Further evidence for lower Columbia River green sturgeon spawning

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Abstract The Green Sturgeon is a long-lived anadromous fish known to spawn in only three locations. Southern Distinct Population Segment (DPS) Green Sturgeon spawn only in the Sacramento drainage, while the Northern DPS spawns in the Klamath and Rogue rivers. In 2011, a young of year (YOY) Green Sturgeon was captured in the Columbia River below Bonneville Dam, providing preliminary evidence of a fourth spawning location. In 2017, four additional Green Sturgeon YOY of similar size were captured in the Columbia River below Bonneville Dam. Genetic analysis of all YOY samples indicates that they belong to the Northern DPS, confirming that the Northern DPS actually spawns in at least three locations. The detection of Green Sturgeon spawning in the Columbia River only in years with relatively high spring flow (2011, 2017), combined with confirmed correlations between flow and spawning for other White and Green Sturgeon populations, suggests that appropriate spawning conditions may only exist above a specific flow threshold. The Columbia River has the potential to play an important role in Green Sturgeon climate change adaptation due to its location at the northernmost end of the species' reproductive range. We recommend future research to better quantify Green Sturgeon recruitment magnitude, frequency and dynamics in the Columbia River.

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Introduction

The Green Sturgeon (*Acipenser medirostris*) is a large, long-lived, anadromous fish distributed from Baja California, Mexico to the Bering Sea, Alaska (Wilimovsky 1964; Moyle 2002; Colway and Stevenson 2007; Rosales-Casián and Almeda-Jáuregui 2009). Despite their wide range, Green Sturgeon spawning has only been documented in three locations. The Southern Distinct Population Segment (DPS), as designated by NOAA (2006), spawns in the Sacramento River system in California (mainstem Sacramento and Feather rivers; Seesholtz et al. 2015) from March to June, while the Northern DPS spawns in the Klamath and Rogue rivers in California and Oregon, from April to June and March to June, respectively (Benson et al. 2007; Erickson and Webb 2007; Heublein et al. 2009). Spawning is suspected in the Eel River, California but to our knowledge, neither eggs nor young of year (YOY) Green Sturgeon have been captured there (Stillwater Sciences 2017). The fact that Green Sturgeon spawn in so few locations increases the species vulnerability to extinction (Musick et al. 2000). Indeed, dependence on a single drainage for spawning was one factor that led to

listing of Southern DPS Green Sturgeon as federally threatened in 2006 (NOAA 2006).

In 2016, we provided preliminary evidence that another Northern DPS spawning population of Green Sturgeon exists in the Lower Columbia River, below Bonneville Dam. A YOY Green Sturgeon was captured in 2011 at rkm 209 and genetic methods indicated that the individual belonged to the Northern DPS (Schreier et al. 2016). At 22 cm FL, the YOY would not have yet developed the salinity tolerance required to migrate through marine habitat to the Columbia River (Allen et al. 2011). Therefore, we concluded that the individual had hatched in the free-flowing portion of the Columbia River below Bonneville Dam.

In 2017, four additional YOY Green Sturgeon were captured in the Lower Columbia River. One was captured in a similar location as the 2011 YOY (Table 1) while the other three individuals were captured further downstream. Here we report genetic analysis of the four YOY samples collected in 2017, including species confirmation and DPS assignment. We then discuss the implications of a third Northern DPS spawning population.

Materials and methods

YOY sampling

Oregon Department of Fish & Wildlife (ODFW) and Washington Department of Fish & Wildlife (WDFW) jointly sample the Columbia River below Bonneville Dam annually as part of routine White Sturgeon (*Acipenser transmontanus*) population assessment. Flows in this portion of the river, while un-dammed, are still influenced by upstream dams on both the Columbia and Snake Rivers. The sampling sites are above the zone of saltwater intrusion but are still tidally-influenced. Small-mesh, bottom-set gillnets (~5 cm stretch-mesh; 91.4 m L × 3.7 m H) are fished at standardized index locations (Fig. 1; Table 1) for 24 h. (Farr 2017). These gillnets have proven to be an effective gear for sampling YOY sturgeon based on many years of research and monitoring studies in impounded, free-flowing and estuarine river systems (Farr and Kern 2005; C. Chapman, ODFW, pers. comm.; O. Langness, WDFW, unpubl. data). Sampling took place from late October through early December 2017. Sampling locations were selected based on a stratified

sampling scheme to ensure a representative distribution of effort while also accounting for net effectiveness and crew safety. Generally, locations selected have moderate flow and substrate ranging from silt to sand to cobble with rooted macrophytes sometimes present.

Three putative Green Sturgeon YOY, as determined through visual inspection of physical morphology, were captured 25 October 2017 just upstream of Rooster Rock (~rkm 209) and the fourth was captured 27 October between Hayden Island and Government Island, OR (~rkm 177). The fish were on average 27.9 cm fork length (FL; range: 24.5–29.3 cm). Each fish had a pectoral fin clip taken by ODFW or WDFW personnel following their standard procedures for sturgeon sampling. Fin clips were taken with scissors, dried, and samples were stored in individual paper envelopes marked with unique identifiers. The dried tissue samples were subsequently transferred to the Genomic Variation Laboratory at the University of California, Davis for genetic analysis.

Molecular methods

DNA was extracted from the four putative Green Sturgeon fin clips using the DNEasy kit (Qiagen, Venlo, Netherlands) following the manufacturer's instructions. DNA was quantified with a Qubit 2.0 fluorometer (ThermoFisher Scientific, Waltham, MA) and normalized to 20 ng. To confirm that the YOY were Green Sturgeon rather than the more abundant White Sturgeon, qPCR was performed on a Bio-Rad Chromo 4 real time detector using species-specific Taqman assays for Green Sturgeon and White Sturgeon following Brandl et al. (2015).

For DPS assignment, we conducted PCR with ten microsatellite loci (AfuG 41, AfuG 43, AfuG 135, AfuG 247, An 76, Aox 27, As 007, Spl 101b, Spl 106, Spl 120b) following Israel et al. (2004) and Israel et al. (2009). One microliter of diluted PCR product was added to 8.8 μl of highly deionized formamide and 0.2 μl Liz 600 size standard (ThermoFisher Scientific, Waltham, MA). Fragment analysis was performed on an ABI 3730 Genetic Analyzer and alleles were called in GeneMapper v 5.0 (both by ThermoFisher Scientific, Waltham, MA). Due to the polyploid nature of the Green Sturgeon genome, allele dosage could not be determined unambiguously. Each allele was converted to a present/absent dominant locus (Rodzen et al. 2004; Israel et al. 2009).

Table 1 Columbia River sturgeon indexing sampling sites by river section. Alternate sampling sites are presented in italics. Locations at which the 2011 and 2017 YOY were captured are bolded

Section	Site ID	RKM	Latitude	Longitude	Depth (m)
1	LCR1 S1	49.5	46° 15.598'	123° 30.620'	30
1	LCR1 S2	57.3	46° 14.658'	123° 25.803'	51
1	LCR1 S3	65.8	46° 11.785'	123° 22.901'	20
1	LCR1 S4	68.5	46° 11.075'	123° 21.382'	43
1	LCR1 S5	84.2	46° 10.559'	123° 12.017'	22
1	LCR1 S6	85.3	46° 11.067'	123° 11.265'	59
1	*LCR1 ALT1*	*60.5*	*46° 13.111'*	*123° 25.301'*	*32*
1	*LCR1 ALT2*	*62.6*	*46° 11.673'*	*123° 26.060'*	*65*
2	LCR2 S1	101.1	46° 08.001'	123° 00.907'	28
2	LCR2 S2	105.4	46° 06.352'	122° 58.192'	33
2	LCR2 S3	107.0	46° 05.928'	122° 57.394'	35
2	LCR2 S4	115.2	46° 03.179'	122° 53.149'	42
2	LCR2 S5	121.2	46° 00.368'	122° 51.407'	33
2	LCR2 S6	127.6	45° 57.589'	122° 48.543'	59
2	*LCR2 ALT1*	*118.0*	*46° 01.794'*	*122° 52.798'*	*29*
2	*LCR2 ALT2*	*102.3*	*46° 07.682'*	*123° 00.122'*	*34*
3	LCR3 S1	134.7	45° 53.526'	122° 48.365'	42
3	LCR3 S2	139.2	45° 51.855'	122° 47.302'	24
3	LCR3 S3	142.6	45° 49.802'	122° 47.747'	51
3	LCR3 S4	148.5	45° 46.759'	122° 46.527'	23
3	LCR3 S5	155.0	45° 43.594'	122° 45.943'	39
3	LCR3 S6	158.4	45° 41.876'	122° 46.501'	40
3	*LCR3 ALT1*	*162.7*	*45° 39.375'*	*122° 46.000'*	*34*
3	*LCR3 ALT2*	*165.6*	*45° 38353'*	*122° 44550'*	*34*
4	**LCR4 S1**	**176.9**	**45° 36.085'**	**122° 36.607'**	**22**
4	LCR4 S2	182.7	45° 35.644'	122° 32.202'	15
4	LCR4 S3	186.8	45° 35.005'	122° 28.994'	21
4	LCR4 S4	191.3	45° 34.090'	122° 25.983'	19
4	LCR4 S5	199.9	45° 33.197'	122° 20.515'	22
4	**LCR4 S6**	**209.5**	**45° 33.504'**	**122° 13.590'**	**35**
4	*LCR4 ALT1*	*205.0*	*45° 32.559'*	*122° 16.003'*	*40*
4	*LCR4 ALT2*	*173.0*	*45° 36.567'*	*122° 39.638'*	*19*

Data analysis

The four YOY were assigned to DPS following two different approaches. First, a maximum likelihood approach was taken in the program AFLPOP (Duchesne and Bernatchez 2002) to allocate the YOY to genetic baselines developed for Northern DPS and Southern DPS Green Sturgeon by Israel et al. (2009). Also, the single Columbia River Green Sturgeon YOY captured in 2011 and 10 adults determined previously to belong either to the Northern or Southern DPS (5 from each DPS; Schreier et al. 2016) were re-allocated along with the 2017 YOY samples. The adults not in the DPS baselines were treated as positive controls in analysis. We used a zero replacement value of 0.004 and a minimum likelihood difference (MLD) of 0.8, as identified previously for Green Sturgeon with simulations in Schreier et al. (2016). Using an MLD threshold of 0.8
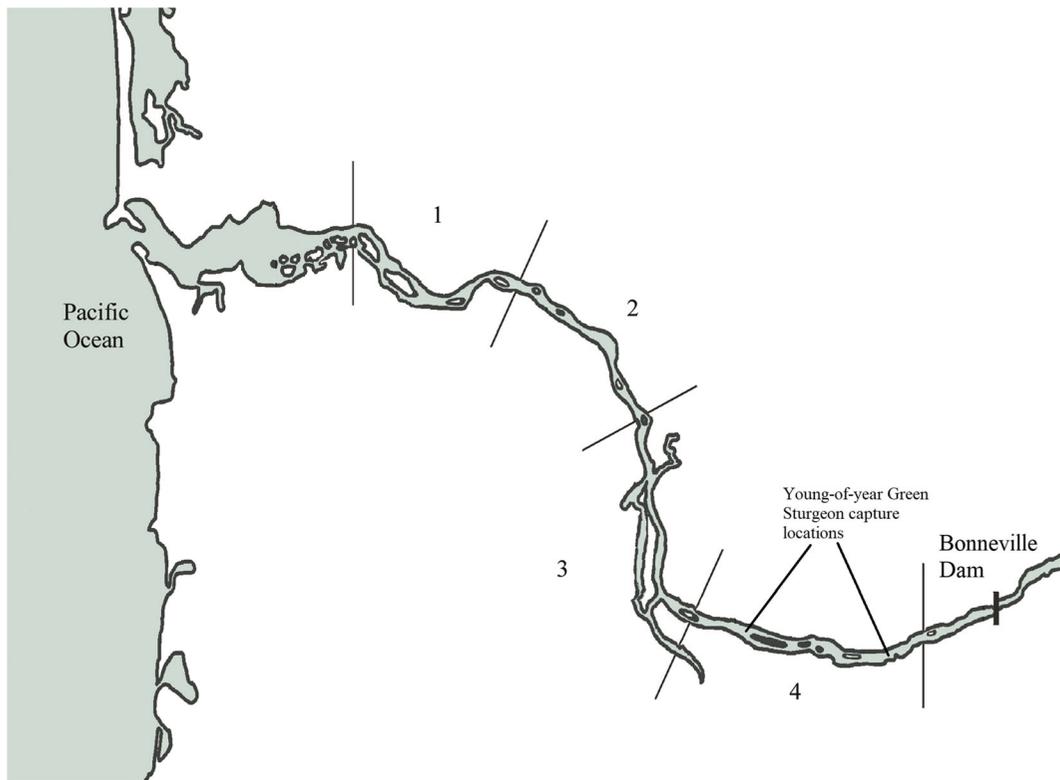
Fig. 1 Columbia River sturgeon indexing sampling sites by river section. Locations at which the 2011 and 2017 YOY were captured are noted

meant that an individual needed to be $10^{0.8}$ ($= 6.3$) times more likely to belong to one DPS than another in order for an allocation to be made. One thousand individuals were simulated using allele frequencies from baseline genotypes to estimate *P*-values for each allocation.

Next, we used the program Structure v. 2.3.4 (Pritchard et al. 2000; Falush et al. 2007) to infer the number of populations (K) in the dataset including the Northern and Southern DPS baseline samples, the 2011 and 2017 YOY samples, and the ten positive control samples. Although we expected that the YOY would belong to one of two known DPS's, we still tested K = 1 through K = 3 to allow for the possibility of originating from a separate population. We applied the LOCPRIOR model, which uses sampling location as a prior if found to be informative, in our initial Structure analysis because this approach has been shown to detect weak genetic differentiation better than the standard model (Hubisz et al. 2009). The YOY samples were given a sample label identical to known Northern DPS individuals to account for the fact that they were sampled nearest the Northern DPS spawning rivers. Burn-in

was 500,000 followed by 500,000 iterations and six replicates were performed for each K. We applied the admixture model and assumed correlated allele frequencies. We determined K using the mean likelihood Pr($X|K$) and ΔK (Evanno et al. 2005) as visualized in Structure Harvester (Earl and vonHoldt 2011). The program Clumpp (Jakobsson and Rosenberg 2007) was used to generate consensus Q values (proportional ancestry in each K) across replicates and the program Clumpak (Kopelman et al. 2015) was used to generate bar plots to visualize individual Q values for each sample.

Finally, we performed a population assignment test in Structure v. 2.3.4, using genetic baseline membership or cluster designation in our initial Structure analysis (for YOY and positive controls) as prior population information. Burn-in was 500,000 followed by 500,000 iterations and K = 2 was selected. We examined Q values to determine the likelihood that each YOY individual originated in the Northern DPS. Final DPS designations of YOY samples were based on interpretation of both AFLPOP and Structure results.

Results

The qPCR species-specific assays confirmed that all 2017 YOY were Green Sturgeon. AFLPOP analysis allocated the 2011 YOY and three 2017 YOY to the Northern DPS, with likelihood differences above the minimum threshold of 0.8 (Table 2). However, one 2017 YOY sample could not be allocated to either DPS and P-values for all YOY allocations were low ($P = 0$–0.001). In AFLPOP, P-values represent the proportion of simulated individuals with allocation likelihoods less than or equal to the likelihood of an unknown sample. Therefore, there is low statistical support for allocating the YOY samples to the Northern DPS with this approach, despite a greater likelihood of originating from the Northern rather than the Southern DPS. All but one positive control sample was allocated to the correct DPS, with only one sample unable to be allocated due to a low likelihood difference of 0.17.

Both the mean likelihood $Pr(X|K)$ and ΔK indicated that there were two populations in the dataset corresponding to the Northern and Southern DPS's ($Pr(X|K) = -11,251$; Fig. 2). As expected, sampling

Table 2 AFLPOP allocations of five Columbia River YOY samples and ten positive controls samples (5 each from Northern and Southern DPS's). N designates Northern DPS (NDPS) and S designates Southern DPS (SDPS) positive control samples. MLD is the minimum likelihood difference (threshold 0.8) and P value refers to the proportion of simulated individuals with allocation likelihoods less than or equal to a sample's likelihood

Sample ID	Allocation	MLD	P value
11–01	NDPS	1.72	0.000
17–1323	NDPS	2.87	0.000
17–1429	None	0.49	0.001
17–1430	NDPS	1.95	0.001
17–1434	NDPS	3.18	0.000
10HE057-S	SDPS	4.55	0.128
10HE060-S	None	0.17	0.003
10HE065-S	SDPS	1.45	0.461
10HE066-S	SDPS	3.61	0.107
10HE071-S	SDPS	4.95	0.262
10HE081-N	NDPS	5.99	0.106
11FA04-N	NDPS	3.06	0.007
11FA26-N	NDPS	5.91	0.023
11FA27-N	NDPS	2.13	0.417
11FA28-N	NDPS	2.12	0.124

location was informative and was used as a prior to assist in clustering (r values for $K = 2$ ranged from 0.055–0.163; mean $r = 0.108$). Most individuals from each baseline dataset showed high proportional ancestry in the expected DPS (Northern DPS mean $Q = 0.912$, Southern DPS mean $Q = 0.939$), although there were some individuals that exhibited ancestry in the other DPS (Fig. 2). The 2011 and 2017 YOY samples exhibited high levels of proportional ancestry in the Northern DPS by this method, with Q values ranging from 0.876–0.978 (mean $Q = 0.931$) (Fig. 2). In the population assignment test, all YOY samples originated from the Northern DPS population with high likelihood, with Q values ranging from 0.932–0.992 (mean $Q = 0.966$).

Discussion

Our genetic analysis indicates that the Green Sturgeon YOY samples collected in the Columbia River in 2017 originate from the Northern DPS. The difficulty AFLPOP encountered in assigning the YOY samples to DPS may be due to minor genetic differentiation between a Columbia River spawning population and the Klamath and Rogue rivers from which our Northern DPS microsatellite genetic baseline was derived. A previous study suggested that some level of population genetic substructure exists within the Northern DPS (Israel et al. 2009), although it cannot be resolved with the dominant genotype data we must use in this ancestral polyploid fish. We did examine Structure bar plots for $K = 3$ and observed a small number of individuals from both DPS baselines showing ancestry in a third cluster, but neither the YOY samples nor the positive control samples contained individuals assigning to the third cluster (data not shown). This finding may result from genotyping the YOY and positive control samples on a different platform than the baseline samples. Future genetic studies should use the SNP genotype baseline developed by Anderson et al. (2017), which includes reference samples from the Sacramento and Klamath rivers. Anderson et al. (2017) demonstrated that the SNP baseline has slightly more statistical power for DPS assignment than the microsatellite baseline and avoids platform related discrepancies.

The results of this paper and Schreier et al. (2016) provide strong evidence that a third Northern DPS spawning population exists, at least intermittently, in the Columbia River. The only alternative explanation
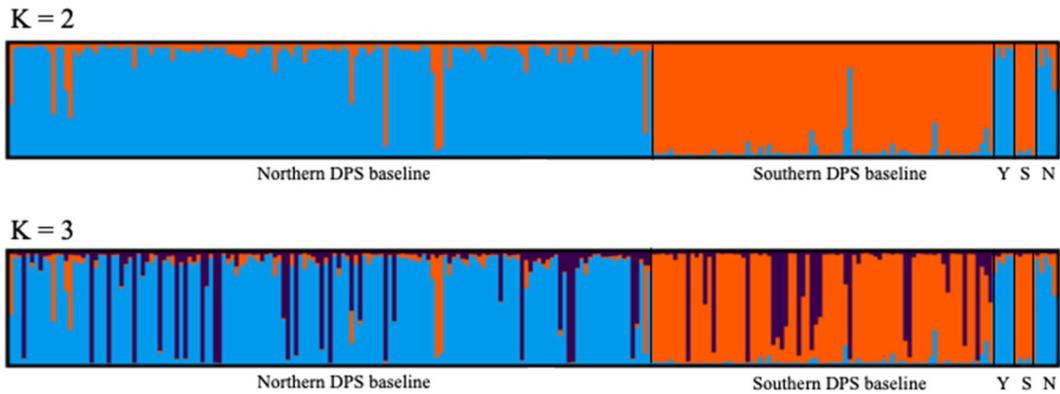
Fig. 2 Structure barplots, generated in Clumpak, illustrating individual Q values when K = 2 and K = 3, for the dataset including the existing Northern DPS and Southern DPS microsatellite baselines, the 2011 and 2017 YOY samples, and the Southern DPS and Northern DPS positive controls. Y is 2011 (N = 1) and 2017 (N = 4) YOY samples, S is Southern DPS positive control samples (N = 5) and N is Northern DPS positive control samples (N = 5)

is that the YOY individuals captured in the Columbia have migrated from another Northern DPS spawning river. Although somewhat larger than the YOY captured in 2011 (22 cm FL), at the time of sampling the 2017 YOY (24.5–29.3 cm FL) were around the minimum mean size at which age-0 Northern DPS Green Sturgeon are able to tolerate saltwater after a prolonged acclimation period (~23.1 cm FL; Allen et al. 2011). Migration from the nearest known spawning population, the Rogue River, would have required the YOY to make a > 400 km migration through marine habitat along the Pacific Coast. It is unlikely that the YOY would have been sufficiently developed to leave freshwater in the Rogue River in the time required for them to reach the Columbia River by their dates of capture.
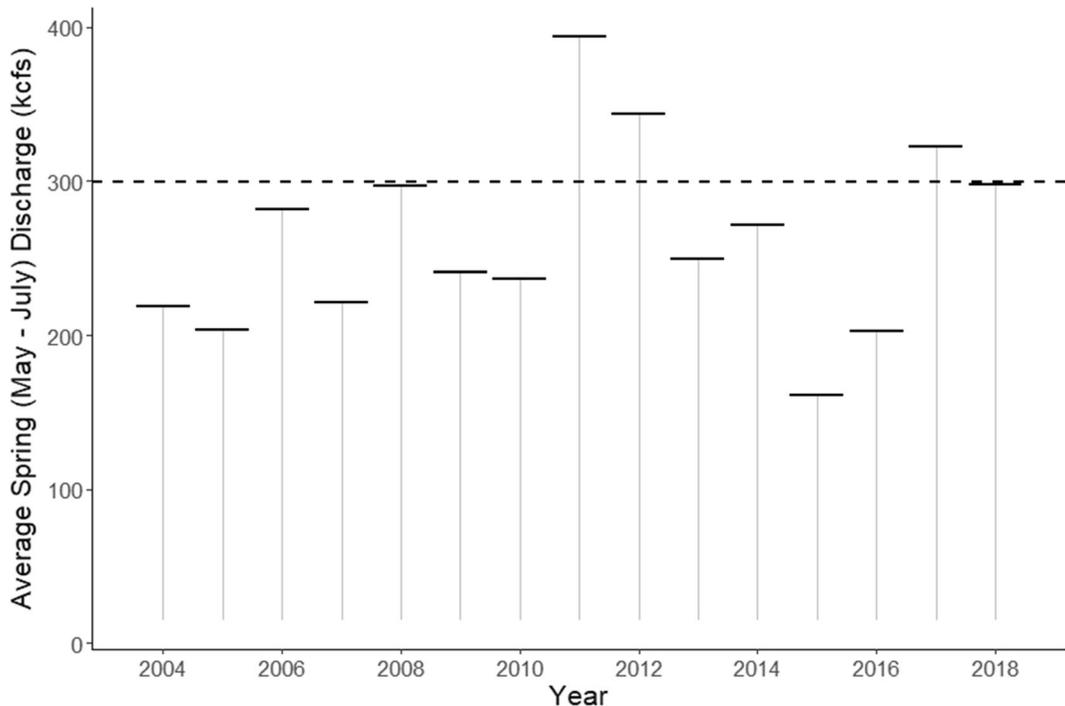

Fig. 3 Annual average spring (May – July) discharge at Bonneville Dam. The dashed line denotes the 300 kcfs level. Discharge above this level have produced detectable Green Sturgeon reproduction in two out of three years

The fact that Green Sturgeon spawning has been detected in the Columbia only in high flow years (2011, 2017) may indicate that higher flows are necessary, if not sufficient, for reproductive success. A positive correlation between spring flows and recruitment success also has been identified in the sympatric White Sturgeon (Hildebrand et al. 2016; Counihan and Chapman 2018) and other sturgeon species (Nilo et al. 1997; Goto et al. 2015), but the exact mechanism underlying the relationship is unclear. In the Sacramento River, Southern DPS Green Sturgeon only spawn when flow increases to 250–350 m^3/s (Poytress et al. 2009) and a similar threshold may exist for Northern DPS Green Sturgeon. During 14 years of YOY sampling in the lower Columbia River, Green Sturgeon YOY have been detected in two (2011 and 2017) of the three years (2011, 2012 and 2017) when average spring (May – July) discharge at Bonneville Dam has exceeded 300 kcfs (Fig. 3). In comparison, White Sturgeon YOY have been found every year (mean: 127 fish; range: 14–543), regardless of flow, indicating that sampling gear and design are sufficient to capture YOY sturgeon when present. Preferred substrate for Green Sturgeon spawning consists of a mix of cobble and gravel with abundant interstitial spaces (Moser et al. 2016), and it is possible that high flows are required to scour out adequate spawning habitat for Green Sturgeon on the Columbia. Both substrate and scour conditions are believed to exist in the Bonneville Dam tailrace.

There are other possible explanations for the lack of evidence of Green Sturgeon spawning between 2011 and 2017. The protracted spawning periodicity of Green Sturgeon (2–4 years for females; Moser et al. 2016) could mean that spawning occurs on the Columbia infrequently and spawning truly didn't occur most years between 2011 and 2017. Alternatively, Green Sturgeon and White Sturgeon YOY could use different habitats, so although gear targeting White Sturgeon is capable of capturing YOY Green Sturgeon, they may not be abundant at locations sampled for White Sturgeon population assessment. Unfortunately, additional financial resources were not available to conduct a Green Sturgeon specific sampling effort nor to expand the White Sturgeon sampling to better sample Green Sturgeon. Studies specifically designed to identify and characterize Green Sturgeon spawning habitat in the Columbia will help managers better understand recruitment in this system.

The Columbia River has the potential to play an important role in Northern DPS Green Sturgeon adaptation to climate change due to its location at the northernmost end of the species' reproductive range. However, increasingly variable precipitation predicted for the North American West Coast by climate change models may limit the role of the Columbia River in Green Sturgeon conservation if recruitment is poor in low flow years. Efforts to identify the mechanisms driving recruitment in the Columbia may reveal factors that can be improved (e.g. by habitat enhancement) to increase the river's value to Green Sturgeon in the face of climate change.

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