



Biology and life history of Green Sturgeon (*Acipenser medirostris* Ayres, 1854): state of the science

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Summary

Green Sturgeon (GRS) *Acipenser medirostris* is one of the most marine-oriented of all sturgeons. It primarily spawns in the Sacramento, Klamath, and Rogue Rivers, yet lives most of its life in estuarine and coastal waters along the West Coast of North America. Spawning is only known to occur in the Rogue, Klamath and Sacramento rivers and optimal temperatures for egg incubation and larval growth are not always maintained in these dammed and highly-regulated systems. Genetic analysis and acoustic telemetry have confirmed the presence of two genetically distinct populations; the southern population is listed as “threatened” under the ESA. Adults only enter natal rivers to spawn every 1–4 years. They make extensive coastal migrations in depths <80 m and move between estuaries where they aggregate in summer. The long marine occupancy of GRS potentially exposes them to mortality from various marine activities such as bottom trawl fishing, dredging, and ocean energy projects, but also provides a theoretical reservoir of fish to support viable populations. Critically-needed information for protection of this species includes: accurate annual population size estimates, data on distribution and habitat requirements for larvae and juveniles, and assessment of mortality due to bycatch, poaching and marine mammal predation.

Taxonomy, phylogeny, and morphology

Acipenser medirostris Ayres, 1854.

AFS English common name: Green Sturgeon.

Adult GRS are olive green in color with an olivaceous stripe on each side, as well as on the abdomen; however, there is individual variability in the amount and actual color pigmentation (Artyukhin and Andronov, 1990). Adults can reach up to 2.5 m in TL and weigh up to 159 kg; however, the average adult size is closer to 2.0 m and 20 kg (Moyle, 2002; Kynard et al., 2005).

Aside from its green coloration and smaller adult size, the GRS is similar in appearance to White Sturgeon (WS) *A. transmontanus*. These two species overlap throughout

their range. Green Sturgeon can be differentiated from WS by position of the barbels, which are closer to the mouth than to the snout. Green Sturgeon has a row of 23–30 lateral scutes, 8–11 dorsal scutes, 7–10 ventral scutes, and one bony plate behind the anal and dorsal fins. All of these scute counts differ from those of WS (Moyle, 2002).

Green Sturgeon is very similar in appearance to the Sakhalin Sturgeon (*A. mikadoi*) of northeastern Asia. However, subtle morphological differences distinguish the two species (North et al., 2002; Vasil’eva et al., 2009). North et al. (2002) found that Sakhalin Sturgeon had longer, narrower heads than GRS from the Columbia River; specifically, the length of the snout anterior to the eyes. North et al. (2002) and Vasil’eva et al. (2009) both found little overlap between these two species in the location of barbels relative to the mouth. North et al. (2002) reported overlap in the number of ventral scutes and gill rakers between Sakhalin Sturgeon and GRS, while Vasil’eva et al. (2009) observed subtle differences in these counts. Vasil’eva et al. (2009) reported “usually not more than nine ventral scutes; generally less than 20 gill rakers” in Sakhalin Sturgeon, but “usually more than nine ventral scutes; generally more than 20 gill rakers” in GRS.

While Birstein (1993) originally considered GRS and Sakhalin Sturgeon as one species, differences in ploidy levels (Blackledge and Bidwell, 1993; Ludwig et al., 2001) and molecular phylogenetic research later revealed them to be distinct species (Birstein and DeSalle, 1998; Birstein et al., 2002; Krieger et al., 2008). Green Sturgeon is a functional tetraploid, with 249 ± 8 chromosomes (Van Eenennaam et al., 1999; Ludwig et al., 2001), similar to Sakhalin Sturgeon, although the karyotype structure is different (Vasil’eva et al., 2009). Birstein and DeSalle (1998) and Birstein et al. (2002) placed the two species in distantly related clades, while Ludwig et al. (2000, 2001) described them as sister species. More recently, Krieger et al. (2008) found the two species closely related, based on 10 synapomorphies. Hence, the earlier controversy over topology probably stemmed from use of the NADH5 gene, which has a high percentage of variable sites relative to other gene regions examined.

Distribution and abundance

Green Sturgeon occurs in the coastal ocean from 200 km south of Ensenada, MX (Rosales-Casian and Almeda-Jauregui, 2009) north to the Bering Sea (Fig. 1; Mecklenburg et al., 2002). Adults and sub-adults move among coastal estuaries and regularly aggregate in estuarine areas for extended periods (Moser and Lindley, 2007; Lindley et al., 2008, 2011). While GRS ranges over an extensive area off the North American Pacific coast, it is known to spawn regularly in only three West Coast river systems: the Sacramento and Klamath in CA and the Rogue in OR (Van Eenennaam et al., 2006; Erickson and Webb, 2007; Webb and Erickson, 2007; Mora et al., 2009; Seesholtz et al., 2015; Fig. 2). Larvae and YOY (2–150 cm FL) are typically found only in rivers where spawning occurs. Due to its reduced abundance, restricted spawning range, and vulnerable life history, Musick et al. (2000) included GRS among other marine and diadromous fishes as a species at risk of extinction.

Green Sturgeon appears to have experienced a contraction in its spawning range, particularly in CA and southern OR (Mora et al., 2009). In the upper Umpqua, Feather, Yuba, and Eel Rivers (Fig. 2), sightings of GRS are few, and there is limited evidence that spawning occurs. In the San Joaquin and South Fork Trinity rivers, GRS populations appear extirpated (Adams et al., 2007). Fish reproducing in the two northernmost rivers are genetically distinct from the Sacramento River population (Israel et al., 2004). For

management and conservation purposes, the Klamath–Rogue rivers meta-population has been designated as the northern distinct population segment (DPS) of GRS under the ESA, while the Sacramento River population has been designated as the southern GRS DPS (Adams et al., 2007).

The proportion of each meta-population found in estuarine aggregation areas has been estimated using both genetic analysis and acoustic telemetry. Green Sturgeon from different natal rivers exhibit different patterns of habitat use; most notably, San Francisco Bay (Fig. 2) was used only by Sacramento River fish, while the Umpqua River estuary was used most by fish from the Klamath and Rogue rivers (Lindley et al., 2011). During 1995–2005, genetic analysis showed that 69–88% of GRS sampled from the Columbia River and Willapa Bay, WA (Fig. 2) were Sacramento River fish (Israel et al., 2009). In contrast, Sacramento River fish made up 41–46% of the genetic assignment for samples from Grays Harbor, WA. Similar results were obtained from genetic analyses of samples collected in 2011–2012 (Schreier and Langness, 2014). Acoustic detection data from 2005 and 2006 indicated that 77% and 82% of GRS entering Willapa Bay were from the Sacramento River. In Grays Harbor, 77% of the 2006 detections were GRS from the Sacramento River. For the Columbia River estuary, the proportions of Sacramento GRS detected were variable: 42% in 2005 and 81% in 2006 (M. L. Moser, NMFS, Seattle, WA, unpublished data).

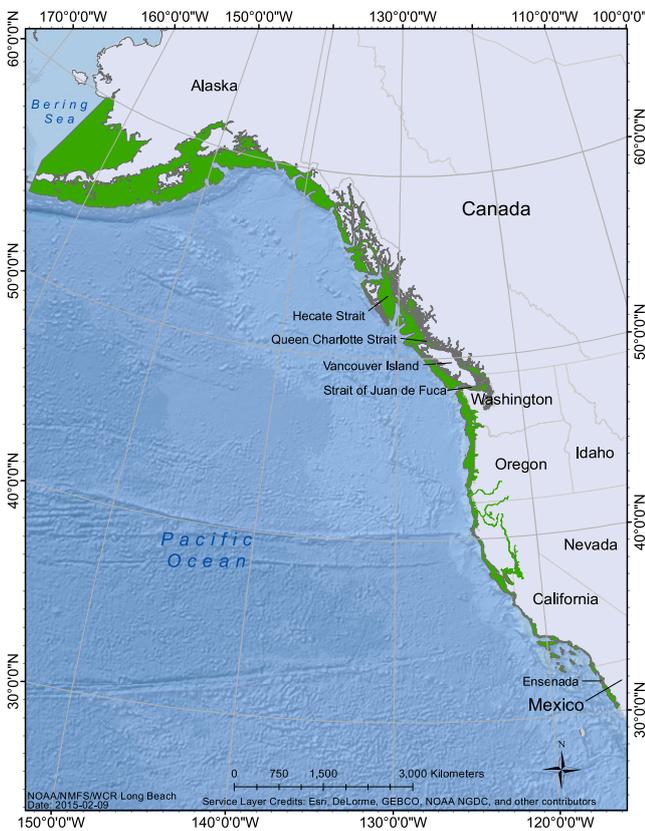


Fig. 1. Distribution of Green Sturgeon in North America

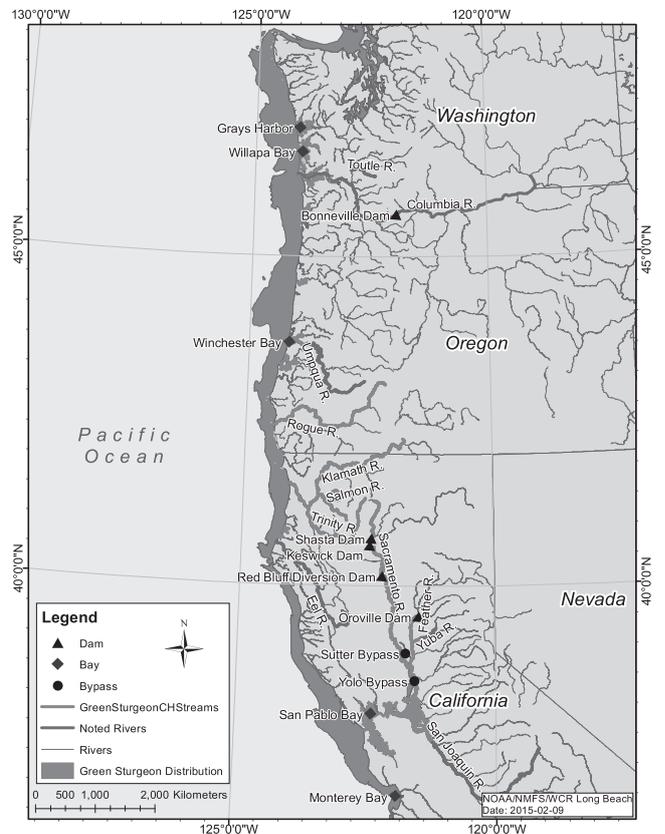


Fig. 2. Detail of Green Sturgeon aggregation areas and spawning rivers

The limited range and abundance of GRS in freshwater may reflect very specific spawning and rearing requirements. The Rogue and Klamath rivers (Fig. 2) are at the southern tip of the North Pacific Coastal ecoregion (defined by Abell et al., 2000), where climate is influenced by the southern, more humid and warmer Mid Coastal ecoregion. The Sacramento River (Fig. 2) is the northernmost drainage of the Pacific Central Valley ecoregion, which also includes the San Joaquin River flowing from south to north. These rivers flow across broad alluvial flatlands where the climate is characterized by dry summers and wet winters and springs (Myers et al., 1998; Abell et al., 2000). While the number of spawners returning to each river annually is unknown, estimates place them in the hundreds for the Rogue and Klamath rivers and probably less for the upper Sacramento (see Population metrics section).

Eggs, larvae, and young-of-the-year

Green Sturgeon eggs, larvae, and YOY typically occur in freshwater portions of the main-stem natal river. While no systematic survey has been undertaken to estimate abundance at these life stages, they have been captured both incidentally and in directed sampling efforts. Recently, GRS eggs were discovered in the Feather River (Fig. 2), providing exciting new evidence that spawning can occur in large tributaries (Seesholtz et al., 2015). This supports historical observations of GRS spawning in other tributary rivers (e.g., South Fork Trinity River) (Adams et al., 2007).

Water temperature is critically important to GRS egg development and larval growth. Eggs do not drift far downstream from the spawning grounds and develop where they are deposited (Kynard et al., 2005). Optimal water temperature for egg incubation under laboratory conditions ranges 14–17°C and temperature higher than 20°C can be detrimental to embryos (Van Eenennaam et al., 2005). Laboratory experiments indicated that larval growth was highest for groups held at 15°C, and was lower for those in water temperature less than 11°C or higher than 19°C (Cech et al., 1984). Similarly, bioenergetic constraints were lowest for GRS larvae held at 15–16°C (Mayfield and Cech, 2004).

Environmental temperatures may be sub-optimal in many GRS spawning and rearing habitats. Toward the end of the spawning season, temperatures can exceed 17°C in spawning habitats on the Klamath and Rogue rivers (Erickson et al., 2002; Van Eenennaam et al., 2005). In summer rearing habitats, temperatures frequently exceed 20°C (Erickson and Webb, 2007). Green Sturgeon eggs were collected in the Feather River at 17.5°C (Seesholtz et al., 2015). In contrast, artificially cold water (released to protect incubating Chinook Salmon, *Oncorhynchus tshawytscha*) occurs in the Sacramento River main-stem. This results in temperatures below 14°C in prime Sacramento River spawning and rearing habitats (Brown, 2007; Heublein et al., 2009).

Little is known about the habitat requirements or behavior of GRS larvae and YOY. As is the case for other sturgeon species, GRS at these life stages are cryptic, and their capture requires specialized gear (Usvyatsov et al., 2013). In the Sacramento River, larvae and YOY (1.8–18.8 cm FL) have

been collected annually using D-nets and rotary screw traps downstream from Red Bluff Diversion Dam (Fig. 2; Poytress et al., 2009, 2014). In the Rogue River, YOY as small as 15.0 cm FL have been captured (Farr et al., 2001). On the Klamath, Trinity, and Salmon rivers, YOY have also been captured in screw traps.

Larvae and YOY utilize riverine areas to forage and rear until they gain the osmoregulatory capacity to tolerate higher salinity concentrations (Allen and Cech, 2007). In fact, recent behavioral choice tests revealed that 200–220 days old GRS (38–52.5 cm TL) preferred the most saline water available (Poletto et al., 2013).

Juveniles

Juvenile GRS (1–3 year olds, <75 cm) are known to reside in freshwater for up to 3 years (Nakamoto et al., 1995); however, they are able to survive in (and seek out) seawater as early as the end of their first year (Allen et al., 2006a,b; Poletto et al., 2013). Green Sturgeon juveniles (<60 cm) use riverine, subtidal, and intertidal habitats in lower main-stem rivers and estuaries (Radtke, 1966; Klimley et al., 2015). Captures in freshwater indicate potential overwintering of more than one age class in main-stem natal rivers (Brown, 2007).

No systematic sampling has been completed on natal rivers and estuaries to characterize GRS habitat or abundance at the juvenile stage. In the Sacramento River system, juveniles are more frequently observed in the San Francisco Bay-Delta than in rivers. For example, 20–60 cm TL fish were captured during the summer in shallow shoals (1–3 m deep) in the lower San Joaquin River (Radtke, 1966). Klamath and Rogue estuaries are orders of magnitude smaller than the San Francisco Bay-Delta estuary (Israel et al., 2004), which likely has consequences for juvenile habitat availability in the northern GRS range.

Subadults and adults

Subadult (<75.0 cm TL) and adult GRS (>75.0 cm TL) occupy coastal waters for most of their life span, usually migrating north from the natal river (Erickson and Hightower, 2007; Lindley et al., 2008, 2011). They make long-distance migrations and can be found offshore from Ensenada, Mexico, to the Bering Sea, AK (Mecklenburg et al., 2002; Moyle, 2002; Colway and Stevenson, 2007; Fig. 1). Subadults tagged in San Pablo Bay, CA (Fig. 2) have been recaptured to the north off Santa Cruz, CA, in Winchester Bay on the southern OR coast, at the mouth of the Columbia River, and in Grays Harbor, WA (Chadwich, 1959; Miller, 1972). Moreover, Erickson and Hightower (2007) found that all adult GRS tagged with pop-up satellite archival tags (N = 7) migrated north immediately after leaving the Rogue River (note, these findings were from a single study year).

Green Sturgeon enter estuaries to feed and mature individuals will migrate upriver to spawning habitats in their natal river system. From January to May, reproductively mature GRS enter the San Francisco Bay Delta and migrate up the Sacramento River (Heublein et al., 2009). Similar migration

periods have been reported for mature adults entering the Rogue River from March to June (Erickson et al., 2002; Erickson and Webb, 2007), and the Klamath River from April to June (Benson et al., 2007). Green Sturgeon spawned in the lower Feather River in mid-June 2011 (Seesholtz et al., 2015), and spawning pairs were captured on underwater video in the Yuba River that same spring (Bergman et al., 2011). These observations occurred when high outflows were sustained into the late spring; summer sightings are extremely limited.

After spawning, most GRS adults exit rivers during periods of changing flow, between October and January. A smaller proportion exit in May and June (Benson et al., 2007; Erickson and Webb, 2007; Heublein et al., 2009). In addition to spawning movements, adult and subadult GRS (>75 cm TL) make regular summer (May–October) entries into estuaries to take advantage of warm waters and abundant food resources. Moser and Lindley (2007) found that GRS occupied Willapa Bay (Fig. 2) when estuarine water temperature exceeded coastal water temperature by at least 2°C.

Population metrics

To date, little population-level data have been collected for any population of GRS. Published abundance estimates for this species are based primarily on counts of spawners in the Rogue, Klamath, and Sacramento rivers made using dual-frequency identification SONAR (DIDSON) and mark-recapture methods (Mora et al., 2015).

Preliminary DIDSON data indicated that the total run size in the Rogue River was roughly 350 fish in 2007 (S. T. Lindley, NMFS, Santa Cruz, CA, unpublished data). During the same year, a slightly larger point estimate of Rogue River spawner abundance (426 to 734) was obtained using mark-recapture methods (D. L. Erickson, ODFW, Newport, OR, unpublished data). More recent estimates of spawner abundance were 223 based on DIDSON (95% confidence interval = 180–266) and 236 based on mark-recapture (95% confidence interval = 150–424; Mora et al., 2015).

Recent abundance estimates for Sacramento River spawning adults have been obtained from genetic studies and DIDSON observations. Estimates of spawning population size using genetic data suggest that between 10 and 28 pairs of GRS have bred annually between 2002 and 2006 in river reaches above Red Bluff Diversion Dam (Fig. 2; Israel and May, 2010). Counts from DIDSON observations were made in 2010–2015 at spawning sites on the Sacramento River and indicated an annual spawning run size of 336–1236 individuals (Mora, 2016). Estimates from DIDSON observations in the Klamath River were similarly low (E. Mora, University of California, Davis, CA, unpublished data).

Limited historical abundance data preclude any rigorous population trend analysis. Lindley et al. (2008) estimated an annual survival of 0.83 based on detections of acoustic-tagged subadults and adults drawn from both meta-populations. Adams et al. (2007) reported fairly stable adult abundance in the Klamath River based on annual tribal harvest of a few hundred spawning adults. However, no effort data were available, so the value of these fishery-dependent

trend data is limited. In the Sacramento River, the GRS population is believed to have declined over the last two decades, with less than 50 adults now sighted annually in the best spawning habitat (R. Corwin, BOR retired, Red Bluff, CA, personal communication).

Age and growth information have been collected from Klamath River and coastal GRS (Nakamoto et al., 1995; Farr et al., 2001). However, growth rings on fin rays were not validated as annuli due to the rarity of fish and the relative brevity of research studies (Farr et al., 2001). Estimated GRS ages for WA and OR rivers and estuaries ranged 7–45 years for females and 8–31 years for males. The age of Klamath River adults was estimated at 16–40 years for females (29–73 kg) and 14–32 years for males (19–56 kg; Van Eenennaam et al., 2006). Maximum size for the northern meta-population ranged 216–260 cm TL (Nakamoto et al., 1995; Rien et al., 2001; Van Eenennaam et al., 2006).

A life-table population model for the Sacramento River GRS was developed by Beamesderfer et al. (2007). Based on available abundance data and equilibrium assumptions, this model predicted that adults comprise 12% of the population while subadults comprise 68%. Mora (2016) used this result to estimate that the total Sacramento GRS population ranges 12 614–22 482 individuals. However, he cautions that this result is uncertain and suffers from a lack of information regarding the abundance of early life stages. Similar to other sturgeons (Boreman, 1997; Tringali and Bert, 1998; Gross et al., 2002; Heppell, 2007), Sacramento River GRS are highly sensitive to increases in mortality.

Species habitat requirements, preferences and tolerances

Water flow

More information is needed to define a riverine flow regime (i.e., velocity, flow rate, frequency, duration, seasonality, and rate of change of freshwater discharge over time) required for normal GRS behavior, growth, and survival. This is particularly critical with the anticipated flow alterations arising from global climate change (Sardella and Kultz, 2014). Stable and sufficient flow rates in spawning and rearing reaches are necessary to maintain water temperatures within the appropriate range for egg, larval, and juvenile survival and development (Mayfield and Cech, 2004; Allen et al., 2006b; Van Eenennaam et al., 2006). Sufficient flow is also needed to prevent egg suffocation in spawning substrates (Deng et al., 2002; Kock et al., 2006; Poytress et al., 2009), reduce the incidence of fungal infestation in eggs (Parsley and Beckman, 1994; Deng et al., 2002; Parsley et al., 2002), and maintain surfaces for larval feeding (Nguyen and Crocker, 2007).

Migratory and spawning behaviors are also associated with water flow and temperature. Within bays and estuaries, sufficient flows are needed for productive feeding grounds and to allow successful adult navigation to spawning areas. It has been hypothesized that current velocity must be sufficient to attract adults to rivers and initiate the upstream spawning migration (Kohlhorst et al., 1991; Erickson and Webb, 2007). Spawning in the Sacramento River is believed to be triggered by increases in river discharge to about

400 m³ s⁻¹ (Brown, 2007; Poytress et al., 2009). Average daily discharge during spawning months in the Sacramento was reported at 198–352 m³ s⁻¹. Erickson and Webb (2007) found that longer spawning migrations in GRS were correlated with increased discharge in the Rogue River, OR. They found that average monthly discharge during the spawning season ranged 58–93 m³ s⁻¹ during 2001, when upstream spawning migration distance was shortest, but ranged 178–260 m³ s⁻¹ during 2003, when upstream spawning migration distance was longest. Post-spawning downstream migrations are also believed to be triggered by increases in discharge, from 174 to 417 m³ s⁻¹ in late summer in the Sacramento River (Vogel, 2005) to over 100 m³ s⁻¹ in winter in the Klamath and Rogue rivers (Erickson et al., 2002; Benson et al., 2007).

Water quality

Optimal water quality requirements differ among GRS life stages. For egg incubation, water temperatures should be relatively stable, ranging 11–17.5°C with an optimum of 13–15.5°C (Van Eenennaam et al., 2005; Poytress et al., 2009). Incubating eggs exposed to experimental temperatures of 11°C resulted in slightly lower hatching success and produced smaller free embryos than those held at warmer temperatures. Factors affecting temperature tolerance of embryos may include egg quality and thermal exposure of the parents (Van Eenennaam et al., 2005). Suitable water temperatures are below 20°C for larvae, and below 24°C for juveniles. At temperatures above this threshold, juveniles exhibit decreased swimming performance (Mayfield and Cech, 2004) and increased cellular stress (Allen et al., 2006a; Werner et al., 2007; Linares-Casenave et al., 2013; Wang et al., 2013). Sub-adults and adults occupy estuaries when water temperature ranges 14.5–20.8°C (Moser and Lindley, 2007).

In comparison to other sturgeons, the GRS exhibits earlier saltwater tolerance and the unique ability to survive abrupt transfer from saltwater to freshwater (Allen et al., 2011). Suitable salinity levels range from freshwater (<3‰) for larvae and YOY (about 100 days post hatch) to brackish water (10‰) for juveniles prior to their transition to saltwater (Poleto et al., 2013). Juveniles transitioning from brackish to saltwater can tolerate high salinities, but prolonged exposure may result in decreased growth, reduced activity, and even mortality (Allen and Cech, 2007; Sardella et al., 2008). In contrast, sub-adults and adults regularly occur in the ocean (>33‰) and in estuaries where they can encounter freshwater, seawater, or anything in between (Kelly et al., 2007; Moser and Lindley, 2007). In estuaries, GRS are exposed to rapid tidally-influenced fluctuations in salinity of up to 1‰ h⁻¹ and temperature changes of up to 2°C h⁻¹ (Moser and Lindley, 2007).

Other water quality factors that may limit sturgeon habitat use, growth, or fitness include inadequate dissolved oxygen and/or high contaminant levels in sediment or pore water. Sturgeon eggs and embryos require adequate flow and dissolved oxygen for proper development (Kynard et al., 2005; Usvyatsov et al., 2013). Respiration rates of juvenile GRS are relatively low (61.78 to 76.06 mg O₂ h⁻¹ kg⁻¹), as are the metabolic costs of osmoregulation (Allen and Cech,

2007). Green Sturgeon tolerance to hypoxia is unknown. Telemetry studies of sub-adults and adults indicated that they occur in estuarine habitats where dissolved oxygen levels are greater than 6.5 mg O₂ L⁻¹ (Kelly et al., 2007; Moser and Lindley, 2007). Contaminants (e.g., pesticides, polycyclic aromatic hydrocarbons, heavy metals, etc.) may be deleterious to all sturgeon life history stages. Adverse developmental effects have been documented in numerous contaminant studies (Holcik, 1989; Fairey et al., 1997; Foster et al., 2001a,b; Kruse and Scarnecchia, 2002; Feist et al., 2005; Greenfield et al., 2005; Linares-Casenave et al., 2015).

Substrate quality

Optimal substrates for GRS egg deposition and development likely include cobble or gravel with interstices or irregular surfaces to provide protection from predators and turbulence. Studies in the Rogue River suggest that spawning occurs in turbulent, deep (>5 m) pools scoured at the base of fast-flowing rapids or in riffles over exposed cobble or boulder substrates (D. Erickson, Oregon Department of Fish and Wildlife, Newport, OR, unpublished data). In the Sacramento River, spawning occurred at or near the deepest portion of pools (0.6–11.3 m), predominantly over gravel substrates (Poytress et al., 2009).

Green sturgeon eggs are initially adhesive for a few seconds after exposure to water and then become highly adhesive after fertilization (Van Eenennaam et al., 2012). In tank spawning, eggs were physically damaged by the spawning adults as they rolled along the flat tank bottom (Van Eenennaam et al., 2012). Hence, during river spawning eggs presumably settle into crevices and adhere to substrate shortly after fertilization (Poytress et al., 2009).

Optimal substrate characteristics for other life stages are unknown. Both free embryos and larvae exhibited a strong affinity for benthic structure during laboratory studies (Kynard et al., 2005), but larvae also used flat-surfaced substrates for foraging (Nguyen and Crocker, 2007). In estuaries where GRS feed, sediment type and quality are of particular concern. Intertidal areas can be vulnerable to the accumulation of contaminants such as heavy metals, polycyclic aromatic hydrocarbons, and organochlorine pesticides, which may adversely affect growth and development (Holcik, 1989). In estuaries, subadult and adult GRS use soft substrate (as opposed to heavily vegetated or hard substrate) to feed on benthic invertebrates (M. Moser, NMFS, Seattle, WA, unpublished data). In the coastal ocean they regularly occur over flat, sandy substrate (Payne et al., 2015), but can also be found near complex, hard-bottom habitats (Huff et al., 2011).

Depth

In freshwater, many sturgeon species exhibit extended holding periods in deep areas (>5 m) to conserve energy (Adams et al., 1997; Hildebrand et al., 1999; McLoed et al., 1999; Sulak et al., 2007). Such deep (≥5 m) riverine pools are favored by adult GRS for holding when adequate water quality and flow are available (see section on adults and sub-adults). In the Sacramento River, acoustic-tagged adult GRS

chose spawning areas deeper than 5 m (Thomas et al., 2014). These deep pools feature turbulence and upwelling that may be critical for egg fertilization or incubation (Vogel, 2005; Benson et al., 2007; Poytress et al., 2009). Adult GRS occupy these deep holding pools for up to 9 months after spawning, presumably for feeding and/or energy conservation (Erickson et al., 2002; Israel et al., 2009).

In marine waters, adult and subadult GRS occupied depths <120 m (Erickson and Hightower, 2007; Payne et al., 2015), and most frequently occupy depths of 40–70 m (Erickson and Hightower, 2007) and 20–80 m (Payne et al., 2015). Green Sturgeon depth distribution in the ocean has been shown to change seasonally, with most acoustically-tagged individuals occupying shallowest depths during summer and fall (e.g., July–November) and deepest depths during winter and spring (e.g., December–May; Payne et al., 2015; D. Erickson, Oregon Department of Fish and Wildlife, Newport, OR, unpublished data). A similar seasonal pattern of depth occupation has been determined (Beardsall et al., 2016) in the Atlantic Sturgeon (*A. oxyrinchus oxyrinchus*).

Erickson and Hightower (2007) found that all GRS tagged with pop-up satellite archival tags (N = 7) made rapid ascents to minimum depths of 0–5 m while in the ocean. Ascents from >40 m to the surface were typically made in 3–5 min. The elapsed time for ascents increased with increasing starting depth, ranging from 2 min at starting depths of 29 m to 11 min for starting depths of 111 m (Erickson and Hightower, 2007). These rapid ascents likely result in GRS breaching the ocean surface; fishermen have reported observing GRS breaching in nearshore ocean waters and GRS are known to breach the surface while in fresh water (D. L. Erickson, Oregon Department of Fish and Wildlife, Newport, OR, personal communication). These ascents are analogous to vertical movements made for buoyancy control by the Gulf Sturgeon (GS) *A. oxyrinchus desotoi* (N. Whitney, Mote Marine Laboratory, Sarasota, FL, unpublished data) and Chinese Sturgeon (*A. sinensis*) (Watanabe et al., 2008).

In WA estuaries (e.g., Grays Harbor, Willapa Bay), adults and subadults were captured in the deepest available habitats, but made forays over mud flats to feed (O. Langness, Washington Department of Fisheries, Vancouver, WA, unpublished data). Acoustic-tagged adults and subadults in the San Francisco Bay estuary primarily occupied waters less than 10 m depth, either swimming near the surface or foraging along the bottom (Kelly et al., 2007). Likewise, juveniles in the Sacramento Delta were captured primarily in waters 1–3 m deep, where they presumably were foraging (Radtke, 1966). In laboratory experiments, juveniles have been observed to stay near the bottom during the day and use shallower portions of the water column at night (Kynard et al., 2005). Adults in the marine environment were also more active and occupied shallower depths at night than during the day (Erickson and Hightower, 2007).

Food resources

Limited data exist on food resources for GRS in freshwater. Based on surrogate information from nutritional studies on

WS, juveniles most likely feed on seasonally-abundant drifting and benthic invertebrates, such as amphipods, bivalves, and dipteran larvae (Schreiber, 1962; Radtke, 1966). Such items are also major food items of juvenile Shovelnose Sturgeon *Scaphirhynchus platyrhynchus* and Pallid Sturgeon *S. albus* in the Missouri River (Gerrity et al., 2006; Wanner et al., 2007), as well as Lake Sturgeon *A. fulvescens* in the St. Lawrence (Nilo et al., 2006), WS in the lower Columbia (Muir et al., 2000), and GS in the Suwannee River (Mason and Clugston, 1993; Sulak et al., 2012). These seasonal food resources are probably important during the summer downstream migration, when temperatures support active juvenile foraging, growth, and development. Although juveniles (<75 cm TL) are opportunists, their diet shifts to larger benthic food items such as mysid shrimp and amphipods (*Corophium*) when they enter estuaries (Radtke, 1966).

Subadult and adult GRS (>75 cm TL) are secondary consumers and opportunistic predators of fish, macrocrustaceans and bivalves in subtidal, and intertidal habitats. Radtke (1966) identified *Corophium* sp. (amphipods) and *Neomysis* sp. (opossum shrimp) in stomachs of GRS from the San Francisco Delta. Stomach contents of GRS from San Pablo Bay contained a diversity of food items including *Corophium* sp. and *Photis californica* (amphipods), *Crangon franciscorum* (Bay shrimp), *Macoma* sp. (clam), *Synidotea laticauda* (isopod), *Neomysis* sp. (mysid shrimp), and unidentified crab and fish (Ganssle, 1966). In Willapa Bay, GRS gut contents included macrocrustaceans (*Neotrypaea* sp., *Upogebia pugetensis*, and *Crangon* sp.), bivalves, and benthic fishes (Dumbauld et al., 2008).

Shallow pits in intertidal areas are created when GRS feed on benthic infauna (Dumbauld et al., 2008). In Willapa Bay, WA, GRS feeding pit density was surveyed over both intertidal and subtidal areas where GRS congregate (M. L. Moser, NMFS, Seattle, WA, unpublished data). Feeding pit densities were highest in mid-summer over intertidal muddy substrates with high densities of Pacific ghost shrimp *Neotrypaea californiensis*. Ghost shrimp have also been indicated as major prey of GS in Choctawhatchee Bay (e.g., Fox et al., 2002).

As is the case for adults of other sturgeon species, GRS adults appear to exhibit trophic dormancy during summer residence in rivers (Mason and Clugston, 1993; Gu et al., 2001; Sulak et al., 2007). While most GRS stomachs sampled from the Rogue River in summer were empty, one specimen (capture date unknown) had the exoskeleton of a crayfish (*Pacifastacus* sp.) as well as algae in its digestive tract (Farr and Kern, 2005). Whether subadults feed during excursions into freshwater is unknown.

Ontogenetic migrations

Laboratory studies have been used to investigate migration in early life stages of GRS. Eggs are not strongly adhesive until fertilized and apparently sink into substrate interstices for incubation (Van Eenennaam et al., 2012). Once exogenous feeding begins, larvae undergo a 12-day nocturnal downstream migration (Kynard et al., 2005). In the laboratory, post-migrant juveniles continued to forage and were most active at

night. They resumed nocturnal downstream migration between days 110–181 and ceased when water temperature decreased to 8°C (Kynard et al., 2005). This may represent the thermal threshold for onset of wintering behavior.

Behavioral choice experiments with older YOY (200–220 days post hatch, 44 cm TL) indicated that, regardless of acclimation history, GRS of this size sought out the most saline water available (Poletto et al., 2013). This suggests that YOY are likely to enter estuaries within the first year. Little is known about movements of juveniles (<60 cm TL) within estuaries.

Movement within and between estuaries by subadult and adult GRS has been intensively studied using acoustic telemetry. In the San Francisco estuary, Kelly et al. (2007) observed an average ground speed during directional movement of 2.01 km h⁻¹ (range 0.00–7.92 km h⁻¹). Mean ground speed was slower (0.76 km h⁻¹; range 0.00–6.98 km h⁻¹) during non-directional movement. Within Willapa Bay (Fig. 2), maximum rates of movement between fixed-site receivers ranged 0.5–2.3 km h⁻¹ (Moser and Lindley, 2007). In both estuaries, GRS moved during day and night. Maximum rates of movement between Willapa Bay and the Columbia River were 12 km d⁻¹ (Moser and Lindley, 2007). Southward movements in the coastal ocean were faster than northward ones, with a maximum migration rate of 58 km d⁻¹ (Lindley et al., 2008).

No straying has been observed between meta-populations of acoustic-tagged GRS subadults and adults. However, GRS tagged in the Rogue River have been observed to enter the Klamath River and vice-versa, suggesting some between-basin mixing within the northern DPS (D. Erickson, ODFW, Newport, OR and B. McCovey, Yurok Tribe, Weitchpec, CA, unpublished data). No tagged GRS from the Sacramento drainage has been detected in the upper reaches of a northern river (Lindley et al., 2008, 2011). The presence of vitellogenic females and pre-meiotic males during spring spawning migration in the Rogue River and vitellogenic females during the fall migration suggests that some non-reproductive adults engage in test spawning runs (Webb and Erickson, 2007).

Adult riverine movements can be categorized into discernible patterns: upstream spawning migration in spring, downstream migration by some fish in spring, holding in summer, and downstream migration after summer holding (Benson et al., 2007; Heublein et al., 2009). In the upper Sacramento River, ground speeds ranged 0.54–2.05 km h⁻¹ (mean 1.19 km h⁻¹) during directed upstream spawning migration, and these movements were often interspersed with periods of milling and holding (Thomas et al., 2014). However, these fish were tracked immediately after tagging and may have exhibited some responses to handling. In the Klamath River, spawning migration rates ranged between 0.05–0.09 km h⁻¹ (Benson et al., 2007). In the lower Rogue River, average upstream migration rates for two individuals were 0.15 and 0.47 km h⁻¹ (Erickson and Webb, 2007). These slower ground speeds recorded in the Klamath and Rogue rivers were not based on continuous mobile tracking and probably included periods of milling and holding observed by Thomas et al. (2014).

Benson et al. (2007) recorded ground speeds of downstream migrants bearing acoustic transmitters and reported mean spring migration rates of 0.21 km h⁻¹ (range 0.02–0.32 km h⁻¹) for males and 0.23 km h⁻¹ (range 0.11–0.46 km h⁻¹) for females. However, the authors caution that this behavior may have been affected by tagging and handling. After holding for the summer, Klamath River GRS moved seaward at mean rates of 0.75 km h⁻¹ for males and 1.72 km h⁻¹ for females. These movements were initiated after the first major flow event of the season, with some individuals exiting as late as December (Benson et al., 2007). Most downstream migration in the Rogue River occurred from October through December, when flow increased and water temperature decreased (Erickson et al., 2002).

Reproduction, spawning, early life history

As is the case for all sturgeon species, the GRS is long-lived, late maturing, and typically does not spawn every year (Boreman, 1997). Males mature earlier and have smaller body sizes and shorter life spans than females (Van Eenennaam et al., 2006; Erickson and Webb, 2007). For example, adult GRS captured in the Rogue River had a mean FL of 175 cm for females and 159 cm for males, while mean TL was 190 cm for females and 172 cm for males (Webb and Erickson, 2007). No statistically significant differences were found between FL or TL and stage of maturity for either sex. The spawning interval for females ranges 2–4 years, while males seem to spawn at higher frequency, potentially every 1–3 years (Erickson and Webb, 2007; Lindley et al., 2008; Heublein et al., 2009). In the Sacramento River, mean spawning interval for both sexes was 3.9 years (N = 48, range 2–6 years; D. Woodbury, NMFS, Sacramento, CA, unpublished data).

Female GRS presumably hold their eggs in an advanced stage of ovarian maturation until spawning is stimulated by optimal water temperature and the presence of males (Van Eenennaam et al., 2001, 2008, 2012). There have been no observations of ovarian atresia in any riverine-captured fish on the Klamath or Rogue rivers (Van Eenennaam et al., 2006; Webb and Erickson, 2007). Fecundity is lower (59 000–242 000 eggs; Van Eenennaam et al., 2006) than for many other sturgeon species, but egg size is large (4.2–4.5 mm diameter; Deng, 2000).

Both field and laboratory studies have been used to document spawn timing and egg incubation and hatching. Like many sturgeon species, GRS exhibits wide variation in the spawning period, with spawning documented from April through June depending on temperature and flow conditions (Erickson et al., 2002; Van Eenennaam et al., 2005; Poytress et al., 2015; Seesholtz et al., 2015). The free embryos hatch after approximately 1 week at 12.6–14.5 mm and begin first feeding at 10–16 days of age (Van Eenennaam et al., 2001; Deng et al., 2002; Gisbert and Doroshov, 2003). In laboratory experiments, larvae deprived of food exhibited progressive deterioration of the digestive system, with the first pathological signs after 5 days (at 16°C) and severe atrophic changes after 10–15 days (Gisbert and Doroshov, 2003). This indicates that larvae have a period of approximately

4–5 days, depending on water temperature, to find exogenous food sources before they reach the point of no return, similar to Chinese Sturgeon (Chai et al., 2011).

The growth of larvae and early YOY (~0.1–10 g) appeared to be temperature independent between 19 and 24°C (Allen et al., 2006b). Specific growth rate, wet weight, and TL were all greater for fish at temperatures >24°C and when temperature was cycled between 19 and 24°C than for fish held at a constant temperature of 19°C. Thus, it seems that elevated and cycling temperature does not have adverse effects on juveniles if food is abundant and dissolved oxygen levels are suitable. Post-migrant larvae and early juveniles forage during both day and night with a nocturnal activity peak (Kynard et al., 2005).

External biology/functional morphology

Green Sturgeon exhibit egg and larval morphologies that equip them for benthic life among cobble or boulders in fast-moving streams or rivers (Kynard et al., 2005). Green and WS often occur in the same drainages, but clearly rely on different early life history strategies. The GRS eggs are larger (4.2–4.5 mm diameter) and denser than WS eggs (3.4–3.6 mm diameter), indicating that they do not drift far and are adapted to sink into the crevices between rocks (Van Eenennaam et al., 2001; Deng et al., 2002; Kynard et al., 2005). At first feeding (10–16 days of age) GRS larvae are also larger (23.0–25.2 mm) than WS larvae (17.3–19.0 mm; Deng et al., 2002).

Juvenile GRS are easily distinguished from WS in that they have the distinctive green color and dark mid-ventral stripe by 45 days of age. They also exhibit a smoother appearance and lack the bony grains and platelets on the head and trunk that give metamorphosed WS a rugose appearance (Deng et al., 2002). Juvenile GRS have proportionately large pectoral fin surface areas and display behaviors (including rostrum wedging and pectoral fin holding) that support station holding in high flow velocity riverine environments (Adams et al., 1997, 2007; Allen et al., 2006a).

Swimming ability has been measured in juvenile GRS. Allen et al. (2006a) examined GRS capacity for sustained swimming in a swim chamber during a series of increasing water velocities. Critical swimming ability (U_{crit}) was also measured and defined as the speed at which the fish is exhausted after incremental increases in the flow. They found that swimming performance increased with size in YOY of 120–266 mm TL ($U_{crit} = 25.5\text{--}62\text{ cm s}^{-1}$) prior to seawater transition, supporting the hypothesis that GRS juveniles migrate to estuaries in their first fall (Kynard et al., 2005). However, swimming performance decreased with size in juveniles of 267–475 mm TL ($U_{crit} = 26.5\text{--}54.5\text{ cm s}^{-1}$) at the same time that salinity tolerance increased. Juveniles of 267–787 mm TL had a mean U_{crit} of $80.4 \pm 16\text{-cm s}^{-1}$ (Mayfield and Cech, 2004; Verhille et al., 2014).

Internal biology

Green Sturgeon exhibits a higher metabolic rate compared to other sturgeon (Mayfield and Cech, 2004), starting with the

endogenous larval feeding phase. Concomitant with organogenesis and conversion of the yolk sac into new tissues, there is a five-fold increase in oxygen consumption (Gisbert et al., 2003). Oxygen consumption continues to increase in exogenously feeding larvae in proportion to the increase in larval weight (Gisbert et al., 2003). This relationship reflects the need for increased energy expenditure for maintenance and activity and the energetic costs associated with proportionally larger red muscle mass (Moyle, 2002; Mayfield and Cech, 2004). Increased oxygen consumption may indicate that juvenile GRS can tolerate elevated summer river temperatures, despite the increased energy cost, if food supply is adequate (Allen et al., 2006b; Verhille et al., 2015).

Rates of oxygen consumption are independent of body mass, although more oxygen is consumed with increasing body length, as GRS attain sizes large enough to enter seawater (1.5 years, Allen and Cech, 2007). Both iono- and osmoregulation improves in GRS with age and size; they enter and osmoregulate in seawater at an earlier age than most sturgeon species (Allen et al., 2011; Haller et al., 2015). Allen et al. (2011) also documented endocrine and enzyme upregulation by juvenile GRS held in freshwater as they prepared for seawater entry. They speculated that this preparatory period was stimulated by natural photoperiod.

Studies on migration of adults to spawning locations have yielded some novel information, including the observation that non-reproductive individuals make this migration. On the Rogue River, 95% of females and 88% of males appeared reproductively active or had recently spawned during April to July (Webb and Erickson, 2007). In that study, vitellogenic females and pre-meiotic males (both non-reproductive adult developmental stages) were also observed in freshwater during the spring (Webb and Erickson, 2007). Female and male GRS captured during fall in the Rogue River showed signs of gonadal tissue repair, with 29 and 44% pre-meiotic, respectively. This indicated that by fall, GRS had already initiated their next gametogenic cycle (Webb and Erickson, 2007).

Genetics

Green Sturgeon is one of two acipenserids that inhabit the northeast Pacific biogeographic province, the other being the WS (Bemis and Kynard, 1997). These two species have an ancestral relationship to species of the Amur River, Sea of Okhotsk, and Sea of Japan northwest Pacific biogeographic province (Bemis and Kynard, 1997; Krieger et al., 2008). Sturgeon inhabiting both of these biogeographic provinces diverged from other acipenserid clades between 55 and 141 million years ago (95% credibility intervals; Peng et al., 2007). More recently, the GRS has been estimated to have diverged from its sister species, the Sakhalin Sturgeon, between 0.5 and 29.5 million years ago (Peng et al., 2007).

As is the case for most sturgeon species, GRS exhibit homing to their natal river. Genetic structure of GRS from WA, OR, and CA was confirmed by analysis of six microsatellite loci developed from published primers (Israel et al., 2004). There was no genetic differentiation between the Klamath and Rogue River collections. However, there

was a significant difference between collections from the northern meta-population (Rogue and Klamath rivers) and the estuarine collections. These data, and subsequent genetic and acoustic telemetry evidence, suggest that there is mixing between the Rogue and Klamath river GRS in saline habitats, but that fish spawning in the southern meta-population Sacramento River are genetically distinct (Israel et al., 2009; Lindley et al., 2011). The genetic analysis displayed additional genetic structure indicating that additional spawning populations remain to be identified (Israel et al., 2004).

Fisheries and impacts

Historically, thousands of GRS were harvested annually as bycatch in commercial, recreational, and tribal fisheries for WS and salmonids (Adams et al., 2007). Even in the last few decades, these fisheries have taken large numbers of GRS and have been cited as factors in the decline of the species (NMFS 2006). For example, from 1985 to 1993, the harvest of GRS in commercial fisheries in the Columbia River and in WA ranged from 3000 to over 7500 fish per year (Adams et al., 2007). Between 1994 and 2003, GRS harvest in some fisheries decreased, due in part to reduced fishing effort (Fig. 3; Adams et al., 2007). Upon ESA listing of the GRS southern DPS in 2006, commercial sale of GRS was prohibited in WA and all Columbia River fisheries. Commercial sale of GRS was prohibited throughout OR in 2010.

Contemporary changes in harvest management are likely to conserve GRS in river and estuarine environments. In-river retention fisheries have been eliminated in all western states. Natural resource agencies in WA, OR, and CA have adopted permanent rules (2007–2010) to prohibit retention of GRS in recreational fisheries. The California Fish and Game Commission also implemented a sturgeon report card system to evaluate the impact of this rule on GRS take in CA. Data collected from returned sturgeon report cards showed 311 and 215 GRS caught in 2007 and 2009. Effective

March 1, 2010, fishing for GRS or WS was prohibited year-round in the upper main-stem Sacramento River (RKM 283–485) to protect spawning adult GRS.

Hoopa and Yurok tribal harvest of GRS in the Klamath River occurs primarily during the spring spawning migration. The number of fish taken ranged 127–810 in the period from 1981–2003 (Adams et al., 2007) but there are no tagging or effort data associated with these takes. GRS are rarely captured during summer or on spawning grounds. Heppell and Hofmann (2002) reported that almost all fish captured in Klamath River gillnet operations were ripe or spawned adults and that juveniles rarely occur in this fishery. To check for evidence of poor recent recruitment to the spawning population, Heppell and Hofmann (2002) looked for a decrease in the proportion of small adults in the Klamath River catch during 1 April to 31 July in 1984–2001. They found no significant trend in the proportion of adult GRS less than 170 cm (Heppell and Hofmann, 2002).

The Yurok Tribe has recently experimented with new regulations for their tribal subsistence harvest that reduce impacts on GRS. This fishery is conducted in a 71-km stretch from the Klamath River mouth to its confluence with the Trinity River. It is regulated to a bag limit of one sturgeon per day in season, with retention of only fish less than 1.8 m. Recently the tribal council has experimented with different combinations of rules in an attempt to find the most effective methods to promote conservation while still allowing tribal harvest. The fishery is closed 3–4 days each week to protect spring Chinook salmon, and other regulations include sturgeon holding area closures, gear restrictions, and handling protocols.

In Canadian waters, GRS appears to be regularly intercepted in fisheries around Vancouver Island. Lindley et al. (2008) noted that the relatively warm, shallow, and productive areas north of Vancouver Island, in Queen Charlotte Sound and in Hecate Strait (Fig. 1) may be important overwintering areas. In US coastal waters, Payne et al. (2015) detected GRS near the Umpqua River estuary year-around,

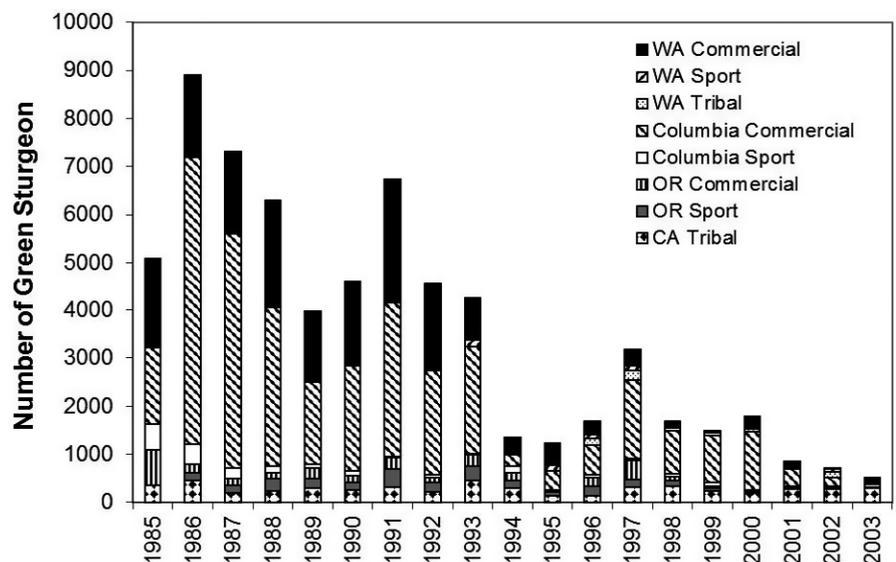


Fig. 3. Fishery data for Green Sturgeon. Washington commercial (mostly gillnet), recreational, and tribal treaty harvest, OR commercial (trawl) and recreational catch, and CA tribal (Yurok and Hoopa) harvest. Adapted from Adams et al. (2007)

with highest concentrations occurring during winter–spring months. This information suggests that where GRS aggregate, they may be particularly vulnerable to fishing mortality.

Green Sturgeon are captured in commercial and tribal coastal gillnet and trawl fisheries in the coastal US. They are regularly reported as bycatch in trawl fisheries, including the California Halibut (*Paralichthys californicus*) fishery. Al-Humaidhi et al. (2012) provided estimates for GRS bycatch based on GRS discards reported by West Coast groundfish observers. The fisheries were divided into those that target California Halibut (state managed trawl fishery that typically operates in less than 30 fathoms (55 m) and south of 40° 10'N, both limited-entry and open-access fisheries) and federally managed limited-entry bottom trawl fisheries targeting groundfish, as identified in the Pacific Coast Groundfish Fishery Management Plan (PFMC, 2016; Fig. 4). Beginning in 2011, an Individual Fishing Quota (IFQ) program was implemented for the limited entry shore-side trawl sector, whereas a system of regulated cooperatives was developed to manage the at-sea Pacific whiting sectors. Under these federal groundfish trawl rationalization programs, both shore-side and at-sea sectors require 100% catch monitoring by human observers or electronic monitoring (PFMC, 2016).

Because observers were not present on all vessels prior to 2011, Al-Humaidhi et al. (2012) extrapolated the observed bycatch rate fleetwide to estimate total bycatch of GRS in all fisheries. Al-Humaidhi et al. (2012) found that GRS bycatch is greatest in the limited-entry sector of the California Halibut trawl fishery, and that far fewer GRS are captured in other groundfish fisheries (Figs 4 and 5). Since 2011, Lee et al. (2015) reported no fleetwide GRS bycatch in the IFQ groundfish fishery in WA and CA waters. However, the estimated fleetwide GRS bycatch for the groundfish fishery in OR waters was 37 in 2011, 21 in 2012, and 10 in 2013 (Lee et al., 2015). For the California Halibut fishery, fleetwide GRS bycatch estimates were 30 in 2011, 80 in 2012, and 526 in 2013 (Lee et al., 2015).

Prior to 2002, GRS were regularly captured in relatively shallow-water (<110 m) groundfish bottom trawls off OR and WA (Erickson and Hightower, 2007). Although GRS is susceptible to bottom trawls, groundfish trawl captures decreased between 2002 and 2010 (Al-Humaidhi et al., 2012). Green sturgeon occurrence in these groundfish trawl fisheries was likely affected by several factors: (i) implementation of rockfish conservation areas within which trawlers cannot fish, (ii) reduction in trawling effort due to the vessel buyback program, (iii) requirement for groundfish trawlers to use a low-rise “selective flatfish trawl” on the shoreside of rockfish conservation areas (e.g., shallow waters) north of 40° 10'N latitude, and (iv) reduced targeting of GRS aggregations.

The limited-entry sector of the California Halibut trawl fishery occurs primarily in relatively shallow water near San Francisco and Monterey bays, so it is likely that fish taken in these fisheries are from the Sacramento River (Lindley et al., 2008, 2011). Green Sturgeon captures were recorded by observers in both summer and winter. Numbers of fish handled by observers ranged widely within a season and between years. This likely reflects varying amounts of fishing effort, changes in fish abundance, and observer distribution. However, observed bycatch in 2013 sharply increased (46 GRS observed), and resulted in the third highest annual fleet-wide total bycatch estimate for the period 2002–2013 (Lee et al., 2015).

Starting in 2007, the fishery observers were instructed to measure and take photographs and genetic samples from captured GRS. Data from sturgeon measured in 2007–2010 (N = 82) indicates that fish caught in California Halibut trawls are typically small (≤ 1.2 m TL; Fig. 6) (Al-Humaidhi et al. 2012). It is probable that larger adults are able to escape this gear or are uncommon in the trawling area. Future sampling will help to determine the sizes of GRS that are most vulnerable to this gear. In addition, genetic sampling will identify which GRS populations may be most impacted by each fishery.

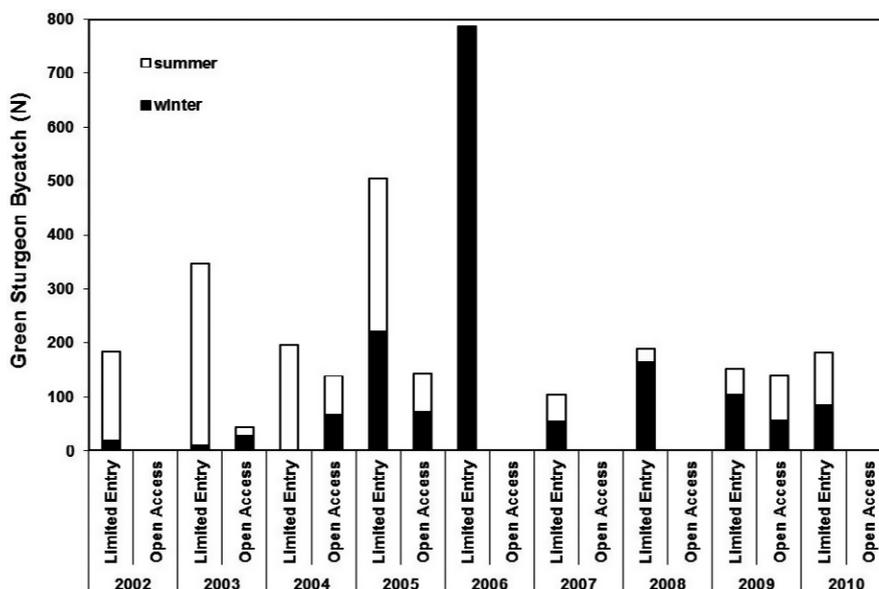


Fig. 4. Estimated Green Sturgeon bycatch in California Halibut fisheries by fishery type and season between 2002 and 2010. Data from Al-Humaidhi et al. (2012)

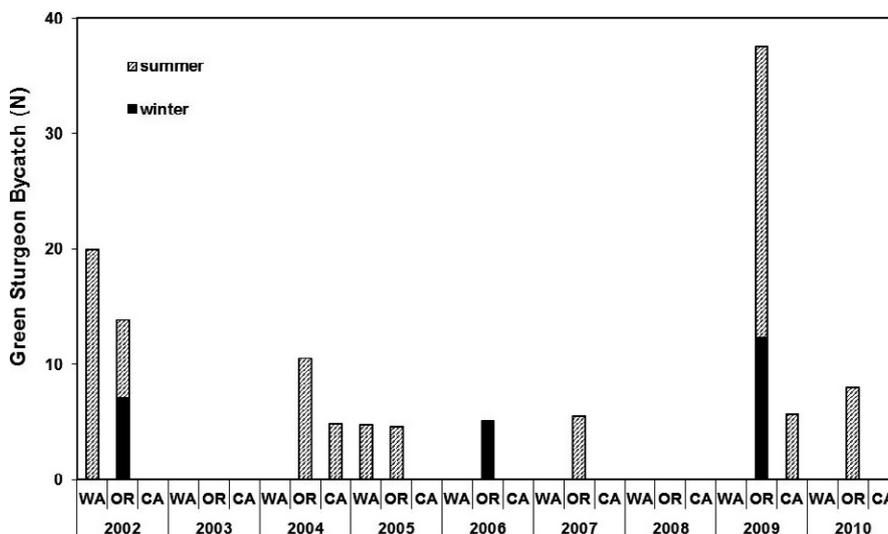


Fig. 5. Estimated Green Sturgeon bycatch from other bottom trawl fisheries (excludes California Halibut trawls). Data from Al-Humaidhi et al. (2012)

Discard survivorship for GRS caught in trawls is unknown, but the stress of capture may lead to delayed effects (Lankford et al., 2003, 2005). Sub-lethal effects of capture are difficult to assess, as they may involve disruption of feeding or migratory activity, reduced growth, or even reproductive failure. Another unknown is resilience of individual GRS to repeated handling. Repeat captures may inflate bycatch estimates and observer marking studies are needed to resolve the degree to which re-captures occurs in individual fisheries.

Major anthropogenic habitat impacts

Habitat alteration

Dams limit GRS access to historical spawning habitats and alter the hydrograph. Mora et al. (2009) constructed a model

of GRS habitat requirements using data from known GRS occupancy in the Rogue and Klamath rivers. This model was then used to predict habitat loss in the Sacramento River drainage that is attributable to dams. The model predicted that in the absence of impassable dams and altered hydrographs, GRS would occupy the upper main-stem Sacramento and San Joaquin rivers, and several major tributaries including portions of the lower Feather River, American River, and Yuba River (Fig. 3). Dams block access to about 9% of historically-available habitat in the Sacramento River Basin, but it is likely that these inaccessible areas contained prime spawning habitat (Mora et al., 2009).

Dams can alter timing of spawning runs, reduce habitat suitability for eggs and larvae, and/or directly reduce survival and recruitment. For example, in the Sacramento River, Red Bluff Diversion Dam (Fig. 3) historically blocked upstream

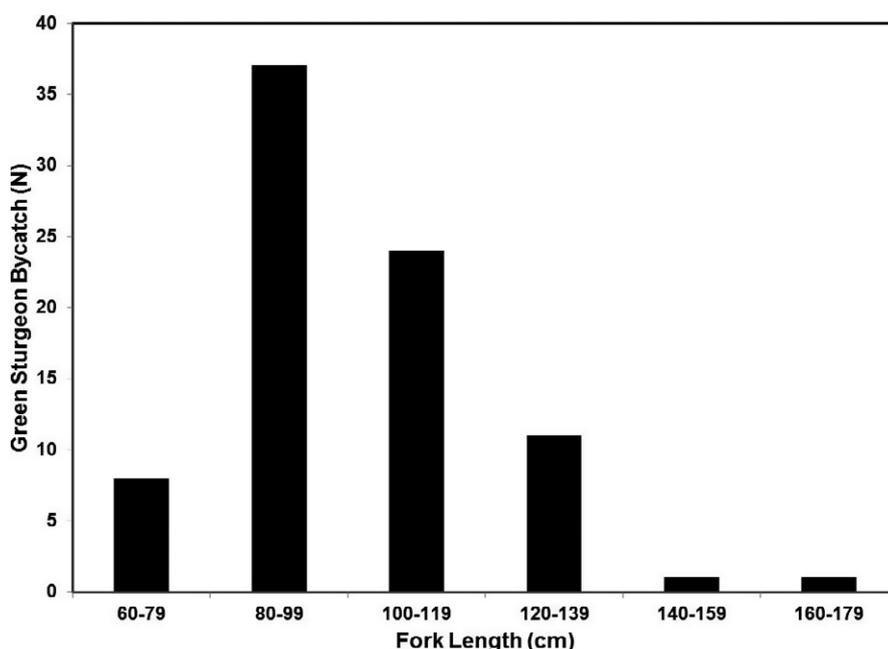


Fig. 6. Size distribution (FL) of Green Sturgeon measured by California Halibut trawl observers in 2007–2010. Data from Al-Humaidhi et al. (2012)

migration of GRS when the gates were lowered annually to impound water (Brown, 2007; Heublein et al., 2009). As a mitigation measure, gates were raised from 15 September to 15 May each year to allow fish passage and to release water to protect and restore spawning and rearing habitats downstream. In 2007, the gates were raised partially between 18 May and 10 June 2007 to accommodate migrating spring-run Chinook Salmon after a dry winter. Thereafter, carcasses of 10 adult GRS (168–226 cm TL) were found at the dam ($n = 2$) and immediately downstream ($n = 8$). Locations of the retrieved carcasses and necropsy results suggested that mortalities resulted from injuries inflicted by the gates. That is, migrating GRS adults were apparently injured either in the course of traversing the gates or when the gates were in the process of closing. Since this incident, the gates have been permanently raised to protect GRS.

In the Sacramento River, water management to restore Chinook Salmon populations may also be affecting temperatures needed for GRS spawning and rearing. To mitigate for effects of dams on salmon, cold water releases are made in spring and summer that alter the normal temperature profiles in prime GRS spawning and rearing habitats in the Sacramento River main-stem. The resulting period of prolonged, artificially-low water temperature may extend the spawning period, reduce growth of larvae and juveniles, and delay seaward migration of adults after spawning (D. Woodbury, NMFS, Sacramento, CA, personal communication).

Egg incubation and rearing of GRS larvae and juveniles may also be affected by increased fine sediment deposition, isolation of low velocity side channels, direct removal or alteration of substrate, and/or obstruction of downstream migration. Increased fine sediment input results from logging, farming, grazing, mining, and bridge and road construction. Suspended and deposited sediment reduces survival and successful development of eggs and embryos of salmonids and other fish species (Scrivener and Brownlee, 1989; Owens et al., 2005) and the effects on GRS eggs and embryos are likely to be similar. Excess fine sediments bury eggs, reducing interstitial dissolved oxygen (Scrivener and Brownlee, 1989), impeding removal of waste carbon dioxide, and filling interstitial spaces used by developing free embryos.

Large scale filling or isolation of split channels and intermittent waters may destroy or block access to rearing habitats, or impede or delay downstream migration by trapping juveniles that have entered these areas. Structures that function to fill in or isolate these areas include tide gates, flood weirs, culverts, and road crossings. Direct removal (dredging and gravel/sand mining) or alteration of substrate impacts both spawning and rearing habitats. Green Sturgeon use specific substrate types at different life stages and removal or disturbance of riparian areas near spawning habitats may reduce early survival. In addition, stranding of adults in altered channels may affect the spawning migration or even the survival of pre-spawning adults (Thomas et al., 2013).

Entrainment and impingement risks

Water diversions, power generating projects, and dredge activities each pose entrainment and impingement threats to

GRS. There are hundreds of unscreened water diversions in the Sacramento River and Sacramento-San Joaquin Delta (Herren and Kawasaki, 2001; Mussen et al., 2014). Laboratory testing indicated that young (<30 cm TL) GRS contacted and were impinged on screens two times more frequently than young WS (Poletto et al., 2014a,b). However, a study of fish entrainment at an unscreened diversion in the Sacramento River did not report any GRS, even though individuals of other fish species ranging 9–59 mm FL were observed during July 2000 and 2001 (Nobriga et al., 2004). Laboratory simulations indicated that the probability of entrainment for GRS of around 35 cm FL would be 52% when passing within 1.5 m of an intake at least three times (Mussen et al., 2014). The authors note that entrainment related GRS mortality could be substantially decreased if water extraction rates were decreased.

Entrainment of juvenile GRS has been documented periodically at state and federal fish facilities in the south Sacramento-San Joaquin Delta, where fish are salvaged before they enter the pumps (Adams et al., 2007). Installation of positive fish screens, adjustment in timing of operations, and continued fish salvage operations may minimize entrainment-related mortality. Evidence exists for the impingement of GRS in the operation of coastal power plants using cooling water intake systems. Two impinged juvenile GRS died on cooling water intake screens at the now-retired Contra Costa Power Plant in 1978–1979 and at the Moss Landing Power Plant in 2006 (C. Raifsnider, Tenera Environmental, Lafayette, CA, personal communication).

Dredging operations in rivers, bays, and estuaries where GRS occur may pose entrainment risk. Although entrainment of GRS in dredging operations has not been documented, it probably occurs. For example, approximately 2000 juvenile WS were entrained during operation of a large suction dredge in the lower Columbia River (Buell, 1992); risks could be similar for GRS. Long-term management strategies for dredging operations have established regional environmental work windows, or periods of time when listed fish species are not likely to be present. However, GRS typically reside in estuarine areas during these work windows, making such risk amelioration strategies ineffective for them. Other strategies to reduce potential dredging risks could include the use of dredging equipment with fish-friendly designs and real-time monitoring to adapt dredging operations to avoid areas of GRS aggregation.

Non-native species introductions

Non-native species are a continuing problem in freshwater rivers and coastal bays and estuaries and may affect GRS. Introduced striped bass (*Morone saxatilis*) in the Sacramento River and the Sacramento-San Joaquin Delta may prey on young GRS. Non-native species may also replace GRS prey and/or result in greater bioaccumulation of contaminants. For example, the Asian Clam (*Potamocorbula amurensis*), a non-native bivalve, has become widespread in the San Francisco Bay and the Sacramento-San Joaquin Delta and has replaced other common prey items for WS. Asian clam is an efficient bioaccumulator of selenium, a reproductive toxin

that causes deformities in embryos and reduced hatchability of eggs, and has been linked with increased selenium levels in WS (Linville et al., 2002; Linville, 2006; Linares-Casenave et al., 2015). Asian clam has also been identified in the gut contents of at least one GRS (Kogut, 2008).

Non-native species may also alter sturgeon habitat or compete with sturgeon for space or food. For example, the non-native Japanese eelgrass *Zostera japonica*, has proliferated in many estuaries and functions to bind sediments, thereby reducing GRS unvegetated sand feeding habitat (K. Patten, Washington State University, Vancouver, WA, unpublished data). Although existing laws prohibit the release of non-native species into the environment, accidental and intentional introductions of non-native species remain a problem. Eradication programs for non-native species, increased public education and outreach, and increased fines or penalties for the release of non-native species would help to alleviate this problem.

Pesticides and discharge of pollutants

Green Sturgeon occupies waterways where pesticides are regularly applied and may be adversely affected by long-term sublethal effects that reduce growth and reproductive success (Lee et al., 2011, 2012; Silvestre et al., 2010; De Riu et al., 2014). Several pesticides have been detected in the Sacramento River Basin at levels that are likely to be harmful to aquatic life (Domagalski et al., 2000). Accumulation of industrial chemicals and pesticides such as polychlorinated biphenyls (PCBs), dichloro-diphenyl-trichloroethanes (DDTs), and chlordanes in WS gonad, liver, and muscle tissues affects growth and reproductive development and results in lower reproductive success (Fairey et al., 1997; Foster et al., 2001a,b; Kruse and Scarnecchia, 2002; Feist et al., 2005; Greenfield et al., 2005). Green Sturgeon may experience similar risks from contaminants, although exposure may be reduced by metabolic depuration during the extended residence of subadults and adults in marine waters.

Pesticides may also either directly or indirectly affect GRS through effects on their prey. For example, GRS enter Willapa Bay, where they may feed on burrowing Bay ghost shrimp (*Neotrypaea californiensis*; Dumbauld et al., 2008). Oyster culture operations in this area control ghost shrimp abundance by direct application of the pesticide carbaryl, with unknown consequences to GRS or their feeding habitats (Moser and Lindley, 2007). Plans are currently in place to phase out use of this pesticide in Willapa Bay and replace it with the neonicotinoid insecticide imidacloprid, which acts on the central nervous system of crustaceans (Frew and Grue, 2012; Frew 2013). Laboratory and field experiments indicated that GRS can take up this chemical through both contaminated pore water or via ingestion of shrimp tissue, with unknown consequences to fish health. Field evidence suggests that GRS are actually attracted to areas that have been treated with imidacloprid, due to the activity of dying shrimp (K. Patten, Washington State University, Vancouver, WA, unpublished data).

Whether national standards for use of pesticides and toxic substances are conservative enough to protect long-lived

fishes like GRS is unknown. Recent jeopardy biological opinions were issued by NMFS to the EPA due to inadequate regulation of harmful pesticides impacting salmonids (NMFS 2000, 2008, 2009b). Thus, programs to assist land managers in attaining NMFS-imposed water quality standards for salmonids may similarly be required to minimize adverse impacts to GRS.

Poaching

Poaching for meat and eggs is a potential threat to GRS throughout its range. In recent years, arrests have been made for illegal harvest of WS in the Sacramento River (CDFG, 2010), Sacramento-San Joaquin Delta (CDFG, 2010), and lower Columbia River (Cohen, 1997). Poachers were convicted for the 2008 take of a gravid female GRS in the Feather River (D. Woodbury, NMFS, Sacramento, CA, personal communication). Increased public outreach and awareness, increased fishery evaluation and enforcement, and heavier sentences and fines for poachers may increase protection of GRS.

Research and monitoring activities

Collection or handling associated with scientific research and monitoring, if not done properly, may result in GRS stress, injury, or mortality. Recent research and monitoring effort has involved tracking the movements and habitat use of subadult and adult GRS by using a variety of tagging techniques. In addition, tissue samples have been taken to identify DPS of origin or natal river. Empirical results from GRS field investigations indicate that netting, tagging, tissue sampling, and telemetry research, when done according to accepted protocols, results in minimal short-term stress (Erickson and Hightower, 2007; Kelly et al., 2007; Moser and Lindley, 2007). The protocols for handling and use of sturgeon can help to minimize handling effects while providing standard, comparable methods for researchers (Damon-Randall et al., 2010; Kahn and Mohead, 2010).

Habitat restoration

The primary purpose of habitat restoration is to re-establish self-sustaining habitats that resemble natural conditions in terms of structure and function. To re-establish natural GRS habitat function, a variety of restoration activities will be needed. These include barrier removal or modification to restore natural water flows, river and estuarine bed restoration, natural bank protection, restoration of native vegetation, removal of non-native species, and removal of contaminated sediments. Although GRS mortalities may occur during restoration activities, none have been reported thus far.

Stochastic natural impacts

Green Sturgeon lives in highly dynamic environments that are subject to occasional catastrophic disturbance. Lindley et al. (2007) considered sources of catastrophic disturbance

in the Sacramento River basin in the context of salmonid conservation. Risks identified there are likely similar to those in the Rogue and Klamath basins, which also drain the Cascade Range, an area of active volcanism. Headwaters of the Rogue River (Fig. 3) arise from Crater Lake, which was created by the explosion of Mt. Mazama 7700 years ago. Presumably, GRS was present in the Rogue River at that time and the population either survived that event or subsequently recolonized the Rogue River.

While Mt. Mazama is now dormant, Mt Shasta is an active volcano dividing the upper Klamath and upper Sacramento basins. Mt. Lassen is another active volcano in the Sacramento basin. Eruption of such volcanoes can create enormous debris flows and deposition of toxic ash that can destroy anadromous fish habitat for many years over a substantial area. A recent example of this phenomenon was the 1980 eruption of Mt. St. Helens and the subsequent devastation of fish populations in the Toutle River (Jones and Salo, 1986). The eruption of Mt. St. Helens released only 1% as much material as the eruption of Mt. Mazama.

Other potential sources of catastrophic risk identified by Lindley et al. (2007) include prolonged and widespread drought, and wildfires that result in large debris flows. On the Sacramento River, temperature is regulated by water releases from Shasta and Keswick dams (Fig. 3). Hydrologic models suggest that it will be increasingly difficult to maintain cool waters during the prolonged droughts that span the GRS spawning season in some rivers or tributaries. Green Sturgeon may be relatively resilient to local catastrophic disturbance, with the bulk of the populations dispersed in the ocean and various estuaries along the West Coast. Hence, only a fraction of the population may be vulnerable to localized catastrophic disturbances with effects lasting less than decades.

Population recovery actions

In 2001, the U.S. National Marine Fisheries Service (NMFS) received a petition from the Environmental Protection and Information Center, Center for Biological Diversity, and WaterKeepers Northern California requesting that GRS be listed under the ESA with concurrent designation of critical habitat for the species. Based on genetic data and tag recoveries prior to 2006, two populations were identified for listing: GRS inhabiting the Sacramento River and its tributaries were considered the southern distinct population segment (DPS), and those spawning in the Klamath, Rogue, or any other rivers north from or including the Eel River were considered the northern DPS.

In April 2006, NMFS made a final determination regarding the ESA status of GRS (NMFS 2006). While NMFS determined that the northern DPS did not warrant listing, it was identified as a species of concern. Species of concern are those species that are at risk, but for which there is insufficient information to warrant listing under the ESA. The southern DPS was found at risk of extinction in the foreseeable future throughout all or a significant portion of its range and was therefore listed as threatened (Adams et al., 2007). Evidence for this listing determination included: (i)

information indicating that the majority of spawning adults are concentrated in one spawning river (i.e., Sacramento River), thus increasing the risk of extirpation due to catastrophic events, (ii) information that threats remain severe and insufficiently addressed by current conservation measures, (iii) evidence of lost spawning habitat in the upper Sacramento and Feather rivers, and (iv) fishery-independent data exhibiting a negative trend in juvenile GRS abundance.

In the April 2006 listing decision, NMFS concluded that the threatened southern DPS of GRS was currently at risk of extinction due to a variety of human-induced "takes". As defined in the ESA, to "take" is to harass, harm, pursue, hunt, shoot, wound, trap, capture, collect or attempt to engage in any such conduct. "Harm" includes any act that actually kills or injures GRS. This includes habitat modification or degradation that results in death or injury by significantly impairing essential behavioral patterns such as breeding, spawning, rearing, migrating, feeding, or sheltering. To "harass" is to increase likelihood of injury by annoying GRS to such an extent as to significantly disrupt normal behavior. The agency published a proposed rule in May 2009 to prohibit the take of GRS from the southern DPS and prohibitions went into effect in summer 2010. A recovery team was selected and convened in 2009 to develop a recovery plan for the southern DPS. This plan will include a threat assessment, a prioritized list of recovery actions, a set of criteria by which to gauge recovery, and a recovery implementation schedule.

In 2009, critical habitat designation for the Southern DPS identified areas within the occupied range of the species (CA/MX border north to the Bering Sea, AK) that contained physical and biological features that are essential to GRS conservation and that may require special management considerations or protection (NMFS 2009a). The rule designated critical habitat comprising approximately 515 km of riverine habitat, 2323 km² of estuarine habitat, and 29 581 km² of coastal marine habitat in and offshore from CA, OR, and WA. In addition, NMFS designated approximately 784 km² of habitat in the Sacramento-San Joaquin Delta, and 350 km² of habitat within the Yolo and Sutter bypasses (Fig. 3). The designation excluded 14 specific areas based on economic or national security impacts: Mare Island Army Reserve Center in San Pablo Bay, three naval restricted areas and one Navy operating area in the Strait of Juan de Fuca, and Indian lands owned by 12 federally-recognized tribes.

Research needs

It is essential that future studies generate population-scale information. This will require sampling to develop estimates of total population size, effective population size, age at maturity, frequency of spawning, and mortality rates for each DPS. These demographic data can be incorporated into predictive models to estimate minimum viable population size of each DPS. This type of research includes conventional mark-recapture investigations for estimates of abundance and mortality. Other methods include tagging of GRS with individually-coded passive integrated transponders, acoustic, and/or satellite transmitters; collection of biological samples

to determine population of origin, age, and reproductive condition; and investigations employing DIDSON and sidescan SONAR technologies to enumerate individuals.

The early life history remains the least investigated, especially for fish <75 cm TL in the wild. Natural mortality and larval drift need to be evaluated, as do larval feeding areas during those critical few days after the yolk has been exhausted. While laboratory experiments have been undertaken to assess suitable abiotic conditions or early life stages, this information has not been used to model energetics or assess habitat use. It is hypothesized that juveniles primarily utilize estuarine habitats and that these habitats differ substantially among river systems. Greater emphasis should be placed on studying this life stage in all natal rivers to characterize GRS habitat preferences. Continuous tracking of juvenile GRS, when combined with epibenthic and benthic sampling could elucidate prey selection and foraging behavior. Juveniles should be sampled and monitored to increase our understanding of the effects of flow, water temperature, and many other physical, chemical, hydraulic, and biological parameters on life history diversity and productivity. This is critical to the management of such watershed-scale activities as cool water releases from Shasta Dam and dam operations on the Klamath and Rogue rivers.

Studies to tag and track subadults will help determine whether their distribution and habitat use expose them to the same anthropogenic threats faced by adults. Hundreds of adult and subadult GRS have been tagged with acoustic transmitters. Further synthesis of telemetry data from these efforts will yield more complete knowledge of spawning intervals, movements, and habitat use. Such information is needed to understand the vulnerability to various threats and mortality rates associated with the subadult life stage. Characterizing patterns of habitat use in nearshore marine and estuarine waters is needed to evaluate the effects of fisheries, bottom disturbing activities, and alternative power generation facilities (e.g., water turbines, wave generation), thereby refining critical habitat designations. Additionally, the use of SONAR technology for systematically estimating abundance of GRS in each spawning river or index reach will provide data on population size and distribution.

Finally, GRS spawning success may be affected by changing environmental conditions, impediments to passage, and losses to poaching and predation (Thomas et al., 2013). Bio-engineering studies are needed to develop structures in freshwater habitats that maximize passage of migrants. Research is needed to determine the effects of contaminants and other anthropogenic effects (e.g., aquaculture, tidal energy development, climate change) on adult GRS feeding, migratory behavior and reproductive maturation/success. The effects of capture and release as bycatch in fisheries is poorly understood and is a critical research need. Finally, with recovery of marine mammal populations, there is a need to re-assess natural mortality rates in addition to capture by poachers.

Current prognosis for the Green Sturgeon

Listing of the southern DPS of GRS should be beneficial; however, the prognosis for this DPS remains unknown.

Adults are observed annually in upper Sacramento River spawning habitat. However, over a number of recent years, no juveniles were captured in downstream-migrant sampling efforts. Listing has led to increased focus on determining population abundance, the spatial distribution of various life stages, and evaluation of migratory behavior. All of this information will potentially lead to better management of stressors and reduction of risks to GRS in the diversity of habitats they inhabit.

A better understanding of population demography is needed to develop a GRS life cycle model similar to that proposed by Beamesderfer et al. (2007). In the near future, river management strategies that improve flows and water temperatures may support rebuilding of GRS populations below Shasta Dam and on suitable tributaries in the CA Central Valley (Fig. 3). Water temperatures in the Sacramento River are currently managed for restoration of Chinook salmon. Unintended negative effects of these actions on GRS spawning and rearing should be addressed. While habitat preservation and improvement is critical, management actions to control predation, poaching, and bycatch mortality are also needed.

In the Klamath and Rogue rivers, GRS from the northern meta-population continue to spawn annually (Fig. 3). River conditions seem favorable to YOY success, as juveniles are detected in downstream migrant sampling within these rivers. Levels of effort for tribal harvest data are needed to determine whether the spawning population of GRS in the Klamath River is stable. Systematic sampling (e.g. DIDSON assessments) should also be conducted to evaluate adult GRS escapement to spawning and holding habitats in the Klamath River.

A recent adult population estimation study on the Rogue River found that there were fewer fish than anticipated by researchers (Mora et al., 2015). Recent changes in harvest regulations will help to minimize GRS mortalities in rivers and estuaries. However, at the same time, managing flow and water temperatures will prove more difficult as climate change, dam operations, and water withdrawals progressively increase in the lower sections of the Klamath and Rogue rivers. Finally, a better understanding and management of losses that occur in nearshore marine and estuaries may be just as important as maintenance of adequate freshwater habitats for this, most marine-oriented of all North American sturgeon species.

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