



Supplement Article

Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future

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Summary

White Sturgeon, *Acipenser transmontanus* (WS), are distributed throughout three major river basins on the West Coast of North America: the Sacramento-San Joaquin, Columbia, and Fraser River drainages. Considered the largest North American freshwater fish, some WS use estuarine habitat and make limited marine movements between river basins. Some populations are listed by the United States or Canada as threatened or endangered (upper Columbia River above Grand Coulee Dam; Kootenai River; lower, middle and, upper Fraser River and Nechako River), while others do not warrant federal listing at this time (Sacramento-San Joaquin Rivers; Columbia River below Grand Coulee Dam; Snake River). Threats that impact WS throughout the species' range include fishing effects and habitat alteration and degradation. Several populations suffer from recruitment limitations or collapse due to high early life mortality associated with these threats. Efforts to preserve WS populations include annual monitoring, harvest restrictions, habitat restoration, and conservation aquaculture. This paper provides a review of current knowledge on WS life history, ecology, physiology, behavior, and genetics and presents the status of WS in each drainage. Ongoing management and conservation efforts and additional research needs are identified to address present and future risks to the species.

Introduction

White Sturgeon (WS), *Acipenser transmontanus* (Richardson, 1863) is the largest freshwater fish in North America and is native to large river systems on the western portion of the continent. Although the order Acipenseriformes originated ~200 MYA, WS have existed as a species for about 46 million years (95% CI 18–85 MY; Peng et al., 2007). They have

shown a remarkable resilience to major geologic and climatic perturbations that have caused mass extinctions of other species. It is a sad irony that within the past 150 years, this prehistoric relic has been brought to the brink of extirpation in many areas of its historical range as a result of anthropogenic effects such as overharvest, pollution, dam construction, and habitat alteration.

Over the past 30 years, considerable effort has been directed towards understanding the basic biology, population metrics, and causes of recruitment limitations for WS. This paper incorporates information from selected published and grey literature sources and builds on previous synopses (e.g., Scott and Crossman, 1973; PSMFC, 1992; McPhail, 2007) to provide contemporary information on WS biology, population status, recovery efforts, and research needs. In presenting such a synopsis, it is important to note that most studies have been conducted on populations in highly altered habitats, and studies in unimpounded or relatively unaltered systems are comparatively limited.

Taxonomy

Scientific name: *Acipenser transmontanus* Richardson, 1863
AFS English common name: White Sturgeon.

Vernacular names: Pacific Sturgeon, Oregon Sturgeon, Columbia Sturgeon, Snake River Sturgeon and Sacramento Sturgeon.

Phylogeny

The WS is part of a Pacific clade of species (Birstein and DeSalle, 1998; Ludwig et al., 2001; Birstein et al., 2002; Peng et al., 2007; Krieger et al., 2008) including Kaluga (*Huso dauricus*; Georgi, 1775), Sakhalin Sturgeon (*Acipenser mikadoi*; Hilgendorf, 1892), Green Sturgeon (GRS; *Acipenser medirostris*; Ayres 1854), Chinese sturgeon (*Acipenser sinensis*; Gray, 1835) and Amur sturgeon (*Acipenser schrenkii*;

*Retired

Brandt, 1869). Peng et al. (2007) and Krieger et al. (2008) include the Yangtze sturgeon (*Acipenser dabryanus*) in this group. Recent phylogenies suggest the Amur Sturgeon is the sister species of WS (Ludwig et al., 2001; Birstein et al., 2002; Peng et al., 2007; Krieger et al., 2008).

All extant sturgeon species are polyploid, derived from an extinct ancestor possessing 60 chromosomes (Dingerkus and Howell, 1976; Birstein and Vasiliev, 1987). Subsequent genome duplication during sturgeon evolution has led to three groups: species with ~120, ~240, and ~360 chromosomes. Due to controversy over whether species with 120 chromosomes should be considered diploid or tetraploid (Fontana, 1994; Ludwig et al., 2001; Birstein, 2005; Vasiliev, 2009), there is still debate whether the WS, with ~240 chromosomes (Hedrick et al., 1991; Fontana, 1994; Van Eenennaam et al., 1998), is tetraploid or octoploid. A recent study of microsatellite inheritance in WS (Drauch Schreier et al., 2011) supports the hypothesis that the WS is an ancestral octoploid.

Distribution

The WS are native to several large North America rivers that drain into the Pacific Ocean; individual WS have been documented along the West Coast from northern Mexico up to the Aleutian Islands in Alaska (PSMFC, 1992; Ruiz-Campos et al., 2011; Fig. 1). Reproducing populations have been identified in the Sacramento, San Joaquin, Columbia, and Fraser river basins. Over most of the species' range, historical WS population structure has been substantially modified by historical overharvest and major habitat changes caused

by dams and resultant river regulation that affect habitat quality, suitability, and connectivity.

Marine movements between basins

While the capacity for long-range movements of WS between river basins is apparent (e.g. Brennan and Cailliet, 1991; Welch et al., 2006), the frequency and details of marine habitat use are poorly understood. WS have been occasionally documented in bays and estuaries in the vicinity of their natal spawning river (Schreier, A., University of California Davis, CA, pers. comm.; DeVore and Grimes, 1993), on the east and west coasts of Vancouver Island (Lane, D., Vancouver Island University, Nanaimo, BC, pers. comm.), in the Aleutian Islands off Alaska (PSMFC, 1992), and near Baja California, Mexico (Ruiz-Campos et al., 2011); these individuals have likely dispersed through marine habitat from nearby natal spawning rivers (i.e., Fraser, Columbia, Sacramento, and San Joaquin, respectively).

While marine movements are clearly undertaken by this species, our current understanding indicates the common reference to WS as anadromous is erroneous. Although historically, all WS potentially had access to the ocean, marine environments are not obligatory to the completion of their life cycle and most populations show no evidence of consistent or recurring movements to marine environments. Within the Columbia and Fraser river basins, WS in the middle and upper sections complete their life cycle in freshwater while WS in the lower sections with access to the ocean, are best described as exhibiting freshwater amphidromy. The Fraser River, a system without mainstem dams or natural barriers, has three or four genetically distinct populations (Smith et al., 2002; Drauch Schreier et al., 2012a), of which only a portion of the lower population shows evidence of marine movements (Lane, 1991; Veinott et al., 1999). Although the lower Columbia River population has access to the Pacific Ocean, only a small proportion enter the marine environment and most marine movements appear to be localized (DeVore et al., 1999a). Adult WS in the Sacramento-San Joaquin system congregate in San Francisco Bay, but catch records do not suggest extensive marine habitat use (Amiri et al., 2009; DuBois et al., 2009, 2010, 2012; DuBois, 2013; DuBois and Gingras, 2011; DuBois and Harris, 2016).



Fig. 1. Historical distribution of White Sturgeon in North America

Within basin movements

Numerous WS movement studies have been conducted over the past five decades. General tendencies are (i) fish tend to remain in relatively localized areas for extended periods (Golder Associates Ltd., 2010a; Nelson and McAdam, 2012; Nelson et al., 2013a,b; BC Hydro, 2016a) and (ii) fish in many areas show repeated seasonal movements between specific locations (Parsley et al., 2008; Golder Associates Ltd., 2010a; Robichaud, 2012; Nelson et al., 2013a). Large-scale movements of WS are influenced by the geographic separation between suitable habitats required for various life-requisite functions such as feeding, spawning, and

overwintering (Apperson and Anders, 1990; Brannon and Setter, 1992). While movements throughout most river basins (except the Fraser River) are limited by the presence of dams, Parsley et al. (2007) provide recent evidence of repeated passage both upstream (through fish ladders) and downstream of a lower Columbia River dam. Despite the greater connectivity in the undammed Fraser River, most movements are still restricted to particular river sections and 'whole' river migratory movements have not been detected (McAdam, S., BC MOE, Vancouver, BC, pers. comm.).

Spawning movements

Spawning migrations are quite variable within and among populations, with individuals exhibiting every migration type as defined by Bemis and Kynard (1997). In the Sacramento-San Joaquin Bay-Delta, some adults move into the delta and lower rivers throughout the fall and winter, and a proportion of these individuals make an upstream spawning migration to the Sacramento or San Joaquin rivers in late February to May (Miller, 1972; Kohlhorst et al., 1991).

Spawning migrations in the Columbia River vary by population or location. In some Columbia River impoundments, spawning movements from wintering habitats in the reservoir occur in spring, often to areas near the base of the upstream dam (Golder Associates Ltd., 2003c; Howell and McLellan, 2013b). In isolated reaches retaining sections of riverine habitats, both upstream and downstream movements to spawning areas have been documented (RL&L, 1994). In some Columbia River reaches, WS overwinter in the vicinity of spawning areas (Golder Associates Ltd., 2003b,c, Columbia Basin Bulletin, 2008). In the Kootenai River (spelled Kootenay in Canada), WS exhibit three migration patterns: fall movements from Kootenay Lake upstream to wintering and staging areas, spring movements from the lake to staging areas, and late spring/early summer movements directly to spawning areas (Paragamian and Kruse, 2001; Paragamian and Duehr, 2005; Neufeld and Rust, 2009).

Non-reproductive movements

Activity levels of WS decline when water temperature drops below 15°C (Haynes et al., 1978; Howell and McLellan, 2007b). In northerly systems that ice-over in winter, fish become torpid or dormant from October to March (RL&L, 2000a). The degree of winter movements varies over the species range and is likely due to differences in physical river conditions (e.g., water temperature and discharge), habitat suitability (e.g., proximity of feeding areas), and food availability. In systems that do not freeze-over, feeding occurs during winter although foraging activity is greatly reduced. In the upper Columbia River (i.e., Lake Roosevelt, WA, and downstream of Hugh L. Keenleyside Dam [HLK], British Columbia) and in free-flowing sections of the Snake River, WS select specific overwintering areas and typically remain in these areas all winter (RL&L, 1994; Lepla et al., 2001; Whittmann-Todd et al., 2001; Howell and McLellan, 2007b).

WS generally move more during the summer than other seasons. Juvenile WS in the upper Columbia in Arrow Lakes

Reservoir used a wider range of depths and exhibited more frequent, longer, and faster movements during the summer than in spring or fall (Golder and ONA, 2013). Adult WS in Lake Roosevelt are most dispersed in the late summer with some fish travelling 100 km from primary overwintering areas, although less movement is exhibited by WS in the riverine areas immediately upstream of Lake Roosevelt (Howell and McLellan, 2013b). In the upper Columbia River below HLK (Brannon and Setter, 1992; RL&L, 1994) and in the Kootenai River (Apperson and Anders, 1990), WS use shallower depths during the spring to summer period and exhibit frequent, short distance forays between shallow and deep-water areas. However, the proportional use of shallow water relative to deep water habitat use in the spring and summer is relatively low in the upper Columbia River (McLellan et al., 2011).

Movements of WS in lower river reaches with ocean access appear more complex. Adult WS in the Sacramento-San Joaquin Bay-Delta intensively forage in the San Francisco, San Pablo, and Suisun Bays, where movements appear to be influenced by tidal or diel cycles (Miller, 1972; Moyle, 2002). Seasonal movements were correlated with salinity levels; WS inhabited areas closer to the delta in low flow years and areas closer to San Francisco Bay in high outflow years (Kohlhorst et al., 1991). In the lower Columbia River, non-spawning adults and juveniles migrate into the estuary in spring, remain over summer, and then most move upstream in fall (Parsley et al., 2008). Movement patterns in the lower Fraser River suggest both upstream and downstream movements in the spring (associated with feeding on eulachon; Envirowest, 1992) and in the fall, associated with feeding on in-migrating salmon (Nelson et al., 2016).

The absence of mainstem dams on the Fraser River allows for the evaluation of WS movements in the most natural large river habitat available within the species distribution. A basin-wide inventory project identified five 'stock groups' based on recapture and telemetry data (RL&L, 2000a). Subsequent studies support the presence of these five spatially defined groups, although there is evidence of limited movements between areas (CSAS, 2016). An early telemetry study in the lower Fraser River identified a mixture of local fidelity and longer distance movements (Envirowest, 1992). Detailed evaluation of movements in the lower Fraser River using a long term recapture database indicated that most fish showed relatively localized movements (e.g. within 100 km) and some, typically older fish, showed more widespread movements (Nelson et al., 2004; Beardsall and McAdam, 2016). In the middle Fraser River, WS showed repeated movements between multiple discrete summer and winter habitats. Seasonal salmon migrations affect WS movements in the lower Fraser River (RL&L, 2000a; Nelson et al., 2013a; Beardsall and McAdam, 2016). In the lower Fraser River, WS movements >60 km at rates >2 km day⁻¹ have been recorded (McDonald et al., 1987). A recent tracking study of 110 WS (Robichaud, 2012; Stoddard, E., BC MOE, Vancouver, BC, pers. comm.) and WS fin ray microchemistry (McAdam, S., BC MOE, Vancouver, BC, unpubl. data) both suggest that WS in the lower Fraser River display a complex set of movement patterns.

Population structure

Criteria for population designation

Determining what constitutes a WS population in a fragmented riverine environment is problematic. WS that inhabit impounded river sections between dams are frequently referred to as 'fragmented populations' because they are perceived to be relatively isolated by the dams. However, range-wide population genetic structure analyses do not support designating WS in impounded reaches as separate populations (Drauch Schreier et al., 2013). The International Union for Conservation of Nature (IUCN) has identified five sub-population groups for WS: Sacramento-San Joaquin, Fraser and Nechako, Columbia-Snake, Upper Columbia, and Kootenai (Duke et al., 2004). For the purposes of this paper, we use population designations made by Canadian and American governments for WS populations (lower Fraser River, middle Fraser River, upper Fraser River, Nechako River, upper Columbia River above Grand Coulee Dam, and Kootenai River). For geographic and management reasons, we also partition the Columbia River below Grand Coulee Dam into the middle Columbia, Snake, and lower Columbia segments and treat the Sacramento-San Joaquin as a separate population. We refer to the numerous groups of WS within these broad geographic designations that are separated either geographically or physically (by dams) as 'population segments' throughout this document. Note that the 'population segment' designation used here is not the same as the Endangered Species Act 'Distinct Population Segment' designation, which has regulatory and legal meaning and implies genetic differentiation.

Genetic diversity

WS with access to marine habitat (Sacramento-San Joaquin Bay-Delta, lower Columbia, and lower Fraser) possess high levels of genetic diversity while WS in more upstream reaches of the Columbia-Snake and Fraser Rivers have lower levels of genetic diversity (Drauch Schreier et al., 2013). The Kootenai River population possesses the least genetic diversity, likely due to the founder effects, isolation from gene flow, and recent population declines (Drauch Schreier et al., 2012b).

Brown et al. (1992a) showed that lower Fraser WS exhibited greater genetic diversity than their lower Columbia counterparts, even though the lower Columbia River is the likely source population for post-glacial recolonization of WS in the Fraser River basin. Differences in genetic diversity between the lower Columbia and lower Fraser may be due to greater anthropogenic disturbance in the Lower Columbia (Brown et al., 1992a) or multiple sources of post-glacial recolonization in the lower Fraser (Drauch Schreier et al., 2012a).

Genetic population structure among basins

Several investigations have revealed population genetic structuring among the Sacramento-San Joaquin Bay-Delta, Columbia, and Fraser River systems. Early studies identified significant differences between these river systems in allozyme allele or mtDNA haplotype frequencies (Bartley et al., 1985;

Brown et al., 1992a,b, 1993). Different patterns in mtDNA heteroplasmy were exhibited by Columbia and Fraser WS, with Fraser River WS possessing a greater mean number of mtDNA types per individual. More recent studies using poly-somic microsatellite markers confirm the presence of genetic substructure among river basins. Rodzen et al. (2004) genotyped 670 WS from the Sacramento-San Joaquin Bay-Delta, Columbia, and Fraser River basins and reported a global F_{ST} value, a measure of among population genetic differentiation, of 0.19 which suggests a moderate amount of genetic divergence exists among basins. A more comprehensive survey of WS population structure that included samples collected throughout the species distribution identified six distinct populations among basins: the Sacramento-San Joaquin Bay-Delta, lower Columbia, middle Snake, Kootenai, lower Fraser (below Hells Gate), and upper Fraser (above Hells Gate; Drauch Schreier et al., 2013).

Genetic population structure within basins

In addition to range-wide population structure, finer scale population genetic analyses have revealed significant genetic structure within some basins (Setter and Brannon, 1992; Smith et al., 2002; Drauch Schreier et al., 2012a, 2013). Population structure was not detected in the Sacramento-San Joaquin Bay-Delta, although spawning is known to occur both in the Sacramento and San Joaquin rivers (Gruber et al., 2011; Drauch Schreier et al., 2013; Jackson et al., 2016), suggesting either high gene flow among Sacramento and San Joaquin spawning sites or unsuccessful spawning in the degraded San Joaquin system.

In the Columbia basin, microsatellite data show a complex pattern of population structure with two populations associated with the extreme ends of the WS distribution (lower Columbia, middle Snake) with WS in intervening reaches showing admixture between them (Drauch Schreier et al., 2013). An 'isolation by distance' pattern was revealed, with an individual's genetic similarity to the middle Snake population increasing with upstream location in the system (Drauch Schreier et al., 2013). The Kootenai River population has been identified as genetically differentiated from all other reaches of the Columbia (Bartley et al., 1985; Setter and Brannon, 1992; Rodzen et al., 2004; Nelson and McAdam, 2012; Drauch Schreier et al., 2013), likely due to its isolation from the lower system by Bonnington Falls ~10 000 years ago (Northcote, 1973). Although Drauch Schreier et al. (2013) found no evidence of population structure within the Transboundary Reach (upper Columbia from Grand Coulee Dam to HLK Dam) using nuclear microsatellite markers, Nelson and McAdam (2012) reported substructure among WS showing fidelity to high use zones using mtDNA control region haplotype data.

In contrast to low levels of genetic divergence within the Sacramento-San Joaquin and the Columbia basins (excluding the Kootenai River population), the Fraser River is characterized by within-basin genetic structuring (Nelson et al., 1999; Smith et al., 2002; Drauch Schreier et al., 2012a). WS in the lower Fraser below Hells Gate (Fig. 7) are strongly differentiated from WS above Hells Gate

(Drauch Schreier et al., 2012a) while weaker but still significant levels of population structure can be detected above Hells Gate (Smith et al., 2002; Drauch Schreier et al., 2012a). WS in the middle Fraser River and the Nechako River are significantly genetically differentiated from the lower Fraser and each other (Drauch Schreier et al., 2012a). Although earlier work with mtDNA and a small number of microsatellites suggested that the upper Fraser River, from the confluence of the Nechako River to McBride, was a distinct population (Smith et al., 2002), Bayesian analyses with a greater number of nuclear markers indicated that the upper Fraser may actually be an aggregation area for individuals originating from the middle Fraser and Nechako Rivers, although to date this has not been verified by movement studies. Genetic structuring in the Fraser River provides important biological insight because it indicates that strong spawning site fidelity can exist even in the absence of physical migratory barriers.

General life history

The five life history stages commonly referred to in fish are embryo, larva, juvenile, adult, and senescence. However, terminology for the early life history periods of sturgeon is variable within the literature, particularly during early life history. For this paper, we have adopted the rationale described in Urho (2002) for the larval period and provide the following definitions of the life stages used herein:

Egg/embryo: These terms are often used interchangeably for the period between fertilization and hatch. Egg is more often used for the first portion of the period and can also refer to the unfertilized ovum.

YSL: This is the period between hatch and the initiation of exogenous feeding. This phase has also been referred to as free embryo or eleutheroembryo (Balon, 1975).

Feeding larvae: This refers to the period between the initiation of exogenous feeding and completion of metamorphosis. Detailed criteria for the initiation of this phase may include the ability to feed, the initiation of feeding, and release of the melanin plug; however, these events may not be simultaneous. This period ends when the full complement of fins is present.

Juvenile: This is the period from metamorphosis to maturity. The first year in this period is referred to as age-0.

Adult: This period extends from maturity onward, as there is no evidence of senescence in WS.

The periodicity of early life stages of WS (egg-feeding larvae) across the species range is provided in Table 1.

Growth and development

Egg/embryo

Mature WS eggs are large (2.5–4.0 mm) and dark grey in color. After oviposition and upon contact with water, embryos become strongly adhesive (Cherr and Clark, 1985; Wang et al., 1985), negatively buoyant, and typically adhere to substrate surfaces near where spawning occurred. Embryo incubation time is temperature dependant, varying from 4 to

21 days (Bajkov, 1949; Wang et al., 1985; Conte et al., 1988; Parsley et al., 2011). About 120 accumulated thermal units (ATU) are required to complete this phase (Boucher et al., 2014) although Jay (2014) identified some variation with ambient temperature. Optimal incubation temperatures range between 14 and 16°C with increasing egg mortality at <8°C and >18°C and complete mortality occurring >20°C (Wang et al., 1985). However, in-situ egg incubation experiments in the upper Columbia have shown hatch rates up to 88% for eggs incubated at a mean temperature of 20.1°C (Golder Associates Ltd., 2010b). Although the long-term viability of the larvae hatched at these temperatures is unknown, the results suggest there may be some population specific variability in the upper lethal temperature.

Yolk-sac larvae

Hatch provides a clear transition defining the initiation of the YSL period. Length at hatch varies with temperature (Wang et al., 1987) with values from 11.2 to 13.0 mm TL at temperatures of 20 and 11°C, respectively. Although mean length has not been widely evaluated, figures from Deng et al. (2002) and Wang et al. (1985) report mean lengths at hatch of 9.0 and 13.6 mm TL, respectively. Temperature and substrate effects on the wet weight of yolk-sac larvae have been identified, although corrections for thermal exposure based on ATU eliminates temperature effects between treatments (Wang et al., 1987; Boucher et al., 2014). More recent work provides evidence that developmental rate deceleration is apparent for both embryos and larvae reared in colder temperatures, even when development is expressed by ATU (BC Hydro, 2016b). This delay appears to be associated with the development of major structures in both egg (neural tube; following stage 19; Parsley et al., 2011) and Yolk-sac larvae (liver development; following stage 40; BC Hydro, 2016b) stages.

Within 3 days post hatch (dph), pectoral fin buds and barbels are evident and the circulatory network is well developed (Conte et al., 1988). Pigmentation increases along the rostrum, head, and post-dorsal fin portion of the trunk. The fin fold narrows along the caudal peduncle and protrudes slightly at the future dorsal, anal, and caudal fin areas. Larvae are about 16.5 mm TL at 5 dph. Development of digestive organs appears similar to other chondrosteans (Buddington and Christofferson, 1985). Development of the spiral valve and intestine proceed from the distal end and connect with the anterior development of the oesophagus and stomach to form an anatomically complete digestive tract at the initiation of exogenous feeding (Buddington and Doroshov, 1986a). However, enzyme production continues to develop (Buddington and Doroshov, 1986b; Gawlicka et al., 1995). Yolk depletion and extrusion of the melanin plug is associated with the initiation of first feeding (Wang et al., 1985) at 7–14 dph (Conte et al., 1988; Deng et al., 2002). However, some exogenous feeding may occur prior to plug extrusion and yolk exhaustion (Buddington and Christofferson, 1985), meaning that different criteria may yield a slightly different timing for the transition to feeding larvae stages (Urho, 2002).

Table 1
Life stage periodicity for White Sturgeon in the Sacramento-San Joaquin Bay-Delta, Columbia, and Fraser river basins

Life stage	Location	J	F	M	A	M	J	J	A	S	O	N	D	Reference
Embryo	Sacramento-San Joaquin River	X	X	X	X	X								(Kohlhorst, 1976; Israel et al., 2009) (Parsley et al., 1993; McCabe and Tracy, 1994; Miller and Beckman, 1996) (Golder Associates Ltd., 2003b,c, c; Counihan et al., 1995) (Golder Associates Ltd., 2006c, 2010b, b, Howell and McLellan, 2013a) (IPC, 2005; Parsley and Kappenman, 2000) (IPC, 2005; Bates, 2015) (Paragamian et al., 2001) (Perrin et al., 2003) No Data (Triton, 2009)
	Lower Columbia River			X	X	X	X							
	Mid Columbia River						X	X						
	Upper Columbia River						X	X	X					
	Lower Snake River				X	X	X	X						
	Mid Snake River				X	X	X							
	Kootenai River					X	X	X						
	Lower Fraser River							X	X					
	Mid & Upper Fraser River													
	Nechako River					X	X							
Yolk sac larvae	Sacramento-San Joaquin River		X	X	X	X								(Kohlhorst, 1976; Israel et al., 2009) (McCabe and Tracy, 1994) CCT, unpubl. data (Golder Associates Ltd., 2009a, 2010b, Howell and McLellan, 2013a) (IPC, 2005; Counihan et al., 1995; Parsley et al., 1996) (IPC, 2005; Bates, 2015) No Data (Perrin et al. (2003) No data (Triton, 2009)
	Lower Columbia River				X	X	X							
	Mid Columbia River						X	X						
	Upper Columbia River						X	X	X					
	Lower Snake River				X	X	X	X						
	Mid Snake River				X	X	X							
	Kootenai River								X	X				
	Lower Fraser River								X	X				
	Mid & Upper Fraser River													
	Nechako River						X	X						
Larvae (feeding)	Sacramento-San Joaquin River		X	X	X	X								(Kohlhorst, 1976; Israel et al., 2009) (Parsley et al., 1993; McCabe and Tracy, 1994) CCT, unpubl. data (Howell and McLellan, 2013a) (IPC, 2005) (IPC, 2005; Bates, 2015) No Data (Perrin et al., 2003) No Data (Triton, 2009)
	Lower Columbia River				X	X								
	Mid Columbia River						X	X						
	Upper Columbia River						X	X	X					
	Lower Snake River				X	X	X	X						
	Mid Snake River				X	X	X	X						
	Kootenai River													
	Lower Fraser River													
	Mid & Upper Fraser River													
	Nechako River						X	X						

Larval rearing conditions influence growth. Larval lengths at the end of the yolk-sac period range from 16.4 to 25.1 mm TL (Wang et al., 1985; Deng et al., 2002), and the availability of interstitial habitat significantly increases larval growth under both laboratory (Baker et al., 2014; Boucher et al., 2014) and field conditions (Crossman and Hildebrand, 2014). Wang et al. (1987) reports wet weights at this phase range from 26.8 to 30.8 mg (11–20°C). Rearing YSL in the presence of interstitial habitat leads to increased weight wet (Baker et al., 2014), with weights near 50 mg observed by Boucher et al. (2014). A decreasing trend for dry weight of early larvae (Wang et al., 1987) reflects their restriction to endogenous yolk reserves to satisfy both metabolic and growth requirements. The increased wet weight during the period when dry weight is declining reflects the incorporation of water in conjunction with cell proliferation and development.

Optimal temperatures for this stage, based on both survival and an absence of abnormal development, fall in the

range between 13.5 and 16.0°C with temperature induced mortality occurring >20°C (Wang et al., 1985; but see Golder Associates Ltd., 2010b). Temperatures in the lower portion of this range may increase survival (Boucher et al., 2014) and reduce cortisol levels (Bates et al., 2014a). This is supported by results from the Kootenai River Conservation Aquaculture Program (KRCAP) where successful egg incubation and larviculture is completed at 14°C (KTOI, 2016).

Feeding larvae

Once exogenous feeding begins, feeding larvae disperse and forage over the open bottom and use less cover with increased age (Brannon et al., 1985). Studies in the laboratory indicate feeding larvae are most active at night (Kynard and Parker, 2005). Searching for food is the primary activity at this final stage of larval development with benthos, periphyton, and zooplankton comprising the majority of their diets (Brannon et al., 1984; Buddington and Christofferson,

1985; Muir et al., 2000). Within 20–45 days, metamorphosis is complete and larvae develop into juveniles (life stage with adult features) with a full complement of scutes and fins (Buddington and Christofferson, 1985; Deng et al., 2002).

Juveniles

A review of growth and temperature literature on North American species of sturgeon and paddlefish by Lebreton and Beamish (2004) reported that optimal temperatures for growth in young WS occur from 20 to 24°C with growth decreasing to zero as temperatures reach 26°C. In laboratory and culture environments, WS juveniles can grow very rapidly with body weight doubling (at 16°C) every 2–3 weeks during their first 4 months of life (Brannon et al., 1984). Supporting Brannon et al. (1984), the KRCAP rears young juveniles, up to 120 dph, at 16–18°C to balance growth and mortality during their first summer (KTOI, 2016). Wild WS juveniles likely exhibit lower growth rates due to temperature and food limitations. Although growth of juvenile WS is initially rapid, it slows with age. For instance, age-0 WS in the middle Snake River (C. J. Strike Reservoir) can achieve 38 cm TL by the end of their first growing season (Lepla, 2008a). Average growth then gradually decreases from 12 cm year⁻¹ for juveniles between 70 and 93 cm TL to ~3.0 cm year⁻¹ for adults >183 cm TL (IPC 2007; Bates, 2013). In the Sacramento River, WS reached sizes of 43–45 cm TL in their first year and then grew 2–6 cm year⁻¹ after attaining a size of 102 cm TL (Brennan and Cailliet, 1989).

Growth rates can vary due to spatial and genetic variability. Golder (2003a, 2005a, 2006a,b) revealed more rapid growth rates for hatchery-reared WS in the upper, riverine portion of the upper Columbia relative to those in the lower reservoir section. Below Bonneville Dam, age-0 WS reached a minimum mean total length of 17.6 cm and a minimum mean weight of 30 g by the end of September (4–7 month old; McCabe and Tracy, 1994). Mean length at age and condition factor for WS were greater for fish ages 1–7 in the three reservoirs immediately upstream of Bonneville Dam than for the population segment downstream from Bonneville Dam (Miller and Beckman, 1993). Due to genetic differences among families, hatchery WS below Shoshone Falls (Snake River) from the same year-class recaptured at age-11 ranged from 86 to 163 cm TL and 2.9–25.4 kg in weight (Lepla et al., 2002).

Growth rates and condition factors for hatchery-reared WS following release may be hindered by difficulty adapting to a natural environment after release. In the upper Columbia River in Canada, 95% of hatchery juveniles released at 10 month old (mean FL = 19 cm; mean weight = 54 g) and recaptured at age-3 exhibited a decrease in relative weight (Golder Associates Ltd., 2006a). In the upper Columbia, annual growth rates ranged 9.5–12.0 cm in fork length for younger fish (fish aged 2–6) and 7.6–8.5 cm per year for older aged juveniles (fish aged 7–12; BC Hydro 2015a). Conversely, average annual weight increases were smaller for the younger fish and larger for older ones (BC Hydro 2015a). In Washington, average relative weight (W_r ; see Murphy et al., 1991) values for 58 hatchery fish from five brood years (BY)

captured in 2009 was 104 (range 80–135; Howell and McLellan, 2013a). Those captured in the same year that they were released (BY2008) had the lowest mean W_r values ($n = 17$; mean = 89; range = 80–106).

In the Kootenai River, juvenile growth rates averaged 4.5–6.4 cm year⁻¹ during 2000–2014, but were highly variable (Ireland et al., 2002a; Ross et al., 2015; Stephenson and Evans, 2015). Average relative weight decreased in the first year after release; however, after several years at large, most fish showed significant increases in length, weight, and relative weight.

Adults

The transition from juvenile to adult occurs at the onset of sexual maturity; however, the size and age at maturity for either sex is variable across the species range. WS males begin to mature at about age-12 (125 cm) while females require a longer period, generally maturing at age-15–32 (PSMFC, 1992). Sexual maturity in captive WS can occur much earlier with males maturing at age-4 and females between age-7–10 (Conte et al., 1988; Doroshov, S., University of California Davis, Davis, CA, pers. comm., as cited in PSMFC, 1992).

The smallest spawning females in the middle Snake River are about 165 cm FL and ~age-15–18 (Bentz and Lepla, 2009; Lepla, K., IPC, Boise, ID, pers. comm.). In the Sacramento-San Joaquin Bay-Delta, females mature at a larger size (95–135 cm FL) and at a later age than males (75–105 cm FL; Chapman et al., 1996). DeVore et al. (1995) state that the median length at first maturity for WS in the Columbia River downstream from Bonneville Dam was 160 cm FL; 95% of the females matured between 124 and 196 cm FL. The median size of mature females has been reported as 158–194 cm FL in the lower Columbia River (Beamesderfer et al., 1995), 188 cm FL in the Snake River upstream from the Salmon River confluence to Shoshone Falls (IPC, 2009), 194–205 cm FL in the middle Columbia River (Golder Associates Ltd., 2003c), and 140 cm FL in the Kootenai River (Paragamian et al., 2005). The small median size of mature females in the Kootenai River was possibly a result of slower growth rates (Paragamian et al., 2005). Kootenai River WS reportedly do not reach sexual maturity until age-30, which may suggest that isolated populations with slow growth mature at smaller sizes and older ages (Beamesderfer, R., Cramer Fish Sciences, pers. comm., as cited in PSMFC, 1992).

Across the species range, spawning occurs between February and August, with late winter spawning occurring at the southern end of their range and continuing into late summer with increasing latitude (Table 1). WS have a non-annual iteroparous reproductive life history strategy. Physiologically, mature females are capable of spawning every 2–3 years (Webb, M., Oregon State University, Corvallis, OR, pers. comm., as cited in Paragamian et al., 2005). Based on the capture of repeat female spawners, 3–5 years spawning intervals have been documented in the Nechako River (Williamson, C., FFSBC, Prince George, BC, pers. comm.) and Kootenai River (Paragamian et al., 2005; Stephenson, S., BC FLNRO, Nelson, BC, pers. comm.), and Snake River (IPC,

2016). In the upper Columbia River, over 100 adults annually have been sexed during broodstock collection programs conducted since 2000; an average of 19.0% ($\pm 0.04\%$) of females collected have been in spawning condition (Hildebrand and Parsley, 2013) which suggests a 5-year spawning interval.

Reports of longer inter-spawning intervals of 9–11 years (Semakula and Larkin, 1968; Scott and Crossman, 1973) were based on interpretation of spawning checks on fin rays and are not supported by more recent studies. In the Kootenai River, however, telemetry and recapture data suggest that some females have spawning intervals of up to 10 year. (Stephenson, S., BC FLNRO, Nelson, BC, pers. comm.)

WS sex ratios in the wild are generally 1 : 1 (Chapman et al., 1996; IPC, 2007; Hildebrand and Parsley, 2013; BC Hydro, 2015b) and where this is not the case, divergence may be attributed to harvest or sampling bias. Beamesderfer et al. (1995) reported that in the lower Columbia River, the sex ratio among larger fish was skewed toward females.

Fecundity in WS increases with size. In the lower Columbia River, fecundity estimates ranged from 39 400 to 713 000 eggs (Wydoski and Whitney, 2003) with size specific estimates of 47 000 eggs for a 100 cm FL female and 210 000 eggs for a 150 cm FL female (Beamesderfer et al., 1989). DeVore et al. (1995) reported fecundities from 98 200 to 699 000 ($N = 38$) for fish from 115 to 215 cm FL sampled in the lower Columbia below Bonneville Dam. In the lower Fraser River, a 240 cm long female was reported to contain 700 000 eggs (Scott and Crossman, 1973).

Behaviour

An understanding of WS behaviour is limited by the cryptic behaviour of early life stages and the deep, large river habitats they occupy. Behaviour of early life stages has been inferred from laboratory studies and a limited number of field studies. Information on juveniles and adults is based mainly on field observations, underwater videography, movement studies, and inference from recaptures.

Early life stage behaviour

A variety of studies have addressed early larval behaviour; however, a comprehensive understanding continues to be limited by differences among laboratory studies and between laboratory and field studies. For example, laboratory studies have identified both hiding and drift behaviours for the yolk-sac larvae life stage, including patterns ranging from immediate post-hatch hiding (McAdam, 2011) to a 1–6 dph drift phase (Brannon et al., 1984, 1985; Deng et al., 2002; Kynard and Parker, 2005). However, variable substrate conditions among studies, and particularly the absence of interstitial habitat in some studies, appears explain the observed differences in larval drift behaviour (McAdam, 2011). In the presence of suitable interstitial habitat, yolk-sac larvae show a strong tendency to hide both under static water conditions (Bennett et al., 2007) and in the presence of moderate flow (McAdam, S., BC MOE, Vancouver, BC, unpubl. data). However, laboratory studies may reflect behaviour under

ideal conditions, and behaviour expression may differ under field conditions of higher water velocity, greater turbulence and more variable substrate.

Under field conditions, drifting yolk-sac larvae are predominantly detected in benthic habitats (Parsley et al., 1993; Howell and McLellan, 2008), although van der Leeuw et al. (2006) collected drifting yolk-sac larvae in surface tows in the lower Columbia River downstream of known spawning areas. Studies in the upper Columbia River detected drift of yolk-sac larvae within about 2 km of known spawning locations. The detection of yolk-sac larvae in drift monitoring studies might be attributed to an innate tendency for short term, non-volitional drift due to the inability to larvae to rapidly hide within interstitial habitats, or a response to degraded or unsuitable habitat conditions (e.g. Triton, 2009). Differentiating between these possibilities is challenging. While the increased retention of 2 dph yolk-sac larvae in response to substrate augmentation that improved interstitial hiding habitat (Crossman and Hildebrand, 2014) suggests that drift at that age is non-volitional, this field study did not examine behaviour immediately post hatch.

In contrast, feeding larvae demonstrate a clear volitional drift that is primarily nocturnal (McAdam, 2012; Howell and McLellan, 2014a). Drift by feeding larvae is also primarily benthic (Parsley et al., 1993; Howell and McLellan, 2008, 2013a,b). In the upper Columbia River substantial numbers of feeding larvae (e.g., approximately 30 000 in both 2014 and 2015) were captured (Colville Confederated Tribes, Spokane, WA, unpubl. data; Spokane Tribe of Indians, Wellpinit, WA, unpubl. data) within 16 km of spawning areas (Howell and McLellan, 2008; Golder 2009a). Drift over greater distances from known egg incubation sites has been reported in the lower Columbia River (McCabe and Tracy, 1994; Parsley and Kofoot, 2013). Larval drift studies in the lower Fraser River also have detected feeding larvae, although sampling has been limited and sampling effectiveness is limited by high debris loads in that river.

Aggregation behaviour

WS juveniles and adults are gregarious and commonly found in large aggregations of various sizes and year-classes (Hildebrand et al., 1999; Parsley et al., 2007). In February 2008, a large aggregation of approximately 30 000–60 000 WS (potentially 5–10% of the entire population in the lower Columbia River) was identified in the stilling basin below the spillways at Bonneville Dam (http://blog.oregonlive.com/breakingnews/2008/05/_when_sonar_surveys_spotted.html; accessed 9/30/2016). The aggregation subsequently dispersed when water temperatures and flows from the dam increased. In March 2009, approximately 1500 adult and juvenile WS were stranded in shallow tidal channels at Port Susan Bay in Puget Sound when the tide went out (<http://www.seattletimes.com/seattle-news/big-appetites-probably-stranded-sturgeon/>; accessed 9/30/2016). Most survived until the tide returned, but the reasons behind this and other reported stranding events remain unknown. Their tendency to form large aggregations may place large numbers of WS at risk of natural or anthropogenic catastrophic events.

Spawning behaviour

Environmental or physiological cues that determine spawn timing and trigger spawning behaviour are poorly understood. However, water temperature is a relatively good predictor of spawning time in any given area. Generally, spawning occurs between 8 and 20°C. In 15 years of monitoring WS at the Waneta spawning area at the Columbia-Pend d'Oreille rivers confluence, the only consistent patterns among all years was that the onset of initial spawning always occurred during the descending limb of the Pend d'Oreille River hydrograph in mid to late June (around the summer solstice) and when mean daily water temperature reached 14°C (Golder Associates Ltd., 2010b). No significant correlations were found between spawn timing and flow as spawning occurred during load shaping operations that resulted in substantial daily flow fluctuations in the spawning and egg incubation areas (van der Leeuw et al., 2006; Golder Associates Ltd., 2010b). In the Kootenai River, temperatures of 6–8°C during March and April trigger movement/migration toward known spawning areas; 10°C typically triggers male and female ripeness and spawning typically occurs during late May and June at 10–12°C on the peak and descending limb of the freshet (Ross et al., 2015; Hardy et al., 2016). WS spawning in the Snake River occurs from mid April through July with corresponding water temperatures between 12 and 18 °C. Egg collections have occurred on peak and descending hydrographs as well as drought years with no spring freshet (Lepla and Chandler, 2001). In the Sacramento-San Joaquin Bay-Delta, Fish (2010) found a positive correlation between year-class index (age-0 and age-1) and both winter ($r = 0.74$) and spring ($r = 0.71$) outflow, hypothesized as corresponding to attraction flows for successful spawning and flows required for early life stage dispersal. Schaffter (1997) suggested a minimum flow of $180 \text{ m}^3 \text{ s}^{-1}$ was required for spawning in the Sacramento River. This was based on the interrupted upstream spawning migration of putative female spawners before reaching spawning sites when flow was less than this threshold.

Spawning behaviour is rarely observed because spawning occurs in deep and sometimes turbid rivers, and because the large size of WS prevents captive studies. Aerial observation of putative spawning behaviour in the Nechako River identified small groups of sturgeon typically consisting of one larger fish (female) with two or three smaller males vying for position beside the female (Triton, 2004). Males typically held positions about two-thirds down the length of the female and crossed from one side of the female to the other. The observed spawning event involved one male-female pair, where the male held a position with its head slightly upstream of the female's while turning its ventral surface towards the female. Gamete release was associated with rapid body undulations as the fish moved upstream in unison. Although communal broadcast spawning has been documented for Lake Sturgeon (LS; *Acipenser fulvescens*; Bruch and Binkowski, 2002) and has been suggested for WS (Anders and Beckman, 1993), the observation of only one spawning WS pair in the Nechako River may reflect the low numbers of spawners present in this system. Pedigree analysis

confirms a polygynadrous mating system with WS adults sharing 3.6 ± 2.8 and 2.0 ± 1.5 partners based on genetic evaluations of larvae captured in 2011 and 2012, respectively (Jay et al., 2014). Questions remain regarding where in the water column WS egg release occurs. Highly aggregated egg captures on egg collection mats placed on the riverbed suggest egg release may occur near the river bottom (Golder Associates Ltd., 2008) as has been observed for LS (Bruch and Binkowski, 2002).

Feeding behaviour

Like other sturgeon species, WS use their inferior mouth and barbels for benthic-oriented feeding. WS larvae in the lower Columbia River fed primarily on amphipods (*Corophium* spp.; Muir et al., 2000). Juveniles (<60 cm TL) feed on tube-dwelling amphipods, mysids, isopods, *Corophium*, and other benthic invertebrates such as chironomids, and on the eggs and fry of other fish species (Schreiber, 1962; Radtke, 1966; Cochnauer, 1983; Partridge, 1983; PSMFC, 1992; Parsley et al., 2010). In the upper Columbia River, diet analysis of age-1 to age-10 juvenile WS indicated that *Mysis relicta* were the primary component of the diet followed by Trichoptera nymphs; other prey items encountered (in decreasing order of abundance) were Ephemeroptera nymphs, snails, Diptera, fish parts, Gammaridae, Hemiptera, and Plecoptera (Crossman et al., 2015). As WS grow (~60–80 cm TL), their diets diversify and they begin to eat fish (Muir et al., 1988; PSMFC, 1992). Larger individuals exploit seasonal prey items such as salmon and lamprey (Galbreath, 1979). Other items found in their diet include small mollusks and crayfish (Bajkov, 1949; McKechnie and Fenner, 1971).

Habitat use

Rearing habitat

Egg incubation habitat is primarily determined by adult spawning site selection. Field collections confirm that embryos tend to be located in discrete areas, and sampled densities suggest a patchy distribution (Golder Associates Ltd., 2002, 2008; Howell and McLellan, 2008; Triton, 2009). The release of gametes into high velocity areas (see Spawning habitat) does provide some potential for short distance embryo dispersal (magnitude unconfirmed), which may help to prevent extreme patchiness that could be prone to density dependant effects (e.g. fungus and bacterial infection of clumped embryos). Eggs are detected in mainstem channels at most spawning sites, although in the lower Fraser River eggs have been found in multiple large seasonal side channels (Perrin et al., 2000; Liebe and Sykes, 2011; pers. comm. Stoddard, E., BC FLNRO, Surrey, BC). At all sites, the benthic detection of eggs contrasts with the suggestion by Coutant (2004) that WS embryos adhere to riparian vegetation. While direct observation of WS embryo incubation habitat is limited, similar to observations by Johnson et al. (2006) of LS embryos, coarse substrates with interstitial spaces would likely provide refugia for the eggs until hatch.

Recent investigations in the laboratory have identified strong effects of substrate on condition during the yolk-sac stage. During the yolk-sac phase, larval use of suitable sized interstitial habitat (e.g. that provided by gravel) leads to faster growth, gut development, swimming performance, and survival (Baker et al., 2014; Boucher et al., 2014) as well as diminished stress responses (Bates et al., 2014a). Energetic trade-offs combined with the limited metabolic scope of larvae appear to be the root mechanism of these effects (Boucher, 2012). Substrate conditions experienced during the yolk-sac phase also have strong carryover effects that manifest during the subsequent feeding larvae stage (Boucher et al., 2014).

Less is known about habitat use of feeding larvae and early juveniles. However, in the Fraser River, juveniles use lower velocity areas such as side channels, sloughs, and deeper areas of the mainstem (Bennett et al., 2005; Glova et al., 2008). The decreased availability of such habitats has been identified as a potential threat to juvenile survival (Nelson et al., 2007).

Spawning habitat

Spawning WS appear to be attracted to a particular reach and then likely select areas within the reach for egg deposition based on velocity, depth, substrate composition, turbulence or a combination of these or other factors. Spawning generally occurs in areas with fast-flowing waters over coarse substrates (Parsley et al., 1993; Hildebrand et al., 1999; Parsley and Kappenman, 2000; Perrin et al., 2003). In the Kootenai River, spawning has been observed over clay and/or sand (Ross et al., 2015), which is considered as sub-optimal spawning substrate. Based on coring and sonar data, substrates in this reach of the Kootenai River historically, were always dominated by sand and clay (Barton et al., 2010). Therefore, the reason (s) for the present apparent selection of these areas (and their apparently unsuitable substrates) by WS for spawning is unknown.

Spawning often occurs in areas with hydraulic complexity such as deep turbulent areas of the mainstem or major tributary confluences (Hildebrand et al., 1999; Parsley and Kappenman, 2000; Howell and McLellan, 2007b; Golder Associates Ltd., 2009a; McDonald et al., 2010), high velocity runs near rapids (Lepla and Chandler, 2001), and immediately downstream from dam outlets (Parsley and Kappenman, 2000, Golder Associates Ltd., 2003b,c, 2005a,b). Potential benefits from spawning in fast, turbulent waters with coarse substrates include suitable attachment surfaces for negatively buoyant adhesive eggs, removal of fine sediments that could suffocate eggs, enhanced egg viability by dispersal of adhesive eggs to prevent clumping and disease, and reduced egg predation (Parsley et al., 1993, 2002; McCabe and Tracy, 1994). Fast turbulent flows also provide increased oxygenation provide more efficient gas exchange for eggs and embryos than would occur under laminar flow conditions (Sulak and Clugston, 1998, 1999). Coarse substrates also provide hiding habitat for hatched larval

WS. Near-bottom velocities in egg deposition areas are typically $>1 \text{ m s}^{-1}$ (Parsley et al., 1993; Perrin et al., 2003; ASL et al., 2007).

While river regulation and upstream passage barriers occur across the species range, studies from populations where dams and impoundments are distant from spawning locations (Kohlhorst, 1976; McAdam et al., 2005; Paragamian et al., 2009) suggest that current spawning locations were also historical spawning locations although habitat conditions within these areas may have changed. Early life history sampling suggest that WS spawning may be widely distributed within long reaches with riverine conditions (McCabe and Tracy, 1994; Parsley and Kappenman, 2000; Perrin et al., 2000; Golder Associates Ltd., 2009a), although spawning may be restricted to a particular reach (e.g. 2 km of the Nechako River near Vanderhoof, BC; 12 km of the Kootenai River near Bonners Ferry, ID) even when extensive riverine habitat is available. For many other population segments, backwater effects from impoundments restrict spawning to areas within a few kilometres downstream of dam outlets (Parsley et al., 1993; RL&L, 1994; Parsley and Kappenman, 2000; Lepla and Chandler, 2001; IPC, 2005; Golder Associates Ltd., 2006c, 2010b). In the Fraser River, recent use of side scan sonar has also identified multiple potential spawning sites based on the presence adult aggregations during the spawning season (English et al., 2014). Egg sampling has now confirmed at least seven spawning locations within a 47 km section of the lower Fraser River downstream of Hope, BC and four sites upstream of Hope (Stoddard, E., BC FLNRO, Surrey, BC, pers. comm.). These locations are a mix of both mainstem and side channel habitat, and use over multiple years has been confirmed for some locations.

Overwintering habitat

WS typically occupy deep, low velocity habitats during the winter period (Apperson and Anders, 1990; Hildebrand et al., 1999). Downstream from Bonneville Dam, WS have been observed congregating in deep water as well as water $<1 \text{ m}$ deep during winter (Parsley et al., 2007). In some population segments, wintering areas are also used for feeding and rearing and extensive migrations to wintering habitats have not been observed.

Population metrics

Currently, the more abundant and productive WS populations are found in lower portions of the Sacramento-San Joaquin Bay-Delta, Columbia, and Fraser river basins (Table 2). Greater productivity in the lower rivers is presumably due to diverse estuarine and marine food resources and favourable water temperatures for maximizing growth (DeVore et al., 1995). WS growth rates generally decrease as distance inland increases, with headwater residents typically showing the slowest growth (Figs 2 and 3). In the Columbia and Sacramento basins, increased modification of the riverine ecosystem by multiple anthropogenic stressors resulting in changes to flow and temperature regimes, water quality, physical habitat, food availability and density, and the biotic

Table 2

Population estimates of wild White Sturgeon in the Sacramento-San Joaquin, Columbia, and Fraser river basins. Note that estimates are relevant to the publication date and have not been standardized

River system	Population segment	Habitat type [Length or Area]	Conservation status	Population estimate (95% CI) [min size – FL]	References
Sacramento	Sacramento-San Joaquin (Bay-Delta)	Riv (600 km) Est (~ 4000 km ²) Del (~2850 km ²)	NL	48 000 [117 cm]	(DuBois and Gingras, 2011)
Lower Columbia	Unimpounded Bonneville	Riv (187 km) Est (48 km)	NL	1 009 635 [54 cm]	(Jones, 2010)
		Res (75 km)	NL	228 249 [61 cm]	(Cox and Martin, 2016)
	The Dalles	Res (39 km)	NL	86 895 [61 cm]	(Cox and Martin, 2016)
	John Day	Res (122 km)	NL	30 989 [61 cm]	(Cox and Martin, 2016)
Mid Columbia	Hanford Reach and McNary	Riv (89 km) Res (80 km)	NL	9241 [54 cm]	(Cox and Martin, 2016)
		Priest Rapids	Res (53 km)	NL	134 (48–2680) [45 cm]
	Wanapum	Res (96 km)	NL	551 (314–1460) [45 cm]	(Golder Associates Ltd., 2003e)
	Rock Island	Res (48 km)	NL	Low abundance; estimate unavailable	
	Rocky Reach	Res (69 km)	NL	47 (23–237) [60 cm]	(Golder Associates Ltd., 2003b,c)
	Wells Chief Joseph	Res (48 km) Res (82 km)	NL NL	31 (13–218) [65 cm] Low abundance; estimate unavailable	(Jerald, 2007)
Upper Columbia	Roosevelt Reach	Res (214 km) Riv (26 km)*	NL	2037 (1093–3223) [70 cm]	(Howell and McLellan, 2007b)
	Keenleyside Reach	Riv (56 km)	E	1160 (415–1900) [50 cm]	(Irvine et al., 2007)
	Arrow Lakes Reservoir	Riv (7 km) Res (225 km) *	E	52 (37–92) [60 cm]	(Golder Associates Ltd., 2006c, 2010b)
	Revelstoke and Kinbasket Reservoirs	Riv (180 km) Res (335 km) *	E	Unknown; presence suspected based on anecdotal sightings	(RL&L, 2000b)
Lower Snake	Ice Harbor	Res (51 km)	NL	4830 [54 cm]	(Ward, 1998)
	Lower Monumental	Res (46 km)	NL	4262 [54 cm]	(Ward, 1999)
	Little Goose	Res (60 km)	NL	6492 [54 cm]	(Ward, 1999)
Mid Snake	Lower Granite	Res (63 km) Riv (162 km)	S1	3816 (3028–4871) [50 cm]	(Bentz, 2015a)
	Hells Canyon	Res (40 km)	S1	Low abundance; estimate unavailable	
	Oxbow	Res (19 km)	S1	Low abundance; estimate unavailable	
	Brownlee	Res (88 km) Riv (190 km)	S1	141 (43–658) [60 cm]	(Bentz, 2015c)
	Swan Falls	Res (17 km) Riv (40 km)	S1	334 (219–700) [60 cm]	(Bentz and Lepla, 2013)
	C.J. Strike	Res (38 km) Riv (68 km)	S1	4025 (2469–6731) [60 cm]	(Bentz and Lepla, 2011)
	Bliss	Res (8 km) Riv (13 km)	S1	54 (47–152) [60 cm]	(Bentz, 2013)
	Lower Salmon	Res (12 km)	S1	88 (68–129) [60 cm]	(Bentz, 2015b)
	Upper Salmon	Res (8 km) Riv (46 km)	S1	297 (233–404) [60 cm]	(Bentz, 2014)
Kootenai	Kootenai River and Kootenay Lake	Riv (126 km) Lak (120 km)	E	1000 (800–1400) [>100 cm]	(Beamesderfer et al., 2009)
Lower Fraser	Estuary to Hells Gate	Riv (175 km), Est (45 km) Lake (85 km)	E	44 713 (42 634–46 792) [40–279 cm]	(Nelson et al., 2013a)
Mid Fraser	Hells Gate to Prince George	Riv (580 km, including 270 km canyon)	E	3745 (3064–4813) [>40 cm]	(RL&L, 2000a)
Upper Fraser	Prince George to McBride	Riv (300 km)	E	815 (677–953) [>40 cm]	(Yarmish and Toth, 2002)
Nechako	Nechako	Riv (230 km) Lak (196 km)	E	571 (421–890) [>50 cm]	(RL&L, 2000a)

Riv, Riverine; Res, Reservoir; Est, Estuarine; Lak, Lake; Del, Delta; E, Endangered (U.S. and Canadian Federal Designations); S1, Critically imperiled (State of Idaho Listing); NL, Not Listed.

*Denotes sections with large storage reservoirs and variable river and reservoir lengths; values provided represent lengths of each habitat type at typical full reservoir level.

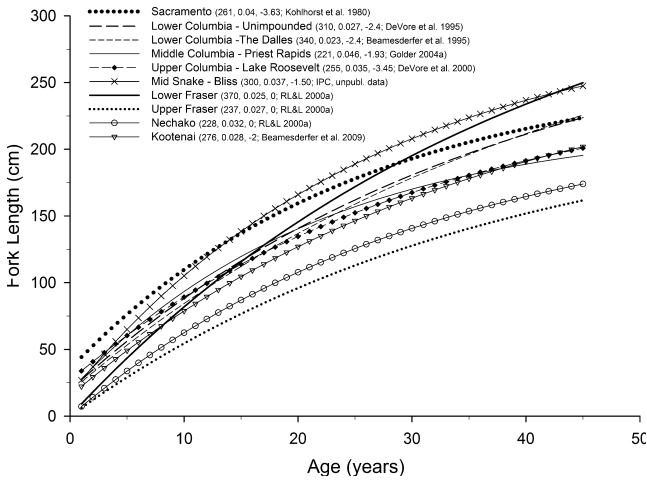


Fig. 2. Von Bertalanffy growth lines (L_{∞} , k , t_0) for White Sturgeon in the Sacramento/San Joaquin, Columbia, and Fraser river basins

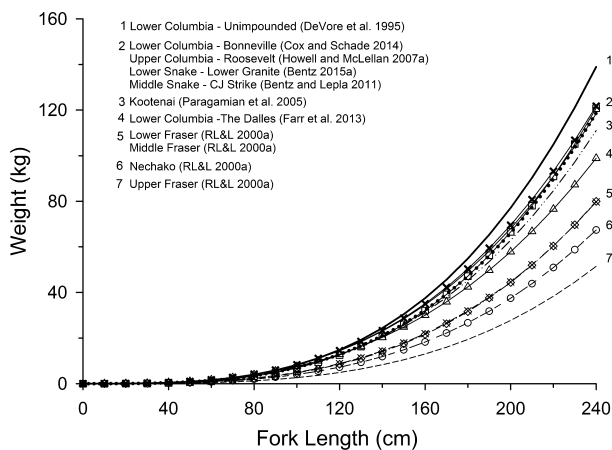


Fig. 3. Weight-at-length relationships for White Sturgeon in the Columbia and Fraser river basins. Comparable data from the Sacramento Basin not available

community all affect WS productivity. For example, bioenergetic modelling identified growth and metabolic differences between two groups of WS in the upper Columbia River. This highlights the interaction between habitat selection and population productivity, and shows that increased water temperatures and limited food resources can reduce energy intake, slow growth, prolong maturity, increase spawning intervals, and lower lifetime fecundity of WS in the upper Columbia (Van Poorten and McAdam, 2010) and middle Snake rivers (Bevelhimer, 2002).

Growth of WS also tends to slow and condition is reduced with increased latitude (Fig. 2) although reach specific habitats (e.g. moderated river temperature from the Snake River aquifer) can provide favourable growing conditions for WS, as observed in the middle Snake River. In northern systems like the Nechako River, reduced growth of WS typically results from cooler temperatures, low system productivity, and increased distance from abundant estuarine and marine food resources (NWSRI, 2004). In the lower Columbia River

downstream from Bonneville Dam, considered the most productive population in the species' range (DeVore et al., 1995), WS have the largest mean W_r observed in any WS population studied to date (Fig. 4).

Annual survival rates for long-lived fish like WS often exceed 90% (Semakula, 1963; Cochnauer, 1983; Kohlhorst et al., 1991; DeVore et al., 1993; Beamesderfer et al., 1995; Irvine et al., 2007; Golder Associates Ltd., 2015a). Natural mortality estimates for adult WS range from 4 to 10% in the lower Columbia River (Beamesderfer et al., 1995; DeVore et al., 1995), 6–16% in the middle Snake River (Cochnauer, 1983; Lukens, 1985; Lepla and Chandler, 1995, 1997), 4–9% for the Fraser (Semakula and Larkin, 1968; Walters et al., 2005; Whitlock, 2007), 4–7% in the Kootenai River (Beamesderfer et al., 2009, 2014b; Dinsmore et al., 2015), and 3% in the upper Columbia River (Irvine et al., 2007).

Survival rates of wild WS juveniles have not been estimated, but in the upper Columbia, using mark-recapture data for hatchery-released WS juveniles between 2002 and 2006, estimated survival was $29 \pm 5\%$ (S.D.) for the first 6 months at-large and thereafter increased to 88% (Irvine et al., 2007). A more recent analysis of 7351 recaptures from 136 914 juvenile WS released from 2002 to 2014 found that annual survival (i.e., survival adjusted to a 1-year period) of the first age-class increased with release weight (Golder et al., 2015a). At release sizes of 100, 200, and 300 g, the 2002-released fish had predicted annual survivals of 90.7, 95.6, and 98.1%, respectively. These values were considerably higher than those previously reported in the analysis of 2002–2006 releases (Golder Associates Ltd., 2009b) but were comparable to the higher range of age-2 survival reported for WS in the Kootenai River (Justice et al., 2009).

Uncertainty regarding both ageing accuracy and imprecision have been identified in WS, and particularly for fish >age-30 (Rien and Beamesderfer, 1994; Paragamian and Beamesderfer, 2003). Age estimation error can confound analyses of age frequencies, relative year-class strengths, and age-related population statistics, and affect estimation of growth, mortality, and sustainable exploitation rates (Rien and Beamesderfer, 1994). Despite concerns regarding accuracy and precision, age estimates can be useful for relative comparisons between groups, if biases are assumed to be similar (Rien and Beamesderfer, 1994) or when comparing younger age classes (McAdam, 2015) where accuracy is typically greater. Further work on age validation in WS is suggested to increase confidence in evaluations that rely on age data.

General physiology

The ancient origin and benthic feeding mode of WS have led to interesting physiological attributes. WS have efficient gas exchange mechanisms (Brauner and Berenbrink, 2007), are oxyconformers (Burggren and Randall, 1978; Cech and Crocker, 2002), and are tolerant to hypoxia (Burggren and Randall, 1978). This may be partly related to adaptations that allow continued gill ventilation during benthic feeding without passing water through the mouth via retrograde gill ventilation and spiracles (Burggren, 1978). Studies of respiratory

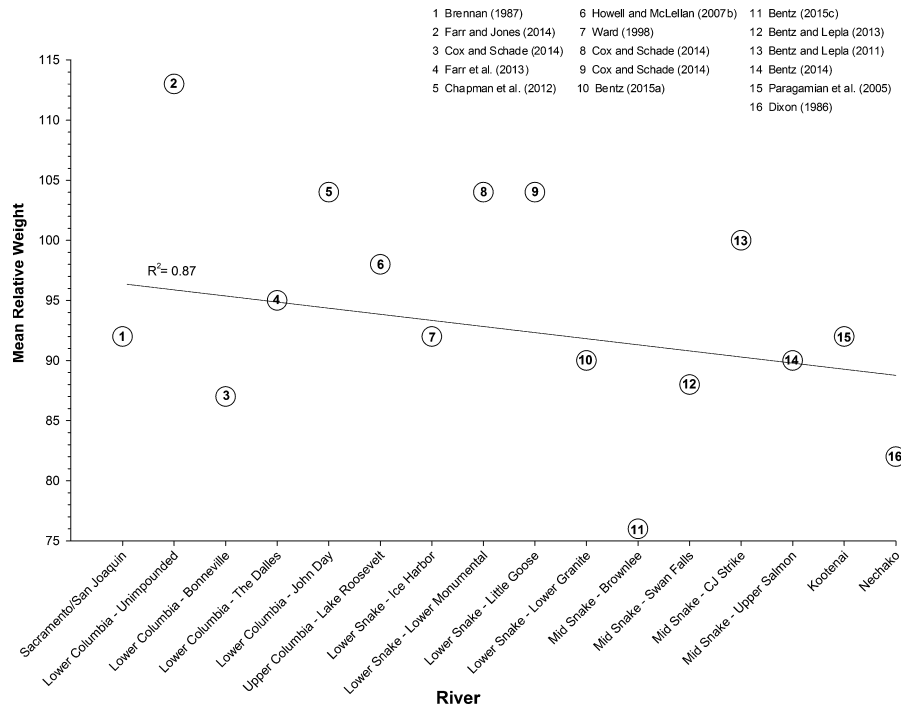


Fig. 4. Mean relative weights for White Sturgeon in the Sacramento, Columbia, and Fraser river basins

physiology indicate that WS are one of the most CO₂ tolerant species studied to date (Crocker and Cech, 1998; Baker et al., 2009; Baker and Brauner, 2012). While tolerance to both hypoxia and hypercarbia may have some relation to benthic resting and feeding habitats, extreme tolerance for these conditions may be related to the evolutionary point of origin for sturgeon during the Devonian Period when such conditions were likely common (Ultsch, 1996).

Stress responses have been fairly well studied for WS under conditions such as air exposure and handling, with stress responses noted via increased cortisol levels (Belanger et al., 2001). Recent studies have demonstrated a stress response in peritoneal fluid and identified the potential utility of modern PIT tag technology to provide a non-invasive means of stress monitoring (Zuccarilli et al., 2008). Studies focused on stress in early life stages demonstrated the endogenous production of cortisol and sex steroids during late embryo development and immediately after hatch as well as an increase in steroid levels around the time of first feeding (Simontacchi et al., 2009; Bates et al., 2014a). Cortisol increases in response to agitation stress were observed as early as 3 dph, with the greatest response magnitude observed at 35 dph (the oldest age tested; Simontacchi et al., 2009). Elevated cortisol levels have also been detected in response to predator odour (Eom, 2016). Lower cortisol levels in response to substrate enrichment with gravel (Bates et al., 2014a) emphasize the utilization of cortisol for multiple signal pathways.

Osmotic stresses related to marine movements have also been examined. Age-1 Fraser River WS showed complete mortality associated with transfer to ≥24 ppt salinity, 25–30% mortality at 16 ppt, and low mortality at ≤8 ppt (Amiri

et al., 2009). Survival of juvenile WS in brackish water did appear to be size-dependent, as larger individuals showed higher survival and greater tolerance to increasing salinities than smaller individuals (McEnroe and Cech, 1985; Amiri et al., 2009). Shaughnessy et al. (2015) suggest that the capability for seawater acclimation occurs between ages 14 month and 2 year, and that acclimation occurred over a 4 day period. The lack of mortality at 15 ppt for juvenile Sacramento River WS (McEnroe and Cech, 1985) of similar sizes to those examined in Amiri et al. (2009) suggests possible population differences in juvenile salinity tolerance.

Reproductive endocrinology of WS has been examined in conjunction with captive reproduction (Doroshov et al., 1997; Feist et al., 2004). Reproductive hormone profiles differ between the sexes and hormonal patterns associated with maturity, final maturation and ovulation appear to follow similar patterns to many other sturgeon species (Webb et al., 2001, 2002). Sex differentiation based on plasma steroids has been demonstrated as early as 21 months of age using radioimmunoassay (Feist et al., 2004) and these authors also indicated the potential identification of males using the simpler and cheaper enzyme immunoassay method as early as 30 months old.

Conservation issues

Fishing effects

In regions where angling and/or harvest are still permitted, WS are the target of subsistence fisheries (Columbia and Snake), or sport fisheries (Sacramento-San Joaquin Bay-Delta, lower and middle Columbia, Snake, and middle and lower Fraser). Due to their longevity and late maturation,

WS are particularly sensitive to overfishing (Boreman, 1997). Rieman and Beamesderfer (1990) reported that intensive management of WS fisheries was necessary and that exploitation >0.10 of wild self-sustaining populations risked stock collapse. Inherent in exploitation rates are losses associated with handling of non-legal fish in direct and indirect fisheries and losses due to illegal harvest; however, these losses have been poorly studied and are rarely incorporated into fishery management models. While intensive mark-recapture programs allow estimation of abundance by length class for the lower Fraser population (Nelson et al., 2013a), for most WS fisheries, there is substantial uncertainty regarding age-specific abundance, the productivity of individual stocks, and population dynamics parameters such as natural mortality rates. Additionally, even when extensive mark-recapture data sets are available, model assumptions (e.g. movement, vulnerability to capture, steepness of recruitment curve) can have strong effects on population predictions (Nelson et al., 2016; Whitlock and McAllister, 2012). A further discussion of fishing effects can be found in the 'Present and Future Risks' section below.

Recruitment limitation

White Surgeon are periodic reproductive strategists, which, coupled with their high fecundity, means that even a slight variation in early life survival creates the potential for highly variable recruitment (Winemiller, 2005). Upstream population segments under regulated flow regimes (e.g. Nechako, Kootenai, and upper Columbia rivers) show the most severe recruitment limitations and all exhibit recruitment collapse. The presence of juvenile year-classes in other regions reflects consistent annual recruitment (e.g. Fraser River mainstem, Columbia River downstream of Bonneville Dam) or episodic recruitment (e.g. Sacramento-San Joaquin, some lower Columbia and Snake river population segments).

There is a general consensus that WS recruitment collapse is due to high mortality during their early life history. This is supported by multiple lines of evidence including theoretical analysis (Gross et al., 2002; Jager et al., 2010; Schueller and Hayes, 2010), and the detection of annual spawning in most population segments. The strongest evidence of early life history bottleneck is provided by the regular detection of viable eggs, yolk-sac larvae (approximately 1–2 dph), and, in some locations, feeding larvae (up to ~15 dph) combined with the failure to capture older sub-yearlings or early juveniles (Howell and McLellan, 2005, 2007a,b, 2008, 2013a,b; Golder Associates Ltd., 2009a; Triton, 2009). Further evidence is provided by the high survival of hatchery progeny released at 10 month of age as discussed previously (see Population metrics; Golder Associates Ltd., 2005a).

Diagnosing the causes of recruitment failure is challenging due to data limitations and the long time period since the initiation of recruitment failure. The influence of substantial flow regulation on all populations undergoing variable recruitment coupled with correlations between flow and recruitment in other populations (Stevens and Miller, 1970; Kohlhorst et al., 1991; Parsley and Beckman, 1994; Fish, 2010), suggests that flow volume is a primary determinant of

recruitment success (*sensu* Burke et al., 2009). Flow regulation leads to a wide variety of secondary effects, which complicates the identification of specific causal mechanisms. Coutant (2004) presented a range-wide evaluation of recruitment patterns and developed a hypothesis that the loss of riparian floodplain vegetation, and in particular egg attachment sites, was the likely cause of recruitment failure. However, the presence of egg deposition and development within the river channel and the absence of riparian areas from some recruiting populations (e.g. middle Fraser and some impounded Columbia and Snake reaches) indicates the importance of other factors. The identification of links between substrate change and recruitment failure in the Nechako River presents valuable insight because the limited range of anthropogenic activities in the Nechako watershed (e.g. flow regulation by a single dam well upstream of spawning habitat) meant their analysis was less confounded by a broad array of impacts such as occurs in the Columbia and Kootenai rivers. For Upper Columbia WS, the use of professional judgement led to the identification of four prevailing recruitment failure hypotheses: (i) changes in flow patterns and turbidity, (ii) diminished habitat quality or quantity downstream of spawning areas, (iii) changes in the fish community resulting in increased predation, and (iv) food availability (Gregory and Long, 2008). A subsequent structured weight-of-evidence evaluation for that population incorporated spatial and temporal patterns in recruitment failure and multiple lines of evidence and identified increased fine substrates in the vicinity of spawning sites as the hypothesis with the most support (McAdam, 2015). Similarly studies regarding the Kootenai River suggest that substrate alteration plays an important causal role (Paragamian et al., 2009).

With regard to the life stages affected, the diminished availability of suitable interstitial habitat due to fine sediment deposition in spawning areas can decrease survival of eggs (Koch et al., 2006) and the retention (Crossman and Hildebrand, 2014) and survival of yolk-sac larvae (McAdam, 2011, 2012; Boucher et al., 2014). Survival effects on feeding larvae may also be important and this is particularly well supported by the capture of substantial numbers of drifting feeding larvae in the 16 km downstream of spawning sites near Northport, WA. The substantial catch of feeding larvae as the latest life stage detected indicates not only the presence of suitable embryo and yolk-sac larvae habitat but also implies that factors affecting the survival of early feeding larvae also contribute to recruitment failure. Food limitations and increased predation offer potential mechanisms that may result from effects such as substrate alteration (McAdam, 2015) or altered larval transport subsequent to upstream flow regulation (Howell and McLellan, 2014b). Despite ongoing analysis, uncertainty regarding the cause(s) of recruitment failure will likely persist until experimentation provides proof of a causal mechanism.

Contaminants/pollutants

Until recently, there were relatively few toxicological studies for WS (e.g., Farrell et al., 1998); however, since 2012, there

have been more than 17 toxicological studies published. Recent studies that addressed the effects of copper, zinc, lead, and cadmium include Calfee et al. (2014), Little et al. (2014), Vardy et al. (2013, 2014, 2015) and Wang et al. (2014). Toxicological effects of selenium and mercury have been investigated by Lee et al. (2012), Huang et al. (2012, 2013) and Zee et al. (2016). For some toxicants (e.g., copper) WS are consistently identified as highly sensitive relative to other fish (Farrell et al., 1998; Dwyer et al., 2005; Doering et al., 2012; Vardy et al., 2013; Calfee et al., 2014; Wang et al., 2014) and Vardy et al. (2014) identified that feeding larvae (40 dph) were more sensitive to copper than yolk-sac larvae (8 dph). Lethal concentrations for most life stage-contaminant concentrations are above current water quality criteria (Vardy et al., 2013). However, sublethal effects such as altered movement, diminished hiding, and loss of equilibrium were detected at contaminant concentrations substantially lower than lethal concentrations (Calfee et al., 2014; Little et al., 2014; Wang et al., 2014). Sublethal effects may be more ecologically relevant as elevated mortality would be expected when swimming and hiding is compromised. The types of toxicants to which WS are exposed and the method of exposure varies throughout the species' range due to regional differences in land use and anthropogenic disturbances. Therefore, river basin specific pollutant concerns related to WS survival and reproduction are summarized below.

Sacramento-San Joaquin Bay-Delta

The WS in the Bay-Delta are exposed to several toxicants, including selenium, mercury, organochlorines, polychlorinated biphenyls (PCBs), and polybrominated diphenyl ether flame retardants (PBDEs). The effects of selenium, originating from agricultural run-off and oil refinery effluent, on Bay-Delta WS have been widely studied. Adult WS in the Bay-Delta ingest high levels of selenium in their bivalve prey. Linares-Casenave et al. (2015) found adult WS in the San Francisco Bay possessed liver selenium levels near thresholds associated with reproductive toxicity in other fish species. Female WS pass selenium to offspring in egg yolk, which causes a high incidence of deformities and mortality in early life history stages (Kroll and Doroshov, 1991; Linville, 2006; DePeters et al., 2013). Dietary selenium also can increase osmoregulatory stress in juvenile WS (Tashjian et al., 2007).

Other contaminants of concern in the Bay-Delta include PCBs and PBDEs. WS in San Francisco Bay contain median PCB concentrations above the threshold considered a concern for human health (Davis et al., 2007). Concentrations of PBDEs in WS tissues have declined over the past decade due to state and federal phase-outs and bans on production and use of those chemicals (Sutton et al., 2015). The effects of PCB and PDBE exposure on WS are unknown.

Columbia River basin

Water quality within the Snake River has been compromised by the cumulative effects of decades of agricultural and industrial activities. Water quality degradation generally worsens during low flow summer periods when irrigation

demands are high and return flows contribute high amounts of nitrogen, phosphorous, pesticides, and sediment (Clark et al., 1998). This has led to degraded water conditions typically associated with highly polluted environments (e.g., anoxia, algal blooms, and bacterial mats). In some years, a combination of low flows, elevated summer temperatures, and low dissolved oxygen levels have led to WS mortality (Grunder et al., 1993, IDFG, 2008).

Endocrine disrupters and carcinogens such as mercury, chlorinated pesticides (e.g. dichlorodiphenyltrichloroethane; DDT) and PCBs have been detected in WS sampled throughout the Columbia River Basin (Kruse, 2000; Foster et al., 2001a,b; USEPA 2002a; IPC 2015). These contaminants have been loosely correlated to reduced WS growth and reproduction (Foster et al., 2001a,b; Feist et al., 2005; Webb et al., 2006).

From 1930 to 1995, sand-sized water-granulated fumed slag released from a smelter into the upper Columbia River at Trail, BC, was transported downstream and deposited in areas frequented by WS (CH2M Hill, 2006). The slag contains elevated levels of several trace elements, such as arsenic, cadmium, copper, lead, and zinc (Majewski et al., 2003). Smelter effluent was lethal to WS larvae (11–14 and 32–35 dph) at high effluent concentrations of 100 and 50%, but in low concentrations (1%) mortality did not differ significantly from controls (Bruno, 2004; online at: http://a100.gov.bc.ca/appsdata/acat/documents/r7629/SturgeonReportMarch2004_1155248340024_842785c393f94c5cabc796dd9297851f.pdf, accessed on 12/01/2016). Numerous laboratory studies regarding the potential toxicity of these metals is reported above. Site specific contaminant studies found that interstitial pore water from slag substrates collected from the Columbia River were above effect thresholds for WS (Vardy et al., 2015); however, ambient water quality (i.e., in the water column overlying substrates) did not increase mortality up to 60 days post fertilization (Tompsett et al., 2014; Vardy et al., 2015). When exposed to sediment containing slag obtained from the upper Columbia River and leachate prepared from upper Columbia River sediment, abnormal behaviors including immobilization and loss of equilibrium were observed among WS larvae during lab studies (Little et al., 2014). In addition, when presented with slag-contaminated sediments, WS larvae remained in close contact to the sediment versus occupying the water column when substrate was not available. Thus, exposure to slag may result in behaviours that reduce early life stage WS survival in the upper Columbia River.

Slag particles have an angular, glass-like structure and WS larvae that come in contact with slag may experience physical trauma (CH2M Hill, 2006). In the upper Columbia River, early larvae contained slag (attached to prey) in their guts (Howell and McLellan, 2011) and 78% of hatchery origin juvenile WS examined had ingested slag (Parsley et al., 2010). Histological examination of the digestive tracts of WS juveniles that had ingested slag indicated significantly greater chronic inflammation relative to controls (fish reared without exposure to ingestible substrate). Whether the inflammatory response would occur in WS ingesting inert sand-sized substrate or if slag ingestion results in reduced survival, growth, or condition is unknown. The high survival, growth, and

condition of hatchery WS released in the upper Columbia River suggest slag ingestion has little effect on older individuals.

Fraser River

The Fraser River is less industrialized than the other two large river systems inhabited by WS. Major potential contaminant sources in upstream reaches include pulp mill and mine effluent. In downstream reaches, Bennett and Farrell (1998) indicated that anti-sapstain, a wood preservative used in the timber industry and detectable in the Fraser River, was about 1000 times more toxic to WS fry as compared to rainbow trout. This contaminant also significantly reduced swimming performance of 60 dph WS juveniles. Although their long life spans would suggest a high susceptibility to toxins that bioaccumulate, relatively low body burdens for a variety of contaminants were found in large WS carcasses retrieved from the lower Fraser in 1993 and 1994 (McAdam, 1995).

Population status

Sacramento-San Joaquin Bay-Delta

The most southerly WS population is found in the Sacramento-San Joaquin Bay-Delta system in California, which includes the Sacramento and San Joaquin rivers and their tributaries (Fig. 5; Moyle, 2002). A smaller WS population segment may exist in the Klamath River in northern California (Kohlhorst and Cech, 2001; Moyle, 2002) but little is known about its status. Within the Bay-Delta system, WS range upstream as far as Shasta Lake on the Sacramento River, where a small number of previously stocked WS may remain isolated from the estuary by Shasta Dam (Moyle, 2002), and upstream in the San Joaquin River to the confluence with the Merced River (Jackson et al., 2016). Tributaries where WS have been detected include the Feather River (Sacramento; DuBois et al., 2009, 2010, 2012; DuBois, 2013) and the Stanislaus River (San Joaquin; Faulkner and Jackson, 2013; Heironimus et al., 2015), although the reason for their movements into these rivers is unknown. At the downstream extent of their range in the Bay-Delta system, WS feed in the estuary and small numbers of adults are encountered in marine habitat along the coast of California (DuBois et al., 2009, 2010, 2012; DuBois, 2013).

Abundance estimates generated for legal-sized WS have ranged widely from 11 200 (Kohlhorst et al., 1991) to 142 000 (Schaffter and Kohlhorst, 1999). The most recent estimate suggests ~48 000 WS between 100 and 200 cm TL (DuBois and Gingras, 2011). Although no commercial fishery currently exists, a popular recreational fishery has occurred in the Bay-Delta system since 1954 (Schaffter, 1997) under increasingly restrictive size and bag limits. Estimated harvest rates in the recreational fishery have ranged from <0.05 to 0.115 (Kohlhorst et al., 1991; Schaffter and Kohlhorst, 1999; DuBois and Gingras, 2011). Variability in annual harvest estimates is partly explained by changes in the proportion of the adult population available for harvest due to evolving legal size restrictions over time (≥ 102 , 107–183, 112–183, 117–183, and 117–168 cm TL; DuBois et al., 2012).



Fig. 5. Historical White Sturgeon population distributions in the Sacramento-San Joaquin Bay-Delta system

Although non-reproductive adults spend most of their time feeding in the estuary (Moyle, 2002), spawning adults make upriver migrations into the Sacramento and San Joaquin Rivers in late winter to spawn in early spring (Heironimus et al., 2015; Klimley et al., 2015). It was once thought that most WS spawning occurred in the Sacramento River (Kohlhorst et al., 1991); however, multiple WS spawning sites were identified on the San Joaquin River between 2011 and 2012 (Jackson et al., 2016). Known spawning areas in the San Joaquin River are dominated by sand, silt, or hard pan clay, although many also contain some gravel (Jackson, Z.; USFWS, Lodi, CA, pers. comm.). This is similar to spawning substrates selected by the Kootenai River WS population but unlike many other WS populations that typically prefer coarse substrates for spawning (Kohlhorst, 1976). Suspected but unconfirmed WS spawning areas are upstream of Colusa and in the Feather River (Kohlhorst, 1976; Schaffter, 1997; DuBois et al., 2009, 2010; Israel et al., 2009).

The Bay-Delta population exhibits highly variable recruitment, with low baseline levels of recruitment punctuated by occasional strong year classes (Kohlhorst et al., 1991; Schaffter and Kohlhorst, 1999). There is a positive correlation between recruitment and both fall and spring discharge (Kohlhorst et al., 1991; Fish, 2010). Whether the magnitude of recruitment variability currently observed represents the normal state of the Sacramento-San Joaquin population or

whether these fluctuations are driven by anthropogenic disturbances, is unknown. Fluctuations in WS recruitment can be traced back to 1938 (Shirley, 1987); however, degradation and modification of important WS habitats in this system began as early as the 1860s with hydraulic mining activity on the upper Sacramento and San Joaquin rivers.

Columbia River

White Sturgeon are distributed throughout the mainstem Columbia River and larger tributaries (Fig. 6). Historically, movements throughout the system were likely possible, although upstream passage was probably limited at times at large rapids such as Celilo Falls and Kettle Falls (Brannon and Setter, 1992). The first mainstem dams, constructed in the 1930s, disrupted any long-distance migration patterns that may have previously occurred. An additional 12 mainstem dams have since been constructed, the last in 1983. The construction of dams has fragmented the Columbia River into a series of reservoirs, which have functionally created isolated population segments of WS. In the past, these population segments have typically been managed separately. Efforts are presently underway to coordinate management over larger geographic scales: lower Columbia (mouth to McNary Dam); middle Columbia (McNary Dam to Grand Coulee Dam); upper Columbia (Grand Coulee Dam to Columbia Lake); lower Snake mouth to Hells Canyon Dam); middle Snake (Hells Canyon Dam to Shoshone Falls); and Kootenai (Upper Bonnington Falls Dam to Libby Dam including Kootenay Lake; Fig. 6; Table 2).

Most impounded WS population segments exhibit recruitment limitation due to a lack of suitable spawning habitat or flow conditions (Parsley and Beckman, 1994; Counihan et al., 1998; Parsley and Kappenman, 2000). Impoundments provide large areas of physical habitat suitable for juvenile and adult WS (Parsley et al., 1993; Parsley and Beckman, 1994), although use of the large impoundment behind Grand Coulee Dam is generally restricted to the upper third of the reservoir (Howell and McLellan, 2008). The reasons that WS do not use the lower sections of the Grand Coulee impoundment are unknown; however, some acoustic tagged hatchery juvenile WS released at various locations in the lower two-thirds of the reservoir remained near their release locations suggesting some suitable habitat was available (Howell and McLellan, 2014a). Stock assessments of impounded populations have found good survival, growth, and condition of resident WS (Beamesderfer et al., 1995; Rien, 2007; Mallette, 2008), suggesting that the available habitat for juveniles and adults is not used to capacity and greater WS numbers could be supported if recruitment and passage were not limiting.

Lower Columbia River

The lower Columbia section extends from the mouth upstream to McNary Dam and includes a lower unimpounded reach that allows access to euryhaline and marine environments and three upstream reservoirs (Fig. 6). In this section, WS have no special state or federal protected status. Upriver storage reservoirs have reduced spring freshets

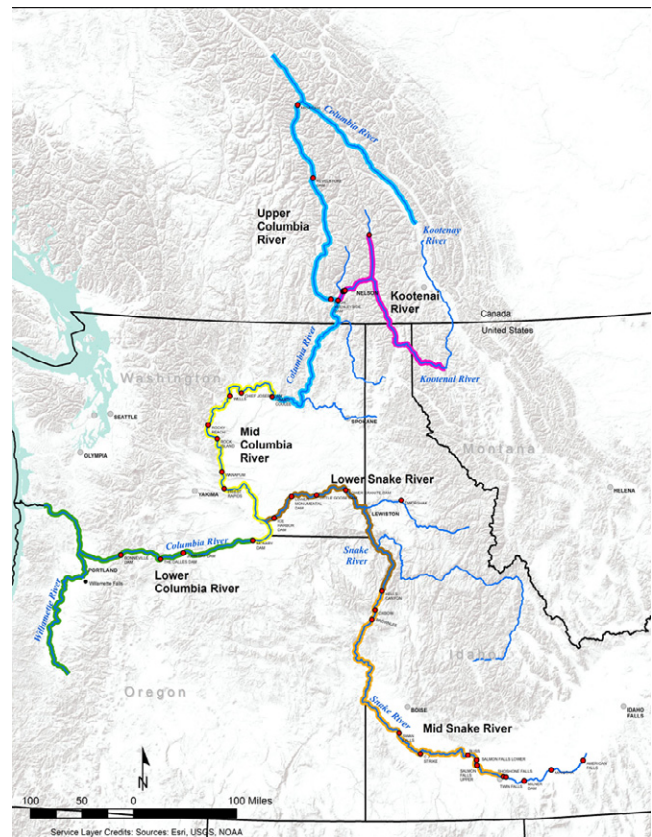


Fig. 6. White Sturgeon population segments in the Columbia River Basin including the Snake and Kootenai rivers

resulting in a substantially reduced peak discharge over a more protracted period. Late summer, fall, and winter flows are generally higher and winter water temperatures warmer than historical (Quinn et al., 1997).

Historical abundance of WS in the lower Columbia River is unknown, but Craig and Hacker (1940) described the species as being 'extremely abundant'. With the completion of Bonneville Dam in 1938, the population became segregated (Warren and Beckman, 1993). Further fragmentation occurred with the completion of McNary, The Dalles, and John Day dams in 1953, 1957, and 1968, respectively. While downstream movement of WS past the dams provides a net benefit to downstream fisheries, with the exception of The Dalles Dam, upstream passage through existing fishways at these facilities is negligible (Warren and Beckman, 1993; Parsley et al., 2007).

WS in the unimpounded section of the Columbia River downstream from Bonneville Dam represent a wild, self-sustaining population segment. Spawning occurs in the first 11 km downstream from Bonneville Dam as well as in the Willamette River downstream from Willamette Falls (Fig. 6; McCabe and Tracy, 1994; Chapman and Jones, 2010). Although flows are highly regulated in both rivers, the area downstream from Bonneville Dam provides good spawning habitat over the range of flows that typically occur (Parsley and Beckman, 1994). WS juveniles and adults have access to

extensive diverse habitats to meet life history needs. Due to its productivity, this population segment supports one of the most productive sturgeon fisheries in the world (Craig and Hacker, 1940; McCabe and Tracy, 1994; DeVore et al., 1995). In the early 1990s, over 1 million WS >54 cm TL were estimated to be present in this area (DeVore et al., 1995) and in the recent past the population sustained an annual harvest of about 40 000 fish (462 000 kg) per year (JCRMS, 2007). The estimated number of legal-length WS that could be retained in fisheries remained relatively stable through 2007, but declined steeply from 131 700 fish in 2007 to a low of 65 300 fish in 2010. Numbers increased to 72 800 in 2011 and 83 400 in 2012 (JCRMS, 2015). These numbers do not include fish that may be in marine waters and will return to the river.

Population segments in Bonneville, The Dalles, and John Day reservoirs support only limited recreational and tribal fisheries and are more vulnerable to overfishing than the unimpounded population segment (Beamesderfer et al., 1995). WS spawn annually in each of these reservoirs, and yolk-sac larvae and feeding larvae have been found downstream from the dams that form their upstream boundaries. Flows are highly regulated and the areas downstream from each of the upstream dams provide some suitable spawning habitat during medium to high flow years (Parsley and Beckman, 1994). WS juveniles and adults have access to a diverse range of physical habitats in each of these reservoirs sufficient to meet life history needs (Parsley and Beckman, 1994) although carrying capacity may be lower than historical pre-regulation levels (Beamesderfer et al., 1995).

Recent estimates of legal-size WS in Bonneville (2015), The Dalles (2014), and John Day (2013) reservoirs were 5890 (97–137 cm FL), 1850 (109–137 cm FL), and 9620 (109–137 cm FL), respectively (Joint Columbia River Management Staff (JCRMS), 2015). For fish >61 cm FL, recent (2016) estimates were 228 249 in Bonneville, 86 895 in The Dalles, and 30 989 in John Day (Table 2). Annual recruitment of age-0 fish is most variable in John Day and least variable in Bonneville (https://www.nwcouncil.org/media/6288813/White_Sturgeon_Framework_review_draft_Feb2013.pdf). Abundance estimates of WS between 91 and 183 cm FL for each reservoir since the late 1980s (Joint Columbia River Management Staff (JCRMS), 2015) had wide ranges: 17 900–117 600 (Bonneville), 6300–76 800 (The Dalles), and 2200–33 800 (John Day).

Snake River

Historically, WS could potentially have ranged freely throughout the 986 km of the Snake River from its confluence with the Columbia River upstream to Shoshone Falls, a natural 65 m high barrier near Twin Falls, Idaho. While overharvest during the late 1880s is believed responsible for the early decline of Snake River WS (Edson, 1956), dam construction beginning at the turn of the century substantially altered the river to provide water for agriculture, hydro-power, and flood control. Today, the Snake River is one of the most extensively regulated and diverted rivers in North America (Palmer, 1991) with almost half of its estimated

volume diverted for agricultural purposes (Miller et al., 2002) and water quality compromised by the cumulative effects of decades of agricultural and industrial activities, particularly in segments of the middle Snake River (Clark et al., 1998; Harrison et al., 2000; USEPA, 2002b). Although WS still exist in most reaches of the Snake River, many contain small population segments with stock structures proportionally skewed toward older adults with few juveniles (Cochner et al., 1985; PSMFC, 1992; DeVore et al., 1999a; Jager et al., 2000; IPC, 2015). Similar to the Columbia River, hydroelectric development coupled with irrigation diversion in the Snake River Basin likely has caused a reduction in WS spawning and recruitment (Parsley and Beckman, 1994; IPC, 2005; van der Leeuw et al., 2006; IDFG, 2008).

The lower Snake River extends from Ice Harbor Dam to Hells Canyon Dam. Ice Harbor Dam is located 15 km upstream from the confluence of the Snake and Columbia rivers, is the first of four hydroelectric projects on the lower Snake River (Fig. 6). In both the Ice Harbor and Lower Monumental reservoirs, the age structure is skewed towards older individuals, indicating those population segments are recruitment limited. Spawning occurs within 1 km below Little Goose Dam (Parsley and Kappenman, 2000). The relatively high catch rates of reproductive females suggest recruitment limitations are not a result of spawner limitations (DeVore et al., 1999b). In both Ice Harbor and Lower Monumental reservoirs, estimates of WS density, growth, and fitness were less than described for other Columbia Basin WS population segments (Beamesderfer et al., 1995; DeVore et al., 1995). This may indicate problems with the forage base or available rearing habitat due to hydroelectric and agricultural development in the region. For instance, anadromous prey has declined with time and other food resources available to other Columbia population segments may not be present in the lower Snake River (DeVore et al., 1998a).

White Sturgeon productivity appears greater in Little Goose Reservoir relative to Lower Monumental and Ice Harbor reservoirs given that proportionally more juveniles were found in Little Goose Reservoir (DeVore et al., 1999b). Spawning occurs at the upstream end of the reservoir near Lower Granite Dam but the origin of the recruited juveniles (i.e., whether from production within Little Goose Reservoir or fish entrained from upstream population segments) is unknown (Parsley and Kappenman, 2000). There appears to be a gradient of reduced juvenile abundance in the lower Snake WS population segments with increased downstream distance from Lower Granite Dam. This suggests that many of the WS in the lower Snake reservoirs may have been entrained through the dams, potentially during flood years with higher than average spring and summer flows (DeVore et al., 1999b).

The Snake River upstream from Lower Granite Dam flows through Hells Canyon, the deepest river-carved gorge in North America, and represents the most natural habitat that remains among all of the impounded Snake and Columbia River sections inhabited by WS. Although isolated from other reaches, WS in this section still have access to diverse habitats that meet life history requirements for all life stages

(Cochnauer, 2002). The only tributary that supports WS is the Salmon River and spawning has also been documented in the lower Salmon River (Everett et al., 2003). However, catch data suggests WS in this system comprise only a minor component of the overall Hells Canyon population segment (IDFG, 2008).

Population surveys over the past 30 years indicate abundance of WS >70 cm TL has remained similar (3800–4100 fish) in the Hells Canyon reach, with a wide range of size classes present from juveniles to mature adults (Coon et al., 1977; Cochnauer et al., 1985; Lukens, 1985; Lepla, 1994; Lepla et al., 2001; Everett et al., 2003; Bentz, 2015a). However, the highest proportions of juveniles were reported in the earlier surveys, which suggested a gradual decline in recruitment (IPC, 2015). The lack of accurate age-length data and slow growth of WS juveniles (<2 cm year⁻¹) in the Hells Canyon population segment (Bentz, 2015a) has limited the ability to identify specific year classes of young fish as well as recruitment status and trends.

In the middle Snake (Hells Canyon Dam upstream to Shoshone Falls), WS abundance within the Hells Canyon complex (Fig. 6) has changed little over the past 30 years. Several surveys have reported low captures (0–42 WS) of predominantly adults with few or no juveniles present (Reid et al., 1973; Cochnauer, 1983; Reid and Mabbot, 1987; Kruse-Malle, 1993; IPC, 2005; Bentz, 2015c). These reservoirs often experience poor water quality conditions, particularly during low flow years, with anoxic conditions developing throughout most of the bottom 2 m (Myers et al., 2001).

The Snake River upstream of Brownlee Reservoir is one of the most degraded sections of the middle Snake River relative to temperature, sediment, organic matter, and nutrients from irrigation returns, industrial, and municipal sources (Harrison et al., 1999). This section, as well as adjacent upstream and downstream reaches, are listed as water quality limited under the §303(d) of the Clean Water Act by Idaho and Oregon. Daily maximum water temperatures can exceed 29°C in summer (IPC, Boise, ID, unpubl. data), and algae and organic matter are many times greater than levels that initiate concern (IDEQ and ODEQ, 2004; Myers et al., 2001). As a result, Brownlee Reservoir experiences severe water quality degradation due to the extremely enriched, hypertrophic waters flowing into it. Modeling investigations suggest poor water quality and habitat degradation within this section is likely the primary limitation to WS recruitment (Jager et al., 2002).

White Sturgeon abundance above Swan Falls Dam appears to be declining (Table 2) and the lack of juvenile WS has been well documented (Cochnauer, 1983; Lepla and Chandler, 1997; Lepla, 2008b; Bentz and Lepla, 2013). Although this segment has 40 km of riverine habitat, it is comprised mainly of low-gradient shallow runs, island complexes, and a few deep pools. There are no rapids or narrow canyon channels to create the turbulent and high-velocity conditions that are commonly associated with other known WS spawning and incubation areas in the Snake River (Lepla and Chandler, 2001). The channel and habitat characteristics suggest this section is better suited for rearing rather than for spawning purposes. An intensive recreational catch

and release fishery also occurs within the upper section of this reach at C.J. Strike Dam.

The 106 km long reach upstream from C.J. Strike Dam supports the most productive and genetically diverse WS population segment in the middle Snake River. Historically, many of the largest WS (272–363 kg) harvested in Idaho came from this section (Cochnauer, 1982). The present population exceeds 4000 fish (>70 cm TL) with stock demographics that indicate periodic natural production and fast growth rates (Bentz and Lepla, 2011). Juvenile WS growth rate in this section is among the highest reported across the species range (Bates et al., 2014b) with individuals exceeding 92 cm FL by age-4 (Bates, 2013). Groundwater springs in this reach moderate river temperature year round, which may result in faster growth rates. Recruitment in this population segment is variable and closely related to the magnitude of springtime Snake River flows (IPC, 2007; Lepla, 2008a; Bates, 2013; Hughes, 2015). Recruitment surveys show successful natural production occurs once spring freshets increase from 17 000 cfs to above 25 000 cfs whereas flow <12 000 cfs has been associated with recruitment failure (Hughes, 2015; IPC, 2015). Large storage reservoirs in the upper Snake basin are operated to meet flood control and irrigation requirements, which can significantly alter spring freshets and reduce river flow volume in downstream reaches during the WS spawning season. Consequently, the lower flow regimes and run-of-river dam operation has not provided for WS recruitment during years absent of large spring freshets.

Stock assessments between Bliss Dam and Shoshone Falls indicate that few wild WS remain within these upper sections of the middle Snake River (Cochnauer, 1983; Lepla et al., 2004; Bentz and Lepla, 2009; Bentz, 2013, 2014, 2015b). An ecological risk assessment of the middle Snake River found that impairment values were generally high for all life stages of WS in these sections (USEPA, 2002b). In particular, survival estimates were lowest for life stages from spawning through larval development because of low river flows and the loss of dynamic spawning and rearing habitats. To improve population abundance and fishing opportunity, approximately 2600 hatchery-reared WS were stocked in the Bliss and 1600 in the Upper Salmon Falls reservoirs from 1989 to 2014 (IPC, 2015).

Middle Columbia River

Prior to the closure of Rock Island Dam in 1933, there were no barriers to WS movement throughout the middle Columbia River, which presently is fragmented into six run-of-the-river reservoirs and one flowing riverine section (the Hanford Reach; Fig. 6). The middle Columbia reservoirs exhibit some of the characteristics of a deep slow-flowing riverine system such as high water transport rates and well-mixed (isothermal) conditions. Water velocities are highest at the outlets of the dams and decrease with downstream distance. WS are present in all middle Columbia reservoirs but intensive studies have only been initiated in most reservoirs within the last decade. All of these population segments have been impacted by hydropower development and operations that have resulted in loss of habitat connectivity, habitat alteration or

destruction due to reservoir creation, and decreased productivity due to reduction of salmon escapements.

WS population segments in the middle Columbia River have been protected by angling and harvest regulations. All angling for WS in Lake Rufus Woods has been prohibited since 2001. Catch and release angling is allowed in the reservoirs between Priest Rapids Dam and Chief Joseph Dam, and sport harvest is allowed in the reach between McNary and Priest Rapids dams. Historical exploitation of local stocks likely occurred but exploitation rates were poorly documented. Low levels of harvest (typically <50 fish year⁻¹) were reported in each reservoir from 1988 to 2000, when Washington State instituted a Volunteer Catch Record Card program. Based on card data collected from 1988 to 2007, annual harvest of WS in the Hanford Reach/McNary Pool averaged 374 fish year⁻¹ (SE = 42; WDFW, Olympia, WA, unpubl. data).

The lower portion of the middle Columbia River includes McNary Reservoir, the Hanford Reach, and the lower 15 km of the Snake River upstream to Ice Harbor Dam. This WS population segment has access to extensive river and reservoir habitats within the Columbia and lower Snake rivers. Spawning has been documented within 44 km of the Columbia River downstream from Priest Rapids Dam (Parsley et al., 1996) and within 7 km of the Snake River downstream from Ice Harbor Dam (Parsley and Kappenman, 2000). The abundance of WS >54 cm FL in this area was estimated to be 8250 in 1995 (Rien and Beiningen, 1997), which increased to 9241 fish in 2011 (Farr et al., 2013); about 50% of the fish in 2011 were <110 cm FL. The greater abundance in the 2011 abundance estimate was likely due to emigration of hatchery WS stocked upstream in 2003 – see Rock Island section below (Farr et al., 2013). The most recent (2016) estimate was 9241 WS >54 cm FL (Cox and Martin, 2016). Low levels of recruitment in most years may limit population abundance, although recruitment was relatively high in 2011 (Farr et al., 2013). Age-0 WS have been captured in bottom trawls and gill nets downstream from the Snake River confluence (Counihan et al., 1995; Farr et al., 2013).

The wild WS population segments in Priest Rapids and Wanapum reservoirs (collectively called the Priest Rapids Project Area – PRPA) prior to 2003 consisted primarily of older adults although ~20% of the total catch in Wanapum Reservoir was composed of wild juveniles, an indication that this population segment either experiences some natural recruitment or receives recruitment from upstream populations (Golder Associates Ltd., 2003c). Natural recruitment to these populations has been sporadic and limited to a strong recruitment period in the mid-late 1950s and a lesser degree of recruitment from 1964 to 1997. WS are distributed throughout both reservoirs, but mainly within the upper two-thirds and exhibited localized concentrations in preferred feeding and overwintering habitats. During the spawning period, mature WS in each reservoir move upstream to the tailrace of the upstream dam between April-June, and some remain until August. Spawning occurs in each reservoir in the tailrace area of the upstream dam from late June-late July.

A White Sturgeon Management Plan (WSMP) was developed for the PRPA in 2009 and has subsequently been implemented (Grant PUD, 2009). The objectives of the Plan are to restore populations of WS in the PRPA to levels commensurate with the carrying capacity of available habitats.

A substantial proportion of the hatchery-reared juvenile WS released into Rock Island Reservoir in 2003 (see Rock Island discussion below) have subsequently moved downstream into the PRPA. From 2010 to 2012, the estimated population size of these hatchery progeny increased from 3550 WS (95% CI = 875–10 768) to 7038 WS (95% CI = 3927–14 637) in Wanapum Reservoir and from 1565 fish (95% CI = 289–6284) to 3096 fish (95% CI = 1304–5227) in Priest Rapids Reservoir (Golder Associates Ltd., 2012). Although estimates of the wild population during these years could not be determined due to an absence of recaptures, based on the 2002 population estimates of 551 (95% CI = 314–1460) wild fish in Wanapum and 134 (95% CI = 48–2680) wild fish in Priest Rapids (Table 2), hatchery juveniles now make up most of the WS population in the PRPA.

The status of the WS population segment in Rock Island Reservoir is unknown, as systematic mark-recapture surveys have not been conducted. A standardized setline stock assessment survey in 1998 resulted in the capture of only four individuals (DeVore et al., 2000). Approximately 12 000 PIT tagged and scute marked hatchery-reared juveniles (age-9 month) from 199–303 mm FL were released into the reservoir April and May 2003 and an additional 8600 scute marked hatchery-reared age-1 juveniles (49–448 mm FL) were released in September 2003 (Kappenman and Parker, 2005). Sampling in 2006 captured 36 of the fish released in 2003; no wild WS were caught (Parker, B., CRITFC, Portland, OR, pers. comm.). Large numbers of the individuals released in Rock Island have subsequently been captured in Wanapum, Priest Rapids, McNary, John Day, and The Dalles reservoirs (Golder Associates Ltd., 2012).

In the early 2000s, approximately half of the wild WS sampled from Rocky Reach Reservoir were juveniles (Golder Associates Ltd., 2003b; Chelan PUD, 2009), a markedly different population composition from adjacent population segments where wild juveniles were a minor component in the catch. The relative abundance of young juveniles in Rocky Reach may either indicate successful reproduction by the resident adults, immigration by recruits from upstream reservoirs, or illegal harvest of adults. To date, WS spawning in Rocky Reach Reservoir has not been verified so spawning activity or success is unknown. Recruitment has been sporadic and apparently limited to strong recruitment periods between 1982 and 1987 and 1995–1997 (Golder Associates Ltd., 2003b). A WSMP was developed for Rocky Reach in 2006 (Chelan PUD, 2009) and was initiated in 2011 with the release of 6376 hatchery juveniles (Wright and Robichaud, 2013). The objectives of the WSMP are to restore populations of WS in Rocky Reach to levels commensurate with the carrying capacity of available habitats. This goal will be achieved using conservation aquaculture to supplement the existing population in conjunction with a monitoring

program to provide the data needed to meet the overall management objectives and obligations.

The reservoirs created by Wells and Chief Joseph dams support very low numbers of WS. Seven fish were captured in a comprehensive set-line survey of Lake Rufus Woods (Chief Joseph Reservoir) in 1998 (DeVore et al., 2000). Recruitment appeared virtually non-existent, as all fish captured were >138 cm FL (DeVore et al., 2000). Abundance in Wells Reservoir was estimated at 31 WS (95% CI 13–218; Jerald, 2007). A small number of juveniles produced in the mid-1990's were captured in Wells Reservoir in 2001 and 2002, but it is unknown if they were from spawning events in the reservoir or entrained from Lake Roosevelt and thus, recruitment was suspected to be limited (Jerald, 2007). A WS management plan was developed in 2008 with a goal to increase the WS population in Wells Reservoir to a level that can be supported by the available habitat and characterized by a diverse age structure with multiple maturity cohorts (Douglas PUD, 2008). A WS broodstock collection and breeding plan (Douglas PUD, 2011) was developed as a prelude to supplementation using conservation aquaculture. Implementation of the plan commenced in 2013 with the collection of wild WS larvae from the Columbia River above Lake Roosevelt and WS eggs from wild WS adult broodstock from the Columbia River downstream of McNary Dam that were that were reared in a hatchery and released into the Wells Reservoir in 2014. The effectiveness of the supplementation will be determined through a long-term monitoring and evaluation program. Interestingly, during the initial year (2015) of the monitoring and evaluation program, seven wild juvenile WS (696–905 mm FL) were captured in Wells Reservoir (Robichaud and Gingerich, 2016). Conditions conducive to low levels of recruitment may occur in Wells Reservoir more frequently than originally thought.

Upper Columbia River

The upper Columbia River extends approximately 1040 km from Grand Coulee Dam in Washington, USA upstream to the headwaters at Columbia Lake in British Columbia, Canada (Fig. 6). This section is regulated by three mainstem storage reservoirs (Roosevelt, Arrow Lakes, and Kinbasket) and one run-of-the-river reservoir (Revelstoke). Upper Columbia WS were subject to recreational angling until 1996 and 2001 in Canada and Washington, respectively when angling for WS was prohibited. WS in the upper Columbia in Canada are listed as Endangered by Species At Risk Act (SARA), but are not listed in the US.

The Columbia River between Grand Coulee Dam to HLK Dam (Transboundary Reach) was first isolated from downstream reaches by the construction of Grand Coulee Dam in 1941 and then further fragmented by the construction of HLK Dam in 1968, Mica Dam in 1973, and Revelstoke Dam in 1984 (Hildebrand et al., 1999). In 2008, the abundance of wild WS in the Transboundary Reach was approximately 3000 fish (Irvine et al., 2007), of which 79% were mature adults >165 cm FL (Howell and McLellan, 2007b). Annual survival rates for wild adult WS in the BC portion of the Transboundary Reach were estimated between 88 and

99%, for the time period 1993–2004 (Irvine et al., 2007). Survival rates of WS in the US portion of the Transboundary Reach are suspected to be similar.

Five spawning areas have been identified in the Transboundary Reach, three in Canada and two in the U.S. (Howell and McLellan, 2007a,b, 2008; Golder Associates Ltd., 2009a). The majority of spawning activity occurs at the confluence of the Columbia and Pend d'Oreille rivers in BC (the Waneta area) and in the mainstem Columbia River near Northport, WA. A lesser degree of spawning activity has been documented at two locations near Castlegar, BC and in the China Bend area downstream of Northport, WA. Despite documented spawning activity, WS recruitment collapse in the Canadian portion of the Transboundary Reach began about 1969 (McAdam, 2015) and became clearly evident by the 1990s (Hildebrand et al., 1999; DeVore et al., 2000; Kappenman et al., 2000).

In the early 2000s, the Arrow Lakes Reservoir supported an estimated population of 52 adult WS (95% CI = 37–92) that pre-date the closure of HLK Dam in 1968 (Fig. 6; Golder Associates Ltd., 2006c). Analysis of fin ray chemistry also suggests that many of the fish that reside immediately downstream of HLK Dam may have originated from upstream (Clarke et al., 2011). WS are distributed mainly in the upper half of the reservoir, which contains suitable habitats for adult feeding and overwintering. Spawning occurs in the Revelstoke Dam tailrace area but spawning intensity is low (one to three spawning events detected per year) and has been documented in nine of 14 years that monitoring has been conducted since 1999 (AMEC, 2016). Evidence to date suggests this population segment has experienced total recruitment collapse. Revelstoke Dam is a load following facility with hypolimnetic withdrawals and as a result, daily flow fluctuations can vary between to 142–2123 m³ s⁻¹ and maximum summer water temperatures rarely exceed 11°C. This is the most northerly spawning location identified for WS in the Columbia River Basin. Spawning occurs from late July to late August, the latest spawn timing documented for the species, at water temperatures of 8.5–11.1°C. This is at the lower end of the reported 10–18°C range for WS in downstream areas of the Columbia River (Parsley et al., 1993), but similar to the 8–14°C range recorded in the Kootenai River (Paragamian et al., 1997).

The presence of WS in Revelstoke Reservoir, Kinbasket Reservoir, and the uppermost Columbia River is suspected based on anecdotal reports but has not been confirmed despite several years of sampling effort (Fig. 6; RL&L, 2000b; Westslope and CCRIFC, 2012). Prior to dam development, WS were reported throughout this section of the Columbia River up to the headwaters at Columbia Lake (Prince, 2001).

Kootenai River and Kootenay Lake

WS historically ranged throughout the Kootenai/Kootenay River drainage below Kootenai Falls, throughout Kootenay Lake, and into the Duncan River system (Fig. 6; Giorgi, 1993; BPA 1997). The construction of Duncan Dam at the outlet of Duncan Lake in 1967 effectively impounded all WS located upstream of the dam. As of 1995, a small remnant

population segment remained trapped in Duncan Reservoir (RL&L, 1998, 1999); the present status of this population segment is unknown. A small remnant population segment of Kootenai WS also are present in Slocan Lake, a tributary to the lower Kootenay River in Canada (RL&L, 2000b).

The Kootenai River is impounded by Libby Dam, which was closed in 1972 (Fig. 6). Within a decade of impoundment, the WS population in the Kootenai River and Kootenay Lake were recruitment limited (Partridge, 1983; Apperson, 1992). In 1994, the Kootenai River population was federally listed by the USFWS as Endangered under the ESA (Duke et al., 1999; USFWS, 1994; USFWS, 1999) and in 2006, WS in the Canadian Kootenay River and Kootenay Lake were listed as Endangered (Canada Gazette 2006).

The wild Kootenai WS population is presently comprised primarily of adults >age-35, within a range of age-30 to age-80 (Paragamian and Beamesderfer, 2003). Near total recruitment collapse since the mid-1970s has resulted in a decline of the wild adult population from approximately 7000 fish in the late 1970s to about 1000 in 2011; <70 wild adults are expected to remain by 2080 (Beamesderfer et al., 2009, 2014b). The population had been declining by ~4% per year based on estimated annual mortality rates (Beamesderfer et al., 2009, 2014b). However, analysis of recent data has shown annual survival has declined from 96 to 71%. Whether this decline is an accurate record of accelerated decline or is an artifact of sampling (e.g., lack of recaptures) in the most recent years, is unknown. Although a few wild juveniles are produced each year (~10 age-1 individuals year⁻¹; Paragamian et al., 2005; Ross et al., 2015; Hardy et al., 2016), annual spawning migrations of reproductive adults and documented spawning activity suggests that recruitment failure is due to environmental rather than demographic limitations. One cause of poor early life stage survival is likely inappropriate spawning substrate in the 12 km 'upper meander reach' spawning habitat (Paragamian et al., 2001). In the absence of natural recruitment, a conservation aquaculture program operated by the Kootenai Tribe of Idaho (KTOI) provides future recruits to the adult population (Ireland et al., 2002b; KTOI, 2012).

Fraser River

The Fraser River is 1375 km in length with a watershed area >220 000 km² (Fig. 7). An absence of mainstem impoundments is one of the unique features of this system, which is reflected in the river's high sediment load (annual total of ~20 million tons). The 270 km long canyon section is the dominant macro-habitat feature in the middle Fraser River, and WS residing in this area may be adapted to fast water habitats. In contrast to the high energy and erosive nature of the middle Fraser River, the lower Fraser River was historically a large meandering braided channel with a floodplain >2000 km². While anthropogenic impacts are present throughout the basin, the greatest concentration of impacts is in the lower section where the human population is most concentrated. For example, substantial portions of the historical floodplain have been lost due to dike construction (Boyle et al., 1997).

Prior to the 1990s, WS studies within the Fraser watershed were limited (though see Semakula and Larkin, 1968). However, a die-off of 36 large fish for unknown reasons during 1993 and 1994 (McAdam, 1995) led to increased interest and research effort. A basin-wide study was undertaken from 1995 to 1999 (RL&L, 2000a), and a basin-wide conservation plan was completed in 2005 (FRWSWG, 2005). Four distinct population segments were identified in the Fraser based on movement patterns and genetics (RL&L, 2000a; Smith et al., 2002). However, Drauch Schreier et al. (2012a) identified only three units, and a recent COSEWIC assessment designated two units (COSEWIC, 2013). Cross population comparisons have identified reduced growth rates in more northerly populations (RL&L, 2000a). Snout shape dimorphisms between populations inhabiting high velocity canyon reaches (middle Fraser) and slower flowing downstream reaches (lower Fraser) have also been observed. The maintenance of population distinctions in the absence of physical movement barriers (e.g. in the Fraser River watershed) supports the need to evaluate mechanisms that influence and maintain population structure (e.g. fidelity, straying).

In the Lower Fraser River, WS range from the river mouth to Yale, situated at the lower end of the Fraser Canyon (Fig. 7). A group of WS that typically resides in the Fraser River from Hope upstream to Hell's Gate appears to be distinct based on spatial and demographic criteria (RL&L,

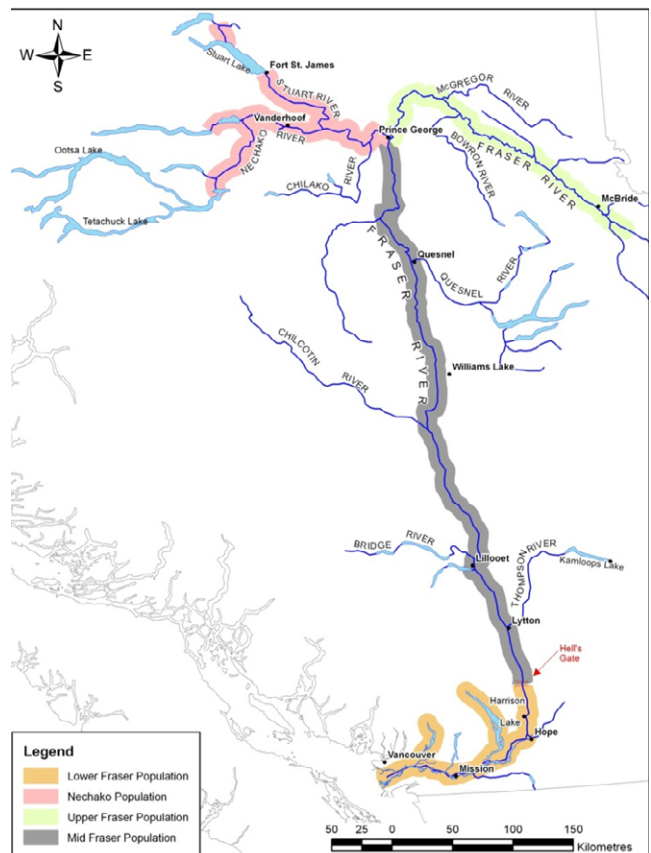


Fig. 7. White Sturgeon population segments in the Fraser River Basin

2000a), but not genetically distinct (Smith et al., 2002; Drauch Schreier et al., 2012a,b). This type of distinction may also apply to WS that use larger tributaries like the Pitt and Harrison rivers. Limited marine movements have been demonstrated by the occasional exchange of tagged fish with the Columbia River (Welch et al., 2006) and by micro-elemental analysis of fin rays (Veinott et al., 1999). However, the extent and prevalence of marine habitat use is not well understood.

The lower Fraser WS population is the largest in Canada, and is currently considered threatened (COSEWIC, 2013) based on a range-restriction criterion. Estimates of historical population size derived from stock reduction analysis range from 100 000–160 000 (Walters et al., 2005; Whitlock and McAllister, 2012). The lower Fraser population declined dramatically in the early 1900's due to fishing pressure (Echols, 1995). The failure to fully recover in the intervening 100 years is likely due to continued by-catch and habitat alterations (Walters et al., 2005). Since 2001, an extensive mark-recapture program has provided the basis for annual population estimates (e.g., Nelson et al., 2013a). Recent analysis suggests a recruitment peak in 1996–1997 (Whitlock and McAllister, 2012). Nelson et al. (2013a) and Carruthers (2015) also identified an apparent recruitment decline in 2005. However, over longer intervals the population has been relatively stable with possible increases in the older age classes (Nelson et al., 2012). Population estimates vary from 46 100 (Nelson et al., 2008) to 78 000 (2004 estimate; Whitlock and McAllister, 2012), with variation reflecting different modelling assumptions. In particular, the steepness of the stock recruitment curve (Whitlock and McAllister, 2012) and vulnerability to capture (Carruthers, 2015) can affect abundance estimates.

Multiple spawning locations have now been detected based on egg sampling, and side scan sonar surveys. Currently, seven locations have been located between 130 and 156 km upstream from the mouth and four more have been detected upstream of Hope, BC (Stoddard, E., BC FLNRO, Surrey, BC, pers. comm.). The continued detection of new locations suggests the presence of additional locations. Confirmed spawning locations in the lower Fraser River are located in both the mainstem and in seasonally inundated large side channels located within a spawning reach that stretches from roughly 130–160 km upstream from the mouth. The collection of eggs and a YSL near Hope, BC, indicates that spawning also occurs in the lower Fraser Canyon area (RL&L, 2000a). This area is quite distinct from the habitats downstream of Hope in areas of lower river gradient. Most spawning locations in the lower Fraser River have been identified based on sampling individual years. However, egg detection over multiple years (Perrin et al., 2003; Liebe and Sykes, 2011; Triton, 2013) suggests some locations are repeatedly used. Spawning occurs near peak flows and during the declining hydrograph at water temperatures from 11 to 18°C.

The WS population in the middle Fraser River between Hell's Gate and Prince George is reasonably healthy due to ongoing recruitment and no evidence of substantial population decline. This population is estimated at 3745 WS

(RL&L, 2000a). The relatively limited impacts on the Fraser River in this area and upstream, and the relatively limited fishery to date, suggest that present population abundance may be similar to historical levels. Spawning locations have not been identified. Feeding movements associated with sockeye migrations also were identified in late August as well as overwintering concentrations as noted for other populations.

White Sturgeon in the upper Fraser River between Prince George and McBride are identified as a population based on geographic and genetic criteria (RL&L, 2000a; Smith et al., 2002) and designated as endangered under SARA due to small population size (~815 individuals, including juveniles; DFO, 2014). However, the divergence of this group from adjacent populations may be limited as recent genetic analyses did not differentiate it from adjacent populations (Drauch Schreier et al., 2012a). Available data suggest WS occupying the upper Fraser River are primarily found in tributary confluences and deeper areas within the mainstem.

The Nechako River, the largest tributary in the upper Fraser Basin, contains a WS population that is demographically (Korman and Walters, 2001), spatially (RL&L, 2000a) and genetically (Smith et al., 2002; Drauch Schreier et al., 2012a) distinct from mainstem Fraser River populations. Fish are found throughout the Nechako River as well as in larger tributaries. Infrequent movements into the mainstem Fraser River also occur. The Nechako population was estimated to contain 571 fish in 1999 (RL&L, 2000a). However, improved movement assumptions and further data support an estimate of 545 fish (2015 estimate; 460–640, 90% probability interval; McAdam, S., BC MOE, Vancouver, BC, pers. comm.). This population has been undergoing recruitment collapse since 1967 (McAdam et al., 2005). Current projections suggest a further decline to 200 individuals in 25 years (16–37 years confidence interval; (McAdam, S., BC MOE, Vancouver, BC, pers. comm.). This population was supplemented by hatchery juvenile releases from 2005 to 2009. A permanent conservation aquaculture program was established in 2014.

Management and recovery efforts

Management and recovery actions have been implemented on individual populations, population segments, and at larger geographic scales that include multiple population segments. An example is the Snake River, which contains nine WS population segments within an 816 km long river section (IDFG, 2008). For relatively healthy populations, management actions generally include trend monitoring of adult abundance trends and restrictions on harvest. For listed populations, recovery programs have been initiated to protect and restore WS populations in jeopardy of extirpation. A summary of relevant information on the management and recovery programs in each of the main geographic areas of the WS range is provided below.

Sacramento-San Joaquin Bay-Delta

The California Department of Fish and Wildlife (CDFW) prioritizes adult WS population monitoring using data from commercial passenger fishing vessels, a mark-recapture

tagging program, and an angler report card program. Annual year-class indexing of age-0 and age-1 WS in the estuary and delta are conducted by otter trawl. Biologists from the USFWS monitor movements of adult WS captured in the San Joaquin River using sonic telemetry receiver arrays situated throughout the Bay-Delta region.

Harvest may be a major stressor on the Sacramento-San Joaquin Bay-Delta WS population. Accordingly, in response to declines in adult abundance, several changes to fishing regulations were made between 2006 and 2013. These included a shift in the legal length slot limit to protect large, fecund females (102–152 cm FL) and the augmentation of a long-standing 1-fish possession limit by a 3-fish annual bag limit (Israel et al., 2009; <https://www.wildlife.ca.gov/Fishing/Ocean/Regulations/Fishing-Map/Central#sturgeon>; accessed 8/11/2016). To monitor harvest of adult WS in the Bay-Delta, a ‘sturgeon report card’ was introduced in 2007 and anglers are required to provide information about the species captured (WS or GRS, whether harvested or released, and the capture location).

Recovery efforts for southern DPS GRS (NMFS 2003) may indirectly benefit WS in the Bay-Delta. An angling closure effective March 1, 2010 on a segment of the upper Sacramento River to protect GRS spawning habitat may also protect WS using this section of the river. Sturgeon report card data document the presence of adult WS in the upper Sacramento (DuBois et al., 2010, 2012) although it is unknown if they use this area for feeding or spawning.

Lower Columbia River

WS abundance in this area collapsed at the end of the 19th century due to overfishing and remained depressed through the first half of the 20th century. Fishery management focused on the commercial fishery during the early 1900s and expanded to encompass recreational fisheries beginning in 1940. After reducing overall harvest and protecting the largest spawning adults, the WS population began to rebuild. Management actions have included adoption of slot length limits, reducing daily and annual catch limits for recreational fisheries, establishing annual quotas for commercial fisheries, and adopting seasonal and area closures to protect spawning fish. Harvest also occurs in marine areas and estuaries outside the Columbia River. Managers monitor tag recovery data and coastal harvest trends to ensure that harvest in these areas is consistent with Columbia River conservation and management needs.

WS assessment, planning, and restoration activities have been conducted throughout the lower Columbia River section. Much of this work was initiated following a WS Research Needs workshop in 1983 (Fickeisen et al., 1984). Initial restoration efforts in Bonneville, The Dalles, and John Day reservoirs emphasized: (i) transplants of juveniles from below Bonneville Dam to upstream areas as an alternative to reengineering of dam passage facilities, (ii) evaluations of flow recruitment relationships to identify critical thresholds and potentially beneficial water management measures, and (iii) intensive fishery management in order to optimize harvest of existing populations at sustainable levels (Rien, 2007;

Malette, 2008). High survival rates of WS transplanted into The Dalles and John Day reservoirs were promising (Rien and North, 2002) but the transportation program was suspended after 2005 due to funding constraints, difficulties in capturing adequate numbers of WS below Bonneville, and concerns about impacts on the unimpounded population segment (Rien, 2007).

The states of Oregon and Washington jointly manage the lower Columbia River WS recreational and commercial fisheries downstream from Bonneville Dam. A WS conservation plan (ODFW, 2011) provides a framework to manage and conserve the species in the lower Columbia River and along the Oregon Coast. The plan is intended to avoid serious depletion of this population segment by setting benchmarks for key population attributes including abundance, distribution, diversity productivity, habitat, and persistence. Reduced recruitment of harvest-sized fish to the lower end of the legal slot length prompted a complete closure of WS harvest in 2014 in the Columbia River and tributaries downstream from Bonneville Dam. The closure was extended to coastal rivers, bays, estuaries, and Puget Sound in the state of Washington. To further increase protection, spawning sanctuaries have been established downstream from Bonneville Dam on the Columbia River and Willamette Falls on the Willamette River (JCRMS, 2015).

Prior to harvest closure, regulations used included: (i) size limits for recreational and commercial fisheries, (ii) daily and annual catch limits for recreational anglers, (iii) gear restrictions for recreational and commercial fisheries, and (iv) the allowance of target seasons in the commercial fishery. The cornerstone of the bi-state management agreement was the adoption of a 3-year average harvestable number that ensures that fishery impacts remain sustainable. Since 1997, this harvestable allocation has been set at 80% for recreational fisheries and 20% for commercial fisheries.

Mark-recapture methods are used every 3 years to estimate the abundance of harvestable sized WS in lower Columbia reservoirs. Harvest guidelines for 2015 allowed a total annual catch of 2200 fish from Bonneville Reservoir, 652 fish from The Dalles Reservoir and 1500 from John Day Reservoir, with the catch allocated to treaty tribes and to recreational fishers (JCRMS, 2015). Because the population segments within each reservoir are naturally self-sustaining, recovery efforts have focused primarily on managing harvest and preventing further habitat loss. Recreational and tribal commercial and subsistence fisheries in these reservoirs are jointly managed by the states and Native American tribes represented by the CRITFC. Populations are monitored through a combination of fishery independent and dependent activities. Fisheries independent activities include WS carcass surveys, monitoring relative abundance of age-0 WS, and periodic population abundance estimates. The reservoir fisheries have been managed for optimum sustained yield (OSY) since 1989 with the goal of optimizing harvest while allowing the continued rebuilding of numbers of spawning adult fish (JCRMS, 2007). The Yakama Tribe conducts subsistence and commercial fisheries in this area and is presently pursuing opportunities to begin supplementing these populations with hatchery-produced fish.

Snake River

Snake River WS are under the jurisdiction of multiple management entities including the IDFG, ODFW, WDFW, and the NPT (IDFG, 2008; NPT, 2005; IPC, 2015). Joint management, conservation, and restoration of Snake River WS by states is shared along the border of the Snake River and with the NPT in Hells Canyon.

The goal of IDFG's Snake River WSMP is to preserve, restore, and enhance populations capable of providing sport fishing opportunities. Plan objectives include providing for coordinated management efforts among stakeholders, providing for a sustainable no harvest recreational fishery, facilitating data collection for stock assessments, integrating and defining the role of artificial propagation, and promoting public awareness and compliance through information and education (IDFG, 2008). Three categories (core conservation, conservation, and sportfish) are used to guide management strategies based on reach designation with an emphasis on protecting habitat, genetic integrity and diversity including measures that evaluate fishing-related mortality, population demographics and temporal trends, and use of conservation aquaculture where necessary to maintain population abundance and fishing opportunity in recruitment limited reaches.

Co-management of Hells Canyon WS includes the NPT WSMP goal of maintaining a viable, persistent population of WS between Lower Granite and Hells Canyon dams that can support an annual sustainable harvest. Plan objectives include: (i) a natural, stable age structure comprising both juveniles and a broad spectrum of spawning age-classes, (ii) stable or increasing numbers of both juveniles and adults, (iii) consistent levels of average recruitment to ensure future contribution to reproductive potential, (iv) stable genetic diversity comparable to current levels, (v) a minimum level of abundance of 2500 adults to minimize extinction risk, and (vi) provide an annual sustainable harvest of 5 kg ha⁻¹ (NPT, 2005).

As part of FERC relicensing, IPC completed a Snake River White Sturgeon Conservation Plan (WSCP) to guide the implementation of protection, mitigation, and enhancement measures for WS population segments impacted by IPC hydroelectric projects (IPC, 2005, 2015). The plan includes nine Snake River population segments from Shoshone Falls downstream to Lower Granite Dam and is coordinated with fishery managers to ensure consistency and support of Snake River WS management objectives.

Middle Columbia River

Status assessments were initiated in McNary Reservoir and Hanford Reach in 1995 (Rien and Beiningen, 1997) and in Lake Rufus Woods and Rock Island Reservoir in 1998 (DeVore et al., 1998b). Additional assessments were conducted as part of FERC re-licensing efforts in the PRPA in 1999–2002 (Golder Associates Ltd., 2003c), Rocky Reach in 2001–2002 (Golder Associates Ltd., 2003b), and Wells in 2001–2002 (Jerald, 2007); monitoring and evaluations programs are ongoing in these areas. All of these projects, except Chief Joseph Dam (USACE) that created Lake Rufus Woods, are owned and operated by Public Utility Districts (PUDs).

White Sturgeon Management Plans (WSMPs), developed under FERC licences for the PRPA, Rocky Reach, and Wells hydroelectric projects, include specific long-term biological objectives such as: (i) attainment of natural reproductive potential via natural recruitment, (ii) increase of the WS population in project reservoirs to a level commensurate with available habitat, (iii) provision of volitional passage (if reasonable and feasible means are developed), and (iv) sustaining of the population through conservation aquaculture until reasonable and feasible means for re-establishing natural recruitment are available (Chelan PUD, 2009; Douglas PUD, 2008; Grant PUD, 2009).

Conservation aquaculture programs will provide the initial foundation for the monitoring and evaluation programs for each project, which are designed to identify existing impediments to achieving the biological objectives, sustain the populations until the existing impediments can be corrected, and mitigate for population losses due to project impacts. No similar management plans are presently being considered for implementation in Lake Rufus Woods.

Upper Columbia River

Canadian assessments of the Transboundary WS population segment began in 1990 and are ongoing (RL&L, 1994; Hildebrand et al., 1999, Irvine et al., 2007; Golder Associates Ltd., 2015a,b, BC Hydro 2016a,b). The upper Columbia WS Recovery Initiative (UCWSRI), an international organization of Canadian and U.S. federal, state, and provincial fisheries agencies, tribes, and industry stakeholders was formed in 2000 and produced an Upper Columbia White Sturgeon Recovery Plan (UCWSRP) in 2002 (subsequently updated; Hildebrand and Parsley, 2013). In 2006, the upper Columbia River population was listed as 'Endangered' under SARA (Wood et al., 2007). A WS Recovery Strategy that addresses the legal requirements of SARA was completed in 2014 (DFO, 2014). A compatible WS recovery project was initiated in the U.S. portion of the Transboundary Reach under the Northwest Power and Conservation Council (NPCC) program in 2003 (Howell and McLellan, 2005).

The UCWSRP outlined short, mid and long-term measures to prevent the extinction of WS population segments above Grand Coulee Dam which included: (i) immediate implementation of a conservation aquaculture program, (ii) evaluation and monitoring of the existing population, (iii) controlling direct sources of WS mortality, (iv) determining genetic stock structure, and (v) research directed at diagnosing and correcting the cause of recruitment failure or collapse. A multi-component monitoring program is ongoing on both sides of the international border for the upper Transboundary population segment. Components of the monitoring program include periodic stock assessment surveys, acoustic telemetry, early life history research, and a juvenile index monitoring program to assess growth, survival, health, distribution, and relative abundance of released juveniles, as well as document any natural recruitment that may occur.

Arrow Lakes Reservoir has been identified by the UCWSRI as a potential location for either a second recovery area or the establishment of a failsafe WS population

segment in the upper Columbia River (Hildebrand and Parsley, 2013). To investigate the feasibility of these objectives, 56 204 hatchery-reared juvenile WS and 1 454 010 WS larvae have been released into Arrow Lakes Reservoir since 2007 (FFSBC, 2016). An annual monitoring program was implemented in 2007 to document the survival of introduced WS, the properties and availability of rearing habitat in this area, and the effects of dam and reservoir operations on the quality and quantity of this habitat. Results indicate a rapid post-release dispersal of juveniles from riverine to reservoir habitats and slow growth rates of released fish (Golder Associates Ltd. and Okanagan Nation Alliance, 2013), and apparent low survival rates of released juveniles based on low recaptures ($N = 30$) despite substantial annual sampling effort (Crossman, J., BC Hydro, Castlegar, BC, pers. comm.).

Kootenai River

Kootenai River WS assessment and conservation efforts under the NPCC Fish and Wildlife Program began in 1989 and are ongoing under a multi-agency cooperative effort (Apperson and Anders, 1990; Paragamian et al., 2005; KTOI, 2007, KTOI, 2012; Ross et al., 2015; Stephenson and Evans, 2015; Hardy et al., 2016). A Kootenai River WS Recovery Team was formed in 1994 to develop and help coordinate implementation of a Recovery Plan (Duke et al., 1999). In 2013, an annual program review was initiated by the KTOI to further assist co-manager decisions/agreements to utilize conservation aquaculture and guide research, monitoring, and evaluation activities (KTOI, 2012). In the Canadian portion of the Kootenai drainage, WS were SARA listed (Endangered) in 2006 and are addressed in the recent Recovery Strategy (DFO, 2014).

Similar to other non-recruiting populations, management actions are focussed on: (i) hatchery supplementation as an interim measure and (ii) habitat restoration to re-establish natural recruitment. Approximately 284 000 hatchery reared WS have been released since 1990. The current estimate of the standing hatchery-reared population of juveniles and sub-adults is 11 000–15 000 (Dinsmore et al., 2015) from 20 year classes. Fish from the earlier releases are expected to begin augmenting the adult population by 2020, after which time the number of hatchery origin adults in the population should rapidly increase through 2030. Meanwhile, experiments with flow augmentation and modification of spawning substrate have been attempted to restore natural recruitment. Experimental flow releases at Libby Dam were found to be unrelated to the initiation of WS spawning activities although maintaining higher discharge is considered beneficial in maintaining a minimum flow in the spawning reach (Paragamian et al., 2001; Paragamian and Wakkinen, 2002, 2011). Recent studies of flow, river substrate, and sediment transport suggest lack of suitable spawning substrate is likely the factor limiting recruitment and indicate that an aggressive habitat enhancement program could reverse recruitment collapse (Paragamian et al., 2009; KTOI, 2009; McDonald et al., 2010). However, an interesting and enigmatic pattern of adult spawning behaviour has been a major determinant

in deciding future restoration activities. Adult WS show high fidelity year after year for spawning sites near Bonners Ferry, ID, that have not supported adequate recruitment for decades. Adults have full access to plentiful upstream habitat that may be deemed 'classical' WS spawning habitat; yet, the wild adults will not migrate farther upstream to these habitats (Ross et al., 2015; Hardy et al., 2016).

Other recovery strategies for Kootenai River WS being investigated include major river channel rehabilitation, spawning substrate enhancement/additions, floodplain/off-channel habitat reconnections/restoration, nutrient enhancement, (KTOI, 2009) and translocation of ripe WS adults to locations with suitable spawning habitat (Rust, 2011). Translocation of reproductively ready adult WS from the current spawning site to upstream areas with cobble and boulder substrate site has been conducted in several years, but most translocated adults rapidly left the release location. Although eggs were collected at the release location, it was uncertain whether they had been fertilized (Rust, 2011).

Fraser River

For the three populations in the mainstem Fraser River, the effort has mainly been focussed on the lower Fraser River population (e.g. Glova et al., 2008; Nelson et al., 2013a), due to habitat changes, a growing catch and release fishery, and other impacts in that region (Hatfield et al., 2004). Assessment in the middle Fraser River has primarily focussed on the identification of spawning habitats, with the aim of supporting habitat protection. Due to the diverse status of WS populations in the Fraser basin, a variety of management objectives have been developed. The conservation plan objectives for the three mainstem populations (FRWSWG, 2005) includes: (i) achieving and maintaining and natural population age structure, (ii) refining understanding of population targets and identifying timeframes for achieving targets, (iii) identifying and quantifying WS habitat availability and making critical habitat recommendations, (iv) tracking the status of WS populations and their responses to management actions, (v) filling in basic biology data gaps (life history, habitat use, etc.) required to support conservation-based management, (vi) addressing specific data gaps to support improved assessment and prioritization of threats, and (vii) identifying the biological and social conditions allowing for beneficial use, where consistent with SARA and conservation objectives.

Since the Nechako River population currently experiences recruitment collapse, the overall Fraser River recovery plan specifically addressing this population (NWSRI, 2004) contains somewhat different objectives. These are: (i) controlling all sources of adult mortality, (ii) implementing conservation aquaculture to preserve as much population diversity as possible in the absence of recruitment, (iii) undertaking research to diagnose cause(s) of recruitment collapse and to identify mitigation options, and (iv) enhancing and maintaining public outreach programs related to WS in the watershed.

Examinations of the geomorphology of the spawning reach in the Nechako River continue to improve our understanding

of both the current habitat condition and what will be required for effective long-term restoration (NHC, 2008, 2013). Experimental investigation of gravel augmentation undertaken in 2008 and 2011 (McAdam, 2012; pers. comm., Williamson, C., FFSBC, Prince George, BC) has shown some success, and both physical and biological monitoring is ongoing (NHC, 2013).

A WS Recovery Strategy that addresses the legal requirements of the Canadian SARA was recently completed (DFO, 2014). Since the entire species within the Fraser River watershed was listed as endangered by COSEWIC (2003) the national recovery strategy will address both the two SARA listed populations (upper Fraser, Nechako) as well as the lower and middle Fraser River populations.

Conservation aquaculture

Conservation aquaculture of WS has benefited from development and refinement of culture techniques driven by the commercial aquaculture industry. At present, WS are farmed commercially for meat and caviar in North America, (California, Washington, Idaho, and British Columbia), Israel, and Italy. Early research into WS aquaculture at the University of California Davis determined an appropriate thermal regime for WS female spawning readiness and developed techniques to induce ovulation/spermiation, evaluate spawning readiness, and remove eggs non-lethally via caesarean (Doroshov et al., 1983; Conte et al., 1988; Moberg et al., 1995; Webb et al., 1999, 2000, 2001, 2002; Linares-Casenave et al., 2002). Conservation aquaculture programs have adapted and expanded on many of these techniques. For example, a less invasive abdominal massage to strip eggs is now common practice (KTOI, 2016).

Recruitment-limited WS population segments in the Kootenai, middle and upper Columbia, Snake, and Nechako rivers have all been supplemented by conservation aquaculture programs, some for over 20 years. Initially, all conservation aquaculture programs were based on a direct gamete take from annual captures of reproductively mature wild WS with subsequent spawning in a hatchery. However, a pilot program conducted in the upper Columbia by the WDFW in 2010 and 2011 evaluated the feasibility of collecting naturally produced WS larvae for hatchery rearing. In 2010 and 2011, the WDFW successfully used this approach to rear and release 522 and 3590 juveniles, respectively, into the upper Columbia. As this method captured more genetic diversity than direct gamete take in the upper Columbia program (Schreier and May, 2012) and reduces the production of spontaneous autopolyploid offspring (Schreier et al., 2013; Fritz, C., FFSBC, Cranbrook, BC, pers. comm.), its adoption in other river systems is being considered.

The longest continually operating WS conservation aquaculture programs occur in the Kootenai River and upper Columbia River. The Kootenai River program was initiated by the KTOI in 1990. To support the long-term population goal of ~8000 sexually mature adults after a generation of conservation aquaculture, 15 000–30 000 age-1 WS (10–70 g) reared using two grow-out regimes, (an accelerated growth regime and an ambient altered-river regime) have been and

will continue to be released annually. The program will continue with adjustments made to cohort sizes based on observed post-stocking survival (KTOI, 2012). The Kootenai River program used two hatcheries that implemented disparate grow-out methods from 2001 to 2015, thus complicating the issue. If juveniles are grown at elevated temperatures throughout year 1, growth is significantly greater/faster than those grown at ambient river temperatures. This allows for earlier release (spring) and/or at a larger-size, which increases in-river survival. The Kootenai River program employed multiple release strategies from 1991 to 2015. In the early years, few older, larger fish were released. Then, higher numbers of young, small fish were released. This was followed by a strategy of releasing intermediate numbers of intermediate-sized fish. All three strategies have resulted in viable year classes (Dinsmore et al., 2015). Given the effect of size on post-release survival, teasing out hatchery-induced effects on survival versus post-release density-dependent effects on survival has been difficult.

In 2001, a broodstock based conservation aquaculture program in the Canadian side of the Transboundary Reach in the upper Columbia was initiated; a similar program was initiated in the US portion in 2004. In 2010, investigations began in the US to examine the feasibility of capturing, hatchery rearing, and releasing wild origin WS through the collection of drifting larva. The success of the capture program and subsequent genetic analysis that confirmed the greater genetic diversity of the wild caught larva versus broodstock based progeny (Schreier and May, 2012) resulted in both the Canadian and US programs switching to a stocking program that presently only uses captured wild eggs and larvae. The Kootenai conservation aquaculture program is based on broodstock collections and uses two rearing locations to guard against disease outbreaks or equipment failure that might significantly decrease egg and/or fry survival in one location.

A pilot conservation aquaculture program was initiated for the Nechako River WS in 2006 to test the feasibility of streamside rearing and to provide initial juvenile survival estimates. A larger permanent conservation aquaculture facility was completed in 2014 leading to the release of the first juvenile cohort in spring 2015. Both the pilot and permanent facilities are located adjacent the spawning reach at Vanderhoof. The decision to use river water in both facilities was made to maintain the potential for olfactory imprinting to wild spawning habitats. Additionally, based on the identified benefits of interstitial habitats during the yolk-sac phase (Boucher, 2012; Boucher et al., 2014) the Nechako and upper Columbia conservation fish culture programs include the provision of substrate during the yolk-sac phase. To support the long-term population goal of ~1500 sexually mature adults after a generation of conservation aquaculture, 12 000 yearlings (150 g) will be released annually, with adjustments made to cohort sizes based on observed post-stocking survival (Williamson, C., FFSBC, Prince George, BC, pers. comm.).

In the middle Snake River, commercial aquaculture of WS began during the late 1980s. In-basin, domestic broodstock were developed for the commercial aquaculture industry

using indigenous WS from the middle Snake River to prevent potential genetic and disease risks from importing non-native WS (Patterson et al., 1992). A portion of the commercial production was then used for experimental stocking (1989–2000) to research growth and survival rates of hatchery-propagated WS (Patterson et al., 1992). Currently, management strategies for conservation aquaculture in the middle Snake River include: (i) native broodstock-produced juveniles and (ii) in-river collection of naturally-produced eggs and larvae to enhance WS population segments where natural recruitment is limited or to establish new sport fisheries (IDFG, 2008; IPC, 2015).

Conservation aquaculture programs for WS in the middle Columbia River were initiated for the PRPA (Golder Associates Ltd., 2015b) and Rocky Reach (Wright and Robichaud, 2013) in 2011 and in Wells Reservoir in 2014 (Robichaud and Gingerich, 2016). Releases in the PRPA and Rocky Reach have primarily used progeny from broodstock captured in downstream reservoirs and reared in several facilities in the region. Investigations into the feasibility of capturing wild larvae in downstream reservoirs for subsequent rearing and release into the PRPA are underway. Supplementation in the Wells Pool prioritizes the use of naturally produced larvae captured from the Columbia River upstream of Bonneville Dam, with the bulk of fish released through June 2016 originating as wild caught larvae from Lake Roosevelt. In the event that larval collection efforts fall short, direct gamete origin fish may be used to achieve stocking targets.

For some population segments such as the Kootenai River, conservation aquaculture has been the only successful mitigation to date to ward off future extirpation (KTOI, 2012). Given the long-term prognosis of eventual extirpation of several population segments due to lack of adequate wild recruitment, conservation aquaculture bridges the gaps in year-classes while restoration strategies can be formulated, implemented, and evaluated. As with any conservation aquaculture program, the inherent risks caused by human intervention should be recognized and minimized as much as possible. For example, the environments experienced during early life history can lead to substantial phenotypic variation for WS, including effects on growth, morphology, and developmental heterochrony (Baker et al., 2014; Boucher et al., 2014). Further attention to unintended effects of captive rearing (e.g. the release of predator naïve juveniles) is required and will improve our ability to release offspring that are representative of their wild counterparts.

One potential side effect of captive rearing that has been investigated extensively in WS is genetic diversity loss that may result from inclusion of too few wild parents as broodstock. Genetic monitoring of broodstock indicates that up to 96% of wild population genetic diversity has been preserved in both the Kootenai River (Drauch Schreier et al., 2012b) and the Transboundary Reach of the upper Columbia River (Schreier and May, 2012) conservation aquaculture programs. However, variability among families in post-release survival due to hatchery management changes and natural selection after release may reduce actual levels of genetic diversity conserved (Schreier et al., 2015). For example, in the KTOI program, full sibling families reared in warmer

water under the recently implemented accelerated growth regime have a significantly higher post-release representation than those reared in the ambient, altered river regime (Schreier et al., 2015).

Another possible negative genetic outcome of conservation aquaculture is exposure of hatchery-reared cohorts to artificial selection pressures, resulting in the transfer of maladaptive genes into native gene pools. Artificial selection has been observed in other sturgeon hatchery programs (Stellate Sturgeon, *Acipenser stellate* and Russian Sturgeon *Acipenser gueldenstaedtii*; Chebanov et al., 2002). In the upper Columbia River, collection of fertilized eggs and down-migrating wild larvae for subsequent hatchery rearing and release has reduced these concerns by reducing artificial selection at the broodstock collection and spawning stages and by preserving natural mate choice behaviours.

Recently, researchers discovered that 15, 10, and 4% of WS produced at a California commercial farm, the Kootenai Tribe of Idaho conservation aquaculture program, and upper Columbia River conservation aquaculture program, respectively, had abnormally large genome sizes (Schreier et al., 2013; Gille et al., 2015; Crossman, J., BC Hydro, Castlegar, BC, pers. comm.). The majority of these spontaneous autopolyploid individuals had genomes 1.5× the normal size, making them genetic triploids. The proportion of spontaneous autopolyploid progeny produced per family ranges from 0 to 47% (Schreier et al., 2013; Gille et al., 2015). Although genetic triploid WS are fertile, they produce offspring of intermediate ploidy when crossed with normal WS (Drauch Schreier et al., 2011). Although the intermediate ploidy progeny are viable, their fertility is unknown and therefore, WS conservation aquaculture programs monitor families for incidences of spontaneous autopolyploids to avoid stocking them into wild populations. The cause of spontaneous autopolyploidy in sturgeon culture is unclear, but its low incidence in wild populations suggests that either some aspect of aquaculture induces this abnormal condition or natural selection eliminates abnormal ploidy individuals at early life stages, likely due to negative physiological consequences caused by abnormal genomes. Investigation of numerous possible factors that may be causing unintended autopolyploidy have found no significant correlations between abnormal ploidy with morphometric characteristics of broodstock used, spawning methods, or early life rearing techniques (Young, S., KTOI, Bonners Ferry, ID, pers. comm.). At this time, the egg quality and/or egg maturity for a given female appears the most likely cause for the high variability in autopolyploidy occurrence in the Kootenai River program, i.e., under common treatment and protocols, some females' offspring are 100% normal while a portion of other females' offspring are genetic triploids. No full sibling family has been identified as 100% autopolyploid (Young, S., KTOI, Bonners Ferry, ID, unpubl. data).

Present and future risks

There are numerous risks to the future status of WS populations. Many of these threats have the potential to impact populations across their range, while others are specific to

population segment(s). The following provides a description of the perceived current and future threats and the population segments to which they apply.

Habitat fragmentation, alteration, and loss

Development of river corridors for economic purposes has reduced the areal extent and complexity of WS habitats across their range through damming, channelization, diking, dredging, and other practices. Construction and operation of dams has fragmented habitat, slowed water velocities, altered the hydrograph and hydraulic conditions, and altered sediment and thermal regimes, all of which affect habitat for WS spawning and early life stage rearing (Parsley and Beckman, 1994; IPC, 2005; van der Leeuw et al., 2006; IDFG, 2008; NHC, 2008).

Fragmentation from dams in the Columbia Basin reduces the quality and quantity of WS habitat, alters migration patterns, and despite limited upstream movement at a few dams (Warren and Beckman, 1993; Parsley et al., 2007), may impose unidirectional downstream gene flow (Jager, 2006; Drauch Schreier et al., 2013). Blocked historical migratory routes and inaccessibility to suitable spawning habitat may be the greatest factors contributing to population declines of most sturgeon species (Auer, 1996). Jager et al. (2001) demonstrated via simulation models that increased habitat fragmentation led to an exponential decline in the likelihood of the persistence of WS populations. At the local scale, ongoing construction of structures at dams (e.g., removable spillway weirs, spill training walls) to improve survival of downstream migrating juvenile salmon may impede movements of WS. These structures also alter water velocities over substantial areas of the riverbed and can thus influence the quality of habitat.

Reduced velocities may disrupt downstream migration of larvae to appropriate nursery areas (Israel et al., 2009). Brannon et al. (1985) reported that during a laboratory study, feeding larvae moved downstream when food was not encountered and a greater proportion of larvae were in the water column at the higher test velocity. In the upper Columbia River, an area with a persistent lack of natural recruitment, larvae have only been collected within 15 km of the most downstream known spawning area and the majority of guts examined were empty (Howell and McLellan, 2013a). The short dispersal distance was likely due to low velocities encountered once larvae entered Lake Roosevelt. Limited recruitment has occurred in some years, such as 1997, when very high river discharge ($>5663 \text{ m}^3 \text{ s}^{-1}$) coincided with the spawning and egg incubation period. High flow is expected to increase drift distances of feeding larvae and may lead to increased survival if larvae are transported to suitable rearing habitat downstream from the river-reservoir interface in most water years. Some WS feeding larvae in the unimpounded lower Columbia River, an area with consistent recruitment, were shown to disperse longer distances (McCabe and Tracy, 1994) and the majority of those examined contained food in their guts (Muir et al., 2000).

The reduction in turbidity resulting from impoundment may contribute to increased predation on early life stages of

WS (Gadomski and Parsley, 2005a); however, the turbidity levels examined in that study exceeded the apparent historical levels in some locations (e.g. upper Columbia River; see McAdam, 2012). However, evaluations of habitat changes relative to historical conditions are limited (often due to an absence of historical data).

Operation of dams has resulted in substantial changes to the natural hydrograph, which can influence year-class success. Before hydro system development, Columbia River flows were characterized by high spring runoff from snowmelt and regular winter and spring floods. Contemporary spring freshet flows have been reduced by ~50% and winter flows have increased ~30% (Quinn et al., 1997). Changes in the timing and magnitude of flows, as well as secondary effects on water temperature, can result in reduced spawning and early rearing habitats for WS (IPC, 2005; IDFG, 2008). Recruitment of juvenile WS has been widely correlated with the volume of spring flow (Kohlhorst et al., 1991; Parsley and Beckman, 1994; Brink and Chandler, 2000; Lepla, 2008a; Fish, 2010). In addition to seasonal changes in magnitude and timing, daily changes in flow caused by hydro electrical load following operations can alter critical habitats or result in stranding of early life stages (van der Leeuw et al., 2006). Load shaping may also disrupt downstream dispersal of larvae by reducing discharge and water velocities at night when WS larval dispersal is greatest (Kynard and Parker, 2010; Howell and McLellan, 2013a, 2014a).

The effects of flow regulation on substrate conditions at spawning sites have received particular attention due to the association of recruitment failure with substrate changes (McAdam et al., 2005; Paragamian et al., 2009; McAdam, 2015) as well as experimental evidence of the positive effects of appropriate substrate on the survival of eggs (Koch et al., 2006) and the retention (McAdam, 2011; Crossman and Hildebrand, 2014), growth (Boucher et al., 2014; Crossman and Hildebrand, 2014) and survival (McAdam, 2012; Boucher et al., 2014) of yolk-sac larvae. An altered hydrograph may change spawning location (e.g. due to an alteration in hydraulic conditions) to areas with low substrate quality and/or modify substrate conditions at long term spawning sites (McDonald et al., 2010; McAdam, 2015).

Habitat reduction due to river channelization, diking, dredging, and agricultural diversions may threaten year-class success through dewatering or destruction of historical spawning sites and rearing habitat. Channelization and diking of the Kootenai River caused deposition of fine sediment in the river channel, rather than the floodplain, potentially covering historical habitat for spawning, incubating, and early rearing of larval WS (Anders et al., 2002). Portions of the navigation channel in the Columbia River downstream from Bonneville Dam are dredged regularly to maintain the authorized shipping channel depth. While dredging sediments from the riverbed can pose a threat (Buell, 1992), the placement of dredged materials at traditional deep in-channel disposal sites generally has little effect on WS rearing habitat (Hatten and Parsley, 2009). This activity historically occurred well downstream of documented spawning and yolk-sac larvae settling areas. Alternately, gravel and rock extraction in the Sacramento-San Joaquin Bay-Delta may remove

important refugia for larval WS and increase predation on this life stage (Israel et al., 2009). Similarly, gravel extraction from the lower Fraser River has the potential to affect WS, particularly when conducted in proximity to spawning locations. Lastly, entrainment in agricultural diversions, power plants, and water projects (particularly in the Sacramento-San Joaquin Bay-Delta) may be an important source of mortality for young WS (e.g. Poletto et al., 2014; Verhille et al., 2014). However, mortality rates appear to be highly variable across locations and dependent on flow rates (Israel et al., 2009).

Predation

Fish, including sculpins, Walleye (*Sander vitreus*), and Small-mouth Bass (*Micropterus dolomieu*; Miller and Beckman, 1996; Gadomski and Parsley, 2005b; Golder and LGL, 2013) and Chinook Salmon (*Oncorhynchus tshawytscha*) fry (McAdam, S., BC MOE, Vancouver, BC, pers. comm.) have been shown to consume WS eggs and age-0 WS. Larger WS have been prey for Broadnose Sevengill Sharks (*Notorynchus cepedianus*) in Willapa Bay, Washington (Langness, O., WDFW, Vancouver, WA, pers. comm.). Predation by Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) on WS below Bonneville Dam has increased annually since 2005 (Tackley et al., 2008a,b; Stansell et al., 2012). In a reach <3 km immediately downstream from Bonneville Dam consumption of WS by sea lions (primarily Stellar sea lions) increased from an observed take of just 1 WS in 2005 to a peak of 3003 in 2011. Sea lions consumed an estimated minimum of 2498, 635, and 147 WS in 2012, 2013, and 2014, respectively. As in the Columbia River system, sea lion predation on adult WS recently has been observed in the Sacramento-San Joaquin Bay-Delta and Fraser Rivers, possibly due to declines in preferred prey such as anadromous salmonids. The magnitude of this stressor on adult biomass has not yet been determined.

Invasive species

Threats posed by non-native aquatic species include a decrease in prey value associated with the replacement of native forage by non-native prey species, loss of benthic prey production areas, competition, disease, habitat alteration, and predation. In the Sacramento-San Joaquin Bay-Delta the invasive Overbite clam (*Corbula amurensis*) has become a major component of the adult WS diet (Zeug et al., 2014) and non-native Asian clam (*Corbicula fluminea*) and American Shad (*Alosa sapidissima*) now make up a considerable part of sub-adult and adult WS diets in the lower Columbia River. Energetic content and nutritional value of exotic species may differ from the natural prey base, and exotic species may compete with preferred prey items. For example, the Overbite clam has been implicated in declines of mysid shrimp (Feyrer et al., 2003), an important food source for juvenile WS in the Sacramento-San Joaquin Bay-Delta (Radtke, 1966).

The recent establishment of the non-native Northern Crayfish (*Orconectes virilise*) in the upper Columbia River in

Washington may be of concern for future WS recovery efforts (Larson et al., 2010) as introduced Rusty Crayfish (*Orconectes rusticus*) were shown to prey on juvenile LS in hatchery experiments (Crossman, 2008). Similarly, invasive Northern Pike (*Esox lucius*) and Walleye in the Columbia River may prey on early life stage WS. Walleye have been documented to consume WS juveniles in lab studies (Gadomski and Parsley, 2005b) and a large Walleye captured in the upper Columbia had consumed three yearling hatchery WS shortly after release (Hildebrand, L., Golder Associates, Castlegar, BC, pers. comm.).

Fishery impacts

White Sturgeon populations in many areas provide unique opportunities for harvest through recreational, commercial, or tribal subsistence fisheries. However, stock status in other areas allows only catch and release fishing. Fishing for WS has been banned in areas where recovery efforts are underway, although this ban is being reconsidered in the PRPA in the middle Columbia River to actively harvest over-abundant hatchery fish from the 2002 release in Rock Island Reservoir that have limited genetic diversity and survival rates that were much greater than expected (Golder Associates Ltd., 2015b).

Recreational fisheries occur in the Fraser, Columbia, and Sacramento-San Joaquin rivers and their associated bays and estuaries. Tribal subsistence fisheries harvest WS from the Columbia and Snake rivers. Harvest is managed primarily through the use of size limits, catch limits, gear restrictions for recreational and commercial fisheries, and fishing seasons during commercial fisheries (JCRMS, 2008; California Department of Fish and Wildlife Freshwater Sport Fishing Regulations, online at: www.wildlife.ca.gov/Fishing/Ocean/Regulations/Fishing-Map/Central/#sturgeon, accessed 8/11/2016). Harvest is monitored via creel surveys and catch records.

The greatest threat to the Sacramento-San Joaquin Bay-Delta population segment may be overfishing. Historically, overharvest in this population lead to the permanent closure of the commercial fishery in 1917 and repeated closures of the recreational harvest over time as the population recovered slowly from overexploitation for caviar at the turn of the 20th century (Moyle, 2002). Harvest mortality estimates made after the recreational fishery re-opened in 1954 have varied from 5 to 11.5% (Kohlhorst et al., 1991; Schaffter and Kohlhorst, 1999; Israel et al., 2009) although a new study of angler reporting bias suggests that estimates of 3.1–4.4% for recent years (DuBois and Gingras, 2011) were substantially underestimated (Gingras, M. CDFW, Stockton, CA, pers. comm.). Illegal harvest is a serious problem for WS and several poaching rings have been discovered and prosecuted over the past decade (Israel et al., 2009).

The biological and population level effects of repeated catch and release angling on WS populations are largely unknown. Booth et al. (1995) indicated that angling could be one of the most severe forms of exhaustive exercise that fish experience. Exhaustive exercise in fishes can result in a variety of physiological disturbances that alter reproductive

performance and cause delayed mortality (Nelson, 1998; Lambert and Dutil, 2000; Schreer et al., 2001). Even low levels of fishing-related mortality could impact population size structure and abundance, especially in reaches with poor habitat and low reproductive success or where fish are concentrated near dams (IDFG, 2008). Angling data collected below C.J. Strike Dam on the Snake River estimated an individual WS in this population was hooked an average of 7.7 times annually. This suggests that a WS in this reach could potentially be hooked several hundred times throughout its life span (Kozfkay and Dillon, 2010).

Other population effects may be less quantifiable. For example, abandoned fishing gear has been shown to contribute to incidental mortality of WS. In the lower Columbia River, efforts to recover lost gill nets 'ghost nets' in areas with heavy commercial and tribal fisheries located 33 lost nets, at large for 1–7 years, that were responsible for incidental mortality of 525 WS (Kappenman and Parker, 2007). In the upper Columbia River, WS with fishing line extending from the anus are commonly encountered. This is a result of ingesting baited tackle that either was being used to fish for smaller game or was snagged on the bottom, broken off by the angler, and then ingested by a WS (Crossman, J., BC Hydro, Castlegar, BC, unpubl. data). The effects of this type of incidental hooking are unknown.

Management agencies must have the ability to quickly reduce exploitation when necessary. For example, when a large aggregation of WS was discovered in a shallow slough in the lower Columbia River, anglers quickly harvested >1000 fish, which comprised >20% of the annual allotment for the management unit in a single month (Monroe, 2010). The substantial short-term harvest from this location required an emergency closure of this localized area to ensure continued fishing opportunities and to protect the resource.

Water quality degradation, and contaminants

Mining, agriculture, irrigation, hydroelectric dams, industrial discharges, urban runoff, grazing, and logging have been associated with degraded water quality in the Columbia (Rinella et al., 1993; Joy and Patterson, 1997; Wentz et al., 1998; Williamson et al., 1998; Schneider, 2002), Snake (Clark et al., 1998; Harrison et al., 2000), Sacramento-San Joaquin (Dubrovsky et al., 1998; Domagalski et al., 2000), Kootenai/ ay (Knudson, 1994; Century West Engineering et al., 2000), and Fraser (Hatfield et al., 2004) river drainages. Much of the mainstem Snake River is listed as impaired or water-quality limited (IDEQ, 1998). In particular, the Snake River between Swan Falls and Brownlee dams is one of the most degraded reaches of the Snake River relative to temperature, sediments, pesticides, organic matter, nutrients and dissolved oxygen (Harrison et al., 1999; Myers et al., 2001; IDEQ, 2003; IDEQ and ODEQ, 2004). As a result, Brownlee Reservoir experiences severe water quality degradation, particularly in low and moderate water years, because of the extremely enriched, hypertrophic waters flowing into Brownlee Reservoir that manifests into algae blooms and fish kills.

Although numerous contaminants have been detected in WS, the susceptibility of WS, particularly early life stages, to a wide variety of pollutants has only recently been studied. Contaminants will continue to be a concern in the future. In the upper Columbia, and Fraser Rivers, the identification of rapidly increasing levels of polybrominated diphenyl ethers (PBDEs) commonly found in flame retardants may represent a contaminant issue affecting future WS recruitment. Environmental toxins may also have sublethal effects, which are more difficult to assess.

Incidental physical trauma

Heavy boat traffic in the San Francisco Bay-Delta causes adult WS mortalities (Gingras, M., CDFW, Stockton, CA, pers. comm.) and the NMFS is currently examining the effects of both recreational and industrial boating activities in the Sacramento-San Joaquin Bay-Delta system on WS survival. Ocean-going vessels transiting the shipping channels of the estuary can result in propeller strike injuries. However, the rate of injury has not yet been quantified (Woodbury, D., NMFS, Santa Rosa, CA, pers. comm.). The risk of collisions between boats and WS is present in most waters with WS. However, there is a greater probability of boat strikes in areas with substantial recreational and commercial boat traffic, such as the Sacramento-San Joaquin Bay-Delta, the lower Columbia River, Puget Sound, and the mouth of the Fraser River. Boat strike mortality has also been reported as a concern for Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) by Brown and Murphy (2010).

Operations and maintenance activities at dams can also result in the direct mortality of WS. Offline turbines being brought online have resulted in fish kills of >1000 individuals at Bonneville Dam. Losses of 1000–3000 WS have occurred in turbine draft tubes when the turbines have been dewatered for maintenance. However, fish kills of this order of magnitude have been rare and are unlikely to occur in the future as operational changes to reduce WS mortality have been developed and implemented. Currently, most mortality events are much smaller (<3 fish killed) although they do happen frequently. In the middle Snake River, at least 11 WS deaths between 1999 and 2016 have been attributed to turbine start-ups at C. J. Strike Dam (Lepla, K. IPC, Boise, ID, pers. comm.). Mortality related to turbine start-up has also been reported in the upper Columbia River. Operational mitigation measures have been developed to exclude WS from draft tubes and modify turbine start-up procedures to reduce impacts. The recently completed Waneta Dam generation station has deployable screens to prevent WS from accessing draft tubes during unit outages (Horan, W., CPC, Castlegar, BC, pers. comm.).

Climate change

Current and future climate changes that alter water temperatures or basin hydrology could affect WS throughout their range. Quinn et al. (1997) report that the Columbia River has been warming to 15.5°C earlier at McNary Dam than in past years (15-day difference between 1954 and 1994).

The date of the annual maximum temperature has not changed but the June–July mean and maximum temperatures increased by 1.5 and 1.2°C, respectively, since 1954, and fall cooling of the river below 15.5°C at McNary Dam has been occurring 12 days later. Hamlet and Lettenmaier (1999) used two global climate models and a hydrology model to predict changes in Columbia River flow over the next 100 year. By 2045, they predicted (depending on models employed) a 11–25% reduction in summer flow at The Dalles Dam and a 1–3°C increase in summer air temperature. Such flow and air temperature changes might translate into additional important changes in water temperature and subsequent changes in WS growth, maturation, spawn timing, and survival. For instance, bioenergetic modelling suggests that WS in the upper Columbia River are at, or possibly beyond, their thermal optimum (Van Poorten and McAdam, 2010). Climate change also is a concern for WS in the Bay-Delta system, as this southernmost population of WS and may be especially vulnerable to increases in water temperature. Intrusion of saltwater into the delta, diminished river flows due to sea level rises, and changes in precipitation patterns projected by California water managers (CDWR, 2009) may influence habitat availability and reproductive success for WS. These same influences are possible for WS inhabiting lower reaches of the Columbia and Fraser rivers. In July 2015, a die-off of as many as 80 large adult WS in the Columbia River was believed to be caused by warmer than average water temperatures (Columbia Basin Bulletin, available <http://www.cbbulletin.com/434540.a.spx>; accessed 4/20/2016). A large number of WS mortalities were observed in the Fraser Rivers in 1993 and 1994 may also have been linked in part to elevated temperature (McAdam, 1995). These incidents suggest that climate warming coupled with flow regulation impacts may increase the risk that this impact will increase in future.

Research focus and needs

While information on WS protection needs and restoration strategies continues to evolve, many aspects of life history, habitat requirements, and threats to population viability and persistence remain poorly understood. This section describes research needs identified for WS populations in the Sacramento-San Joaquin, Columbia, and Fraser river basins (Table 3).

Identify critical habitats by early life stages and environmental variables affecting year-class strength

Additional research is required to evaluate the complex relationships between disturbance, environmental factors, and WS recruitment success. While dam construction, and channel modifications (Beamesderfer and Farr, 1997) and overfishing (Dumont, 1995; Echols, 1995) are considered major causes of decline for sturgeon populations, the loss of spawning grounds and suitable sites for incubation and rearing of early life stages appear most critical (Coutant, 2004; McAdam, 2015). As early life stage survival of WS is a crucial determinant of year-class strength (Gross et al.,

2002; Parsley et al., 2002), priority should be placed on developing methods to quantify vital rates, population abundance, and habitat requirements during the first year of life (Secor et al., 2002). As flow (Stevens and Miller, 1970; Kohlhorst et al., 1991; Parsley and Beckman, 1994; Fish, 2010) and substrate quality (Koch et al., 2006; McAdam, 2011, 2012) may be primary determinants of recruitment success (*sensu* Burke et al., 2009), quantitative work focused on characterizing the relationship between these variables and early life stage survival should be conducted so that effective restoration measures can be developed. There is also a need for recruitment monitoring to document natural production trends and the environmental conditions that produce detectable year classes within the population.

Assess contaminant effects on health and productivity

White Sturgeon are exposed to a variety of pollutants and contaminants through direct contact or bioaccumulation through the food chain. As opportunistic bottom feeders, WS frequently come into contact with sediments that could contain sediment-absorbed hydrophobic pollutants such as PCBs, chlorinated pesticides (e.g. DDT), and chlorinated dioxins and furans. Laboratory studies have shown some pollutants to be particularly toxic to WS, and correlative evidence suggests that WS may be susceptible to bioaccumulation of environmental pollutants because of their life history characteristics (long-lived, late-maturing, benthic association, piscivorous at larger sizes) (Foster et al., 2001a,b; Feist et al., 2005; Webb et al., 2006). The effects of many contaminants and degraded water quality conditions on WS health, reproduction, and early development are poorly understood with no direct links between pollutants and WS productivity. More research is needed to evaluate the impacts of chemicals for which there are no water quality standards or published effects benchmarks. The synergistic effects of contaminants with other non-chemical stressors, such as flow, dissolved gas levels, catch-and-release angling, and invasive species also is an area that requires further study.

Determine spawning periodicity

While our understanding of gonadal cycles and reproductive physiology of WS is improving, substantial limitations remain particularly in the wild (Doroshov et al., 1997). Repeated detection of mature fish in hatchery broodstock programs suggest that females in the wild may spawn every 3–5 years, which differs from prior reports indicating 2–11 years (Conte et al., 1988; PSMFC, 1992; Paragamian et al., 2000). Similarly, hatchery broodstock capture programs indicate that males spawn more frequently, possibly every other year (Paragamian et al., 2005). The lengths of reproductive cycles also appear to be driven by environmental (e.g. food supply) and genetic factors. Further study is needed to determine the roles of endogenous and environmental factors in WS reproduction, which is critically important for both aquaculture and conservation (Doroshov et al., 1997).

Table 3
Priority (check marks) and secondary (asterisks) research needs for White Sturgeon throughout the species geographic distribution

Research need	Research needs by river section											
	Sacramento San Joaquin Bay Delta	Columbia River			Snake River			Kootenai River	Fraser River			
		Lower	Mid	Upper	Lower	Mid	Lower		Mid	Upper	Nechako	
Spawning and early life												
Identify critical habitats used by early life stage and effects of environmental variables on year-class strength	√	*	√	√	√	√	√	√	√	√	√	√
Contaminant effects on reproduction	√	√	*	√	√	√	*					
Spawning periodicity	√		*	*	*			*		*	*	*
Population characteristics												
Validate length-at-age relationships	√				√	√						
Characterize population dynamics and carrying capacity	√	√	√	√	√	√	√	√	√	*	*	*
Population viability analysis model											√	
Stock composition of coastal and marine population segments	*							*				
Genetic characteristics of population segments	*	√	√	*	√	√		*				
Understand movements, behaviour, and habitat use by juvenile and adult life stages	√		√		*	*	√	√	√	√	√	√
Ecological interactions												
Pinniped predation	*	√										
Influence of invasive species	*	*	*	*				*				*
Climate change effects on pop. productivity	*			*		*	*			√		*
Nutritional value of the prey base	*	*		*	*	*	*	√	√	√	√	*
Management												
Quantify anthropogenic mortality	*		*	√		√	*	√	√			√
Long-term population trend data	*	√		*	√	√		*	*			√
Conservation aquaculture programs		*	√	√		√	√					√
Passage studies	*		*	*								

Population characteristics

Validate length-at-age relationships

Ageing methods that provide for higher accuracy and precision need to be developed for WS. Use of fin rays to age WS is neither precise nor accurate for larger individuals, and assigned ages tend to underestimate their true value (Rien and Beamesderfer, 1994; Paragamian and Beamesderfer, 2003). Accurate age assessments are crucial for understanding and managing long-lived species such as sturgeon. When compounded over many years, even small aging errors may have large effects on estimates of growth rate, mortality rate, age of maturation, spawning periodicity, reproductive potential, year-class strength, and population productivity (Archibald et al., 1983; Beamish and McFarlane, 1983; Bradford, 1991; Richards et al., 1992). These population parameters are the basis of management models used to evaluate protection and recovery measures for weak stocks of sturgeon (Kincaid,

1993; Morrow et al., 1999; Secor and Waldman, 1999; Pine et al., 2001) and sustainable fishing rates for strong sturgeon stocks (Rieman and Beamesderfer, 1990; Boreman, 1997; Quist et al., 2002). The recent use of bomb radiocarbon methods for otolith-based age verification of LS (Bruch et al., 2009) suggests that aging inaccuracy might not be as extreme as previously thought. Bomb radiocarbon dating was attempted for upper Columbia WS but was not successful (McAdam, S., BC MOE, Vancouver, BC, pers. comm.). Therefore, similar age verification is still required for WS.

Characterize population dynamics and carrying capacity

The optimal abundance level, size, age, or maturity stage structures for WS populations or population segments are currently unknown. Mark-recapture methods used to estimate abundance may be biased due to non-random distribution of mark or recapture effort, uncertainty regarding fish

movement patterns, and uncertainty regarding vulnerability to capture and emigration among population segments. Post-release mortality of tagged fish has been rigorously evaluated for several population segments (Israel et al., 2009; Justice et al., 2009; Beamesderfer et al., 2014a; Dinsmore et al., 2015; Golder Associates Ltd., 2005a; though see Robichaud et al., 2006). Gear selectivity may have a large effect on uncertainty in the abundance estimates of WS at various life stages with differential catchabilities.

Estimating total mortality and partitioning it among natural and anthropogenic causes is a challenge for long-lived WS. The uncertainties surrounding the accuracy of aging techniques (Rien and Beamesderfer, 1994; Paragamian and Beamesderfer, 2003), tag loss [71% for spaghetti tags after 48 months (DeVore et al., 1995); 3% for PIT tags from 0.5 to 2.5 year post-release (Howell and McLellan, 2007a,b)] and capture efficiency of gears used to assess fish that range in size from a few centimetres to a few metres in length need to be resolved to refine mortality estimates. Confounding the traditional assignments of fishing and non-fishing (i.e. natural) mortality is the component of human influenced non-fishing mortality from such causes as turbine mortality from hydropower system operation and propeller strikes from vessels.

In other fisheries, the adult abundance necessary to sustain populations is typically determined through stock-recruitment relationships and their corresponding functions. Specific stock-recruit (S-R) relationships have not been developed for any WS population and may vary due to differences in spawner abundance and widespread modification of rearing habitats.

Carrying capacity is a critical unresolved issue for listed populations of WS and there is no established method for measuring this in WS (IDFG, 2008). Although estimates of historical population abundance provides some information about carrying capacity (e.g. Walters et al., 2005; Whitlock and McAllister, 2012), habitat alterations through the species' range suggest that such an approach may overestimate current carrying capacity.

Develop a forward forecasting model

The probability of long-term persistence is currently low for many WS populations. Although chances of long-term persistence can be augmented with mitigation and management techniques, it can be difficult for resource managers and regional stakeholders to perceive the benefits of alternate approaches without a modeling tool. Population viability analysis (PVA) is one example of a modeling tool that can be used to examine the likelihood that a population will persist for some arbitrarily chosen time into the future (Boyce, 1992; Jager et al., 2000; Paragamian and Hansen, 2008). Using an iterative process, PVA can evaluate various risks to long-term persistence of WS populations (Jager et al., 2001) and assist in developing population recovery criteria (Paragamian and Hansen, 2008). PVA or similar analyses have been conducted for the middle Snake River (Jager et al., 2000), Kootenai River (Paragamian and Hansen, 2008), and all Canadian populations (Hatfield et al., 2004; Wood et al.,

2007), but have not been developed for WS in the lower Columbia River or Sacramento-San Joaquin Bay-Delta.

Determine stock composition of coastal and marine population components

The spatial and temporal distribution and interchange of WS between saline and freshwater is currently unknown. WS are known to move into marine environments (Bajkov, 1951; Chadwick, 1959; Brennan and Cailliet, 1991; Veinott et al., 1999; Welch et al., 2006). However, the extent of their marine habitat use and the relative proportion of populations actively moving into marine environments are not known. WS harvested in recreational and commercial fisheries in Washington and Oregon coastal waters and tributaries are assumed to be of Columbia River origin. However, movement between the Sacramento-San Joaquin, Columbia, and Fraser rivers does occur (Chadwick, 1959; Galbreath, 1985; DeVore and Grimes, 1993; Welch et al., 2006). Further research should clarify the composition of WS aggregations in marine and non-natal estuarine habitat, which may have implications for interjurisdictional management.

Determine population structure

A variety of indicators can be used to evaluate WS population structure to delineate population units for both resource management and scientific analyses. Current efforts to evaluate spatial population structure (e.g. Clarke et al., 2011; Nelson and McAdam, 2012; McAdam, 2015; Beardsall and McAdam, 2016) suggest further research into methods for mapping spatial habitat use patterns may be useful. Evaluations of large recapture databases, increased availability of acoustic tagging data, fin ray chemistry, and side scan sonar could provide valuable insights in this area. With regard to genetic population structure, the development of more powerful genetic markers will improve our understanding of population level processes such as movement behaviour and adaptive genetic differences. For example, the development of single nucleotide polymorphism (SNP) markers will allow the scoring of gene dosage, which in turn will allow more varied and powerful population genetic analyses. SNP and genome sequence data will also allow geneticists to ask questions about adaptive differences between WS populations to determine if there are differences in allele frequency or gene expression patterns among populations that historically have completed their life cycle in freshwater (e.g. Kootenai River population) versus those that use both freshwater and brackish habitat and the genes involved in facilitating marine movements. Increasing our knowledge about adaptive processes can inform management and recovery of WS populations.

Investigate movement behaviour and habitat use by juvenile and adult life stages

Habitat use and movement varies across the WS range [see Movement and Distribution] and the environmental and physiological cues that cause WS to move are poorly

understood. Most telemetry studies have been of relatively short duration, in terms of the WS life span, and whether the selection of a discrete area over several years represents life-long site fidelity or a more transitory use pattern is unknown. Long-term movement studies, such as those initiated in the Kootenai, upper Columbia, and Fraser rivers, are needed to provide additional insight into this aspect of WS movement and habitat use.

Ecological interactions

Assess pinniped predation mortality

The magnitude and effect of pinniped predation WS population productivity in the lower Columbia and Sacramento-San Joaquin needs to be quantified. Increased predation by sea lions below Bonneville Dam has been identified as a possible contributing factor to the recent trend in declining abundance of WS in the lower Columbia River.

Investigate climate change effects on WS productivity. Although certain impacts to the physical habitat from global climate change can and have been modeled, their exact effect on WS populations remains unknown. As well, the effect of climate change on already altered post-development river thermal regimes is poorly understood. Bioenergetics modeling is required to describe potential changes in growth resulting from altered thermal regimes (Van Poorten and McAdam, 2010).

Determine the influence of invasive species

The introduction of exotic species into North American waterways may have direct and indirect effects on the native communities in which WS are a part. In heavily invaded systems such as the Sacramento-San Joaquin and lower Columbia, studies examining WS diets are necessary to evaluate how changes in the biotic composition of these ecosystems may affect survival or condition of different WS life stages. Studies identifying invasive predators and quantifying rates of predation, particularly for early life stage WS are required in all systems.

Assess the nutritional value of the WS prey base

Historically, WS fed on abundant and energy-rich Pacific Lamprey (*Lampetra tridentate*), Eulachon (*Spirinchus thaleichthys*), and juvenile and adult salmonids. While declines in the abundance of these important food resources may affect WS growth and reproductive potential (Nelson et al., 2013a), the population scale effects are unknown. The types of suitable prey necessary for wild early feeding larvae is also poorly understood and requires additional research to determine the importance of early prey availability on recruitment success.

Management

Quantify sources of anthropogenic mortality

Indirect mortality associated with catch and release of WS in recreational and commercial fisheries has not been

sufficiently assessed, although carcass surveys in the lower Columbia River routinely find deceased WS with fishing gear embedded internally or with hook scars in the tongue, mouth, or gills (WDFW, Vancouver, WA, unpubl. data). WS exhibit a hormonal stress response when handled during commercial or recreational fishing activities but latent mortality or physiological disturbances associated with handling stress has received limited investigation (Robichaud et al., 2006; Webb and Doroshov, 2011). Exhaustive exercise also can result in a variety of physiological disturbances that alter reproductive performance and cause delayed mortality (Nelson, 1998; Lambert and Dutil, 2000; Schreer et al., 2001). Research is needed to quantify the indirect mortality of WS from recreational and commercial fisheries as well as the biological and population level effects of repeated handling stress on WS productivity. Also, additional research is needed to determine the extent of WS mortality associated with dam operations and boat traffic and develop measures to prevent or minimize these occurrences.

Because of the monetary value of WS, particularly caviar, illegal harvest (poaching) is a serious and ongoing threat to many WS populations. Methods to assess the magnitude of poaching losses and to identify of the source of poached WS materials need to be developed so estimates can be incorporated into management and assist enforcement programs that target poaching activity.

Develop long-term, standardized monitoring programs

Long-term trend data on population size or density are generally lacking for all populations, although both historical reconstruction and repeated population estimates are now available for the lower Fraser River (Walters et al., 2005; Whitlock and McAllister, 2012; Nelson et al., 2013a). Standard methods and sampling protocols should be employed so long-term trend data can be developed to monitor temporal changes within and among WS populations. New methods such as side scan sonar, which has been used successfully to identify and enumerate other sturgeon species (Flowers and Hightower, 2013, 2015; Nelson et al., 2013a,b), should also be used where feasible.

Maintain conservation aquaculture programs

Data from several ongoing supplementation programs indicates that hatchery-produced WS will survive to adulthood, based on the survival and growth of released progeny. For instance, the largest hatchery WS sampled in the middle Snake River have achieved lengths up to 200–244 cm TL (18–25 year of age) with cohorts from multiple years classes (1988, 1990, 1993) in reproductive condition (Bentz, 2014). As such, hatchery-produced WS are expected to eventually contribute to fisheries and to spawning populations (Clements, M, Grant County PUD, Moses Lake, WA, pers. comm.; Bentz, 2014). Beamesderfer et al. (2014b) and Dinsmore et al. (2015) both found that WS reared to a larger size on an un-naturally accelerated temperature regime have significantly higher post-release survival in the degraded Kootenai River, particularly compared to wild spawned fish that

have a survival rate approaching zero. Similar results of increased survival with increased size at release have been reported for the upper Columbia program (Golder Associates Ltd., 2005a). These results have guided both programs to employ accelerated growth to avoid the bottlenecks faced by earlier life stages, i.e., smaller fish that have severely limited recruitment. Therefore, continued research, monitoring, and evaluation is needed to adaptively manage conservation aquaculture programs in order to (i) maximize post-release survival, (ii) balance post-release density dependent effects with continued year-class formation, and (iii) promote adequate levels of genetic diversity in restored populations.

Conduct passage studies

Dam construction has largely blocked upstream movement of WS throughout the upper Sacramento-San Joaquin and Columbia basins (Warren and Beckman, 1993; Parsley et al., 2007) and may impose unidirectional (downstream) gene flow (Jager, 2006). The benefits of fish passage for WS could include restoring historical migratory routes, providing access to more suitable rearing/feeding and spawning habitats, improving genetic diversity, increasing fishing opportunities, and increasing production in isolated river segments where populations are sparse. However, unintended consequences must be given consideration as they can reduce benefits or prove detrimental to individuals and the metapopulation (Jager, 2006). For instance, passage could be detrimental to net productivity if adults moved from favorable into unfavorable habitat or migrants become injured upon returning downstream. A better understanding of WS migratory behaviors is needed in order to evaluate the benefits and potential tradeoffs associated with increased passage opportunities (Beamesderfer et al., 2012).

In addition, many existing fish passage structures, such as fish ladders, are largely ineffective for sturgeon passage because of sturgeon physiology, large size, and uncertainty regarding movement behavior. Most fish passage facilities have been designed primarily for smaller migrating species such as salmonids (Lauder and Liao, 2000; Cech and Doroshov, 2004). More recent research has identified more specific information on WS swimming performance that will assist in designing passage facilities that will adequately accommodate this species (Anderson et al., 2007).

Prognosis for the future

Sacramento-San Joaquin Bay-Delta

Uncertainty around previous abundance estimates and fairly low current population size projections (Gingras and DuBois, 2013) suggest that WS in the Sacramento-San Joaquin system may be vulnerable to present and future threats. As adult WS in California experience harvest pressure due to an intensive recreational fishery and unknown levels of illegal poaching, continued monitoring of harvest rates and total population abundance is essential to avoid overexploitation. Recruitment dynamics and reproductive success also should be further examined, as the detection of little or no

recruitment in most years raises concern about long-term population viability (Schaffter and Kohlhorst, 1999). Recent dry years in the Central Valley (2007–2010; 2012–2015) likely will be characterized by low recruitment, as larval survival appears to be positively correlated to river outflows in this system (Kohlhorst et al., 1980, 1991; Fish, 2010). Other anthropogenic changes to the Bay-Delta system, such as reduced water quality and heavy invasion of non-native species provide additional threats to this WS population over time. Therefore, continued monitoring across several WS generations, robust abundance and harvest estimates, and a more thorough understanding of variables affecting recruitment will be essential to refine our prognosis for the population.

Columbia River

Impounded populations that remain at low or very low levels and areas upstream from McNary Dam are at risk of extirpation (DeVore et al., 1999b, 2000; Mallette, 2008; Chelan PUD, 2009; Grant PUD, 2009; Douglas PUD, 2011). Fishing opportunities on impounded populations remain very limited and continue to decline (Fig. 3). Over 20 years of dedicated WS research and management has failed to restore adequate levels of natural WS recruitment (Mallette, 2008). The viability of the population segment in the Transboundary Reach of the upper Columbia River is uncertain, due to the continued lack of natural recruitment (Irvine et al., 2007). However, the relatively abundant adult population, high survival, long life span, and excellent success of conservation aquaculture programs provide hope that natural recruitment can be restored, ensuring long-term persistence. The development of either a failsafe or a self-sustaining population of WS in Arrow Lakes Reservoir, however, is rated as having a low to moderate level of feasibility due to several key uncertainties related to availability and suitability of spawning and early life-stage rearing habitats (Gregory and Long, 2008).

Snake River

The extent of habitat alteration to the Snake River ecosystem from dams, river regulation, degraded water quality, flood control and irrigation diversions are substantial and complex, and present substantial challenges to achieving natural populations in several reaches of the Snake River. A population viability analysis for Snake River WS (Jager et al., 2001) between Lower Granite Dam and Shoshone Falls predicted long-term persistence (beyond the next 200 years) of natural population segments upstream of Lower Granite and C. J. Strike dams. Factors predicted by the model to influence WS recruitment clearly showed a distinction between river segments limited by episodic poor water quality (e.g. Brownlee segment) and those with adequate water quality. WS population segments in shorter river reaches (e.g. Bliss to Upper Salmon Falls and Hells Canyon to Brownlee dams) were also less likely to persist due to fragmented habitat and downstream export of sturgeon, which gradually erodes population abundance. In addition, flood control and water management practices in the upper Snake

River basin can alter the timing and volume of spring freshets which, at times, can reduce river flow during WS spawning in the middle Snake River. Consequently, conservation aquaculture is now employed in recruitment-limited population segments upstream from Brownlee Dam to increase WS abundance and preserve natural patterns of population structure and genetic diversity unique to the middle Snake River. The ability to restore recruitment-limited population segments will depend on the degree to which limiting factors can be effectively addressed and an adaptive approach will be necessary to guide future research and restoration efforts.

Kootenai River

Paragamian and Hansen (2008) simulated future abundance of WS in the Kootenai River and found that the wild population would decline to only 57 individuals after 25 years and six individuals after 50 years if recruitment collapse continued. The population would reach the target carrying capacity of 7000 adults within 25 years only when each adult produced an average of 0.4 age-1 recruits annually, a recruitment rate equivalent to reaching the target level of recruitment in the Recovery Plan every year. In contrast, the population would grow to only 1200 individuals if the target level of recruitment was reached in only three of every ten years. Although a revised abundance estimate by Beamesderfer et al. (2009, 2014b) suggests the wild Kootenai River WS population may be larger than previously thought, the prognosis for the wild population remains unchanged. A host of actions will be needed to restore natural recruitment and these actions will need to act in synergy. At present, these include: (i) alternative operation of Libby Dam towards a hydrograph and thermograph to support fish populations, (ii) restoration of nutrients to promote ecosystem productivity, and (iii) strategic placement of coarse substrate in combination with physical habitat improvements are the main courses of action to restore nature recruitment by means of promoting early life history survival.

Fraser River

Future scenarios for Fraser basin WS vary depending on the current status of the population. In the worst case, the Nechako population faces extirpation as it is expected to decline to <200 fish within 25 years without human intervention (Wood et al., 2007). Hatchery releases are an essential interim measure due to the long history of recruitment collapse (since 1967) and completion of a full scale hatchery in 2014 will begin to address the current absence of juveniles. The long-term restoration of natural spawning and recruitment for this population is focussed on in-stream habitat restoration approaches. This includes ongoing physical and biological monitoring associated with experimental spawning habitat restoration that began in 2011. The long-term prognosis for natural recruitment for this population will depend on the successful implementation of habitat restoration works.

The prognosis for WS in the Fraser River is distinct from other rivers since all three mainstem populations currently

show sustained recruitment. In both the middle and upper Fraser River, populations are expected to be similar to historical levels; barring any unforeseen impacts these populations are expected to remain healthy. For the upper Fraser population the biggest threat is its small size, but is none the less, expected to persist (Wood et al., 2007). WS in the lower Fraser River currently show persistent but variable recruitment (e.g. a pulse in 1996–1997; Whitlock and McAllister, 2012) and hence do not face imminent extirpation like many other populations. There are concerns that recruitment may decline from 2005 onward (Nelson et al., 2013a). While this population is the most abundant in Canada, it is below historical levels. Decreased juvenile growth suggest that food supply may be limiting (Nelson et al., 2013a) although more recent data suggest this effect may be transitory (Nelson et al., 2016). Habitat loss and alteration in the past 60–80 year has restricted potential productivity for juvenile WS rearing (Nelson et al., 2007) as well as the productivity and abundance of key prey species for juveniles and adults. In particular, decreased abundance of Eulachon and many Fraser River salmon stocks may limit the long-term carrying capacity in the lower Fraser River.

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