Notes

Filling Knowledge Gaps for a Threatened Species: Age and Growth of Green Sturgeon of the Southern Distinct Population Segment

Marta E. Ulaski,* Michael C. Quist

M.E. Ulaski

Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho 83844

M.C. Quist

U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho 83844

Abstract

The Green Sturgeon *Acipenser medirostris* is an anadromous, long-lived species that is distributed along the Pacific coast of North America. Green Sturgeon is vulnerable to global change because of its sensitive life history (e.g., delayed maturation) and few spawning locations. The persistence of Green Sturgeon is threatened by habitat modification, altered flows, and rising river temperatures. In 2006, because of persistent stressors, the U.S. Endangered Species Act listed the southern distinct population segment as threatened. Despite increased research efforts on this species after the listing, substantial gaps in basic population information for Green Sturgeon remain. We present the only published information on age structure and growth of a threatened population of Green Sturgeon. By analyzing archived fin rays collected from 1984 to 2016, we revealed highly variable growth among individuals. We detected several age classes from 0 to 26 y and found similar growth rates of southern distinct population segment Green Sturgeon compared with northern population Green Sturgeon. Although limited, this analysis is an important first step to understanding Green Sturgeon population dynamics and highlights critical research needs.

Keywords: Green Sturgeon; age; growth; threatened; von Bertalanffy; distinct population segment; Sacramento River

Received: October 2020; Accepted: March 2021; Published Online Early: March 2021; Published: June 2021

Citation: Ulaski ME, Quist MC. 2021. Filling knowledge gaps for a threatened species: age and growth of Green Sturgeon of the southern distinct population segment. *Journal of Fish and Wildlife Management* 12(1):234–240; e1944-687X. https://doi.org/10.3996/JFWM-20-073

Copyright: All material appearing in the *Journal of Fish and Wildlife Management* is in the public domain and may be reproduced or copied without permission unless specifically noted with the copyright symbol ©. Citation of the source, as given above, is requested.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: ulaskimarta@gmail.com

Introduction

Monitoring population dynamics is an essential component of fisheries management and conservation (Hilborn and Walters 1992; Quinn and Deriso 1999). Even simple population models can inform critical tools for managing species of concern such as population viability and elasticity analyses (Morris and Doak 2002). However, scarcity of population data, such as distribution and trends in abundance, is a problem in conservation because the extinction risks for data-deficient species are unknown (Morais et al. 2013). For example, the population status is known for only 10% of the 2,000 fish species that are commercially exploited (Ricard et al. 2012; Kindsvater et al. 2018). Nontarget species represent an even more pronounced problem regarding knowledge of their population status. Such data deficiencies make it difficult to identify priorities for management

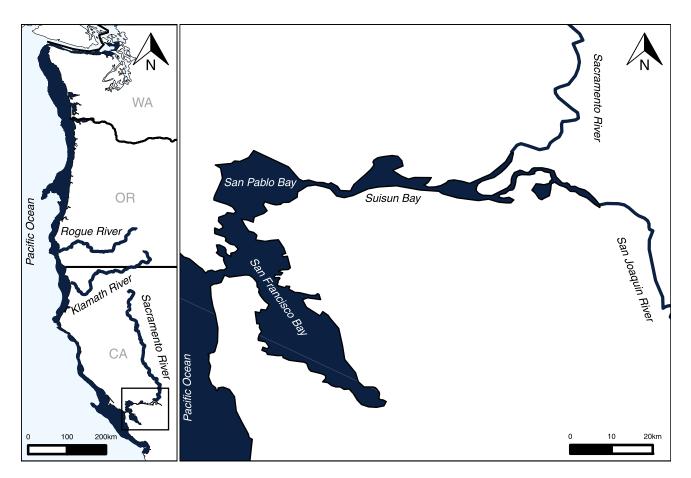


Figure 1. Distribution of Green Sturgeon *Acipenser medirostris* along the Pacific Coast of the United States (dark blue). Major spawning rivers for Green Sturgeon include the Rogue, Klamath, and Sacramento rivers. Fin rays collected from southern distinct population segment Green Sturgeon in San Pablo Bay, Suisun Bay, and throughout the Sacramento-San Joaquin River basin from 1984 to 2016.

action (Jarić et al. 2015). When population trends are unknown, monitoring population age structure and growth can reveal early warning signs of population decline (Quist et al. 2004). For example, increases in growth rate can indicate decreasing population density (Balazik et al. 2010), and age structure can indicate patterns of recruitment and mortality (Ricker 1975; Quist 2007). Thus, age structure and individual growth rate can be important population indicators for data-deficient, nontarget species.

The Green Sturgeon *Acipenser medirostris* is an example of a nontarget species with limited population data. The Green Sturgeon is an anadromous species with a marine-oriented life history (Beamesderfer et al. 2007). It is distributed along the Pacific Coast of North America (Figure 1). Adults migrate upriver from January to June every 2–4 y to spawn, and success of spawning events is dependent on environmental conditions (Erickson and Webb 2007; Heublein et al. 2009). Green Sturgeon deposit their eggs in rocky substrate, and larvae are typically found in rivers where spawning occurs (Moser et al. 2016). Juveniles can reside in freshwater for up to 3 y (Nakamoto et al. 1995), but can be found in seawater as early as the end of their first year (Allen et al. 2006). Postspawning, mature adult

Green Sturgeon exit rivers from October to January or from May to June (Erickson et al. 2002; Benson et al. 2007; Heublein et al. 2009). Adult and subadult Green Sturgeon occupy coastal waters for most of their life, but concentrate in estuaries in the summer and fall when estuarine temperatures are warm and food is abundant. It appears that adults migrate seasonally from northern overwintering areas, such as Vancouver Island, off Canada's Pacific Coast, to estuaries of natal or nonnatal rivers (Moser and Lindley 2007). However, individual migration patterns vary, and some Green Sturgeon migrate south along the Pacific Coast of the United States and Canada (Erickson and Hightower 2007). Green Sturgeon are known to spawn regularly in only three river systems: the Sacramento and Klamath rivers in California and the Rogue River in Oregon (Moser et al. 2016). Limited evidence suggests that spawning also occurs in the lower Columbia, Feather, Trinity, Umpgua, Yuba, and Eel rivers (Adams et al. 2007; Poytress et al. 2015; Seesholtz et al. 2015; Schreier and Stevens 2020). Two distinct population segments (DPSs) exist for Green Sturgeon: a northern DPS that spawns in the Rogue and Klamath rivers and a southern DPS that spawns in the Sacramento, Feather, and Yuba rivers. A DPS is the smallest division of a taxonomic species

Table 1. Number of southern distinct population segment (DPS) Green Sturgeon *Acipenser medirostris* fin rays that were aged and measured. Fin rays were collected from 1984–2016 from several locations in the Sacramento-San Joaquin River basin, San Francisco Bay, and surrounding area.

Year of			Total with associated
capture	Location	Total	length
1984	Monterey Bay	1	1
1984	San Pablo Bay	1	1
1984	Unknown southern DPS location	1	1
1985	Unknown southern DPS location	1	0
1985	Sacramento River	2	0
1987	San Pablo Bay	2	2
1989	Sacramento-San Joaquin River Delta	4	4
1989	Sacramento River	1	0
1989	San Joaquin River	1	1
1989	San Pablo Bay	2	2
1989	Unknown southern DPS location	2	2
1990	Suisun Bay	1	1
1990	Sacramento River	3	3
2001	San Pablo Bay	154	65
2015	Sacramento River	1	1
2015	San Pablo Bay	9	9
2016	Sacramento River	1	1
1984–2016	All locations	187	94

permitted to be protected under the U.S. Endangered Species Act (ESA 1973, as amended). Currently, the southern DPS is the only Green Sturgeon DPS listed as threatened under the U.S. Endangered Species Act.

Green Sturgeon is considered a species of concern because of its reduced abundance, limited spawning locations, and vulnerable life history (Musick et al. 2000). Threats to Green Sturgeon throughout their range include alteration to habitat and bycatch mortality (Adams et al. 2007). For example, large water-storage reservoirs block areas with a high amount of likely suitable spawning habitat (Mora et al. 2009). The effects of climate change, including rising river temperatures, exacerbate altered flow and temperature regimes from large water projects. Early developmental stages of Green Sturgeon are sensitive to changes in environmental conditions. Temperatures and flows may be suboptimal for egg incubation and larval growth in many Green Sturgeon spawning and rearing areas (Moser et al. 2016; Poletto et al. 2018). However, relationships among environmental conditions and Green Sturgeon recruitment are poorly understood. Historically, harvesting in commercial and recreational fisheries was underway until 2006, when recreational and commercial fishing for Green Sturgeon closed. The Yurok and Hoopa tribes still harvest a small number of Green Sturgeon on lower reaches of the Klamath and Trinity rivers. In addition, Green Sturgeon are caught as bycatch in the White Sturgeon Acipenser transmontanus recreational fishery and coastal groundfish trawl fisheries along the Pacific Coast (Adams et al. 2007). Estimates of trawling bycatch survival rate exist (i.e., 82%; Doukakis et al. 2020), and records of the number of Green Sturgeon caught as bycatch are known (Richerson et al. 2020), but effects of bycatch mortality on Green Sturgeon population dynamics are not well defined. The southern DPS faces additional threats including barriers to adult migration, insufficient flow, juvenile entrainment, predation by nonnative fishes, illegal harvest, and water contamination. Because of persistent stressors and uncertainty of population status, the U.S. Endangered Species Act (ESA 1973) listed southern DPS Green Sturgeon as threatened in 2006.

Despite an increase in directed research on Green Sturgeon since 2006, basic population information such as age structure and growth data continue to be deficient for management purposes. Age and growth information is especially lacking for the southern DPS, limiting the use and scope of population models and status monitoring. Fortunately, management agencies collected Green Sturgeon fin rays from 1984 to 2016 during several sampling events, the most substantial being 154 fin rays collected in 2001 during White Sturgeon population surveys in San Pablo Bay, California. We aimed to age and measure growth of Green Sturgeon by using archived fin rays to describe southern DPS Green Sturgeon age structure and estimate growth model parameters.

Methods

The southern DPS encompasses spawning populations south of the Eel River, California, mainly comprised of Green Sturgeon spawning in the Sacramento River (Figure 1). The majority of production occurs in the mainstem of the Sacramento River, with some spawning documented in the Feather and Yuba rivers (Seesholtz et al. 2015). Collections of entire pectoral fin rays or small sections near the body occurred sporadically from 1984 to 2016 from several locations throughout the study area (Table 1). Collections of eight Green Sturgeon fin rays were made from 1984 to 1987 during an age estimation study for White Sturgeon by various methods of capture including hook and line, gill nets, trammel nets, and angler recovery (Brennan and Cailliet 1989). The California Department of Fish and Wildlife collected 10 fin rays in 1989 during juvenile sturgeon sampling with gill nets, trammel nets, and trawls. The California Department of Fish and Wildlife collected the largest sample of fin rays (n = 154) during White Sturgeon population monitoring in San Pablo Bay by trammel net in 2001 and nine fin rays via similar methods in San Pablo Bay in 2015. In addition, the U.S. Fish and Wildlife Service recovered two fin rays from Green Sturgeon mortalities in 2015 and 2016. In total, 187 fin rays were available for age and growth analyses; unfortunately, length data were available for only 94 of those structures (Table 1). When length data were available, we used recorded fork length. Otherwise, we estimated fork length from total length by using linear regression analysis.

We mounted fin rays in clear epoxy and thinly sectioned them by using an IsoMet low-speed saw (Buehler, Lake Bluff, IL). We polished sections with fine

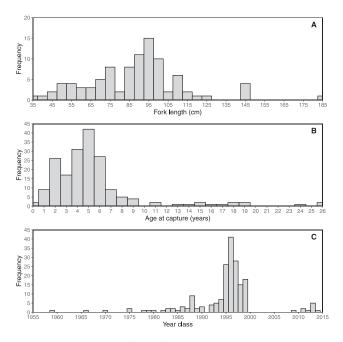


Figure 2. Summary of (**A**) fork length (n = 94), (**B**) age at capture (n = 187), and (**C**) year class of Green Sturgeon *Acipenser medirostris* (n = 187) sampled from 1984 to 2016 in San Pablo Bay and the Sacramento-San Joaquin River basin.

grit sandpaper and viewed them with a dissecting microscope and transmitted light (Koch and Quist 2007). Management agencies archived many fin rays as three thin sections mounted on a glass slide and we analyzed these samples without further processing. We used Image-Pro Plus software (Media Cybernetics, Rockville, MD) to measure the distance between annuli and a reader enumerated annuli without prior knowledge of fish length. The reader was trained to age Green Sturgeon fin rays by aging known-age White Sturgeon fin rays that exhibit similar growth patterns to Green Sturgeon. In addition, a second reader aged a subsample of fin rays with high agreement. Back-calculated lengthat-age was estimated for individual structures with length information (n = 94) by using the Dahl-Lea method. We used mean back-calculated length-at-age data from the 2001 sampling period (n = 65) to model growth described by the von Bertalanffy growth model:

$$L_t = L_{\infty} \times \left[1 - e^{-K(t-t_0)} \right] \tag{1}$$

where L_t is fork length (cm) at time t, L_{∞} is the mean maximum fork length (cm), K is the growth coefficient, and t_0 is the theoretical age when length is zero.

Results

Green Sturgeon varied in age from 0 to 26 y, although most individuals (92%) were younger than age 10 y (Figure 2; Table S1, *Supplemental Material*). The largest Green Sturgeon was 184 cm, with an estimated age of 24 y, and the smallest Green Sturgeon was 34 cm, with an estimated age of 1 y. The median age of Green Sturgeon

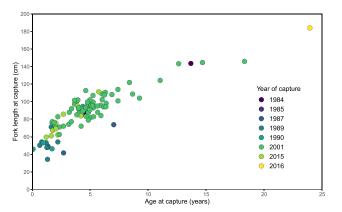


Figure 3. Length-at-age of Green Sturgeon *Acipenser medirostris* captured from 1984 to 2016 in San Pablo Bay and throughout the Sacramento-San Joaquin River basin. Small amounts of random noise added to data to reduce over plotting.

sampled from 1984 to 2016 was 5 y, and we estimated that only three individuals were older than age 20 y. We detected year classes from 1959 to 2014 in this analysis, with most individuals produced in 1996. Growth appeared to be rapid from ages 0 to 10 y and was highly variable among individuals (Figure 3). The fitted von Bertalanffy growth model had an asymptotic fork length (L_{∞}) of 155 cm, a *K* value of 0.125, and a t_0 value of -1.318 (Figure 4). The values fitted by the von Bertalanffy growth model for Green Sturgeon sampled in 2001 had good agreement with mean back-calculated lengths-atage ($r^2 = 0.99$, P < 0.001) and reasonable agreement with individual back-calculated lengths-atage ($r^2 = 0.84$, P < 0.001).

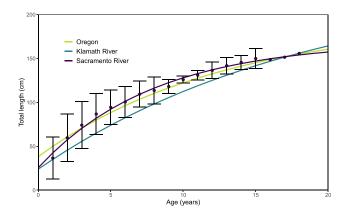


Figure 4. Von Bertalanffy growth model for Green Sturgeon *Acipenser medirostris* of the Klamath River (1979–1982), Oregon coast (2000–2002), and Sacramento River (2001). Klamath River von Bertalanffy equation: $L_t = 238.35 \times [1 - e^{-0.0532(t+1.9943)}]$. Oregon von Bertalanffy equation: $L_t = 176.6 \times [1 - e^{-0.0788(t+2.8111)}] \times 1.09$. Sacramento River von Bertalanffy equation: $L_t = 155.27 \times [1 - e^{-0.125(t+1.318)}] \times 1.09$. We multiplied Oregon and Sacramento River von Bertalanffy equations by 1.09 to translate fork length to total length. Points represent mean back-calculated lengths-atage of Green Sturgeon of the Sacramento River, and error bars indicate 95% confidence intervals.

Discussion

Our analysis of archived fin rays for southern DPS Green Sturgeon revealed highly variable growth among individuals. We detected several age classes of Green Sturgeon from the limited number of samples that were available; however, we need more information to assess recruitment variability and year-class strength. In addition, a scarcity of samples across age and size classes limited estimation of mortality and error associated with the von Bertalanffy growth model. We present the only published information on age structure and growth of a threatened population of Green Sturgeon. Although limited, this analysis is an important first step toward understanding Green Sturgeon population dynamics and identifying research needs.

Our analysis revealed not only significant gaps in research on a threatened population of Green Sturgeon but also pointed to limited information on other populations of Green Sturgeon throughout their range. Only two other studies analyzed age structure and growth of Green Sturgeon: the Oregon Department of Fish and Wildlife analyzed Green Sturgeon fin rays from the Rogue River, Umpqua River, and Oregon coastal estuaries (Farr and Rien 2002); and the U.S. Fish and Wildlife Service analyzed fin rays from the spawning population of the Klamath River (Adair et al. 1983). Growth appeared similar among populations, although southern DPS Green Sturgeon had a higher growth coefficient (K = 0.125) than individuals in the Klamath River (K = 0.0532) and Oregon coast (K = 0.0789) and appeared to have a lower L_{∞} (155 cm in Sacramento River; 219 cm in Klamath River; 177 cm along the Oregon coast). Because of changing population density, temperature, and food availability, Klamath River Green Sturgeon fin rays collected from 1979 to 1982 may not be directly comparable because growth may change (Mayfield and Cech 2004; Hamda et al. 2019). Carried forward, estimates of age and growth for southern DPS Green Sturgeon collected in 2001 may not represent contemporary growth rates and age structure for this population.

We detected fewer age classes older than 20 y compared with age structure described for Green Sturgeon in the Klamath River (Adair et al. 1983) and in the Oregon coast (Farr and Rien 2002). For example, we estimated the oldest Green Sturgeon that we observed to be age 26 y, and the oldest Green Sturgeons observed in the Klamath River and the Oregon coast were >50 y. Differences in age structure are likely a result of differences in sampling gear, location, and timing. Adair et al. (1983) sampled Green Sturgeon in the Klamath River with gill nets for harvest monitoring and a beach seining program at the mouth of the Klamath River from April to October. Therefore, most individuals sampled were mature adults. Similarly, Farr and Rien (2002) collected Green Sturgeon fin rays from the Rogue River, Umpgua River, and Oregon coastal estuaries and included more mature adults than sampling that occurred in San Pablo Bay. Older age classes of southern DPS Green Sturgeon are likely not represented by

sampling efforts in San Pablo Bay. Thus, the L_{∞} value that we report (i.e., 155 cm) is likely an underestimate for southern DPS Green Sturgeon.

Despite age analyses on a few other populations of Green Sturgeon, the accuracy and precision of ageing techniques for Green Sturgeon fin rays are unknown. Aging long-lived anadromous sturgeon may be complicated by reduced growth rates of older fish, spawning periodicity, complex marine movements, and changing environmental conditions (USFWS 1993). The described variability in individual length-at-age is a commonly observed pattern for both Green Sturgeon and White Sturgeon populations (Semakula and Larkin 1968; Kohlhorst et al. 1980). Another limitation of the current study is a lack of older age classes that may represent a clear bias for reported growth parameters. In addition to obtaining a representative sample of the population, a more comprehensive sampling design may support a growth model that accounts for the random effects of individuals and allows for estimation of prediction error. Nevertheless, the 95% confidence interval of mean back-calculated lengths-at-age overlapped with lengths predicted by the von Bertalanffy growth model.

A lack of population information represents a barrier to the effective management and recovery of Green Sturgeon. Our analysis of archived fin rays contributes to removing this barrier, but many substantial limitations for understanding Green Sturgeon population dynamics remain. Current research needs include estimating natural mortality, monitoring year-class strength and recruitment, and assessing trends in population abundance. Collecting basic population information is essential to better understand the effects of environmental conditions and water management on recruitment and to assess effects of management actions on Green Sturgeon population trends (Heppell 2007). There is still a need for contemporary estimates of age and growth from a representative sample of southern DPS Green Sturgeon. Population parameters are useful for predicting future outcomes for Green Sturgeon in a modeling framework and can guide an effective management plan for this threatened population. Green Sturgeon continue to face multiple stressors, and their extinction risk associated with global change is poorly understood. Thus, the effective management and conservation of this long-lived species hinges on future research of Green Sturgeon population dynamics.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Age and growth information for Green Sturgeon *Acipenser medirostris* of the southern distinct population segment including fork length (cm) and age

(y) at capture, radius of fin ray at capture and each annulus (pixels), and year of capture.

Found at DOI: https://doi.org/10.3996/JFWM-20-073.S1 (25 KB CSV).

Reference S1. Adair R, Harper W, Smith J, Eggers S, Klemp S. 1983. Klamath River Fisheries Assessment Program. Annual Report 1982. U.S. Fish and Wildlife Service, Arcata, California.

Found at DOI: https://doi.org/10.3996/JFWM-20-073.S2 (7.19 MB PDF).

Reference S2. Farr RA, Rien TA. 2002. Green Sturgeon population characteristics in Oregon. Oregon Department of Fish and Wildlife Fish Research Project Annual Report F-178-R.

Found at DOI: https://doi.org/10.3996/JFWM-20-073.S3 (962 KB PDF).

Reference S3. Nakamoto RJ, Kisanuki TT, Goldsmith GH. 1995. Age and growth of Klamath River Green Sturgeon (*Acipenser medirostris*). U.S. Fish and Wildlife Service, Arcata, California.

Found at DOI: https://doi.org/10.3996/JFWM-20-073.S4 (375 KB PDF).

Reference S4. Richerson KE, Jannot JE, Lee YW, McVeigh JT, Somers KA, Tuttle VJ, Wang S. 2020. Observed and estimated bycatch of Green Sturgeon in 2002–17 U.S. west coast groundfish fisheries. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NWFSC-158.

Found at DOI: https://doi.org/10.3996/JFWM-20-073.S5 (5.57 MB PDF).

Reference S5. [USFWS] U.S. Fish and Wildlife Service. 1993. Klamath River fisheries investigations 1980–1993 annual reports. Arcata, California.

Found at DOI: https://doi.org/10.3996/JFWM-20-073.S6 (280 KB PDF).

Acknowledgments

We thank J. Kelly and J. Hobbs of the California Department of Fish and Wildlife and J. Heublein of the National Oceanic and Atmospheric Administration, whose comments improved this article. We gratefully acknowledge Z. Jackson and three anonymous reviewers for helpful comments on an early draft of the article. We also thank J. DuBois for assistance with assembling data used in these analyses. Support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, Idaho Department of Fish and Game, and Wildlife Management Institute.

Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Adair R, Harper W, Smith J, Eggers S, Klemp S. 1983. Klamath River Fisheries Assessment Program. Annual Report 1982. U.S. Fish and Wildlife Service, Arcata, California (see *Supplemental Material*, Reference S1).
- Adams PB, Grimes C, Hightower JE, Lindley ST, Moser ML, Parsley MJ. 2007. Population status of North American Green Sturgeon, *Acipenser medirostris*. Environmental Biology of Fishes 79:339–356.
- Allen PJ, Hodge B, Werner I, Cech JJ. 2006. Effects of ontogeny, season, and temperature on the swimming performance of juvenile Green Sturgeon (*Acipenser medirostris*). Canadian Journal of Fisheries and Aquatic Sciences 63:1360–1369.
- Balazik MT, Garman GC, Fine ML, Hager CH, McIninch SP. 2010. Changes in age composition and growth characteristics of Atlantic Sturgeon (*Acipenser oxy-rinchus oxyrinchus*) over 400 years. Biology Letters 6:708–710.
- Beamesderfer RCP, Simpson ML, Kopp GJ. 2007. Use of life history information in a population model for Sacramento Green Sturgeon. Environmental Biology of Fishes 79:315–337.
- Benson RL, Turo S, McCovey BW. 2007. Migration and movement patterns of Green Sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA. Environmental Biology of Fishes 79:269–279.
- Brennan JS, Cailliet GM. 1989. Comparative age-determination techniques for White Sturgeon in California. Transactions of the American Fisheries Society 118:296–310.
- Doukakis P, Mora EA, Wang S, Reilly P, Bellmer R, Lesyna K, Tanaka T, Hamda N, Moser ML, Erickson DL, Vestre J, McVeigh J, Stockmann K, Duncan K, Lindley ST. 2020. Postrelease survival of Green Sturgeon (*Acipenser medirostris*) encountered as bycatch in the trawl fishery that targets California Halibut (*Paralichthys californicus*), estimated by using pop-up satellite archival tags. Fishery Bulletin 118:63–73.
- Erickson DL, Hightower JE. 2007. Oceanic distribution and behavior of Green Sturgeon. American Fisheries Society Symposium 56:197–211.
- 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, USA. Journal of Applied Ichthyology 18:565–569.
- Erickson DL, Webb MAH. 2007. Spawning periodicity, spawning migration, and size at maturity of Green Sturgeon, *Acipenser medirostris*, in the Rogue River, Oregon. Environmental Biology of Fishes 79:255–268.
- Farr RA, Rien TA. 2002. Green Sturgeon population characteristics in Oregon. Oregon Department of Fish and Wildlife Fish Research Project Annual Report F-178-R (see *Supplemental Material*, Reference S2).
- Hamda NT, Martin B, Poletto JB, Cocherell DE, Fangue NA, Van Eenennaam J, Mora EA, Danner E. 2019. Applying a simplified energy-budget model to explore the effects of temperature and food availability on the

life history of Green Sturgeon (*Acipenser medirostris*). Ecological Modelling 395:1–10.

- Heppell SS. 2007. Elasticity analysis of Green Sturgeon life history. Environmental Biology of Fishes 79:357–368.
- Heublein JC, Kelly JT, Crocker CE, Klimley AP, Lindley ST. 2009. Migration of Green Sturgeon, *Acipenser medirostris*, in the Sacramento River. Environmental Biology of Fishes 84:245–258.
- Hilborn R, Walters CJ. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman & Hall, New York.
- Jarić I, Gessner J, Lenhardt M. 2015. A life-table metamodel to support the management of data deficient species, exemplified in sturgeons and shads. Environmental Biology of Fishes 98:2337–2352.
- Kindsvater HK, Dulvy NK, Horswill C, Juan-Jordá MJ, Mangel M, Matthiopoulos J. 2018. Overcoming the data crisis in biodiversity conservation. Trends in Ecology and Evolution 33:676–688.
- Koch JD, Quist MC. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management 27:782–784.
- Kohlhorst DW, Lee MW, Orsi JJ. 1980. Age and growth of White Sturgeon collected in the Sacramento-San Joaquin Estuary, California: 1965–1970 and 1973– 1976. California Fish and Game 66:83–95.
- Mayfield RB, Cech JJ. 2004. Temperature effects on Green Sturgeon bioenergetics. Transactions of the American Fisheries Society 133:961–970.
- Mora EA, Lindley ST, Erickson DL, Klimley AP. 2009. Do impassable dams and flow regulation constrain the distribution of Green Sturgeon in the Sacramento River, California? Journal of Applied Ichthyology 25:39–47.
- Morais AR, Siqueira MN, Lemes P, Maciel NM, De Marco P, Brito D. 2013. Unraveling the conservation status of data deficient species. Biological Conservation 166:98–102.
- Morris WF, Doak DF. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sunderland, Massachussetts: Sinauer.
- Moser ML, Israel JA, Neuman M, Lindley ST, Erickson DL, McCovey BW, Klimley AP. 2016. Biology and life history of Green Sturgeon (*Acipenser medirostris ayres*, 1854): state of the science. Journal of Applied Ichthyology 32:67–86.
- Moser ML, Lindley ST. 2007. Use of Washington estuaries by subadult and adult Green Sturgeon. Environmental Biology of Fishes 79:243–253.
- Musick JA, Harbin MM, Berkeley SA, Burgess GH, Eklund AM, Findley L, Gilmore RG, Golden JT, Ha DS, Huntsman DR, McGovern JC, Sedberry GR, Parker SJ, Poss SG, Sala E, Schmidt TW, Weeks H, Wright SG. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). Fisheries 25:6–30.
- Nakamoto RJ, Kisanuki TT, Goldsmith GH. 1995. Age and growth of Klamath River Green Sturgeon (*Acipenser medirostris*). U.S. Fish and Wildlife Service, Arcata, California (see *Supplemental Material*, Reference S3).

- Poletto JB, Martin B, Danner E, Baird SE, Cocherell DE, Hamda N, Cech JJ, Fangue NA. 2018. Assessment of multiple stressors on the growth of larval Green Sturgeon *Acipenser medirostris*: implications for recruitment of early life-history stages. Journal of Fish Biology 93:952–960.
- Poytress WR, Gruber JJ, Van Eenennaam JP, Gard M. 2015. Spatial and temporal distribution of spawning events and habitat characteristics of Sacramento River Green Sturgeon. Transactions of the American Fisheries Society 144:1129–1142.
- Quinn TJ, Deriso RB. 1999. Quantitative fish dynamics. Oxford: Oxford University Press.
- Quist MC. 2007. An evaluation of techniques used to index recruitment variation and year-class strength. North American Journal of Fisheries Management 27:30–42.
- Quist MC, Stephen JL, Guy CS, Schultz RD. 2004. Age structure and mortality of Walleyes in Kansas reservoirs: use of mortality caps to establish realistic management objectives. North American Journal of Fisheries Management 24:990–1002.
- Ricard D, Minto C, Jensen O, Baum JK. 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. Fish and Fisheries 13:380–398.
- Richerson KE, Jannot JE, Lee YW, McVeigh JT, Somers KA, Tuttle VJ, Wang S. 2020. Observed and estimated bycatch of Green Sturgeon in 2002–17 U.S. west coast groundfish fisheries. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NWFSC-158 (see *Supplemental Material*, Reference S4).
- Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191. Ottawa, Canada: Department of the Environment Fisheries and Marine Service.
- Schreier AD, Stevens P. 2020. Further evidence for lower Columbia River Green Sturgeon spawning. Environmental Biology of Fishes 103:201–208.
- Seesholtz AM, Manuel MJ, Van Eenennaam JP. 2015. First documented spawning and associated habitat conditions for Green Sturgeon in the Feather River, California. Environmental Biology of Fishes 98:905–912.
- Semakula SN, Larkin PA. 1968. Age, growth, food, and yield of the White Sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. Journal of the Fisheries Research Board of Canada 25:2589–2602.
- [ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available: http://www.fws.gov/endangered/esa-library/ pdf/ESAall.pdf (May 2021).
- [USFWS] U.S. Fish and Wildlife Service. 1993. Klamath River fisheries investigations 1980–1993 annual reports. Arcata, California (see *Supplemental Material*, Reference S5).