and occasional catches in July and August (USFWS 1995).
1993	Fisheries graduate student obtained specific descriptions of green sturgeon from anglers, observed green sturgeon photos in local bait shops, and reported catches of seven adult green sturgeon by anglers fishing in the Themolito Afterbay Outlet (CDFG 2002).
2000	Informal survey of local anglers and bait shops found no information on recent sturgeon catches (CDFG 2002).
2000-2004	Intensive angling, scuba surveys, and egg and larval sampling efforts in the Feather River fail to locate significant numbers of adult green sturgeon or evidence of spawning (Schaffter & Kohlhorst 2002, Seescholtz 2003).
2004	Survey of fishing guides reports occasional catches of green sturgeon in the Feather River (Beamesderfer et al. 2004).
2004	California Department of Water Resources field technician reported seeing two adult sturgeons (one green and one white) while angling at Shanghai Bend during June (Beamesderfer et al. 2004).
<u>Yuba and Bear Rivers (Feather River tributaries)</u>	
1989-1992	Adult sturgeon were observed in shallow pools of the Bear River between the Highways 70 and 65 bridges during 1989, 1990, and 1992 (USFWS 1995). During 1989, approximately 100 sturgeon were trapped in pools and at least 30-40 sturgeon (weighing from 60 to 100 pounds and at least 5 feet long) were illegally harvested from this area during a 2-week period in July. All seven sturgeon confiscated by game wardens were white sturgeon.
--	Two reports of sturgeon were documented in the pool below Daguerre Point Dam on the Yuba River (Beamesderfer et al. 2004).
--	A fishing guide also provided a credible report of a sturgeon (unidentified species) sighting in the Yuba River upstream from Hallwood (Beamesderfer et al. 2004).

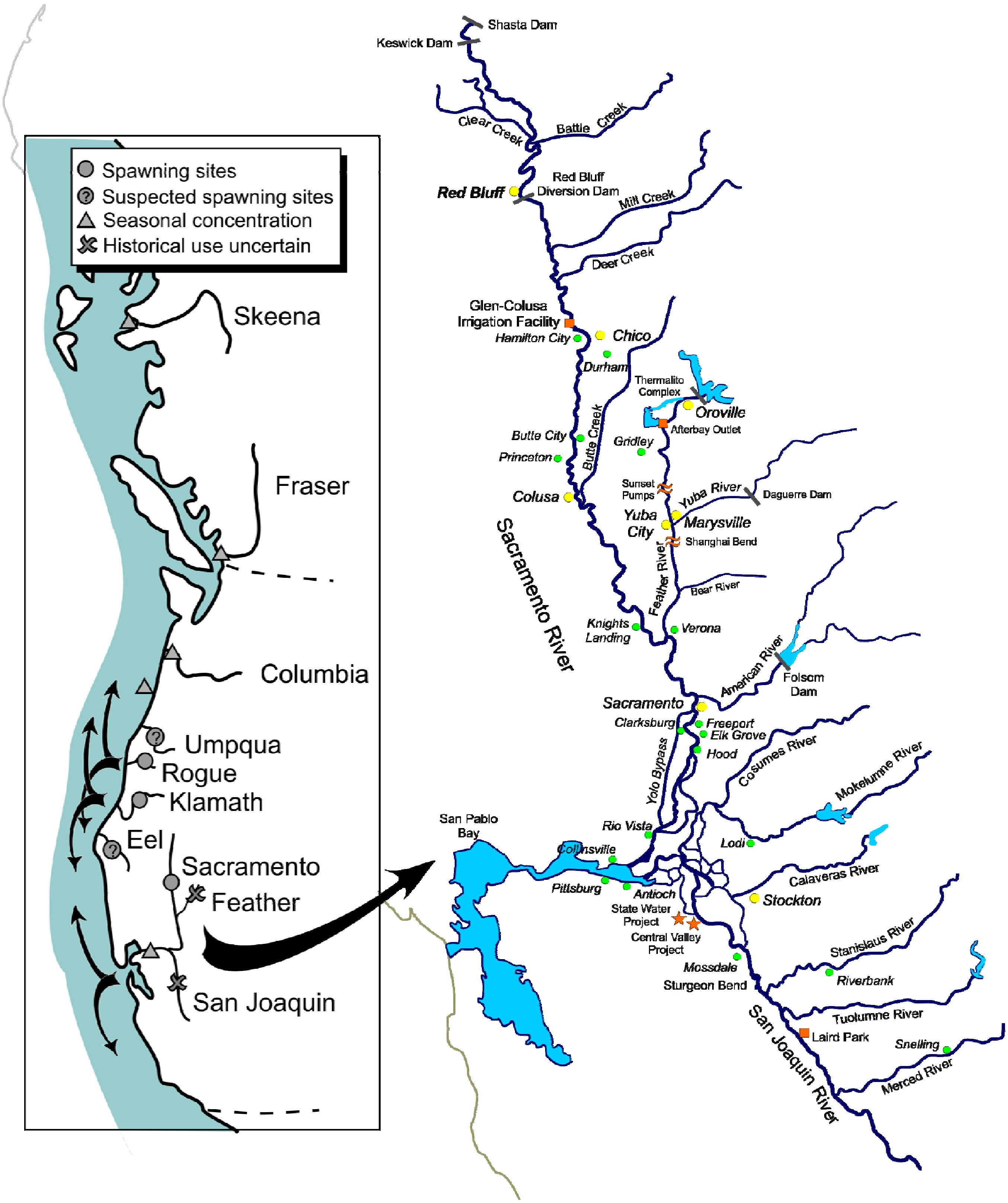

Figure 1. Map of Sacramento and San Joaquin Rivers of California's Central Valley.

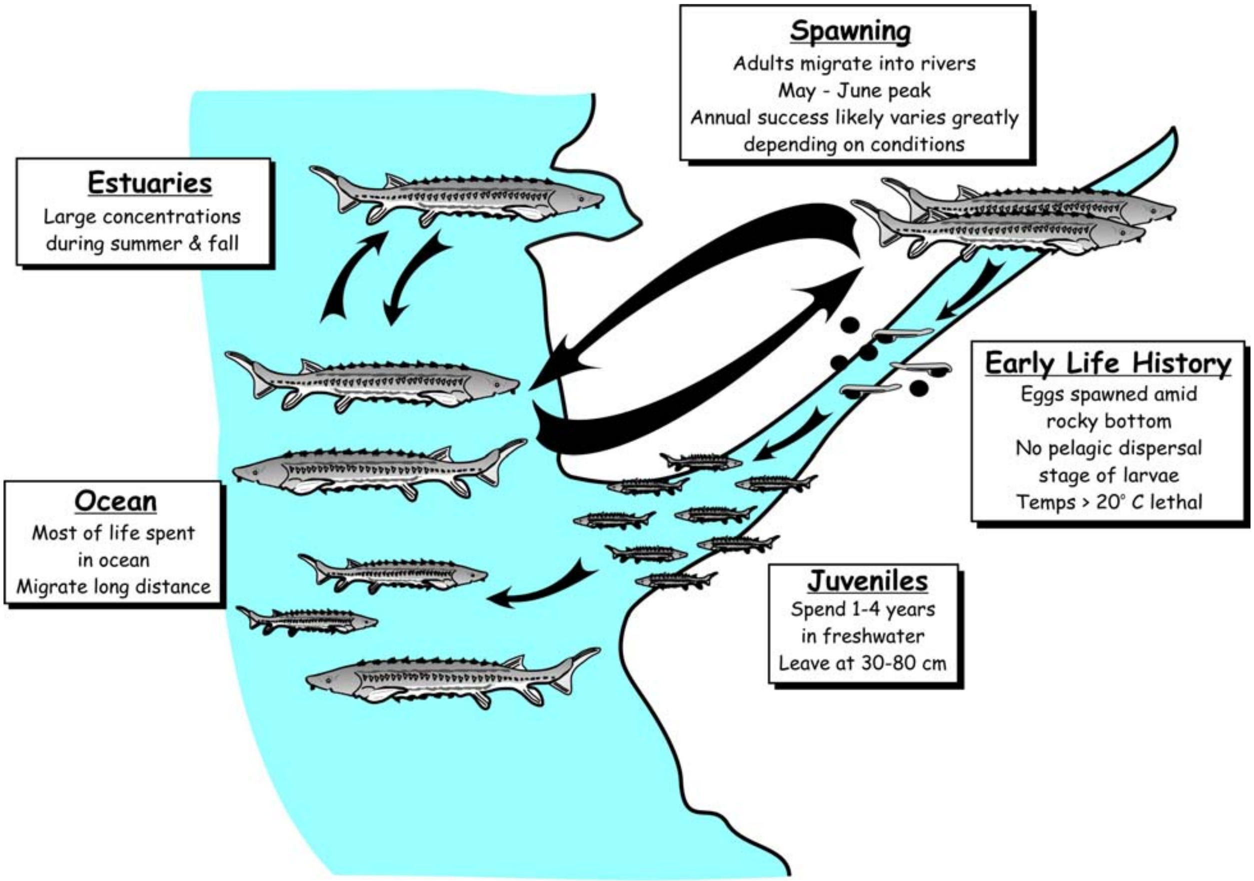

Figure 2. The green sturgeon life cycle.

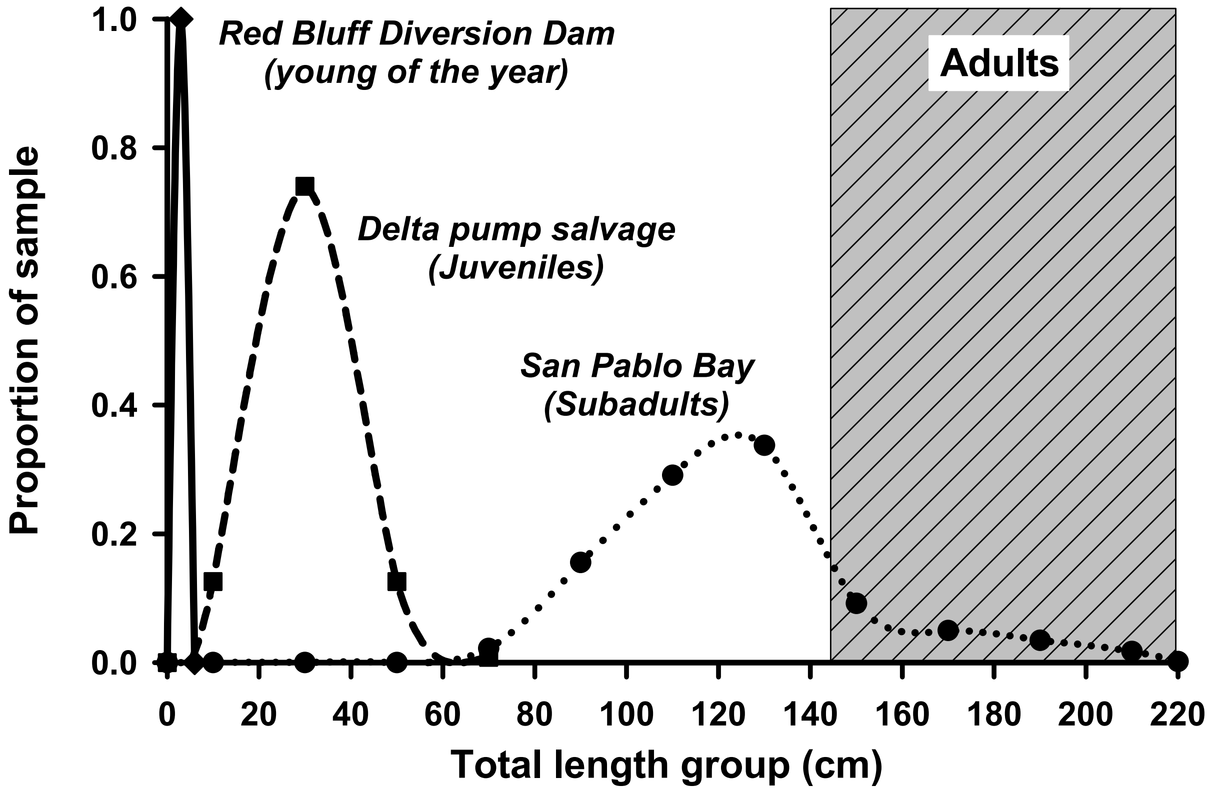

Figure 3. **Length distributions for segments of the Sacramento River green sturgeon population from Red Bluff Diversion Dam juvenile traps (Gaines and Martin 2002), delta pump salvage facilities (CDFG 2004), and semi-annual San Pablo Bay sturgeon stock assessments (Schaffter and Kohlhorst 1999, CDFG 2002).**

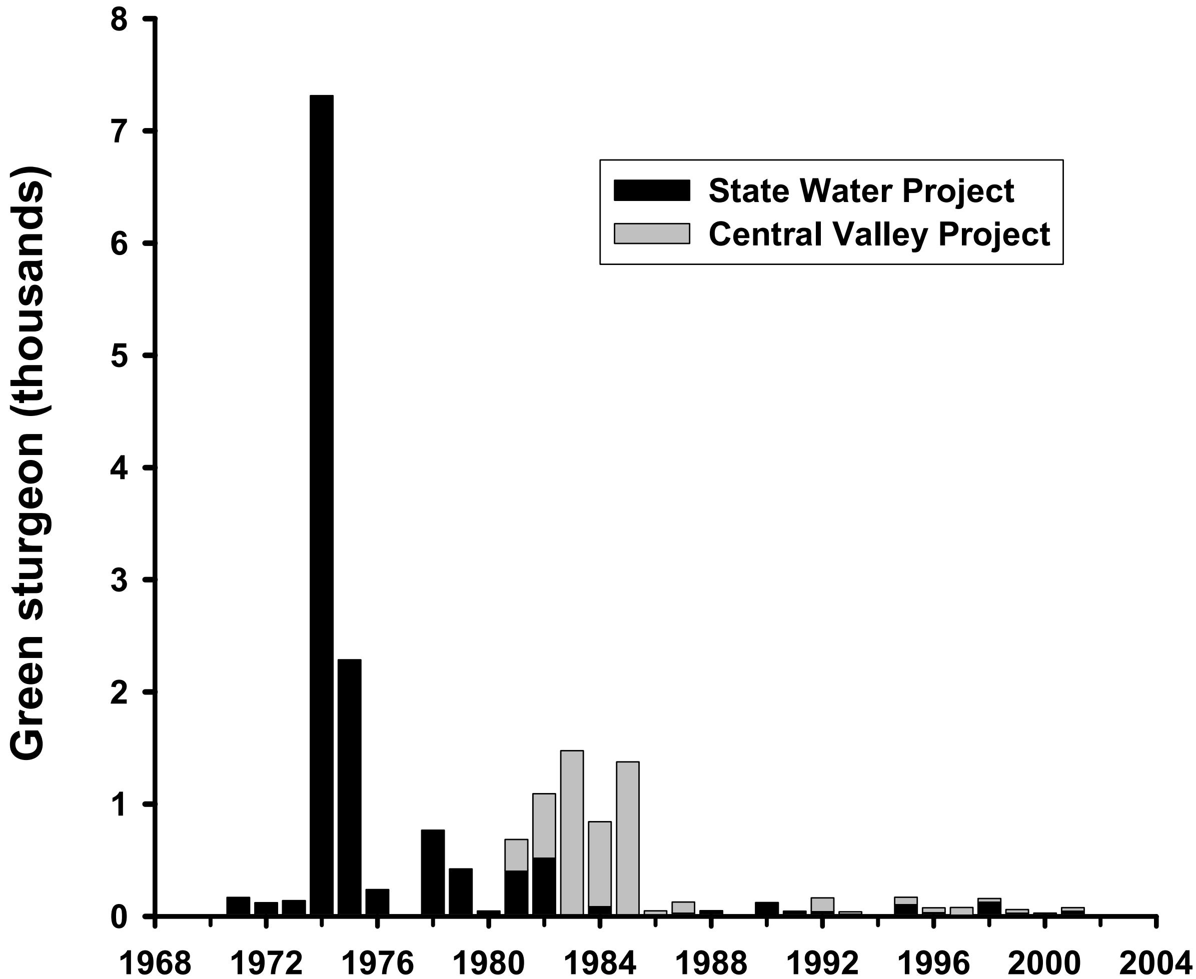

Figure 4. Estimated annual salvage of green sturgeon at State Water Project (SWP) and Central Valley Project fish facilities in the South Sacramento-San Joaquin River delta. Green sturgeon were not counted at the federal Central Valley Project prior to 1981. (Data from CDFG 2004).

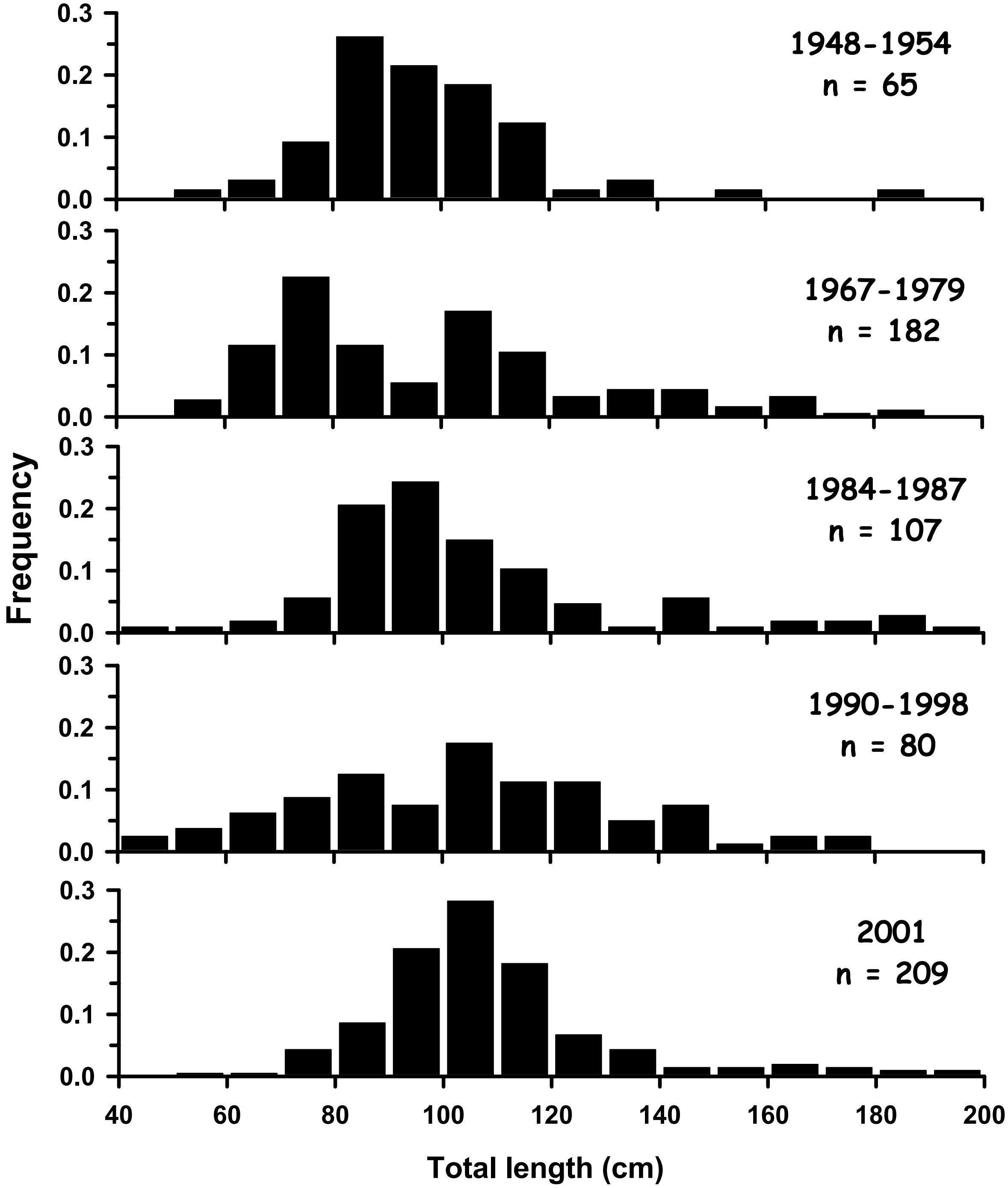

Figure 5. **Changes in length distribution over time based on trammel net sampling of subadult green sturgeon in San Pablo Bay (CDFG 2002).**

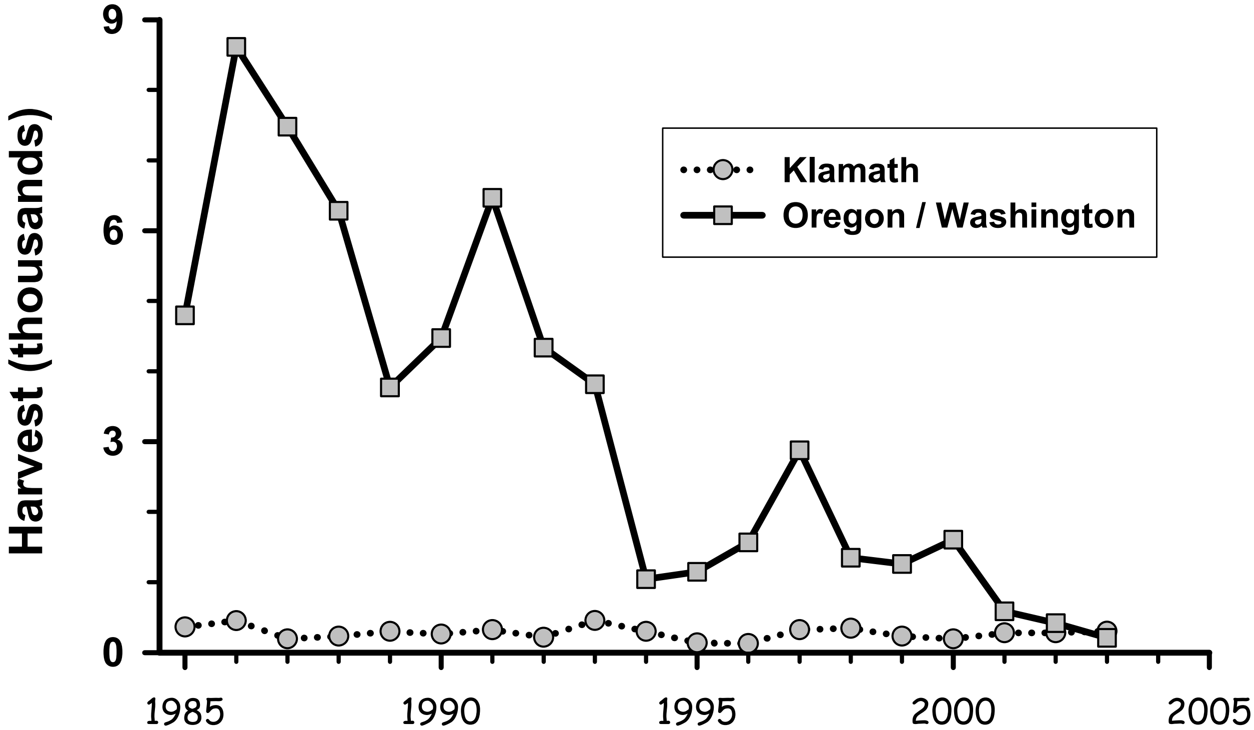

Figure 6. **Recent annual harvest of green sturgeon (NOAA 2005). Klamath includes Yurok and Hoopa subsistence fishery harvests. The Oregon / Washington total includes sport and commercial fishery harvests from ocean and estuary fisheries including the Columbia River, Willapa Bay, and Greys Harbor.**

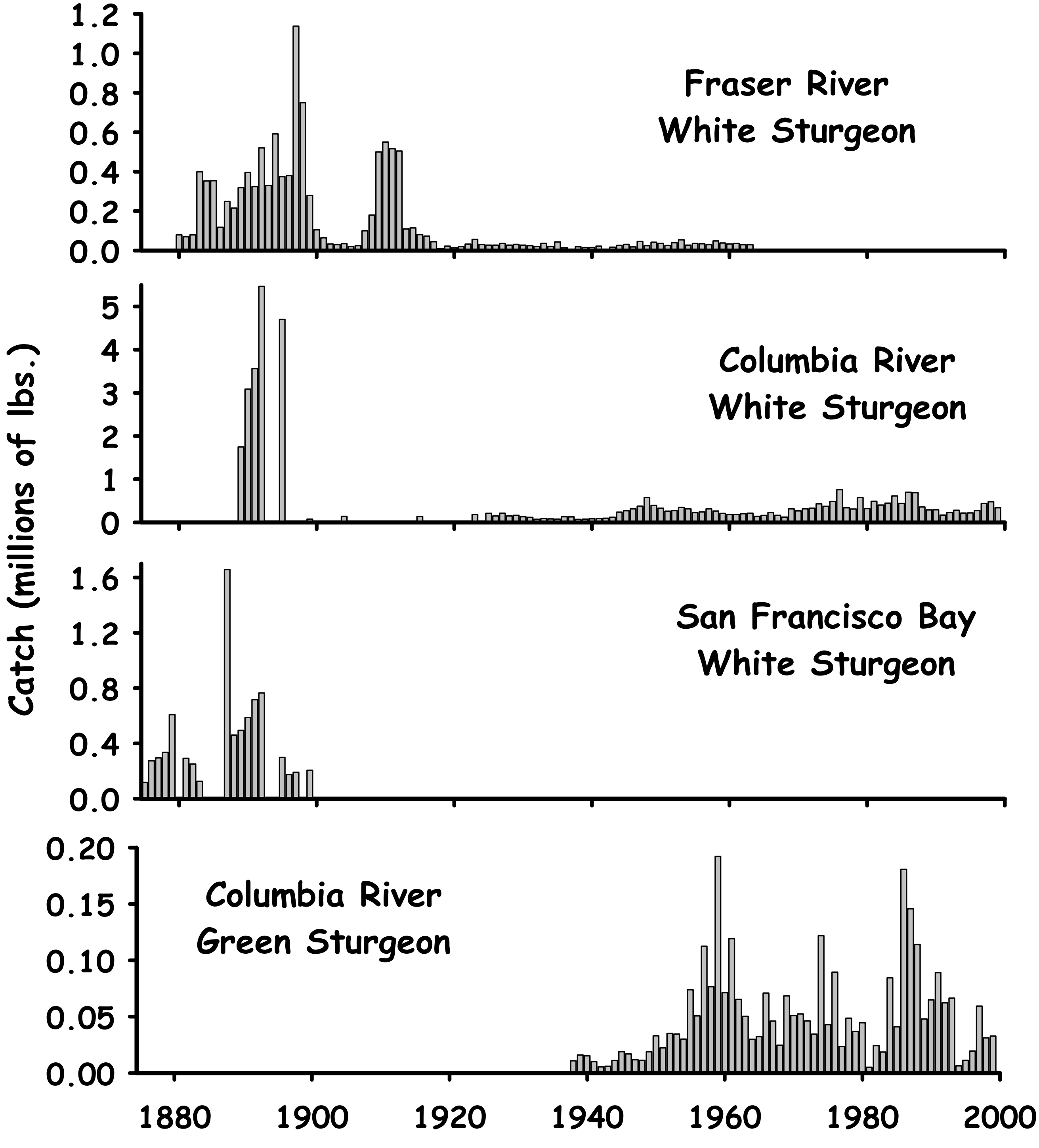

Figure 7. **Historical yield of white sturgeon in the Fraser River commercial fishery (years 1880-1963: Semakula and Larkin 1968), white sturgeon in the Columbia River commercial and sport fisheries (Years 1889-1999: ODFW and WDFG 2004; S. King, Oregon Department of Fish and Wildlife, unpublished data), white sturgeon in San Francisco Bay commercial fisheries (years 1875-1917: Skinner 1962) and green sturgeon in the Columbia River sport and commercial fisheries (Years 1938-1999: ODFW and WDFG 2004). Note differences in the scales of the y axes.**

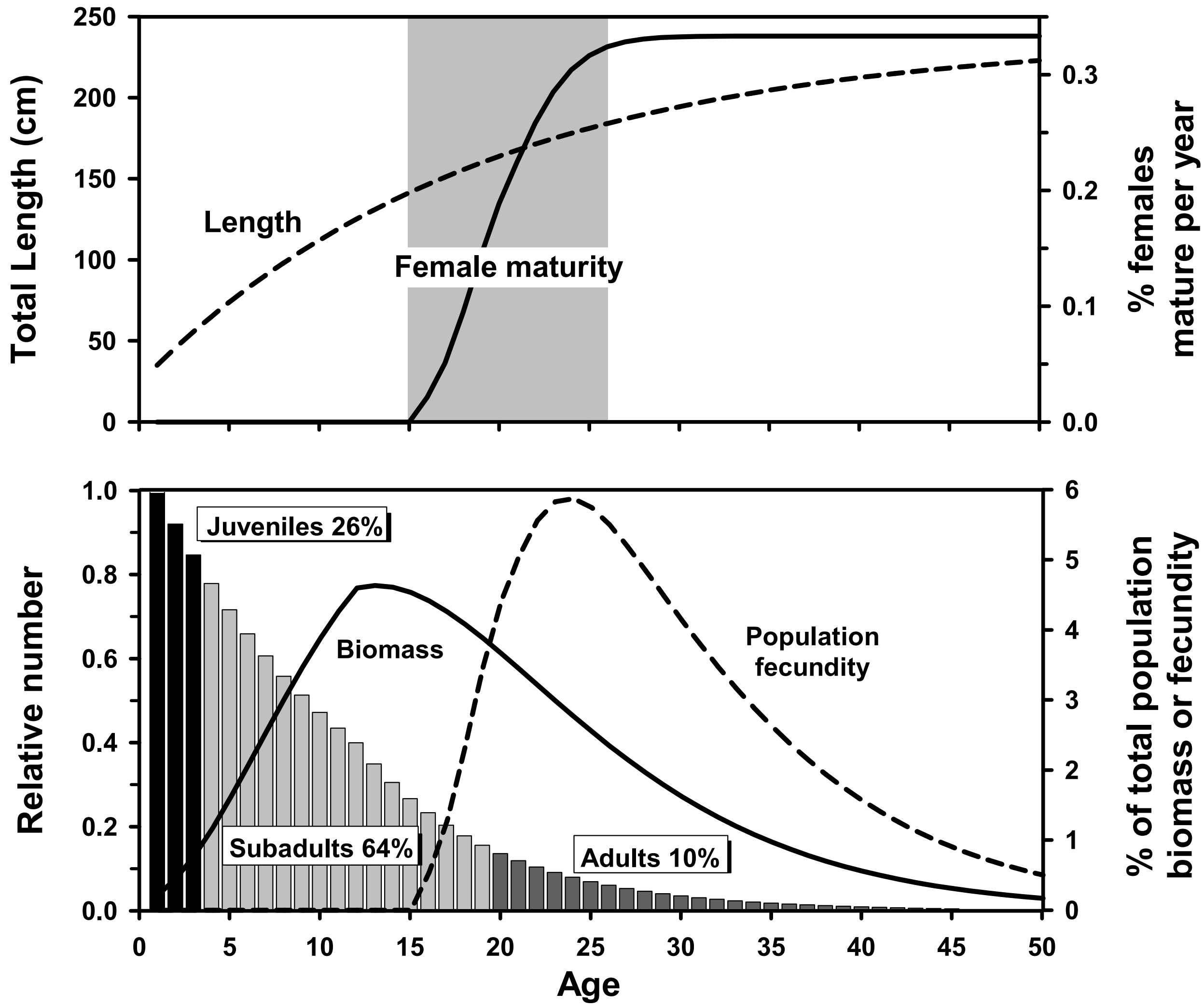

Figure 8. Green population structure based on representative values identified in Table 3. Length at age relationship is von Bertalanffy function reported for the Klamath River population. Female maturity at age relationship (Beamesderfer et al. 2005) is inferred from range in age of maturity of Klamath green sturgeon (Van Eenennaam et al. 2004) and spawning periodicity Rogue River green sturgeon (Erickson and Webb 2005). Number, biomass, and population fecundity at age are based on an equilibrium population model assuming constant recruitment, length and female maturity at age as depicted, an assumed annual natural mortality rate of 8%, and a hypothetical annual exploitation rate of 15% on adults.

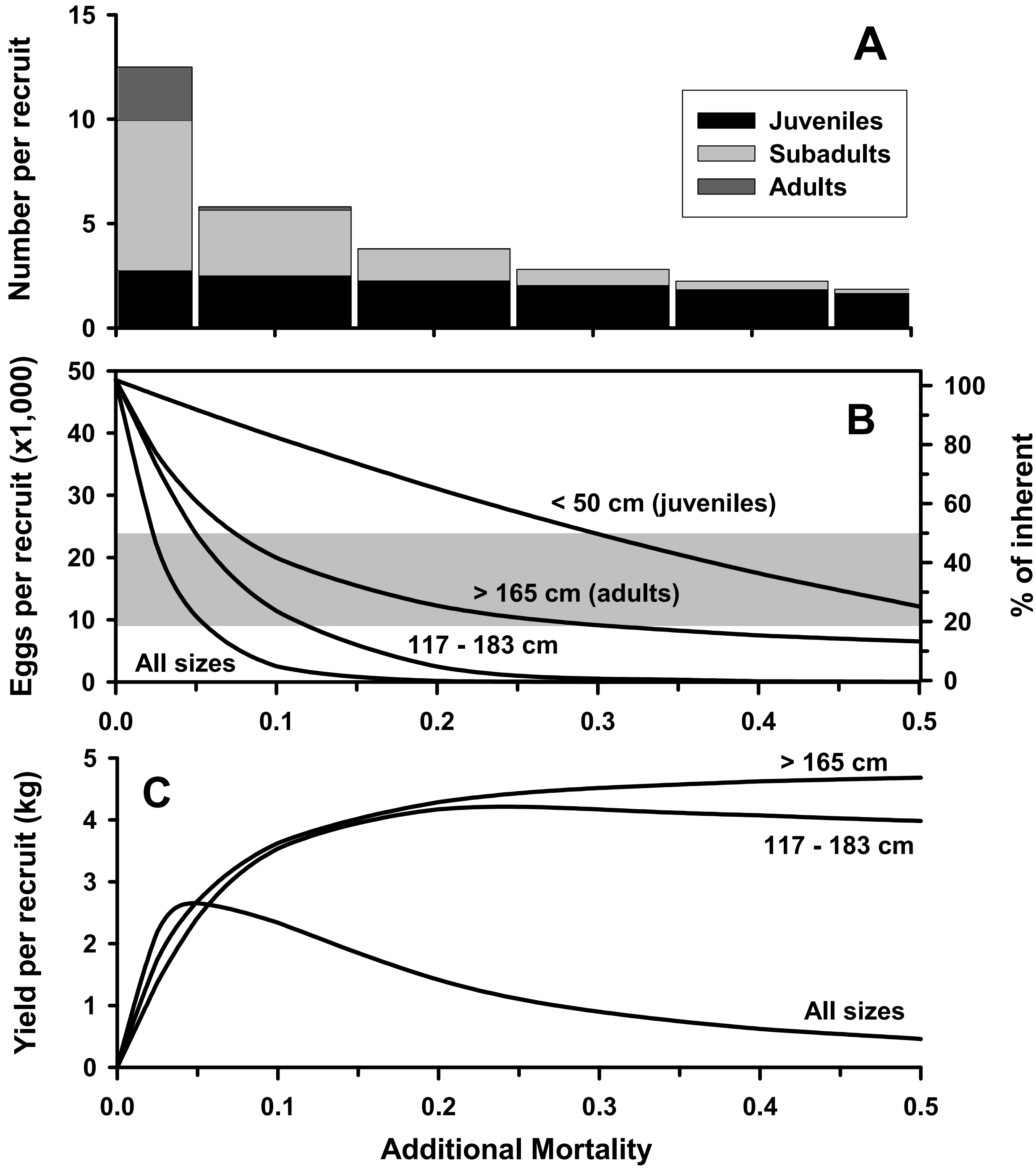

Figure 9. **Fish number, egg production, and yield per recruit as a function of additional mortality or exploitation based on a hypothetical equilibrium population model. Multiple lines on a graph depict the effects of varying size of vulnerability to additional mortality. Values of 20-50% egg production per recruit (shaded) are reference points often associated with sustainable fishing rates. Inherent values for eggs per recruit are relative to values in the absence of the additional mortality.**