Environ Biol Fish (2007) 79:315–337
DOI 10.1007/s10641-006-9145-x

Use of life history information in a population model for Sacramento green sturgeon

Raymond C. P. Beamesderfer · Michele L. Simpson · Gabriel J. Kopp

Received: 27 June 2006 / Accepted: 13 September 2006 / Published online: 1 November 2006

Abstract We review the available life history information on green sturgeon and develop a simple population model to inform interpretations of status and threats in the Sacramento River and throughout their range. A review of general life history information provides a context for interpretation of model results that are based on population parameters specific to the Sacrament River and inferences from other populations where Sacramento data were lacking. The simple life table model consisted of an age-specific schedule of demographic parameters including average length, weight, natural mortality, fishing mortality, sex ratio, and maturity that are used to project age-specific population size, biomass, fecundity, harvest, and yield for any given level of recruitment. While model assumptions of constant recruitment, population equilibrium, stable size and age structure, and a lack of density dependence are rarely met, the model provided useful descriptions of a hypothetical green sturgeon population based on current estimates of demographic parameters. The data available for Sacramento green sturgeon included young-of-year from juvenile salmon migrant traps in the river, pump salvage samples of juveniles from the Sacramento–San Joaquin delta, San Pablo Bay trammel net samples dominated by subadults, and Columbia River commercial fishery landings of subadults and adults. Life table results indicate that green sturgeon are vulnerable to salvage pumps for one or two years of age and that fishery slot limits of 117 cm to 183 cm included 14 years of vulnerability on average. Subadults that rear primarily in bay and ocean habitats would comprise the majority (63%) of an equilibrium population with adults only 12% of average numbers and only a fraction of adults spawning each year. 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. The sensitivity of sturgeon to increasing mortality is highlighted by abrupt declines in numbers, reproductive potential, and potential yield in hypothetical life table analyses. This review and modeling exercise identified significant research needs for green sturgeon and supports a precautionary approach in conservation and management in the face of uncertain assessments of status and risk.

Keywords Life table · Distribution · Abundance · Mortality · Fecundity · Recruitment · Harvest

---

R. C. P. Beamesderfer (✉)
Cramer Fish Sciences, 600 NW Fariss Road,
Gresham, OR 97030, USA
e-mail: beamesderfer@spcramer.com

M. L. Simpson · G. J. Kopp
Cramer Fish Sciences, 636 Hedburg Way,
Suite 22, Oakdale , CA 95361, USA

Introduction

Green sturgeon *Acipenser medirostris* 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. A far-flung ocean distribution and use of large, turbulent, and often remote rivers has limited effective sampling of this species. Until recently, several spawning populations were known only from anecdotal accounts (Moyle 2002; NOAA 2005).

A life history strategy involving a long lifespan, large size, delayed maturation, high fecundity, iteroparity, and anadromy has proven 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 and Beamesderfer 1990; Beamesderfer and 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 status and threats. This lack of information was particularly acute in 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 life history information on green sturgeon and develop a simple population model to inform interpretations of status and threats for green sturgeon in the Sacramento River and throughout their range. Although no comprehensive survey of biology and status is available for any green sturgeon population, significant information exists from limited and often unpublished studies, results of other fish sampling activities, anecdotal observations, and information from other green sturgeon populations. A review of published and unpublished literature on green sturgeon life history provides a background and context for analyzing and interpreting the limited and incomplete data on this species. A population model is useful for organizing quantitative life history information to make inferences regarding the implications of specific population parameters. General life history review and specific model results each inform interpretation and application of the other. Considered in total, the complementary life history and life cycle modeling results begin to paint of what we know about green sturgeon as well as what critical information is lacking.

Review of life history information

Distribution

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 2002; Beamesderfer and Webb 2002). Green sturgeon spawning has been documented in the Sacramento, Klamath and Rogue rivers and is suspected in the Umpqua and Eel rivers (NOAA 2005). Southern (Sacramento) and Northern (Klamath, Rogue, and Umpqua) groups of populations are genetically distinct (Israel et al. 2004). Fish 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 and 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 with the southern DPS apparently comprising the majority of the samples (Israel et al. 2004).

Local distribution and metapopulation structure of green sturgeon is unclear, particular in California's Central Valley (Fig. 1). The occurrence and wide distribution of green sturgeon in the Sacramento–San Joaquin delta has been well documented since the late 1800s (Table 1). Spawning in the upper Sacramento River mainstem was undetected until recently but is currently thought to occur from Hamilton City (Rkm 320) to above Red Bluff Diversion Dam (Rkm 391) and possibly as far upstream as Keswick Dam (Rkm 486) (CDFG 2002). 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 but only white sturgeon were historically reported from areas upstream of Shasta Dam, primarily in the Pit River (USFWS 1995).

Green sturgeon occasionally range into the Feather River but numbers are low and there is no data documenting current or historical spawning (Table 1). 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 in focused sampling efforts (Schaffter and Kohl-

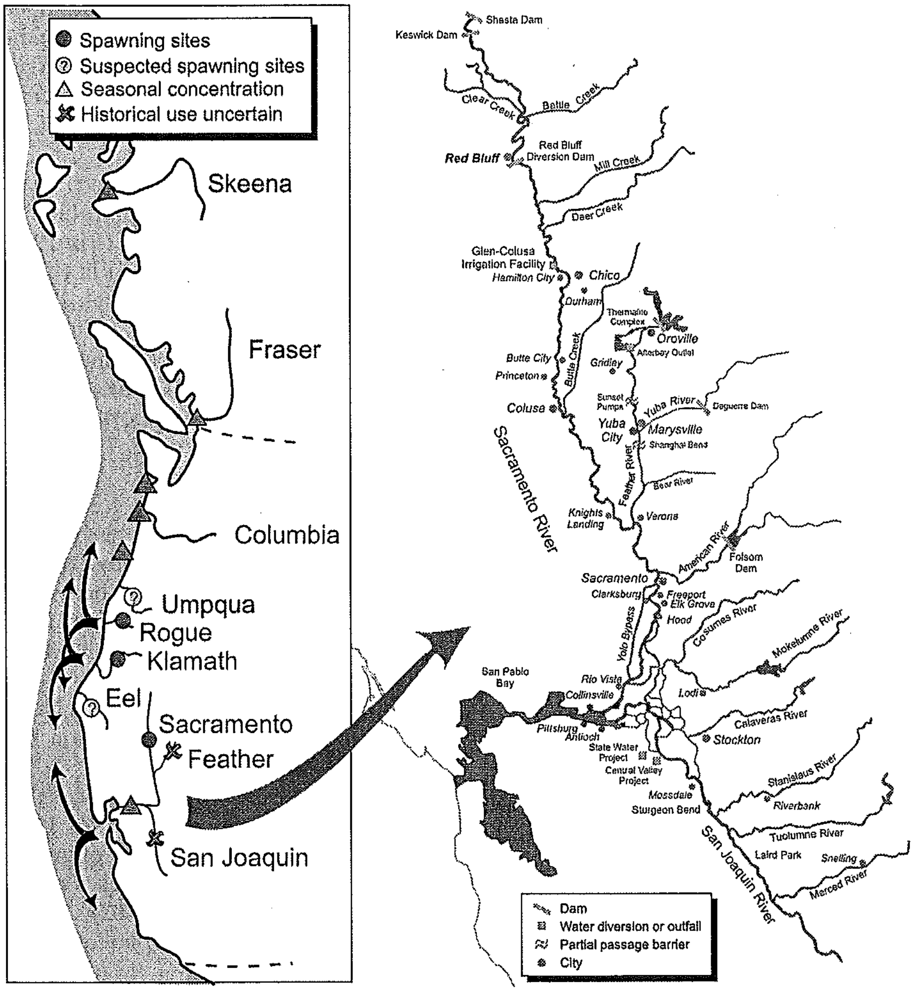

Fig. 1 Map of Sacramento and San Joaquin Rivers of California's Central Valley

Table 1 Historical references for 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 and Kohlhorst 1999).
1954–2001	5–110 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; Radtke 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 and Miller 1970).
1968	Juvenile green sturgeon identified in fish samples at south Delta water pumping facilities (Adams et al. 2002; CDFG 2004).
1967–present	Green sturgeon tagged in the delta are reported in California, Oregon, and Washington commercial fishery catches (Miller 1972; Langness 2005).
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 (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 (Rkm 339). Catches have ranged from 23 in 1994 to over 700 in 1993 (CDFG 2002).
1992–present	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).
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 to 2000 (Johnson and Martin 1997; Gaines and Martin 2002). All sturgeon grown to identifiable size were green sturgeon (Gaines and Martin 2002).
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).
Feather River	
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).

Table 1 continued

Year	Observation
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 and 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).
Yuba and Bear Rivers (Feather River tributaries)	
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).

horst 2002; Niggemyer and Duster 2003; Seesholtz 2003; Beamesderfer et al. 2004). Potential confusion of green and white sturgeon often confounds interpretation of historical records. White sturgeon have been documented in the Feather River system on numerous occasions (Anonymous 1918; Talbitzer 1959; Miller 1972; USFWS 1995; Schaffter and Kohlhorst 2002; Beamesderfer et al. 2004).

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 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) but no green or white sturgeon appear to have been trapped behind Friant Dam 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). White sturgeon are regularly observed in the San Joaquin River upstream from the Delta (Beamesderfer et al. 2004) and spawning is suspected to occur in wet years (Shaffter, CDFG retired, 2004 personal communication). Small fisheries for sturgeon occur in late winter and spring between Mossdale and the Merced River (Kohlhorst 1976; Kohlhorst et al. 1991; Scott 1993; Lewis 1995; Palomares 1995; Keo 1996; Jardine 1998).

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 and Webb 2005), and Sacramento rivers (Brown 2002; CH2M Hill 2002). Sacramento River spawning is estimated to occur from late April through June 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).

Spawning occurs in large, turbulent river mainstems (Moyle et al. 1995). Specific spawning habitat requirements appear to include: (1) large, deep pools where adults rest during upstream migration and post-spawn periods; (2) large gravel, cobble, or boulder substrates where unadhesive eggs broadcast by green sturgeon can settle into cracks (Moyle et al. 1995; Deng et al. 2002; Van Eenennaam et al. 2001; Brown 2002); and (3) optimal temperatures of 17–18°C and maximum temperatures less than the 20–22°C determined to be lethal in laboratory experiments (Cech et al. 2000; Van Eenennaam et al. 2006). 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). Turbulent areas of high velocity near lower velocity resting areas are a common denominator of spawning sites among other sturgeon species (Parsley et al. 2002).

Freshwater rearing

Green sturgeon larvae disperse downstream from Sacramento River spawning areas soon after emergence and rear for several years throughout the Sacramento–San Joaquin delta before migrating into the ocean (Fig. 2). 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 laboratory studies at 16°C (Deng et al. 2002). Larvae began to display a nocturnal swim-up behavior at 6 days post hatch, hiding during the day from the onset of exogenous feeding to metamorphosis (Cech et al. 2000; Deng et al. 2002). Downstream nocturnal migration is initiated around the onset of exogenous feeding (Kynard et al. 2005). Downstream dispersal of larval green sturgeon in the upper Sacramento River occurs from May through August at sizes of 20–60 mm based on trap samples at Red Bluff Diversion Dam (Gaines and Martin 2002) and the Glenn Colusa Irrigation District (CDFG 2002). Juveniles may spend one to four years in freshwater and estuarine environments before entering saltwater habitats based on observations in the Klamath River (Nakamoto and Kisanuki 1995). Laboratory tests indicate that juvenile sturgeon less than six months of age are sensitive to salinity (Allen and Cech 2005). Bioenergetic performance of age 0 and 1 green sturgeon is optimal between 15°C and 19°C (Mayfield and 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

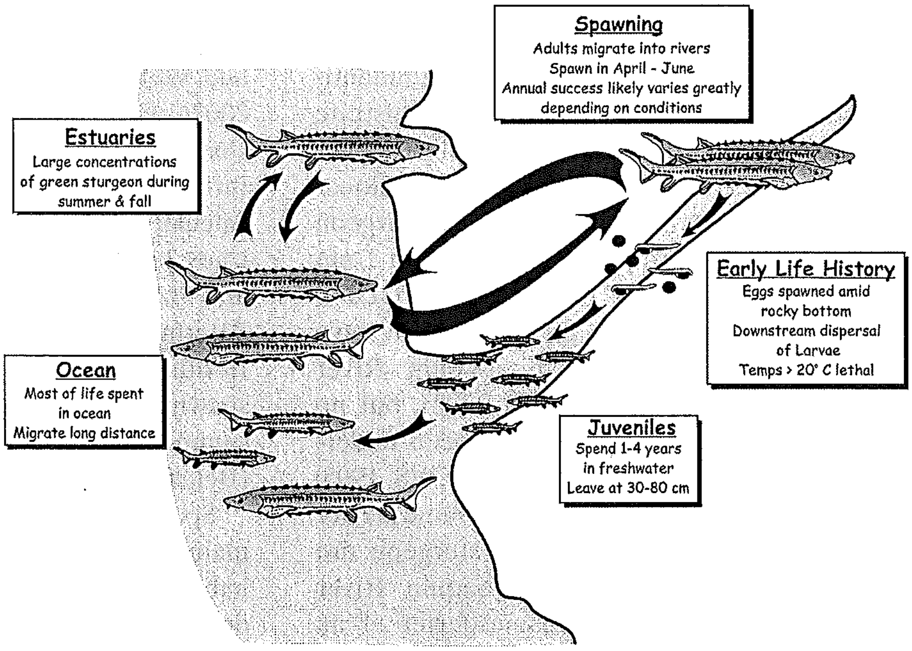

Fig. 2 The green sturgeon life cycle

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 m and 70 m (Erickson and Hightower 2006). Summer concentrations in coastal estuaries might represent feeding aggregations or thermal refugia. In the Sacramento–San Joaquin River system, significant numbers of green sturgeon are found in San Pablo Bay.

Abundance

Empirical estimates of abundance are not available for any green sturgeon population. Interpretations of available time series of abundance index data are confounded by small sample sizes, intermittent reporting, fishery-dependent data, lack of directed sampling, subsamples representing only a portion of the population, and potential confusion with white sturgeon (Heppell and Hofmann 2002; Adams et al. 2002). The most consistent sample data for Sacramento green sturgeon is for subadults captured in San Pablo Bay during periodic white sturgeon assessments since 1948. Low catches of green sturgeon preclude estimates or indices of green sturgeon abundance from this data (Schaffter and Kohlhorst 1999; Gingras 2005). Length distributions vary substantially among sample periods (Fig. 3). Peak numbers at size can reflect fish availability, multiple year and age cohorts, and trammel net selectivity. It is unclear if patterns indicate variable recruitment and abundance or are an artifact of small sample sizes, pooling of sample years, or variable distribution patterns between freshwater and ocean portions of the population.

Recruitment

Recruitment data are practically nonexistent for green sturgeon and it is unclear if observed patterns are an artifact of low sampling efficiencies.

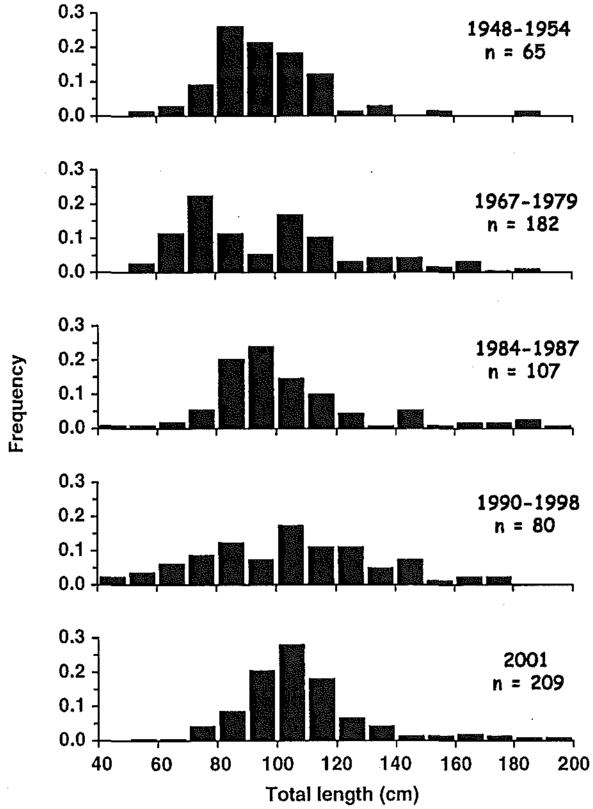

Fig. 3 Changes in length distribution over time based on trammel net sampling of subadult green sturgeon in San Pablo Bay (CDFG 2002)

Incidental catches of postlarval green sturgeon in Red Bluff Diversion Dam traps (Gaines and Martin 2002) and Glenn Colusa Irrigation District traps (CDFG 2002) suggest that Sacramento green sturgeon reproduce successfully in many years but that year class strength may be highly variable. The success of subsequent population recruitment is unclear. Decreases in salvage catch of juvenile green sturgeon at two large Sacramento–San Joaquin River delta water diversion facilities since 1986 (Fig. 4) have led to a concern that recruitment of Sacramento green sturgeon may have declined (NOAA 2005). In the Klamath system, juvenile green sturgeon are consistently observed (Adair et al. 1983; Rueth et al. 1992; Craig and Fletcher 1994; USFWS 2000) but Nakamoto and Kisanuki (1995) describe changes in size frequencies of juveniles among years that could be indicative of variable recruitment success.

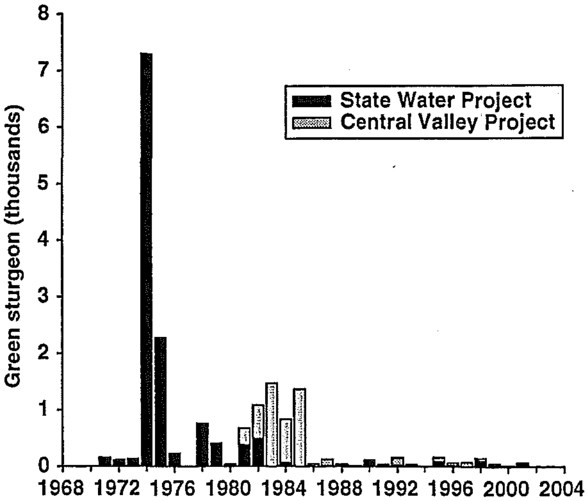

Fig. 4 Estimated annual salvage of green sturgeon at State Water Project (SWP) and Central Valley Project fish facilities in the South Sacramento–San Joaquin River delta. Green sturgeon were not counted at the federal Central Valley Project prior to 1981. (Data from CDFG 2004)

Mortality

The longevity of sturgeon is clearly associated with low natural mortality rates beyond the first few years of age but empirical estimates have not been reported. With the exception 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 in other areas (ODFW & WDFW 2004; Hillemeier 2005). Harvest rates has not been reported but harvest have been well documented over the last 20 years. A series of regulations enacted for sturgeon protection have reduced harvest of mixed populations in Oregon and Washington fisheries from a peak of over 8,000 per year in 1986 to less than 1,000 fish per year since 2001 (Fig. 5). Sport fishery harvest of green sturgeon in the Sacramento system has been regulated since 1990 by a slot limit which limits harvest to green sturgeon 46–72 inches in total length which is approximately 117–183 cm total length. Significant numbers of Sacramento green sturgeon are also likely taken in a Columbia River estuary commercial fishery where the harvest slot was 48–72 inches total length (122–183 cm total length) through 1992 and 48–66 inches total length (122–168 cm total length) since 1993.

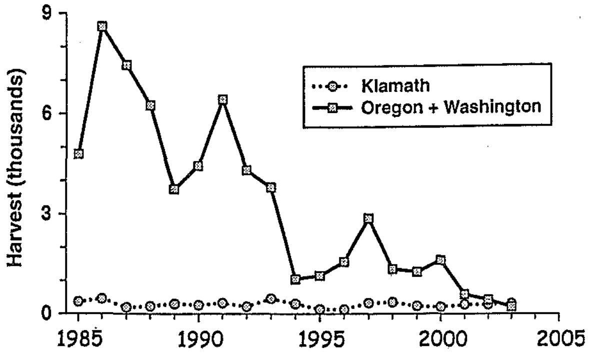

Fig. 5 Recent annual harvest of green sturgeon (NOAA 2005). Klamath includes Yurok and Hoopa subsistence fishery harvests. The Oregon and Washington total includes sport and commercial fishery harvests from ocean and estuary fisheries including the Columbia River, Willapa Bay, and Greys Harbor

Age and growth

The largest confirmed green sturgeon in the Sacramento River is 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 samples but ages as great as 53 have been reported in Columbia River estuary samples based on pectoral fin rays (Farr et al. 2002). Green sturgeon grow 30 cm in their first year and 7–10 cm per year from ages 1 through 10 based on age–length relationships reported from Klamath River and Columbia estuary samples (Table 2). Highly variable individual growth is indicated by scatter in age-length plots (USFWS 1983; Nakamoto and Kisanuki 1995; Farr et al. 2002).

Maturation and fecundity

Male green sturgeon typically mature at younger ages and smaller sizes than females (Table 2). Interpretations of size and age of adulthood for sturgeon are complicated by a wide range of sizes and ages over which first maturity occurs (Beamesderfer et al. 1995; Erickson and Webb 2005). Although a few female green sturgeon may mature at small sizes (e.g. 146 cm), most do not mature until 165 cm or greater (Nakamoto and

Table 2 Green sturgeon vital statistics reported in the scientific literature (TL = total length, FL = fork length)

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 and Kisanuki 1995)
	Females 242 cm TL (223 cm FL) Males 216 cm TL (199 cm FL)	Klamath River (Van Eenennaam et al. 2006)
	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. 2006)
	148 kg (females) 112 kg (males)	Klamath River (Nakamoto and Kisanuki 1995)
	175 kg	(Moyle 2002)
Maximum age	53	Misc. Oregon locations (Farr et al. 2002)
	45	Klamath River (Nakamoto and Kisanuki 1995)
	40 (females), 32 (males)	Klamath River (Van Eenennaam et al. 2006)
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 and Kisanuki 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. 2006) *N* = 62 (males), *N* = 82 (females)[a]
Age–Length	$FL = 176[1-e^{-0.081\ (AGE\ +\ 2.377)}]$	Misc. Oregon locations (Farr et al. 2002) *N* = 258 (Ages 0–53)
	$TL = 238[1-e^{-0.053\ (AGE\ +\ 1.9943)}]$	Klamath River (USFWS 1983; Nakamoto and Kisanuki 1995) (Ages 0–40)[a]
Size at maturity	120–165 cm TL (males) 145–185 cm TL (females)[a]	Klamath River (Nakamoto & Kisanuki 1995)
	152–185 cm TL (males) 165–202 cm TL (females)[a]	Klamath River (Van Eenennaam et al. 2006)
	146–180 cm 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. 2006)
	8+ (males), 13+ (females)	Klamath River (Nakamoto and Kisanuki 1995)
Spawning periodicity	2–4 years	Erickson and Webb (2005)[a]
Fecundity	59,000–242,000	Klamath River (Van Eenennaam et al. 2006)
Length–Fecundity	$Eggs = 4.875E\text{–}5FL^{4.188}$	Klamath River (Van Eenennaam et al. 2006)[a] *N* = 60
Length–oocyte diameter	$mm = 4.875E\text{–}5\ FL + 3.354$	Klamath River (Van Eenennaam et al. 2006)
Annual mortality	0.19 (males), 0.24 (females)	Klamath River (Van Eenennaam et al. 2006)[a,b]
	0.14 (combined sexes)	Columbia River Estuary (Rien et al. 2001)[b]
Total–Fork length	$TL = 1.09\ FL$	Columbia River estuary (Rien et al. 2001) *N*=1,244 (Fork length 100–180 cm)
	$TL = 1.1374\ FL\text{–}4.6131$	Klamath River (Nakamoto and Kisanuki 1995) *N* = 91 (length in cm)
	$TL = 1.083\ FL + 1.1582$	Klamath River (Van Eenennaam et al. 2006)

[a] Values used in life table model

[b] Catch curve estimates from this article were based on reference data

Kisanuki 1995; Van Eenennnaam et al. 2006). Not all females that have reached first maturity will spawn every year (Erickson and Webb 2005). Fecundity and egg size increase with body size (Table 2). Eggs and larvae of green sturgeon are substantially larger and fecundity is less than in other sturgeon species (Van Eenennaam et al. 2001).

Life table model

Materials and methods

Despite our many unknowns about green sturgeon in California, life history parameters from this and other populations can be used to develop a basic model to provide insight on how population characteristics may contribute to vulnerability of green sturgeon populations in the Central Valley. We developed a simple life table model of the Sacramento River green sturgeon population based on a review of life history and demographic characteristics. Information missing for the Sacramento population was inferred from species data for other systems.

Model description

The life table model is simply an age-specific schedule of demographic parameters including average length, weight, natural mortality, fishing mortality, sex ratio, and maturity that are used to project age-specific population size, biomass, fecundity, harvest, and yield for any given level of recruitment. Key model assumptions include constant recruitment, population equilibrium, stable size and age structure, and a lack of density dependence. While these assumptions are rarely met under normal circumstances in a dynamic natural system, the life table model provides a useful representation of: (1) average relationships among individual parameters by size and age; (2) average age and size distribution values for a population over time or a brood cohort over it's life span; and (3) relative sensitivity and response of selected population characteristics to changes in demographic parameters.

The life table model is not intended to realistically represent the dynamic historical population patterns of Sacramento green sturgeon, current status in terms of numbers or population structure, or to predict future trends. Rather, it is a descriptive snapshot of a hypothetical population based on a summary and synthesis of the available data. The life stage model is obviously an oversimplification of much more dynamic population behavior, but one that organizes, captures, and illustrates key aspects of the sturgeon life history strategy and provides a useful construct for evaluating and interpreting the data on hand. The simple modeling approach is mandated by the limited available information.

The life cycle model formulation calculates relative numbers by age (N_x) based on an assumed number of age one recruits and annual survival rates (S_x).

$$N_x = (N_{x-1})(S_x) \tag{1}$$

For the purposes of the life table model, the number of age one recruits (N_1) is assumed to be a constant, independent of spawner number. Annual survival (S_x) is estimated from conditional annual natural (n_x) and fishing (m_x) mortality rates (Ricker 1975):

$$S_x = 1 - [n_x + m_x - n_x\, m_x] \tag{2}$$

Age-specific individual characteristics are estimated from functional relationships based on empirical data. Thus, average length at age (L_x) was calculated from a von Bertalanffy age–length function (Ricker 1975; Moreau 1987):

$$L_x = L_\infty\{1 - \exp[-k(x - t_0)]\} \tag{3}$$

where L_∞ = asymptotic maximum length (length at infinity); k = growth coefficient describing growth rate toward the maximum; and t_0 = hypothetical age at which fish would have been zero length.

Average individual weight at age (W_x) was calculated as an exponential function of length (Ricker 1975):

$$W_x = (a_\mathrm{W})(L_x)^{b_\mathrm{w}} \tag{4}$$

where a_w = length–weight equation coefficient, and b_w = length–weight equation exponent.

Average individual female fecundity (egg number) at age (F_x) was calculated as an exponential function of length:

$$F_x = (a_\mathrm{f})(L_x)^{b_\mathrm{f}} \tag{5}$$

where a_f = length–fecundity equation coefficient, and b_f = length–fecundity equation exponent.

The proportion of the population of females of each age class that spawn in any year (ps_x) was calculated as a sigmoid function of length as (Welch and Foucher 1988):

$$\mathrm{ps}_x = 1 - [1/(1 + \theta/C_\infty)] \quad \text{for } L_x \leq \mu \tag{6a}$$

$$\mathrm{ps}_x = 1 - \{1/[1 + (1 - \theta)/C_\infty]\} \text{ for } L_x > \mu \tag{6b}$$

where μ = mean length of female sexual maturity; C_∞ = female spawning periodicity at maturity; and θ = cumulative normal distribution function dependent variable,

$$\theta = 1/(2\pi)^{0.5} \exp\left[-(L_x - \mu)^2/\sigma^2\right] \sum_{i=1}^{5} bi\{1 + p \mid (L_x - \mu)/\sigma \mid \}^{1-i} \tag{7}$$

where σ^2 = Variance about mean length of female sexual maturity, $b1,\ldots,b5$ = Constants (0.31938153, –0.356563782, 1.781477937, –1.821255978, 1.330274429), and p = Constant (0.2316419).

The female length–maturity function reflects a wide range of female sturgeon size (and age) of first maturity as well as the effect of spawning periodicity of females upon reaching age of first maturity (Beamesderfer et al. 1995). The function parameter for female spawning periodicity at maturity (C_∞) reflects the multi-year maturation cycle that is typical among sturgeon. Even after all females have reached maturity, only a portion of the adult population spawns in each year because the egg development process (vitellogenesis) typically requires more than one year (Erickson and Webb 2005).

Age-specific population values for biomass, fecundity, harvest, and yield are calculated as the product of abundance and individual characteristics. Biomass at age (B_x) is the product of abundance and average weight:

$$B_x = N_x W_x \tag{8}$$

Population fecundity at age (reproductive potential or P_x) is the product of abundance, female proportion (pf), maturation, and individual fecundity:

$$P_x = N_x \,\mathrm{pf}\, \mathrm{ps}_x F_x \tag{9}$$

Harvest by age (H_x) in number of fish is the product of abundance and fishing mortality rate:

$$H_x = N_x m_x \tag{10}$$

Yield by age (Y_x) is the product of harvest and average weight:

$$Y_x = H_x W_x \tag{11}$$

Cumulative population values for biomass ($B.$), fecundity ($F.$), harvest ($H.$), and yield ($Y.$) were calculated as the sum across all ages:

$$B. = \Sigma B_x \tag{12}$$

$$F. = \Sigma F_x \tag{13}$$

$$H. = \Sigma H_x \tag{14}$$

$$Y. = \Sigma Y_x \tag{15}$$

Finally, cumulative population values were analyzed on a per recruit basis (Ricker 1975; Gulland 1983; Prager et al. 1987; Goodyear 1993; Boreman 1997; Haddon 2001) because we lack information on the direct relationship between spawning stock and number of age one recruits. Thus egg production per recruit (EPR) was calculated:

$$\mathrm{EPR} = P./N_1 \tag{16}$$

Yield per recruit (YPR) was calculated:

$$\mathrm{YPR} = Y./N_1 \tag{17}$$

This model formulation is similar to white sturgeon models developed and evaluated by Beamesderfer et al. (1995) and Paragamian et al. (2005). The approach is conceptually similar to the Leslie Matrix model commonly applied in non-fishery population dynamics problems (Caswell 2001; Heppell and Hoffman 2002). Many of the population parameters developed in this paper for use in the life table model could also be adapted for use in a matrix modeling framework.

Model parameters

Life table inputs were based on data reported for the Sacramento and other populations (Table 2) and are summarized in Table 3. In the absence of specific recruitment or recruitment variability estimates for the Sacramento River population, the model arbitrarily assumed a constant annual age one recruitment value of 10,000 sturgeon per year in order to calculate population values for each age on a per recruit basis. The available data (Figs. 3, 4) suggests that recruitment is not constant but model analyses on a per recruit basis provide model results applicable to a variety of recruitment levels.

Total annual survival and mortality rates were estimated based on a catch curve analysis of age-frequency data of mature fish in Klamath River fisheries and subadults in Columbia River estuary fisheries. Age frequencies of the Klamath River harvest were reported by Van Eenennaam et al. (2006). Age frequencies of the Columbia estuary harvest were derived from length frequencies reported by Rien et al. (2001) and an age–length key reported by Farr et al. (2002). Catch curves are widely used in fisheries biology to estimate average annual recruitment rates (Ricker 1975; Hilborn and Walters 1992). Instantaneous annual mortality rates (Z) are estimated from the declining (right) limb of a plot of Ln(catch) by age. The declining limb is assumed to represent ages that are fully recruited to the sample gear and catch is assumed to be proportional to abundance. Annual survival (S) is calculated as (e^{-Z}) and total annual mortality (A) as (1–S). Catch curve analyses involve a series of assumptions including random sampling, uniform survival rates across ages, consistent recruitment across ages (or randomly distributed about an average recruitment), and no trend in mortality over time (Ricker 1975; Hilborn and Walters 1992). While several assumptions are likely violated to some degree for a long-lived species like green sturgeon, we were forced to rely on this simplistic method to develop approximate order-of-magnitude estimates. Mortality rates and inferences should be treated with due caution. While corresponding estimates might be biased, they provide a useful reference point particularly where the nature and direction of the bias is known.

It is unclear how much of the total mortality estimated using catch curves is comprised of fishing mortality or natural mortality (which also includes non-harvest human impacts). Catch curve estimates of total annual mortality rates of 14% for Columbia River subadults and 19%–24% for Klamath River adults provide obvious upper bounds. Based on harvest numbers, we suspect that fishing mortality historically comprised a significant fraction of total mortality. For representative modeling purposes of the Sacramento population, we assumed a conditional annual natural mortality rate (n_x) of 7% and a conditional annual fishing mortality rate (m_x) of 7%, which when combined equal the estimate for

Table 3 Values of input variables and parameters used in life table model

Term	Definition	Value
N_1	Annual recruitment	10,000
n_x	Natural mortality rate	0.08
m_x	Exploitation (harvest mortality rate)	0.08[a]
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
a_w	Length–weight equation coefficient	4.0E–06
b_w	Length–weight equation exponent	3.11
pf	Proportion of the population that is female	0.5
C_∞	Female spawning periodicity at maturity	3 years
μ	Mean length of female sexual maturity	165 cm
σ^2	Variance about mean length of female sexual maturity	10 cm
a_f	Length–fecundity equation coefficient	5.3E–05
b_f	Length–fecundity equation exponent	4.19

[a] Applied to sizes within a fishery slot limit of 117–183 cm

Columbia River subadults ($A = n_x + m_x - n_x m_x$). We assumed that Sacramento fish are subject to and represented by the Columbia estuary fishery. We also assumed that terminal harvest rates on Sacramento River green sturgeon were likely to be less than in the Klamath River because there is no terminal fishery on spawners in the Sacramento River. This assumption is supported by exploitation rates of 1%–4% per year estimated for white sturgeon in the Sacramento system (Schaffter and Kohlhorst 1999) because green sturgeon are less preferred by anglers. Thus, fishing rates were applied in the representative life table analysis to age classes within the range of the regulatory slot limit in the Sacramento system (117–183 cm total length) as well as the historical Oregon and Washington slot limit (122–183 cm total length).

Model parameters for the von Bertalanffy length–age function (Eq. 3) and female exponential length–weight (Eq. 4) functions were based on Klamath River samples that encompassed the greatest reported range of fish sizes (Table 2). Data on the length–fecundity relationship (Eq. 5) was available only from Klamath samples (Van Eenennaam et al. 2006). Estimates of the size-specific proportion of the female population that is mature were based on a calibration of the cumulative normal probability function (Eqs. 6 and 7) to the reported size range of female maturation (145–202 cm: Table 2). The proportion of the population that is female (pf) was assumed to be 50% in the absence of specific data. Relationships were translated between fork and total lengths as necessary based on the relationship (TL = 1.09 FL) derived by Rien et al. (2001).

For model description purposes, size and age classes of green sturgeon were categorized as juveniles, subadults, or adults based on general life history patterns described earlier in this paper. Juveniles included fish during freshwater rearing prior to migration to the ocean (generally one to three years of age and 0–60 cm in length). Adults included fish larger than the median size and age of female maturation (approximately 165 cm and 20 years of age). For reporting convenience, the model represented adulthood as knife-edge recruitment, when in reality, first sexual maturation occurs over a wide range of sizes and ages. An adult definition based on median female maturation was selected to represent the size and age where a majority of fish were sexually mature. Fish over 165 cm are primarily adults (but may include some late maturing individuals). Immature fish comprise the majority of the population at smaller sizes and younger sizes. Fish under 165 cm are primarily subadults (but may include some early maturing individuals). Subadults include all fish that were not juveniles or adults. Subadults include the majority of the wide-ranging ocean distribution.

Model analyses

The most direct application of the life table model is for cross reference of individual characteristics or population parameters. Common questions such as how old is a sturgeon of a given length, how much does a given fish weigh, when are sturgeon recruited to fishery slot limits, do size limits protect mature fish, and how many age groups are vulnerable to a specific threat are easily answered from a simple lookup table or a graphical representation of the nominal relationships included in the model. Each of these questions can have direct application in sturgeon conservation and management. The life table also simplifies interpretation of life history stage from sample data. For instance, green sturgeon of various sizes are collected in widely dispersed areas of the Sacramento–San Joaquin system, and the life table can be used to clarify what portion of the life cycle is being sampled in each area. This application is illustrated with data from screw traps in the Sacramento River, delta pump facility salvage samples, San Pablo Bay trammel net samples, and Columbia River commercial fishery landings.

Model results are also useful for characterizing average population size, age, biomass, and reproductive structure over time. While actual population structure varies with fluctuations and trends in recruitment, survival, and growth, the hypothetical population structure from the model provides a representative baseline for comparison and interpretation of sample data. Model results based on assumed demographic rates can be used to determine average relative numbers of juvenile, subadult, and adult life stages in an equilibrium population, the distribution of sturgeon biomass by age and size, and size and age ranges that account for the majority of the reproduction. Comparisons of sample data and hypothetical distributions can inform considerations of representative sampling or departures from the equilibrium population assumptions. Equilibrium distributions might be used to extend inferences from a sampled segment of the population to other population components that are not vulnerable to sampling. While obviously less desirable than direct empirical estimates of each population segment, inferences from partial samples are the rule rather than the exception for green sturgeon.

One of the most powerful applications of the life table model is for evaluating population sensitivity to changes in demographic rates. This paper includes sensitivity analysis of the effects of mortality operating over different size ranges (all sizes, juveniles, adults, and sizes vulnerable to the fishery slot limit) 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. Results were expressed on a per recruit basis and are most informative when considered relative to the population size in the absence of additional mortality. Model results expressed relative to an assumed baseline (e.g. no additional mortality) are a robust application of this model because both test and control conditions are similarly affected by population assumptions.

Effects of added mortality on the demographic potential of a sturgeon population to reproduce were based on EPR. EPR is calculated as the hypothetical lifetime fecundity of one age one 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 were identified by Boreman (1997) as useful biological reference points for considering the effects of fishing on reproductive potential. Goodyear (1993) recommended maintenance of spawning stock biomass per recruit of at least 20% of maximum, unless evidence exists for strong density dependence in the population. Boreman et al. (1984) used a 50% spawning stock biomass per recruit as a target for rebuilding of shortnose sturgeon (*Acipenser brevirostrum*). Boreman (1997) noted that target levels based on EPR should be similar to those based on spawning stock biomass because fecundity and female body weight are linearly related. We note that the validity of these reference points to assessments of sturgeon sustainability is unproven and these reference points are most useful for evaluating the relative effects of different fishery strategies on reproductive potential.

Appropriate fishing rates depend on the sizes of fish vulnerable to the fishery in concert with the effects of other human mortality factors. These inferences assume that spawning and rearing habitat is adequate for effective reproduction. Assumptions of no density dependence in the reproductive response to increasing mortality will provide precautionary estimates of effects because the actual reduction in EPR due to harvest may be less than the model estimate where compensatory changes in growth or survival are significant.

YPR provided an index of productivity related to potential fishery value and the effects of fishing on different size ranges (Ricker 1975; Gulland 1983; Haddon 2001). Yield refers to the weight of fish harvested at any given fishing rate. Estimates of YPR 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 YPR assume no relationship between spawning stock biomass or status and recruitment. As a result, fisheries based solely on simple maximum sustained yield models have often led to overexploitation and more precautionary management strategies are appropriate in the face of uncertain population productivity.

Considerations of EPR and YPR split the essential components of sturgeon population dynamics into two elements. While EPR and YPR are estimated using an equilibrium modeling approach and constant recruitment, treatment of results on a per recruit basis allows exploration of population sensitivities when recruitment is related to spawning stock size. EPR indirectly considers potential stock–recruitment relationships under the assumption that as long as mortality rates are limited to protect high levels of population fecundity, then prospects for significant recruitment are high so long as habitat is favorable and other human mortality factors are not excessive. Thus, knowing the fraction of unfished EPR that will lead to decreases in recruitment can provide a useful reference point for inferences about the level of mortality that could lead to "recruitment overfishing". Recruitment overfishing would occur where excessive exploitation did not allow for adequate reproductive potential for population replacement or growth. For sturgeon fisheries managed with a slot limit that includes subadults and adults, recruitment overfishing might occur if the slot limit were too wide or the exploitation rates within the slot limit were too great to allow for adequate survival to maturity. Other mortality sources might also contribute to recruitment failure in green sturgeon populations by precluding significant survival to maturity and adequate spawning potential to utilize available habitats. In contrast, YPR addresses a lifetime harvest schedule that potentially maximizes yield and avoids growth overfishing. In long-lived fish like sturgeon, EPR clearly outweighs YPR as a basis for fishery management but YPR can provide guidance for optimizing fishery value of any given sturgeon cohort within the limits identified by EPR reference points.

Results

Mortality rates

Total annual mortality rates estimated from catch curves of age frequencies in fishery harvest were 19% for Klamath River males, 24% for Klamath River females, and 14% for a Columbia River sample including males and females (Fig. 6). The linear descending limbs of catch curves for all samples produced confidence intervals on annual mortality estimates that were generally ±30%–40% of the estimated value.

Life stage interpretation

Life history table results provide a simple cross reference for interpretation of age and size data for green sturgeon. For instance, the life table makes it easy to determine that while a small number of females reach first maturity at about age 16 and 146 cm in total length, the majority of the females mature and the bulk of the egg production occurs after full adulthood at ages older than 20 years and sizes greater than 165 cm (Table 4, Fig. 7). Similarly, a 2-m fish is on average about 33 years of age and weighs about 44 kg. Green sturgeon were recruited to the 117 cm to 183 cm California fishery slot limit at about 11 years of age and remain vulnerable for 14 years on average.

Population descriptions suggest that green sturgeon catches in delta pump salvage samples

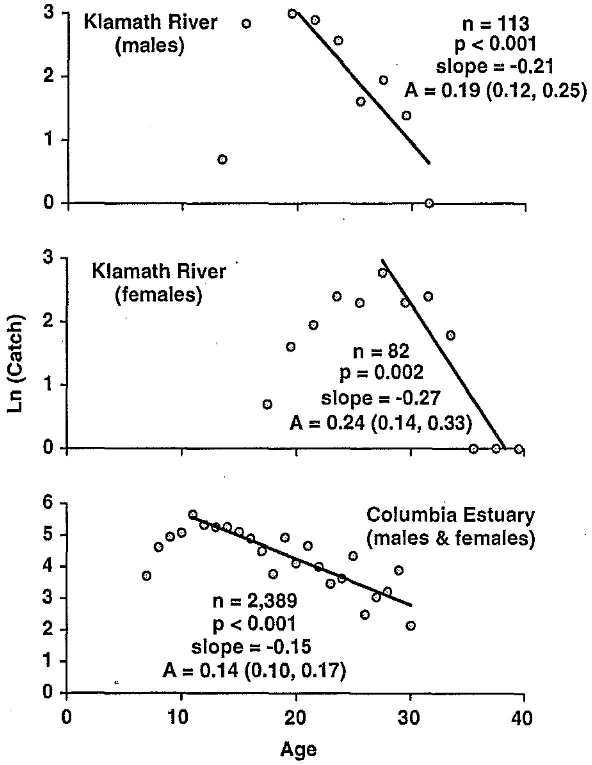

Fig. 6 Catch curves fit to catch-at-age data from fishery samples in the Klamath River (Van Eenennaam et al. 2006) and the Columbia River estuary (Rien et al. 2001; Farr et al. 2002). 'A' is annual total mortality rate (numbers in parentheses are 95% confidence intervals based on regression estimates of the slope of the descending limb which represents the instantaneous total mortality rate)

Table 4 Life table for green sturgeon based on a simple equilibrium model and population parameters reported for various populations

x (years)	L_x (cm)	W_x (kg)	n_x	m_x	S_x	N_x	B_x (kg)	pf	ps	F_x (϶1,000)	P_x (϶1,000)	H_x	Y_x (kg)
1	35	0.2	0.07	0.00	0.930	10,000	1,927	0.5	0.000	0.0	0	0	0
2	45	0.4	0.07	0.00	0.930	9,300	4,054	0.5	0.000	0.0	0	0	0
3	55	0.8	0.07	0.00	0.930	8,649	6,978	0.5	0.000	0.0	0	0	0
4	65	1.3	0.07	0.00	0.930	8,044	10,584	0.5	0.000	0.0	0	0	0
5	74	2.0	0.07	0.00	0.930	7,481	14,716	0.5	0.000	0.0	0	0	0
6	82	2.8	0.07	0.00	0.930	6,957	19,201	0.5	0.000	0.0	0	0	0
7	90	3.7	0.07	0.00	0.930	6,470	23,872	0.5	0.000	0.0	0	0	0
8	98	4.7	0.07	0.00	0.930	6,017	28,573	0.5	0.000	0.0	0	0	0
9	105	5.9	0.07	0.00	0.930	5,596	33,171	0.5	0.000	0.0	0	0	0
10	112	7.2	0.07	0.00	0.930	5,204	37,552	0.5	0.000	0.0	0	0	0
11	118	8.6	0.07	0.07	0.865	4,840	41,630	0.5	0.000	0.0	0	339	2,914
12	125	10.1	0.07	0.07	0.865	4,186	42,165	0.5	0.000	0.0	0	293	2,952
13	130	11.6	0.07	0.07	0.865	3,620	42,061	0.5	0.000	0.0	0	253	2,944
14	136	13.2	0.07	0.07	0.865	3,131	41,410	0.5	0.000	0.0	0	219	2,899
15	141	14.9	0.07	0.07	0.865	2,708	40,303	0.5	0.000	0.0	0	190	2,821
16	146	16.6	0.07	0.07	0.865	2,342	38,832	0.5	0.022	39.7	1,002	164	2,718
17	151	18.3	0.07	0.07	0.865	2,026	37,082	0.5	0.051	45.4	2,346	142	2,596
18	156	20.0	0.07	0.07	0.865	1,752	35,132	0.5	0.095	51.3	4,259	123	2,459
19	160	21.8	0.07	0.07	0.865	1,516	33,048	0.5	0.144	57.5	6,283	106	2,313
20	164	23.6	0.07	0.07	0.865	1,311	30,890	0.5	0.189	63.8	7,893	92	2,162
21	168	25.3	0.07	0.07	0.865	1,134	28,708	0.5	0.225	70.3	8,959	79	2,010
22	171	27.1	0.07	0.07	0.865	981	26,541	0.5	0.258	76.9	9,736	69	1,858
23	175	28.8	0.07	0.07	0.865	848	24,421	0.5	0.285	83.6	10,102	59	1,709
24	178	30.5	0.07	0.07	0.865	733	22,374	0.5	0.304	90.3	10,073	51	1,566
25	181	32.2	0.07	0.07	0.865	634	20,419	0.5	0.316	97.1	9,748	44	1,429
26	184	33.8	0.07	0.00	0.930	549	18,566	0.5	0.324	103.9	9,235	0	0
27	187	35.5	0.07	0.00	0.930	510	18,093	0.5	0.328	110.6	9,269	0	0
28	189	37.0	0.07	0.00	0.930	475	17,578	0.5	0.331	117.3	9,209	0	0
29	192	38.6	0.07	0.00	0.930	441	17,029	0.5	0.332	124.0	9,083	0	0
30	194	40.1	0.07	0.00	0.930	410	16,455	0.5	0.333	130.5	8,912	0	0
31	197	41.6	0.07	0.00	0.930	382	15,862	0.5	0.333	137.0	8,706	0	0
32	199	43.0	0.07	0.00	0.930	355	15,256	0.5	0.333	143.3	8,476	0	0
33	201	44.4	0.07	0.00	0.930	330	14,643	0.5	0.333	149.5	8,227	0	0
34	203	45.7	0.07	0.00	0.930	307	14,028	0.5	0.333	155.6	7,963	0	0
35	204	47.0	0.07	0.00	0.930	286	13,415	0.5	0.333	161.6	7,690	0	0
36	206	48.2	0.07	0.00	0.930	266	12,807	0.5	0.333	167.4	7,408	0	0
37	208	49.4	0.07	0.00	0.930	247	12,207	0.5	0.333	173.0	7,122	0	0
38	209	50.6	0.07	0.00	0.930	230	11,619	0.5	0.333	178.5	6,834	0	0
39	211	51.7	0.07	0.00	0.930	214	11,044	0.5	0.333	183.8	6,545	0	0
40	212	52.8	0.07	0.00	0.930	199	10,484	0.5	0.333	189.0	6,258	0	0
41	214	53.8	0.07	0.00	0.930	185	9,941	0.5	0.333	194.0	5,973	0	0
42	215	54.8	0.07	0.00	0.930	172	9,416	0.5	0.333	198.8	5,694	0	0
43	216	55.8	0.07	0.00	0.930	160	8,909	0.5	0.333	203.5	5,419	0	0
44	217	56.7	0.07	0.00	0.930	149	8,421	0.5	0.333	208.0	5,151	0	0
45	218	57.5	0.07	0.00	0.930	138	7,952	0.5	0.333	212.3	4,891	0	0
46	219	58.4	0.07	0.00	0.930	129	7,504	0.5	0.333	216.5	4,638	0	0
47	220	59.2	0.07	0.00	0.930	120	7,074	0.5	0.333	220.5	4,393	0	0
48	221	60.0	0.07	0.00	0.930	111	6,664	0.5	0.333	224.4	4,157	0	0
49	222	60.7	0.07	0.00	0.930	103	6,274	0.5	0.333	228.1	3,930	0	0
50	223	61.4	0.07	0.00	0.930	96	5,902	0.5	0.333	231.7	3,712	0	0

This example assumes a 7% annual natural mortality rate and a 7% annual fishing mortality rate for fish 177–183 cm in fork length

Where x, age; L_x, total length; W_x, weight; n_x, natural mortality rate; m_x, exploitation rate; S_x, annual survival rate; N_x, number; B_x, biomass; pf, proportion female; ps, annual proportion of mature females; F_x, fecundity; P_x, reproductive potential; H_x, harvest; Y_x, yield

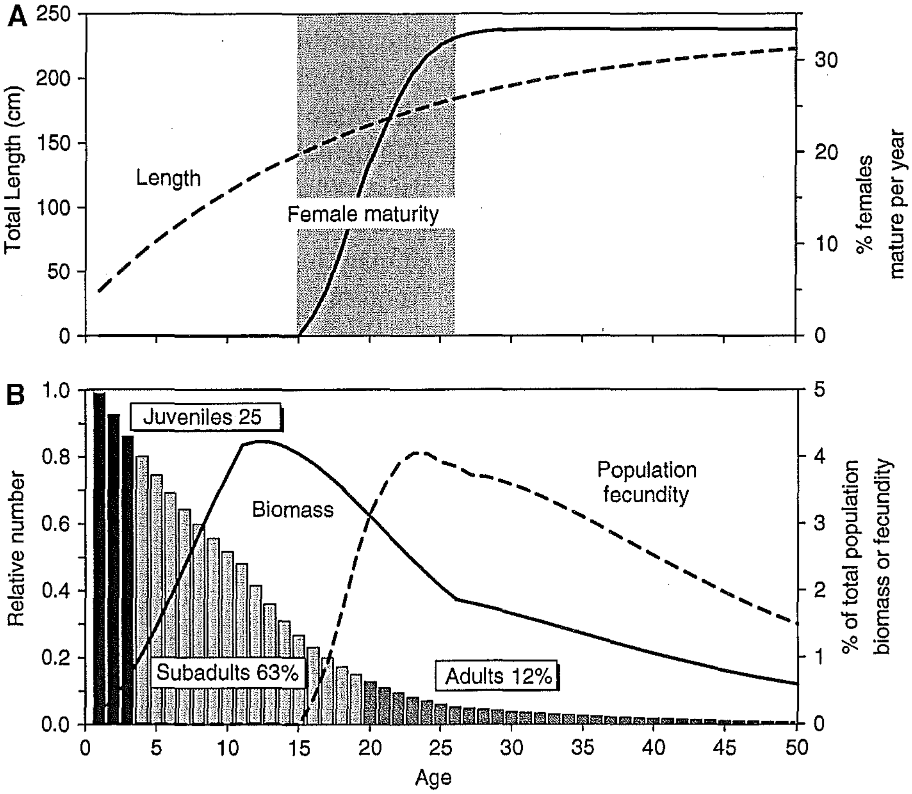

Fig. 7 Green population structure based on representative values identified in Tables 3 and 4. Length at age relationship (graph **A**) is von Bertalanffy function reported for the Klamath River population (Nakamoto and Kisanuki 1995). Female maturity at age relationship (graph **A**) is inferred from range in age of maturity of Klamath green sturgeon (Van Eenennaam et al. 2006) and spawning periodicity of Rogue River green sturgeon (Erickson and Webb 2005). The gray box in graph **A** highlights the size range over which female maturity occurs. Number, biomass, and population fecundity at age (graph **B**) 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 7%, and a hypothetical annual exploitation rate of 7% on sizes within the Sacramento fishery slot limit of 117–183 cm

consist primarily of age one juveniles that are substantially larger than young of the year collected in summer at Red Bluff Diversion Dam screw traps (Fig. 8). Thus, salvage samples might provide a reasonable signal of year class strength in the previous year if the available population is representatively sampled but juvenile green sturgeon appear vulnerable to entrainment at a limited number of ages. San Pablo Bay trammel net samples consist primarily of subadults which are 80–140 cm in length and 7–15 years of age. Adults are poorly represented in San Pablo Bay samples. Columbia River estuary commercial fishery landings include both subadults and adults. Juveniles between 50 cm and 90 cm (3–7 years of age) are poorly represented in existing samples.

Equilibrium population structure

Life table model analyses based on representative population parameters suggest that subadults would comprise the majority (63%) of a population at equilibrium (Fig. 7B). Juveniles in the approximately 3-year freshwater rearing stage would represent 25% of total population numbers. Adults would comprise only 12% 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 perhaps 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. Note the obvious inflection points in Fig. 7B graphs of relative number, biomass, and population fecundity after age 25 where fish were assumed to be no longer subject to fishery mortality.

Mortality effects on abundance

The sensitivity of sturgeon to increasing mortality is highlighted by the abrupt decline in numbers in hypothetical life table analyses (Fig. 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% expressed throughout the life span would result in virtually no green sturgeon surviving to adulthood.

Mortality effects on reproductive potential

Egg production per recruit of green sturgeon is approximately 49,000 in an unexploited hypothetical population. Reproductive potential declines rapidly with increasing mortality concurrent with the decline in survival to adulthood (Fig. 9B). Additional rates of only 2%–5% throughout the life cycle reduce EPR to less than the 20%–50% biological reference points (Fig. 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

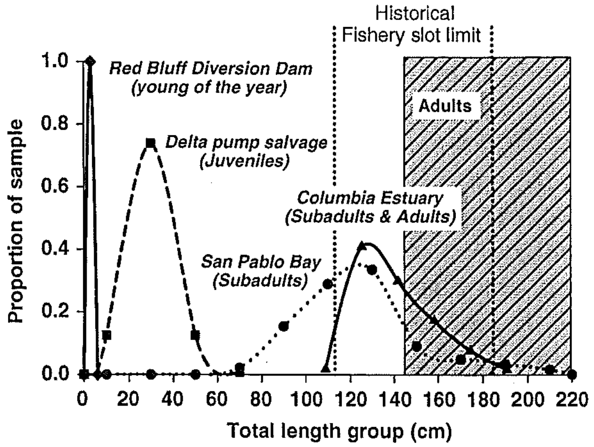

Fig. 8 Length distributions for segments of the Sacramento River green sturgeon population from Red Bluff Diversion Dam juvenile traps (Gaines and Martin 2002), delta pump salvage facilities (CDFG 2004), semi-annual San Pablo Bay sturgeon stock assessments (Schaffter and Kohlhorst 1999; CDFG 2002), and Columbia River estuary commercial fishery landings (Rien et al. 2001). Historical fishery slot limits for green sturgeon were 117–183 cm in California and 122–183 cm in the Columbia River

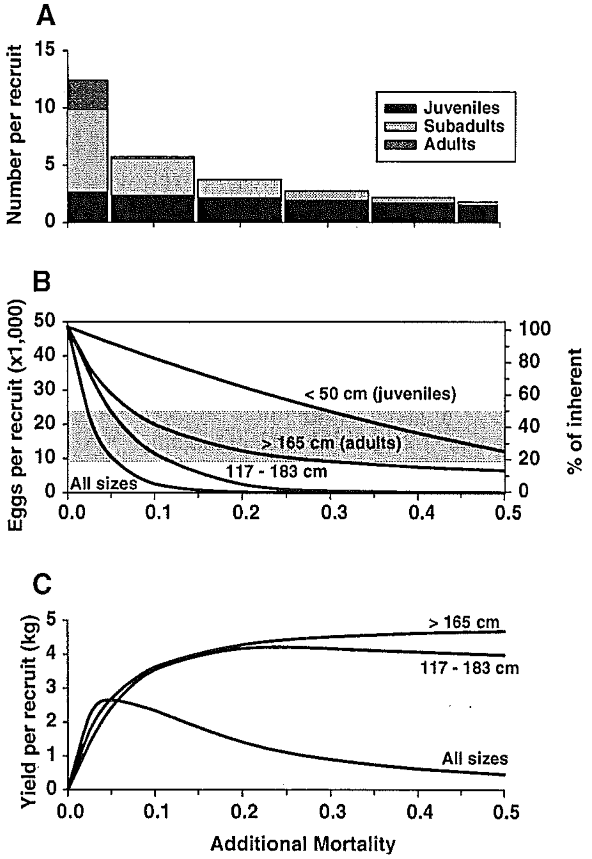

Fig. 9 Fish number, egg production, and YPR as a function of additional mortality or exploitation based on a hypothetical equilibrium population model. Graph **A** illustrates the effects of additional mortality on all size and age groups. Multiple lines in graphs **B** and **C** depict the effects of varying size of vulnerability to additional mortality. Values of 20%–50% egg production per recruit (shaded in graph **B**) are reference points often associated with sustainable fishing rates. Inherent values for eggs per recruit in graph **B** are relative to values in the absence of the additional mortality

be extremely susceptible to overfishing. EPRs of 20%–50% occur at fishing rates of 5%–10% on fish 117–183 cm in length as prescribed by California's historical sport fishery regulations. Fishing rates of 7%–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).

Mortality effects on yield potential

Because green sturgeon grow to large sizes and natural mortality rates are low, potential YPR generally increases when fishing is focused on larger fish (Fig. 9C). Maximum yields are achieved in slot limit (117–183 cm) and adult (>165 cm) fisheries at fishing rates of 15%–20% (Fig. 9C). However, fishing rates that maximize YPR from a cohort will substantially reduce lifetime egg production such that recruitment overfishing could result. Our YPR estimates assumed no relationship between spawning stock biomass or status and recruitment when recruitment may in fact be highly correlated with spawner numbers. Rates that maximize YPR appear to exceed rates that preserve significant reproductive potential under an adult-focused (>165 cm) and subadult fishery slot limit (117–183 cm) alternatives. 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.

Discussion

This paper reviews life history information on green sturgeon and uses that information to develop a simple equilibrium population model. A major problem in the assessment was the lack of species-specific, non-fishery dependent data, intermittent reporting, and at least occasional failure to distinguish green sturgeon and white sturgeon in mixed species catches. Conservation and management decisions with potentially costly consequences for green sturgeon and resource users are currently being made based on the best available information. Assessments have necessarily relied on often subjective inferences for distribution, life history, and population characteristics. The life table model, while subject to a variety of assumptions, provides a systematic tool for integrating and interpreting what we know. The model highlights the extreme sensitivity of a green sturgeon population to even small incremental increases in mortality where multiple ages are affected.

Model results are subject to substantial uncertainty in parameter input values. Analyses considered the effects of different mortality rates but did not evaluate sensitivity to differences in other key parameters such as growth or maturation rates. The data were too sparse to get a reasonable representation of the potential uncertainty in each parameter and the uncertainties are likely to be greater than the range of the few available estimates. Thus, we lack the estimates of reasonable ranges for each parameter needed to place sensitivity analyses in context. Directional effects of parameter differences can be inferred from life table results. For instance, lower than projected growth rates like those that could result from an underestimation aging bias will result in later age of maturation, more ages subject to stage-specific threats such as fishing, a lesser net reproductive potential, and increased sensitivity of adult numbers and potential reproduction to additional mortality. Life table results for female reproduction may be particularly biased by the lack of sex-specific growth and survival parameter estimates. Application of the model must recognize the limitations of these uncertainties on the precision of results and focus on relative comparisons that are generally more robust to potential biases in parameter point estimates.

This review and modeling exercise highlights significant research needs for green sturgeon. These include historical changes in the amount and distribution of suitable habitat, the significance of any portions of the range that have been lost, critical habitat requirements in freshwater, limiting factors, migration patterns, population size, spawner–recruitment relationships, and effective sampling methods. It is particularly unclear whether threats to long-term persistence are significant, existing habitat and fishery improvements for other species provide significant protection for green sturgeon, and which additional actions are necessary for conservation. The most critical information for reducing uncertainty in status and risks includes estimates of spawner abundance by population, strength and consistency of juvenile recruitment, population parameters by sex, and significant human-caused mortality rates.

Accurate assessments of status, productivity, and risk must consider the unique features of the sturgeon life history strategy. Eons of existence in the face of tremendous upheavals over geological time have demonstrated the success of this strategy. It remains to be seen whether these same attributes can withstand the persistent large-scale changes that pervade the modern world. 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. However, the available information remains inadequate to resolve questions of sustainability. These uncertainties may ultimately pose the greatest risk to the protection of this species. A precautionary approach to conservation and management is appropriate.

Acknowledgements M. Webb, J. Inman, and A. Fuller assisted in the collection and review of reference material. C. Ackerman provided assistance with figures and graphs. The manuscript was substantially improved by comments and recommendations of the reviewers and editors.

References

Adair R, Harper W, Smith J (1983) Klamath River fisheries investigation program annual report. U.S. Fish and Wildlife Service, Arcata, CA

Adams PB, Grimes CB, Lindley ST, Moser ML (2002) Status review for North American green sturgeon, *Acipenser medirostris*. National Marine Fisheries Service, Santa Cruz, California, 50 pp

Allen PJ, Cech JJ (2005) Salinity and effects on metabolism in green sturgeon. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Anonymous (1918) Few sturgeon left. Calif Fish Game 4:86

Beamesderfer RCP, Farr RA (1997) Alternatives for the protection and restoration of sturgeons and their habitat. Environ Biol Fish 48:407–417

Beamesderfer RCP, Webb MAH (2002) Green sturgeon status review information. Report by S.P. Cramer and Associates to State Water Contractors, Sacramento, CA

Beamesderfer RCP, Rien TA, Nigro AA (1995) Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Trans Am Fish Soc 124:857–872

Beamesderfer R, Simpson M, Kopp G, Inman J, Fuller A, Demko D (2004) Historical and current information on green sturgeon occurrence in the Sacramento and San Joaquin Rivers and tributaries. Report by Cramer SP and Associates to State Water Contractors, Sacramento, CA

Bemis WE, Findeis EK, Grande L (1997) An overview of Acipenseriformes. Environ Biol Fish 48:25–71

Belchik M (2005) Adult green sturgeon (*Acipenser medirostris*) migration, movements, and habitat use in the Klamath River, California, 2002–2004. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Birstein VJ (1993) Sturgeons and paddlefishes: threatened fishes in need of conservation. Conserv Biol 7:773–787

Boreman J (1997) Sensitivity of North American sturgeons and paddlefish to fishing mortality. Environ Biol Fish 48:399–405

Boreman J, Overholtz WJ, Sissenwine MP (1984) A preliminary analysis of the effects of fishing on shortnose sturgeon. National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole Laboratory Reference Document 84-17, 23 pp

Brown K (2002) Spawning areas of green sturgeon, *Acipenser medirostris*, in the upper Sacramento River, California. Red Bluff Fish and Wildlife Office, U.S. Fish and Wildlife, Service, Red Bluff, CA, 26 pp

Caswell H (2001) Matrix population models. Sinauer, Sunderlund, MA

CDFG [California Department of Fish, Game] (2002) California Department of Fish and Game comments to NOAA Fisheries regarding green sturgeon listing. 129 pp

CDFG [California Department of Fish, Game] (2004) Central Valley Bay Delta Branch Fish Monitoring. www.Delta.dfg.ca.gov/Data/Salvage/SalvageOverview.asp

Cech JJ Jr, Dorshov SI, Moberg GP, May BP, Schaffter RG, Kohlhorst DM (2000) Biological assessment of green sturgeon in the Sacramento-San Joaquin watershed (phase 1). Final Report to Calfed Bay-Delta Program (Project 98-C-15, Contract B-81738)

CH2M Hill (2002) Environmental impact statement/environmental impact report for fish passage improvement project at the Red Bluff Diversion Dam. Report to the Tehama-Colusa Canal Authority and the U.S. Bureau of Reclamation

Craig JL, Fletcher TS (1994) Klamath River fisheries investigation program annual report, 1992. U.S. Fish and Wildlife Service Report AFF1-FRO-94-03, Arcata, CA

Deng X, Van Eenennaam JP, Doroshov SI (2002) Comparison of early life stages and growth of green and white sturgeon. In: Van Winkle W, Anders PJ, Secor DH, Dixon DA (eds) Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, MD, pp 237–248

EPIC, CBD, WKNC [Environmental Protection Information Center, Center for Biological Diversity and WaterKeepers Northern California] (2001) Petition to list the North American green sturgeon (*Acipenser medirostris*) as an endangered or threatened species under the ESA. 70 pp

Erickson DL, Hightower JE (2006) Oceanic distribution and behavior of green sturgeon. N Am J Fish Manage (in press)

Erickson D, Webb M (2005) Spawning periodicity, spawning migration, and size at maturity of green sturgeon (*Acipenser medirostris*) in the Rogue River, Oregon. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Erickson DL, North JA, Hightower JE, Weber J, Lauck L (2002) Movement and habitat use of green sturgeon *Acipenser medirostris* in the Rogue River, Oregon. J Appl Ichthyol 18:565–569

Farr RA, Hughes ML, Rien TA (2002) Green sturgeon population characteristics in Oregon. Oregon Department of Fish and Wildlife Fish Research Project Annual Report F-178-R

Fry DH (1973) Anadromous fishes of California. California Department of Fish and Game, 111 pp

Gaines PD, Martin CD (2002) Abundance and seasonal, spatial and diel distribution patterns of juveniles salmonids passing the Red Bluff Diversion Dam, Sacramento River. U.S. Fish and Wildlife Service Final Report to U.S. Bureau of Reclamation. Red Bluff Research Pumping Plant Report Series Volume 14. Red Bluff, CA

Galbreath JL (1985) Status, life history, and management of Columbia River white sturgeon *Acipenser transmontanus*. In: Binkowski FP, Doroshov SI (eds) North American sturgeons: biology and aquaculture potential. Dr. W. Junk, Dordrecht, pp. 119–125

Ganssle D (1966) Fishes and decapods of San Pablo and Suisun bays. In: Kelley DW (compiler) Ecological studies of the Sacramento-San Joaquin Estuary, part I. California Department of Fish and Game Bulletin 133, pp. 64–94

Gingras M (2005) (San Pablo Bay white sturgeon abundance) X (green sturgeon:white sturgeon catch ratio): Is the product an index of green sturgeon abundance? Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting. Sacramento, CA

Gobalet KW, Schultz PD, Wake TA, Siefkin N (2004) Archaeological perspectives on Native American fisheries of California, with emphasis on steelhead and salmon. Trans Am Fish Soc 133:801–833

Goodyear CP (1993) Spawning stock biomass per recruit in fisheries management: foundation and current use. In: Smith SJ, Hund JJ, Rivard D (eds) Risk evaluation and biological reference points for fisheries management. Canadian Special Publication Fisheries and Aquatic Sciences 120, pp 67–81

Gulland JA (1983) Fish stock assessment: a manual of basic methods. Wiley, New York

Haddon M (2001) Modeling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton, FL

Hart JL (1973) Pacific fishes of Canada. Bull Fish Res Board Can 180:83–84

Heppell SS, Hofmann L (2002) Green sturgeon status assessment. Oregon State University report to National Marine Fisheries Service Southwest Fisheries Science Center

Hilborn R, Walters C (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York

Hillemeier D (2005) Assessing the Klamath River green sturgeon population – an evaluation of the Yurok tribal fishery. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Houston JJ (1988) Status of the green sturgeon, *Acipenser medirostris*, in Canada. Can Field Nat 102:286–290

Israel JA, Cordes JF, Blumberg MA, May B (2004) Geographic patterns of genetic differentiation among western U.S. collections of North American green sturgeon (*Acipenser medirostris*). N Am J Fish Manage 24:922–931

Jardine J (1998) Poachers' growing craftiness makes wardens' jobs tough. August 24, 1998. The Modesto Bee. Modesto, CA

Johnson RR, Martin CD (1997) Abundance and seasonal, spatial and diel distribution patterns of juvenile salmonids passing the Red Bluff Diversion Dam, Sacramento River, July 1994–June 1995. Red Bluff Research Pumping Plant Report Series, vol 2. U.S. Fish and Wildlife Service, Red Bluff, CA

Kelly JT, Klimley AP, Crocker CE (2005) Movements of adult and sub-adult green sturgeon in the San Francisco Bay estuary. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Keo D (1996) Nature gives sturgeon a little added protection. February 26, 1996. The Modesto Bee. Modesto, CA

Kohlhorst DW (1976) Sturgeon spawning in the Sacramento River in 1973, as determined by distribution of larvae. Calif Fish Game 62(1):32–40

Kohlhorst DW, Botsford LW, Brennan JS, Cailliet GM (1991) Aspects of the structure and dynamics of an exploited central California population of white sturgeon (*Acipenser transmontanus*). In: Williot P (ed)

Acipenser: Actes du premier colloque international sur l'esturgeon. CEMAGREF, Bordeaux, France, pp 277–283

Kynard B, Parker E, Parker T (2005) Behavior of early life intervals of Klamath River green sturgeon, *Acipenser medirostris*, with a note on body color. Environ Biol Fish 72:85–97

Langness O (2005) Green sturgeon utilization of coastal estuaries of Washington State. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Lewis M (1995) Catch of night: Angler accused in poaching case. August 16, 1995. The Modesto Bee, Modesto, CA

Lockington WN (1879) Report on the food fishes of San Francisco. In: Biennial Report of the Commissioners of Fisheries of the State of California for the years of 1878–1879, pp 17–63

Mayfield RB, Cech JJ (2004) Temperature effects on green sturgeon bioenergetics. Trans Am Fish Soc 133:961–970

McDonald M (1894) Notes on the fisheries of the Pacific Coast, sturgeon and the sturgeon fishery. Bulletin of the United States Fish Commission No. 14

Miller LW (1972) Migrations of sturgeon tagged in the Sacramento-San Joaquin Estuary. Calif Fish Game 58(2):94–106

Moreau J (1987) Mathematical and biological expression of growth in fishes: recent trends and further developments. In: Summerfelt RC, Hall GE (eds) The age and growth of fish. Iowa State University Press, Ames, IA, pp 81–113

Moser ML, Lindley S (2005) Use of estuarine habitats by green sturgeon in Washington. Symposium on green sturgeon and their environment at Cal-Neva American Fisheries Society Annual Meeting, Sacramento, CA

Moyle PB (2002) Inland fishes of California. University of California Press, Berkeley

Moyle PB, Foley PJ, Yoshiyama RM (1992) Status of green sturgeon, *Acipenser medirostris*, in California. Report by University of California at Davis to the National Marine Fisheries Service, Terminal Island, CA

Moyle PB, Yoshiyama RM, Williams JE, Wikramanayake ED (1995) Fish species of special concern in California, 2nd edn. Final report (Contract 21281F) to the California Department of Fish and Game

Musick JA et al (2000) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of pacific salmonids). Fisheries 25(11):6–30

Nakamoto RJ, Kisanuki TT (1995) Age and growth of Klamath River green sturgeon (*Acipenser medirostris*). U.S. Fish and Wildlife Service Report 93-FP-13, Yreka, CA

Niggemyer A, Duster T (2003) Final assessment of potential sturgeon passage impediments SP-F3.2 Task 3A. Oroville Facilities Relicensing FERC Project No. 2100. Surface Water Resources, Inc., Sacramento, CA. pp 27. http://orovillerelicensing.water.ca.gov/pdf_docs/09-24-03_env_att_11.pdf

NOAA (National Oceanic, Atmospheric Administration) (2005) Green sturgeon (*Acipenser medirostris*) status review update. Southwest Fisheries Science Center, Long Beach, CA

ODFW & WDFW (Oregon Department of Fish and Wildlife, Washington Department of Fish and Wildlife) (2004) Status report: Columbia River fish runs and fisheries, 1938–1999. Clackamas, OR, and Vancouver, WA

Palomares R (1995) Big fish yields big fine. August 29, 1995. The Modesto Bee, Modesto, CA

Paragamian VL, Beamesderfer RCP, Ireland SC (2005) Status, population dynamics, and future prospects of the endangered Kootenai River white sturgeon population with and without hatchery intervention. Trans Am Fish Soc 134:518–532

Parsley MJ, Anders PJ, Miller AI, Beckman LG, McCabe GT (2002) Recovery of white sturgeon populations through natural production: understanding the influence of abiotic and biotic factors on spawning and subsequent recruitment. Am Fish Soc Symp 28:55–66

Prager MH, O'Brien JF, Saila SB (1987) Using lifetime fecundity to compare management strategies: a case history for striped bass. N Am J Fish Manage 7:403–409

Radtke LD (1966) Distribution of smelt, juvenile sturgeon, and starry flounder in the Sacramento-San Joaquin Delta with observations on food of sturgeon. In: Ecological studies of the Sacramento-San Joaquin Estuary, part II. Fish Bulletin 136, pp 115–129

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bull Fish Res Board Can 191:1–382

Rieman BE, Beamesderfer RC (1990) White sturgeon in the lower Columbia River: is the stock overexploited? N Am J Fish Manage 10:388–396

Rien TA, Burner LC, Farr RA, Howell MD, North JA (2001) Green sturgeon population characteristics in Oregon. Oregon Department of Fish and Wildlife Fish Research Project Annual Report F-178-R

Rochard E, Castelnaud G, LePage M (1990) Sturgeons (Pisces: Acipenseridae); threats and prospects. J Fish Biol 37A:123–132

Rueth JC, Kisanuki TT, Polos JC (1992) Klamath River fisheries investigation program annual report, 1990 and 1991. U.S. Fish and Wildlife Service Report AFF1-FRO-92-05, Arcata, CA

Schaffter RG (1997) White sturgeon spawning migrations and location of spawning habitat in the Sacramento River, CA. Calif Fish Game 83(4):1–20

Schaffter RG, Kohlhorst DW (1999) Status of white sturgeon in the Sacramento-San Joaquin Estuary. Calif Fish Game 85:37–41

Schaffter RG, Kohlhorst DW (2002) Determination of green sturgeon spawning habitats and their environmental conditions. California Department of Fish and Game. In Biological assessment of green sturgeon in the Sacramento-San Joaquin Watershed, phase 1. Final report to the CALFED Bay-Delta Program

Scott G (1993) Waiting to snag some snaggers. April 4, 1993. The Modesto Bee, Modesto, CA

Seesholtz A (2003) Final assessment of sturgeon distribution and habitat use SP-F3.2 Task 3a. Oroville Facilities Relicensing FERC Project No. 2100. State of California, The Resources Agency, Department of Water Resources. pp 26. Available at http://oroville-relicensing.water.ca.gov/pdf_docs/12-17-03_env_att_11.pdf

Skinner JE (1962) An historical review of the fish and wildlife resources of the San Francisco Bay area. California Department of Fish and Game Water Projects Branch Report No. 1

Stevens DE, Miller LW (1970) Distribution of sturgeon larvae in the Sacramento-San Joaquin River system. Calif Fish Game 83:1–20

Talbitzer B (1959) Case of the virgin sturgeon: the story of Butte County's largest fish catch. Butte County Hist Soc Diggin's 3:6–8

USFWS (U.S. Fish, Wildlife Service) (1983) Annual report (1982) of the Klamath River fisheries investigation program. Arcata, CA

USFWS (U.S. Fish, Wildlife Service) (1995) Working paper on restoration needs: habitat restoration actions to double natural production of anadromous fish in the Central Valley of California, vol 2. USFWS, Stockton, 78 pp

USFWS (U.S. Fish, Wildlife Service) (2000) Annual report of the Klamath and Trinity River juvenile salmonid monitoring program. Arcata, CA

Van Eenennaam JP, Webb MAH, Deng X, Doroshov SI, Mayfield RB, Cech JJ Jr, Hillemeier DC, Willson TE (2001) Artificial spawning and larval rearing of Klamath River green sturgeon. Trans Am Fish Soc 130:159–165

Van Eenennaam JP, Linares-Casenave J, Dorsohov SI, Hillemeier DC, Wilson TE, Nova AA (2006) Reproductive conditions of Klamath River green sturgeon. Trans Am Fish Soc 135:151–163

Vogel D (2005) Evaluation of adult sturgeon migration at the Glenn-Colusa Irrigation District Gradient Facility on the Sacramento River during 2003. Report by Natural Resource Scientists, Inc. Red Bluff, CA

Wang JC (1986) Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: a guide to the early life histories. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary, Technical Report 9

Welch DW, Foucher RP (1988) A maximum likelihood methodology for estimating length-at-maturity with application to Pacific cod (*Gadus macrocephalus*) population dynamics. Can J Fish Aquat Sci 45:333–343