

Coldwater Lake and Reservoir Research Projects

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Annual Report

Colorado Parks & Wildlife

Aquatic Research Section

317 West Prospect Road

Fort Collins, Colorado

May 2018

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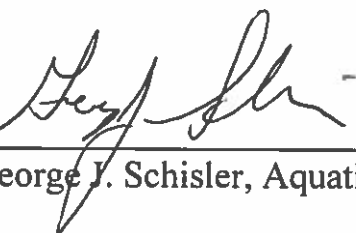
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The results of the research investigations contained in this report represent work of the authors and may or may not have been implemented as Parks and Wildlife policy by the Director or the Wildlife Commission.

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Acknowledgments: Work described in this report was completed with assistance in the field and laboratory from the following: CPW Aquatic Research Technicians—Lauren Hargis, Kyle LaCombe, Sirena Mares, Michael Miller, Jedidiah Thompson, and Ben Wasserstein; CPW Area Aquatic Biologists—Kyle Battige, Dan Brauch, Jon Ewert, Tory Eyre, Ben Felt, Eric Gardunio, and Estevan Vigil; CPW Aquatic Research Scientists—Andrew Treble; Colorado State University collaborators—Dr. Brett Johnson and Bill Pate.

I. Limnology, Zooplankton and *Mysis*

Project A. Physical limnology, zooplankton and *Mysis* collections from Blue Mesa Reservoir, Lake Granby, and Taylor Park Reservoir (2016-2017)

Status: Ongoing

Purpose and Objectives: Zooplankton density, size-structure, and community-composition are timely indicators of fish community-structure and ecosystem health. The primary objective of this ongoing research is to measure zooplankton and *Mysis diluviana* density and distribution in relation to physical habitat conditions (i.e., vertical gradients of temperature and dissolved oxygen) in key reservoirs supporting kokanee salmon to (1) improve our understanding of *Mysis*-zooplankton-kokanee interactions, and (2) monitor for potential changes in reservoir health related to increasing anthropogenic nutrient inputs and water use, shifts in climate, new invasive or illegally introduced species, or other factors.

Methods

Vertical gradients in food supply (e.g., density of *Daphnia*), temperature, dissolved oxygen (DO), light, and turbidity influence the distribution, growth, and survival of key predators like lake trout and prey like kokanee in Colorado's coldwater reservoirs. Diel-seasonal changes in these factors can aggregate or segregate predators and prey depending on how each variable affects the growth efficiency and foraging capability of different species, and the profitability and predation risk associated with feeding in different habitats (Martinez and Wiltzius 1995; Stockwell and Johnson 1999; Hardiman et al. 2004; Hansen et al. 2013).

Because of these complexities, periodically evaluating the seasonal dynamics of zooplankton in a reservoir can strengthen the value of a long-term monitoring program. Therefore, in 2016, we collected depth-stratified zooplankton and temperature and dissolved oxygen profiles twice each month April through November from a standard offshore station in Iola, Cebolla, and Sapinero basins in Blue Mesa Reservoir. We only sampled Blue Mesa once during August 2017, and those samples were archived. *Mysis* tows were not conducted in either year, but are planned for 2018. Standard zooplankton and *Mysis* stations on Lake Granby were sampled on 9/7/2016 and 9/18/2017. Standard stations for Taylor Park Reservoir were only sampled on 8/22/2017. Sampling stations followed (Martinez et al. 2010).

At each station, 1-2 vertical zooplankton tows with a 153- μm Wisconsin style net were conducted during daylight hours through 0-10 m (epilimnion during peak thermal stratification) and 0-20 m depths (incorporated the thermocline) on Blue Mesa, but only through 0-10 m depths on Lake Granby and Taylor Park. Zooplankton samples were preserved in 4% sugared formalin (buffered) and processed in the laboratory to estimate species-specific densities (# individuals/L) and size-structures following the protocol of Martinez et al. (2010). *Mysis* stations were sampled by towing a 1-m diameter 500- μm mesh net vertically from the bottom to the surface at night near the new moon. *Mysis* were preserved in 70% ethanol, counted to estimate density (# individuals/m²), and measured for total length (tip of rostrum to end of telson excluding setae) to the nearest mm in the laboratory.

Results and Discussion

Blue Mesa Reservoir

The average density of dominant zooplankton in Blue Mesa varied by depth (0-10 m versus 10-20 m), basin (Iola, Cebolla, and Sapinero), and month (**Figure 1**).

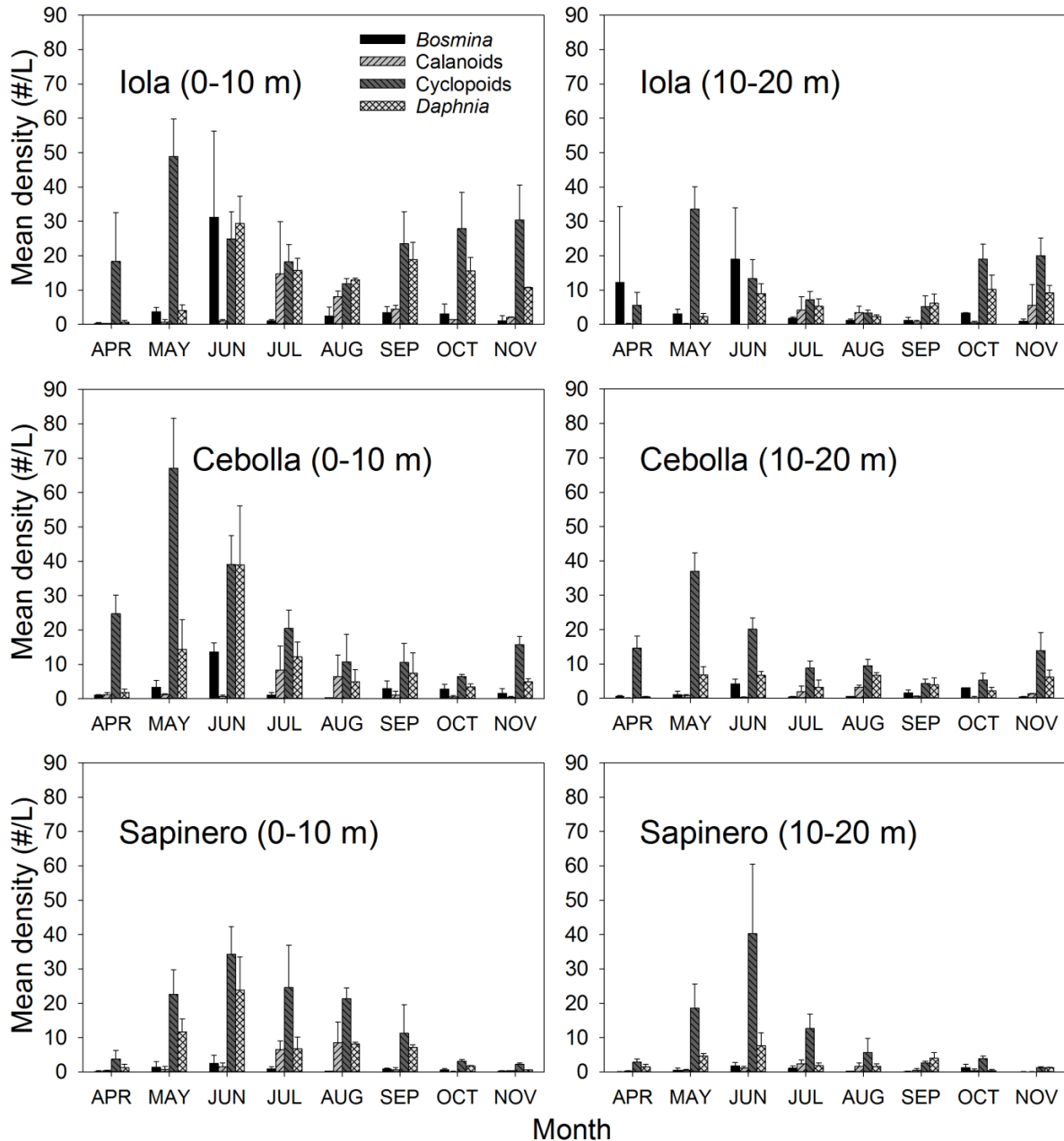


Figure 1. Estimated mean monthly, depth-specific densities of dominant crustacean zooplankton sampled in Blue Mesa Reservoir during 2016. Error bars represent two SEs. Average densities estimated for each depth-stratum were computed from two replicate vertical tows conducted twice each month at the standard station within each basin.

In general, zooplankton densities were highest in Iola and Cebolla and lowest in Sapinero across months. Additionally, zooplankton densities were highest in the 0-10 m depth interval across months, but predominately so for *Daphnia* (**Figure 2**), preferred prey for kokanee at densities as low as 0.4 individuals/L (Beauchamp et al. 1995; Stockwell and Johnson 1997; Scheuerell et al. 2005).

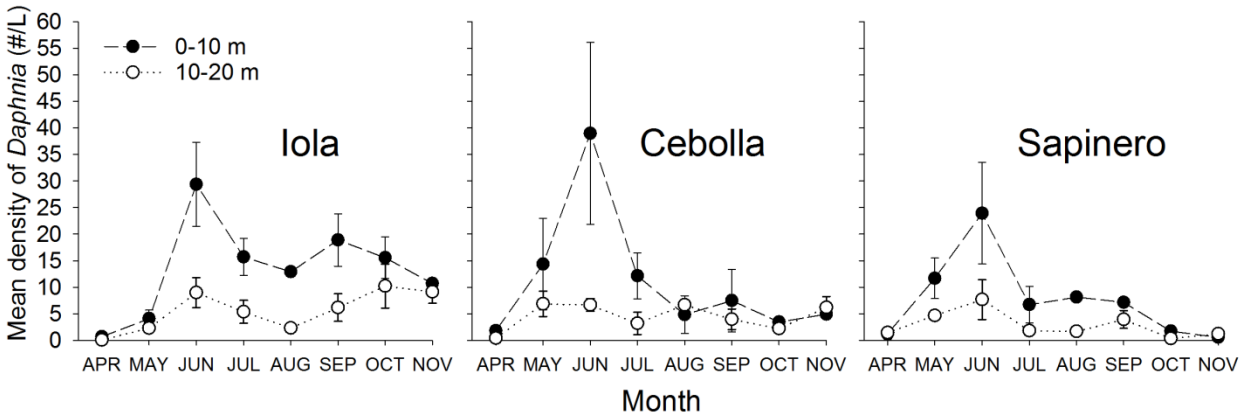


Figure 2. Estimated mean monthly and depth-specific density of *Daphnia* in each basin of Blue Mesa Reservoir during 2016. Error bars represent two SEs.

During April and May (the period when kokanee fry are released from Roaring Judy Hatchery, enter, and disperse throughout the reservoir; Hardiman et al. 2004), the zooplankton community was dominated by Cyclopoid copepods (**Figure 1**). The density of copepods during these months were high, indicating that there was ample food available for stocked kokanee fry prior to the peak bloom of *Daphnia*. Relatively high densities of *Daphnia* appeared in May, but peaked in June, and then dropped below 10 individuals/L July through November in both 0-10 m and 10-20 m depths in Cebolla and Sapinero. *Daphnia* densities remained above 10 individuals/L in 0-10 m depths in Iola from June through November (**Figure 2**).

At densities of 10 *Daphnia*/L, juvenile kokanee can typically fill their stomachs within ≤ 3 hours of feeding under light conditions reminiscent of twilight. Thus, this density represents a reasonable benchmark for gauging the quality of feeding conditions for kokanee (Koski and Johnson 2002). See Koski and Johnson (2002) for more detailed discussion regarding how the observed densities of *Daphnia* translate into juvenile kokanee feeding rates and the corresponding profitability of foraging at different depths during different months based on experimentally derived functional response curves developed under different light levels.

Kokanee selectively eat large *Daphnia* (i.e., body lengths ≥ 1.0 mm; BL) when available, but they can eat *Daphnia* with BLs of 0.6-0.8 mm (Schneidervin and Hubert 1987). Therefore, it is important to not only measure the density of *Daphnia*, but also their size-structure. Large-bodied *Daphnia* were available to kokanee during each month in 2016, but the relative frequency of these individuals varied across months (**Figure 3**).

During 2016, the depth-interval containing the highest densities of *Daphnia* (0-10 m) corresponded with the warm epilimnion during peak thermal stratification in July and August when surface temperatures reached 20-21°C in Iola and Cebolla and 19-20°C in Sapinero

(Figure 4). Temperatures within intermediate depths containing lower densities of *Daphnia* (10-20 m) ranged from approximately 13-18°C. Dissolved oxygen concentrations remained favorable across most depths and months in Iola and Sapinero, but started to dip below 3 mg/L in September at deeper depths in Cebolla (Figure 4). Collectively, environmental and feeding and growth conditions were favorable for kokanee in 2016.

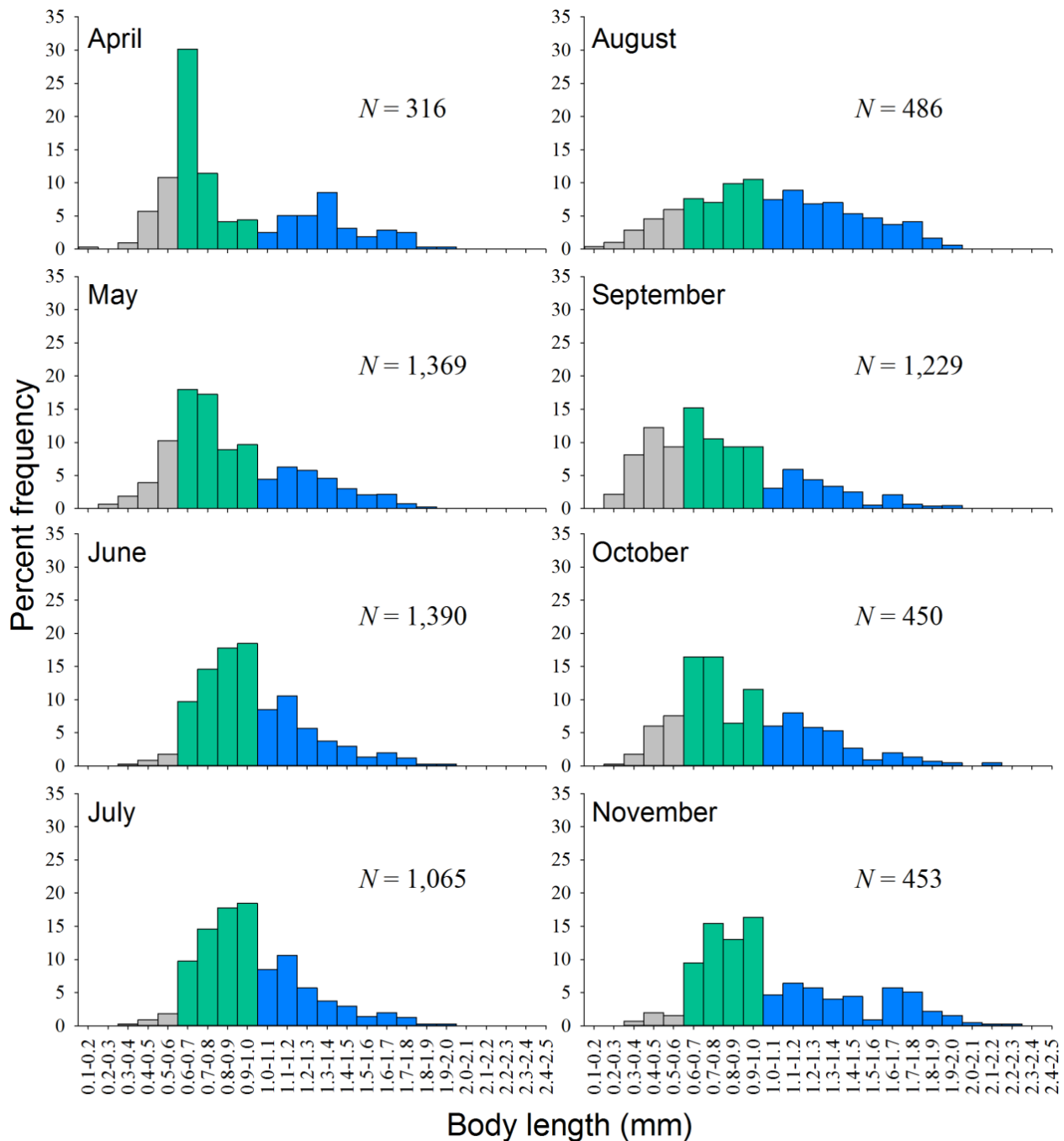


Figure 3. Monthly length-frequency distributions of *Daphnia* sampled from all basins in Blue Mesa Reservoir in 2016. The bars and corresponding size groups of *Daphnia* highlighted in blue are typically preferred by kokanee, but size groups highlighted in green are also edible.

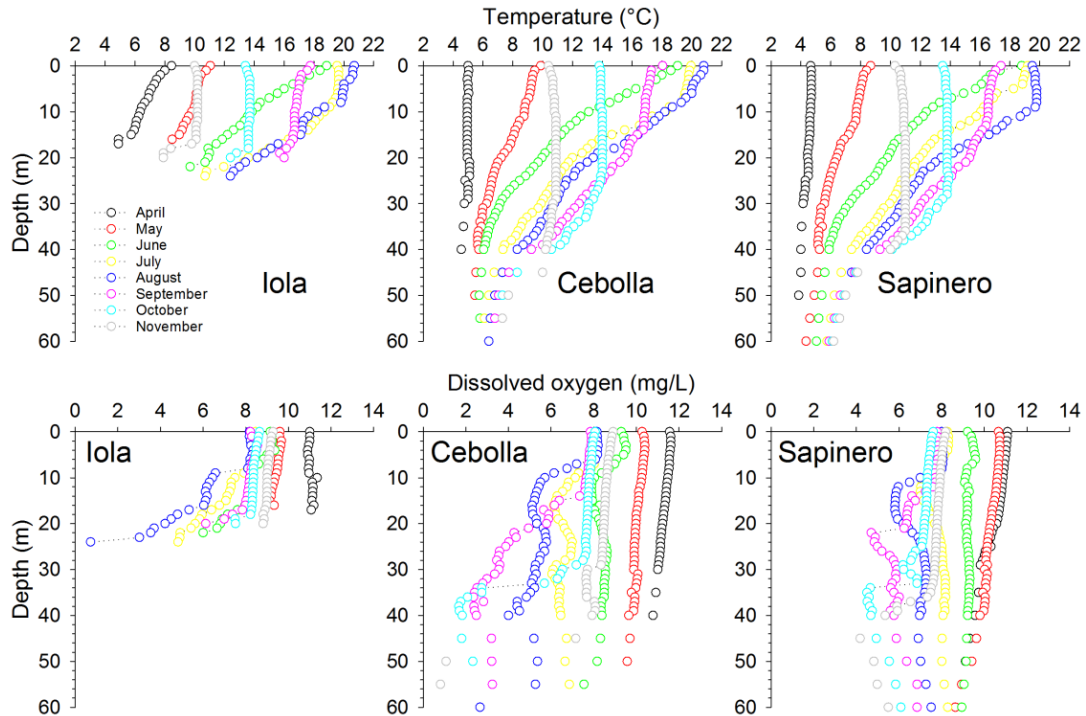


Figure 4. Mean monthly temperature and dissolved oxygen profiles collected in each basin of Blue Mesa Reservoir during 2016.

Lake Granby and Taylor Park Reservoir

Zooplankton and *Mysis* collections from Lake Granby and Taylor Park during 2016-2017 were less intensive and followed standard long-term monitoring protocols outlined by previous investigators (Martinez et al. 2010; Lepak 2014). Dr. Brett Johnson in the Department of Fish, Wildlife, and Conservation Biology at Colorado State University is conducting comprehensive analyses on *Mysis*-zooplankton dynamics in these reservoirs using the full time series of data collected by CPW. The following tables (1-16) contain the raw data I provided to Dr. Johnson:

Table 1. *Mysis* density estimated for each standard station sampled ($N = 10$; one vertical tow at each station) on Lake Granby on 9/7/2016. Mean density was $677.83/m^2$ (SE = 223.93).

Station	Time collected (h)	Tow depth (m)	Tow type	Bottom depth (m)	Preservative	Total <i>Mysis</i> count	Density (#/m ²)
M1	2143	55.0	VERTICAL	56.0	70% ETOH	1,854	2,361.78
M2	2114	38.0	VERTICAL	38.9	70% ETOH	221	281.53
M3	2220	30.0	VERTICAL	30.5	70% ETOH	993	1,264.97
M4	2130	36.0	VERTICAL	36.2	70% ETOH	102	129.94
M5	2104	34.0	VERTICAL	34.7	70% ETOH	505	643.31
M6	2050	25.0	VERTICAL	25.6	70% ETOH	148	188.54
M7	2228	24.5	VERTICAL	24.9	70% ETOH	811	1,033.12
M8	2212	11.5	VERTICAL	12.0	70% ETOH	86	109.55
M9	2155	20.0	VERTICAL	20.5	70% ETOH	241	307.01
M10	2040	17.1	VERTICAL	18.1	70% ETOH	360	458.60

Table 2. *Mysis* density estimated for each standard station sampled ($N = 10$; one vertical tow at each station) on Lake Granby on 9/18/2017. Mean density was $422.42/m^2$ ($SE = 116.14$).

Station	Time collected (h)	Tow depth (m)	Tow type	Bottom depth (m)	Preservative	Total <i>Mysis</i> count	Density ($\#/m^2$)
M1	2125	49.5	VERTICAL	49.5	70% ETOH	1,068	1,360.51
M2	2058	53.7	VERTICAL	53.7	70% ETOH	240	305.73
M3	2156	32.0	VERTICAL	32.0	70% ETOH	454	578.34
M4	2111	27.9	VERTICAL	27.9	70% ETOH	109	138.85
M5	2045	34.7	VERTICAL	34.7	70% ETOH	291	370.70
M6	2033	26.3	VERTICAL	26.3	70% ETOH	356	453.50
M7	2206	19.9	VERTICAL	19.9	70% ETOH	302	384.71
M8	2147	15.1	VERTICAL	15.1	70% ETOH	43	54.78
M9	2137	19.1	VERTICAL	19.1	70% ETOH	116	147.77
M10	2023	21.5	VERTICAL	21.5	70% ETOH	337	429.30

Table 3. *Mysis* density estimated for each standard station sampled ($N = 10$; one vertical tow at each station) on Taylor Park Reservoir on 8/22/2017. Mean density was $282.29/m^2$ ($SE = 69.93$).

Station	Time collected (h)	Tow depth (m)	Tow type	Bottom depth (m)	Preservative	Total <i>Mysis</i> count	Density ($\#/m^2$)
M1	2135	37.5	VERTICAL	37.5	70% ETOH	550	700.64
M2	2200	39.1	VERTICAL	39.1	70% ETOH	452	575.80
M3	2148	25.0	VERTICAL	25.0	70% ETOH	200	254.78
M4	2213	28.5	VERTICAL	28.7	70% ETOH	297	378.34
M5	2250	18.0	VERTICAL	18.4	70% ETOH	204	259.87
M6	2223	22.5	VERTICAL	23.0	70% ETOH	233	296.82
M7	2302	8.2	VERTICAL	8.5	70% ETOH	7	8.92
M8	2314	7.8	VERTICAL	8.0	70% ETOH	29	36.94
M9	2243	12.5	VERTICAL	12.7	70% ETOH	103	131.21
M10	2232	11.5	VERTICAL	12.0	70% ETOH	141	179.62

Table 4. Station-specific length-frequency distributions of *Mysis* collected from Lake Granby on 9/7/2016. All intact *Mysids* from each sample were measured.

STATION	TOTAL LENGTH BIN (mm)																		Totals	
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		23
M1		3	12	19	44	60	55	40	15	19	44	240	527	389	138	36	7	1		1,649
M2			2	6	6	13	9	6	4	1	4	21	57	35	15	11	2	0	1	193
M3		15	21	41	73	65	51	24	9	6	34	126	288	175	44	15	1			988
M4			2	1	5	2	1	2	2	1	5	10	25	20	12	7	1	1		97
M5	2	4	9	17	30	42	26	21	10	5	28	75	119	62	20	10	4			484
M6		1	3	1	3	13	9	2	1	1	4	10	34	22	8	7				119
M7	1	28	52	68	83	88	68	21	7	11	31	85	159	72	26	10				810
M8		1	0	3	6	6	5	3	4	7	11	15	20	5						86
M9			2	10	13	8	14	8	6	8	16	42	66	33	11	3				240
M10			4	3	12	25	14	20	11	10	18	16	62	93	50	20	2			360
Totals	3	52	107	169	275	322	252	147	69	69	195	640	1,357	906	324	119	17	2	1	5,026
Percent	0.06%	1.03%	2.13%	3.36%	5.47%	6.41%	5.01%	2.92%	1.37%	1.37%	3.88%	12.73%	27.00%	18.03%	6.45%	2.37%	0.34%	0.04%	0.02%	100.0%

Table 5. Station-specific length-frequency distributions of *Mysis* collected from Lake Granby on 9/18/2017. All intact Mysids from each sample were measured.

STATION	TOTAL LENGTH BIN (mm)																		Totals	
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		23
M1	1	17	61	134	201	107	48	45	69	88	139	93	52	9	1					1,065
M2	4	7	24	34	29	13	9	13	23	31	25	20	8							240
M3		16	53	70	57	26	29	32	42	26	52	30	11	6						450
M4		5	2	9	12	4	12	16	12	11	11	11	4							109
M5		14	16	29	41	20	17	18	22	33	44	23	7	4						288
M6	1	27	27	28	18	14	6	17	23	56	73	43	20	3						356
M7		10	36	54	29	17	33	48	43	14	10	4	1	1						300
M8		1	2	2	2	8	6	9	10	3								3		43
M9			3	6	7	10	8	9	14	23	18	7	2	1	1					109
M10		24	37	32	16	12	11	16	21	38	70	39	12	4	1					333
Totals	6	121	261	398	412	231	179	223	279	323	442	270	117	28	3	-	-	-	-	3,293
Percent	0.18%	3.67%	7.93%	12.09%	12.51%	7.01%	5.44%	6.77%	8.47%	9.81%	13.42%	8.20%	3.55%	0.85%	0.09%	0.00%	0.00%	0.00%	0.00%	100.0%

Table 6. Station-specific length-frequency distributions of *Mysis* collected from Taylor Park Reservoir on 8/22/2017. All intact Mysids from each sample were measured.

STATION	TOTAL LENGTH BIN (mm)																		Totals	
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		22
M1			24	60	72	79	58	20	18	96	76	38	6	2						549
M2		1	23	44	44	36	36	33	21	84	82	37	9	1	1					452
M3			7	26	26	42	30	8	10	26	16	8	1							200
M4		3	14	17	28	36	49	27	16	45	43	16	3							297
M5		2	13	12	17	34	46	34	9	15	14	6								202
M6		5	21	23	14	18	17	21	12	36	46	16	3							232
M7					3	1	1	2												7
M8					4	12	10	3												29
M9	1	5	4	12	11	27	26	10	0	1	1									98
M10		13	14	13	19	25	36	18	2											140
Totals	1	29	120	207	238	310	309	176	88	303	278	121	22	3	1	-	-	-	-	2,206
Percent	0.05%	1.31%	5.44%	9.38%	10.79%	14.05%	14.01%	7.98%	3.99%	13.74%	12.60%	5.49%	1.00%	0.14%	0.05%	0.00%	0.00%	0.00%	0.00%	100.0%

Table 7. Estimated density (individuals/L) of different zooplankton taxa collected from a single vertical tow through 0-10 m depths at five standard stations on Lake Granby on 9/7/2016.

Zooplankton taxon	Station P1	Station P2	Station P3	Station P4	Station P5	Lakewide mean	Standard deviation
<i>Daphnia pulicaria / pulex</i>	0.00	0.07	0.10	0.00	0.11	0.05	0.05
<i>Daphnia rosea</i>	0.00	0.20	0.00	0.00	0.00	0.04	0.09
Unknown <i>Daphnia</i>	0.24	0.27	0.39	0.53	0.63	0.41	0.17
<i>Bosmina longirostris</i>	0.08	0.13	0.00	0.00	0.11	0.06	0.06
<i>Diacyclops thomasi</i>	10.34	9.85	13.81	15.37	14.00	12.67	2.44
<i>Leptodiptomus nudus</i>	2.21	2.39	3.45	1.79	1.79	2.33	0.68
<i>Leptodiptomus</i> spp.	0.47	0.07	0.00	0.63	0.00	0.23	0.30
Copepod nauplius	0.24	0.00	0.20	0.00	0.53	0.19	0.22

Table 8. Estimated density (individuals/L) of different zooplankton taxa collected from a single vertical tow through 0-10 m depths at five standard stations on Lake Granby on 9/18/2017.

Zooplankton taxon	Station P1	Station P2	Station P3	Station P4	Station P5	Lakewide mean	Standard deviation
<i>Daphnia pulicaria / pulex</i>	0.47	0.79	0.55	0.00	0.16	0.39	0.32
<i>Bosmina longirostris</i>	0.00	0.08	0.08	0.08	0.08	0.06	0.04
<i>Diacyclops thomasi</i>	8.53	9.63	10.66	11.13	12.47	10.48	1.50
<i>Diaphanosoma brachyurum</i>	0.00	0.16	0.08	0.08	0.08	0.08	0.06
<i>Leptodiptomus nudus</i>	0.95	1.34	4.42	1.50	4.10	2.46	1.66
<i>Leptodora kindtii</i>	0.00	0.00	0.00	0.00	0.24	0.05	0.11
Copepod nauplius	0.63	0.71	0.87	0.55	1.50	0.85	0.38

Table 9. Estimated density (individuals/L) of different zooplankton taxa collected from a single vertical tow through 0-10 m depths at five standard stations on Taylor Park Reservoir on 8/22/2017.

Zooplankton taxon	Station P1	Station P2	Station P3	Station P4	Station P5	Lakewide mean	Standard deviation
<i>Daphnia pulicaria / pulex</i>	3.82	1.18	1.18	4.21	2.05	2.49	1.44
<i>Diacyclops thomasi</i>	8.53	9.63	10.66	11.13	12.47	10.48	1.50
<i>Leptodiptomus nudus</i>	0.95	1.34	4.42	1.50	4.10	2.46	1.66

Table 10. Average body length of different zooplankton taxa collected from a single vertical tow through 0-10 m depths at five standard stations on Lake Granby on 9/7/2016.

Zooplankton taxon	Station P1	Station P2	Station P3	Station P4	Station P5	Lakewide mean	Standard deviation
<i>Daphnia pulicaria / pulex</i>	--	2.08	2.03	--	0.75	1.62	0.75
<i>Daphnia rosea</i>	--	0.75	--	--	--	0.75	--
Unknown <i>Daphnia</i>	1.23	1.08	1.06	1.24	1.38	1.20	0.13
<i>Bosmina longirostris</i>	0.25	0.30	--	--	0.28	0.28	0.02
<i>Diacyclops thomasi</i>	0.74	0.76	0.73	0.74	0.71	0.74	0.02
<i>Leptodiptomus nudus</i>	0.79	0.64	0.73	0.79	0.62	0.72	0.08
<i>Leptodiptomus</i> spp.	0.51	0.68	--	0.46	--	0.55	0.11
Copepod nauplius	0.33	--	0.31	--	0.34	0.32	0.01

Table 11. Average body length of different zooplankton taxa collected from a single vertical tow through 0-10 m depths at five standard stations on Lake Granby on 9/18/2017.

Zooplankton taxon	Station P1	Station P2	Station P3	Station P4	Station P5	Lakewide mean	Standard deviation
<i>Daphnia pulicaria / pulex</i>	1.35	1.12	0.93	--	1.3625	1.19	0.21
<i>Bosmina longirostris</i>	--	0.30	0.225	0.25	0.33	0.28	0.05
<i>Diacyclops thomasi</i>	0.64	0.65	0.64	0.70	0.64	0.66	0.03
<i>Diaphanosoma brachyurum</i>	--	0.79	0.68	0.70	6.00	2.04	2.64
<i>Leptodiptomus nudus</i>	0.63	0.68	0.75	0.73	0.72	0.70	0.05
<i>Leptodora kindtii</i>	--	--	--	--	0.99	0.99	--
Copepod nauplius	--	--	--	--	--	--	--

Table 12. Average body length of different zooplankton taxa collected from a single vertical tow through 0-10 m depths at five standard stations on Taylor Park Reservoir on 8/22/2017.

Zooplankton taxon	Station P1	Station P2	Station P3	Station P4	Station P5	Lakewide mean	Standard deviation
<i>Daphnia pulicaria / pulex</i>	1.79	1.96	1.83	1.94	1.56	1.81	0.16
<i>Diacyclops thomasi</i>	0.65	0.64	0.62	0.65	0.64	0.64	0.01
<i>Leptodiatomus nudus</i>	0.97	0.94	1.04	0.94	1.00	0.98	0.04

Table 13. Additional information associated with zooplankton samples taken from five standard stations on Lake Granby on 9/7/2016.

Station	Lake depth (m)	Tow depth (m)	Tow type	Time (h)	Secchi depth (m)	Cond. (uS/cm)	pH
P1	23.4	10.0	Vertical	1658	3.0, 2.9	61.2	8.74
P2	8.9	8.9	Vertical	1715	2.9, 2.5	60.8	8.41
P3	15.3	10.0	Vertical	1727	2.5, 2.3	59.8	8.58
P4	26.3	10.0	Vertical	1742	2.9, 3.0	59.8	8.38
P5	34.0	10.0	Vertical	1802	-	59.0	8.48

Table 14. Additional information associated with zooplankton samples taken from five standard stations on Lake Granby on 9/18/2017.

Station	Lake depth (m)	Tow depth (m)	Tow type	Time (h)	Secchi depth (m)	Cond. (uS/cm)	pH	Salinity (ppm)
P1	23.7	10.0	Vertical	1751	4.125	62.8	8.54	34.30
P2	15.6	10.0	Vertical	1805	3.875	61.2	8.00	33.60
P3	38.7	10.0	Vertical	1814	3.875	60.8	7.97	33.70
P4	52.9	10.0	Vertical	1825	3.875	60.9	7.93	33.60
P5	35.3	10.0	Vertical	1852	-	60.2	8.04	33.50

Table 15. Additional information associated with zooplankton samples taken from five standard stations on Taylor Park Reservoir on 8/22/2017.

Station	Lake depth (m)	Tow depth (m)	Tow type	Time (h)	Secchi depth (m)	Cond. (uS/cm)	pH
P1	12.0	10.0	Vertical	1625	3.875	98.2	8.23
P2	40.0	10.0	Vertical	1642	4.375	98.5	8.27
P3	40.0	10.0	Vertical	1652	4.375	98.5	8.25
P4	13.5	10.0	Vertical	1704	3.875	98.5	8.20
P5	12.0	10.0	Vertical	1713	3.875	98.4	8.22

Table 16. Temperature and dissolved oxygen profiles collected from different standard stations on Lake Granby and Taylor Park Reservoir during 2016-2017.

Depth (m)	Lake Granby (9/7/2016)				Lake Granby (9/18/2017)		Taylor Park Reservoir (8/22/2017)			
	Station P4		Station P5		Station P4		Station P2		Station P3	
	Temp (°C)	DO (mg/L)	Temp (°C)	DO (mg/L)	Temp (°C)	DO (mg/L)	Temp (°C)	DO (mg/L)	Temp (°C)	DO (mg/L)
Surface	16.4	7.51	16.4	7.53	15.7	7.26	15.5	7.44	15.4	7.36
1	16.4	7.50	16.4	7.53	15.8	7.24	15.6	7.41	15.4	7.34
2	16.4	7.49	16.4	7.52	15.8	7.23	15.7	7.39	15.5	7.33
3	16.4	7.46	16.4	7.51	15.8	7.22	15.7	7.38	15.5	7.31
4	16.4	7.44	16.4	7.50	15.8	7.20	15.5	7.00	15.5	7.21
5	16.3	7.44	16.4	7.48	15.8	7.18	15.3	6.76	15.4	7.03
6	16.3	7.42	16.4	7.48	15.8	7.17	15.2	6.66	15.3	6.94
7	16.3	7.40	16.4	7.46	15.8	7.14	15.1	6.56	15.3	6.85
8	16.3	7.36	16.4	7.45	15.7	7.12	15.0	6.37	15.1	6.64
9	15.9	7.15	16.4	7.43	15.7	6.99	14.9	6.31	15.0	6.56
10	15.3	6.78	16.4	7.43	15.6	6.97	14.8	6.06	14.9	6.34
11	13.7	5.87	16.4	7.41	15.6	6.81	14.7	5.95	14.7	6.08
12	13.4	5.67	16.3	7.38	15.4	6.17	14.6	5.83	14.4	5.78
13	12.0	5.20	16.3	7.35	14.4	5.01	14.2	5.53	14.2	5.56
14	9.5	5.20	11.5	5.00	13.6	4.74	13.7	5.23	13.8	5.33
15	8.3	5.33	10.8	4.95	11.8	4.60	13.6	5.10	13.7	5.31
16	8.1	5.37	9.6	5.11	10.8	4.68	13.4	5.05	13.6	5.32
17	8.0	5.38	9.1	5.25	9.9	4.91	13.3	5.00	13.4	5.27
18	7.9	5.41	8.8	5.29	9.4	5.00	13.2	4.98	13.3	5.24
19	7.8	5.41	8.4	5.35	9.1	5.02	13.1	4.98	13.2	5.23
20	7.6	5.43	8.1	5.44	8.9	5.08	13.0	4.98	13.0	5.23
21	7.5	5.45	7.9	5.54	8.6	5.07	12.9	4.98	12.8	5.12
22	7.6	5.44	7.6	5.64	8.5	5.05	12.8	4.98	12.7	5.06
23	7.4	5.44	7.5	5.65	8.3	5.05	12.6	4.96	12.5	5.02
24	7.4	5.42	7.4	5.67	8.1	5.03	12.5	4.92	12.3	5.01
25	7.3	5.41	7.2	5.74	8.0	5.05	12.3	4.91	12.1	4.90
26			7.1	5.75	7.9	5.05	12.2	4.91	12.0	4.94
27			7.0	5.76	7.9	5.03	12.0	4.94	11.9	4.93
28			6.9	5.75	7.8	5.02	11.8	4.89	11.8	4.78
29			6.9	5.73	7.8	5.01	11.8	4.84	11.7	4.68
30			6.8	5.63	7.7	5.01	11.7	4.84	11.6	4.66
31										
32										
33										
34										
35			6.6	5.18	7.7	4.97	11.4	4.56	11.3	4.34
36										
37										
38										
39										
40					7.6	4.94	11.2	4.41		
41										
42										
43										
44										
45					7.5	4.89				

Acknowledgments

Assessing the seasonal thermal and dissolved oxygen regimes and dynamics of zooplankton in Blue Mesa Reservoir during 2016 was completed in collaboration with Dan Brauch, Area Aquatic Biologist.

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II. Species and Trophic Interactions

Project A. Response of yellow perch and brown trout to an annual pulse of stocked kokanee salmon fry in Blue Mesa Reservoir

Status: Complete

Introduction

The unauthorized introductions of nonnative sport fish or other aquatic fauna is a global problem (Eby et al. 2006). Illegal stocking not only undermines efforts to conserve native fish (Tyus and Saunders 2000), it exposes existing economically important recreational fisheries comprised of innocuous nonnative or native fish to unnecessary risk (Hickley and Chare 2004; Tabor et al. 2007; Runicman and Leaf 2008; Johnson et al. 2009; Johnson et al. 2017a). The Upper Colorado River Basin (UCRB), USA, is at the forefront of this issue. The Upper Colorado River contains critical habitat for the endemic Colorado pikeminnow *Ptychocheilus lucius*, humpback chub *Gila cypha*, bonytail chub *Gila elegans*, and razorback sucker *Xyrauchen texanus*. The basin is heavily impounded and most reservoirs contain nonnative piscivores, many originating from illegal stockings (Johnson et al. 2009; Wolff et al. 2012).

Nonnative piscivores in UCRB reservoirs not only threaten endemic native fish downstream through entrainment or assisted dispersal, they complicate the management of reservoir fisheries. Reservoir fisheries management in the region emphasizes nonnative salmonids because of their limited effects on native fish, but illegally introduced piscivores such as northern pike (*Esox lucius*) and walleye (*Sander vitreus*) often select for and have strong predatory effects on salmonids in western reservoirs (McMahon and Bennett 1996; Yule et al. 2000; Baldwin et al. 2003; Lepak et al. 2012; Johnson et al. 2017a).

High profile predators such as northern pike, walleye, and smallmouth bass are not the only cool or warm water nonnative sport fish sought after by anglers in the UCRB and elsewhere. Lower profile centrachids and percids such as bluegill (*Lepomis macrochirus*), crappie (*Pomoxis spp.*), and yellow perch (*Perca flavescens*) are illegally introduced at similar rates (Martinez et al. 2014). Yellow perch in particular are both capable planktivores and piscivores. They can influence zooplankton community composition and size structure by selecting for larger bodied forms such as *Daphnia* (Galbraith 1967; Shrader 2000; Johnson and Kitchell 1996), which are important prey for stocked kokanee (*Oncorhynchus nerka*) and rainbow trout (*O. mykiss*) (Schneidervin and Hubert 1987; Johnson et al. 2002). They also begin feeding on fish at a total length of 100-170 mm (Mittelbach and Persson 1998). Yet, the direct and indirect effects of these secondary species on salmonids are poorly studied despite their unauthorized presence potentially adding predatory or competitive pressures within reservoir food webs.

Predation on focal prey can be acute (i.e., restricted in time and space) or persistent depending on how variable environmental conditions or other factors mediate predator-prey overlap (Beauchamp et al. 2007; Hansen et al. 2013; Hansen and Beauchamp 2014). The primary objective of this study was to assess the spatial-temporal dimensions of predation by illegally introduced yellow perch on kokanee salmon fry stocked annually into Blue Mesa Reservoir, a mesotrophic system within the UCRB, to improve understanding of the role lower profile warm

water sport fish play as piscivores in salmonid dominated reservoir food webs. We quantified the seasonal and size-dependent diet composition and distribution patterns of yellow perch and brown trout (*Salmo trutta*) in relation to environmental conditions in different ecologically relevant regions of Blue Mesa Reservoir. We compared the response of yellow perch to that of brown trout and to known (Johnson and Koski 2005; Hardiman et al. 2004) and supplemented (present study) distribution and growth patterns of age-0 kokanee. Brown trout are naturally reproducing, nearshore oriented predators in many western reservoirs and have been present in Blue Mesa Reservoir for decades. Therefore, brown trout provided a complementary reference point for assessing the relative importance of predation by illegally stocked yellow perch.

Methods

Study system.—Blue Mesa Reservoir (BMR) is a 3,793 ha impoundment on the Gunnison River with a maximum depth of 101 m and a mean depth of 27.9 m (Johnson and Koski 2005). The reservoir is comprised of three distinct basins: Iola where the Gunnison River enters, Cebolla (middle basin), and Sapinero (Figure 1).

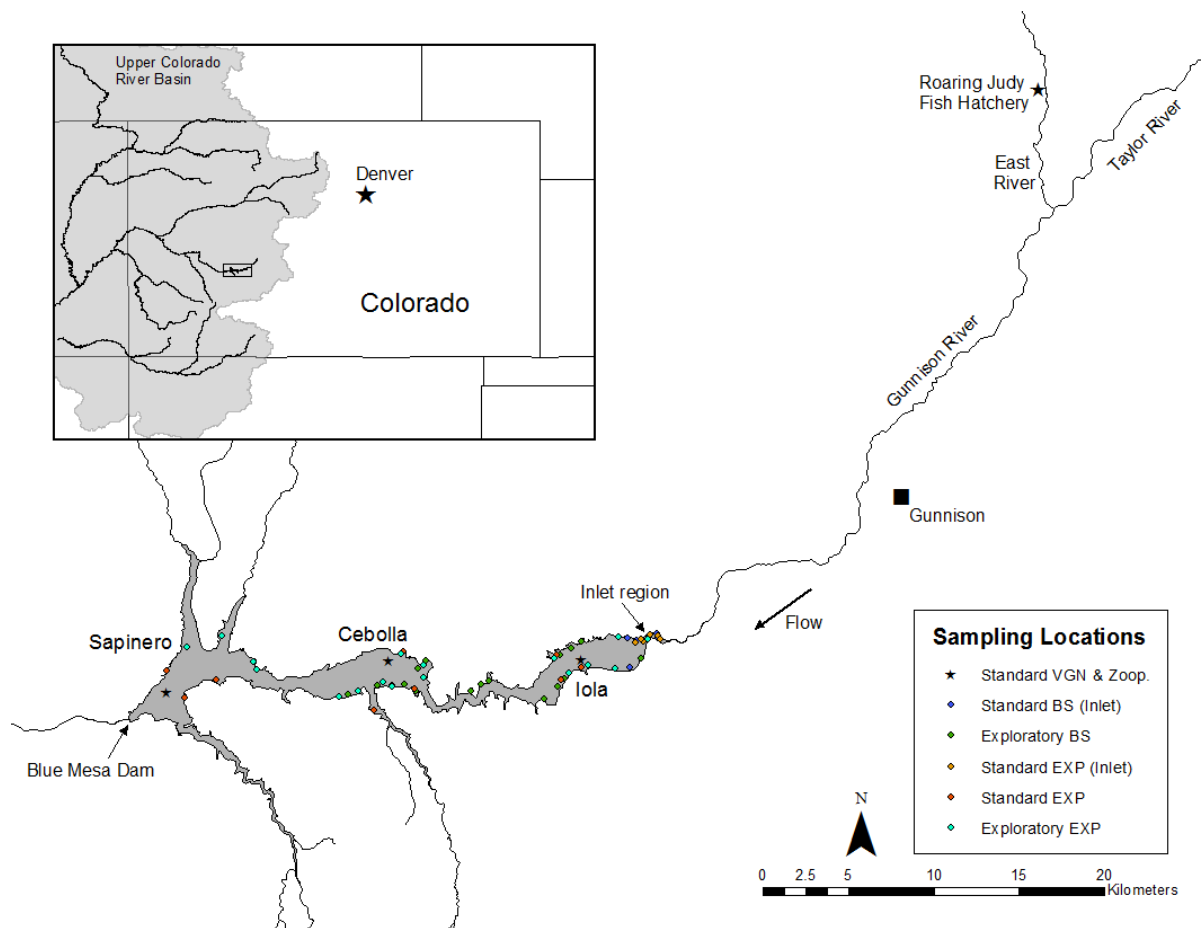


Figure 1. Map of Blue Mesa Reservoir in relation to Roaring Judy Fish Hatchery where kokanee fry are released annually during spring. Black lines within the inset panel represent dominant rivers within each major sub-basin of Colorado. Within the legend: VGN = vertical gill net, BS = beach seine, and EXP = experimental gill net.

Kokanee are a keystone species. They dominate angler catch and harvest, are energetically dense prey (Johnson et al. 2017b) that support a trophy lake trout (*Salvelinus namaycush*) fishery, and produce the majority (as high as 90-100%) of hatchery eggs needed to sustain kokanee populations throughout Colorado (Johnson and Martinez 2000; Pate et al. 2014). The number of kokanee fry stocked into BMR has remained stable at 3.1-3.6 million since 2009. Fry are released annually in March or April from Roaring Judy Fish Hatchery into the East River, a tributary of the Gunnison River. The release occurs after sunset during the new moon to minimize predation as fry migrate to the reservoir. The rate of dispersal is flow dependent, but fry can reach the inlet region of the reservoir (**Figure 1**) in less than 12 hours at most flow levels (D. Brauch, *unpublished data*). Yellow perch first appeared in creel surveys in 2001. Their abundance remained relatively low until recent years (D. Brauch, *unpublished data*) and yellow perch were present in each basin of BMR during our study.

Size-distribution of kokanee fry.—We measured fork lengths (FL; mm) and wet weights (WW; g) from a random subsample ($N = 25-30$) of kokanee fry from each of twenty-two raceways holding fish at Roaring Judy Fish Hatchery on 12 April 2016 to characterize their initial size-distribution immediately prior to the release. The overall size-distribution was adjusted for unequal representation of fish from each of thirteen individual egg lots collected during the October-November 2015 spawning run.

Fish sampling.—Previous research and seasonal hydroacoustics surveys suggested that kokanee fry disperse to deeper offshore waters within Iola and down reservoir to Cebolla and Sapinero within one month post release (Hardiman et al. 2004; Johnson and Koski 2005). However, whether kokanee fry occupy nearshore habitat after reservoir entry and their duration of residence within the shallow inlet region where yellow perch are present and where fry could be particularly vulnerable to predation has not been evaluated. Therefore, fish sampling was designed to (1) assess short-term predator-prey interactions within the confined inlet region during April-May 2016 and (2) seasonal predator-prey interactions within each basin of BMR May-November 2016 (**Figure 1**).

Inlet and nearshore residence by kokanee fry.—We used a 61 m long \times 1.8 m deep beach seine with 4.8 mm knotless mesh (**Figure 2**) and deployed by boat to monitor for the presence of kokanee fry at six standard sites within the inlet region starting 14 April 2016 and repeated on 19 April 2016. Because fry catch on 19 April dropped considerably, we did not continue seining the inlet after this date. Lastly, we conducted a series of exploratory seine hauls ($N = 19$) 18-19 April 2016 throughout Iola and Cebolla (**Figure 1**) to assess whether fry occupy nearshore habitat as they disperse down reservoir.

Inlet predation.—Yellow perch and brown trout were sampled using sinking horizontal gill nets (46 m long \times 1.8 m deep; panels of 2.5, 3.8, 5.1, 6.3, 7.6, and 10.2 cm stretch mesh) set within 2-10 m depths at six standard sites within the inlet region (**Figure 1**) on 13 April 2016 as kokanee fry funneled into the reservoir. Nets were set for short periods (1-2.5 hours) to maintain the integrity of diet samples. We repeated this sampling on 20 April 2016 and 24 May 2016. For all captured fish, mesh size, FL, WW, and sex were recorded. Stomachs were collected and frozen immediately. Gonads from yellow perch were weighed to assess reproductive investment.

Opercles from yellow perch and otoliths from brown trout were collected for age and growth analysis.



Figure 2. Beach seine used to capture kokanee fry within the inlet region of Blue Mesa Reservoir.

Seasonal distribution and diet composition.—We conducted standardized sampling seasonally (May, August, and November 2016) to quantify the distribution, size-structure, and diet composition of yellow perch and brown trout (Beauchamp et al. 2007). Horizontal gill nets used in the inlet were fished overnight at two or three standard nearshore sites in each basin. Two gill nets were set at each site, one within 0-10 m depths (warm epilimnion during peak thermal stratification), and one within 10-30 m depths to capture fish within the cooler thermocline. Because fish captured in standard overnight sets were often degraded by crayfish, we supplemented these efforts with short-term gill nets set within the same depth strata at exploratory locations within each basin May-August to obtain fresh biological samples. Lastly, we fished a suite of three to six vertical gill nets (3 m wide \times 55 m deep) with stretch mesh sizes ranging from 2.5 to 10.2 cm overnight at a standard offshore station in each basin (**Figure 1**) during 9-12 May 2016 (prior to thermal stratification) and 1-4 August 2016 (peak thermal stratification). Captured fish were processed as described above.

Diet analysis.—We analyzed the diets of yellow perch and brown trout as input to a bioenergetics model (Kitchell et al. 1977; Dieterman et al. 2004). Stomach contents were identified to species for prey fish and to order for invertebrates and the blotted wet weight of each group was recorded (Chipps and Garvey 2007). We summarized diet composition seasonally and for relevant size classes of yellow perch and brown trout. The lengths of prey fish and crayfish found in the diets were measured or reconstructed from diagnostic bones (Hansel et al. 1988).

Results and Discussion

Inlet and Nearshore Residence by Kokanee Fry

Catch of kokanee fry in standard beach seine hauls within the inlet region of BMR were highly variable, but indicated that kokanee fry migrate through the confined inlet within days after release. Even though we did not find a significant difference in median catch per haul between sampling days ($W = 9$; $P = 0.17$; Mann-Whitney-Wilcoxon test), mean catch per haul dropped from 10.5 fry ($N = 6$; range = 0-43) on 14 April to 1.7 fry ($N = 6$; range = 0-6) on 19 April. No fry were captured in the exploratory seine hauls throughout Iola and Cebolla indicating that fry move to deeper offshore waters quickly, and are therefore, largely segregated from nearshore predators soon after reservoir entry.

Inlet Predation

Brown trout were the dominant piscivore present within the inlet region of BMR during the kokanee fry release. The mean catch rate (fish per hour) of brown trout in short-term gill nets set at standard sites was 13-fold greater than yellow perch on 13 April and 3 fold greater on 20 April. Rainbow trout were present at relative abundance levels similar to yellow perch on both sampling dates. The mean catch rate of yellow perch on 24 May 2016 was similar to April. Conversely, the mean catch rate declined for both brown trout and rainbow trout indicating that the pulse of kokanee fry generated a numerical response from these predators (**Figure 3**).

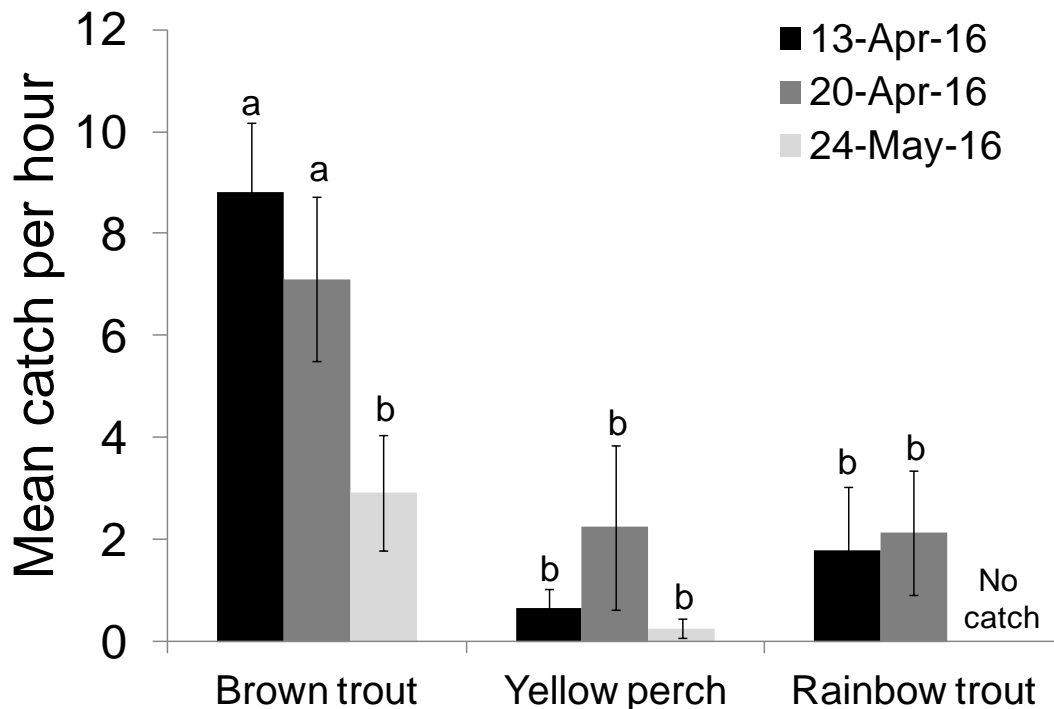


Figure 3. Mean catch per hour in short-term horizontal gill nets set at six standard sites within the inlet region of Blue Mesa Reservoir the morning after kokanee fry were released from Roaring Judy Fish Hatchery (13 April 2016), one week post release on 20 April 2016, and on 24 May 2016. Error bars represent one SE. Letters denote results from a two-factor ANOVA.

The diet composition (mean proportion by weight) of brown trout and yellow perch captured within the inlet region on 13 April, the day kokanee fry funneled into the reservoir, were similar and all size-classes of predator incorporated notable fractions (40-68%) of kokanee fry (**Figure 4**). However, kokanee fry disappeared from the diet of brown trout and yellow perch on 20 April, one week after fry were released (**Figure 5**). Thus, fry were only vulnerable to predation from nearshore predators within the inlet for a very brief period. This result corresponded with observations from our beach seine hauls. Lastly, we did not see any evidence for size-selective predation on kokanee fry released from Roaring Judy from either predator (**Figure 6**) indicating that there were no apparent size-related survival advantages or disadvantages regarding predation during the dispersal life-stage of kokanee fry in BMR.

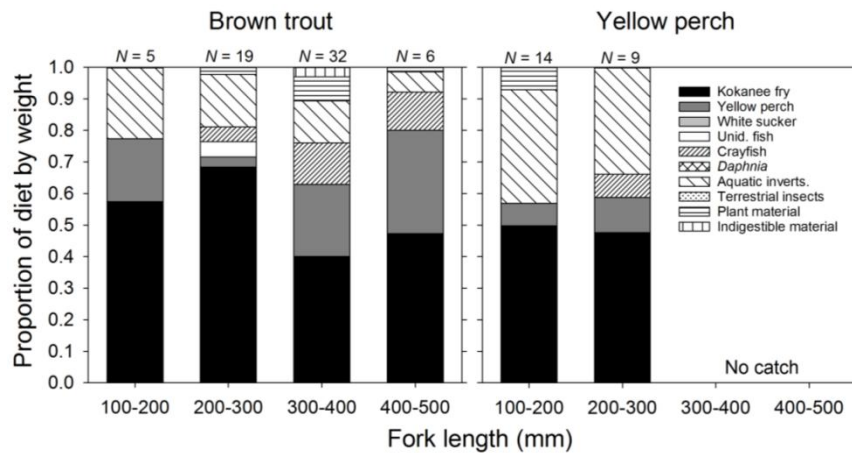


Figure 4. Diet composition (mean proportion by weight) of different size-classes of brown trout and yellow perch captured in short-term horizontal gill nets set at six standard sites within the inlet region of Blue Mesa Reservoir on the morning of 13 April 2016 as kokanee fry funneled into the reservoir. Values denote the number of non-empty stomach samples analyzed.

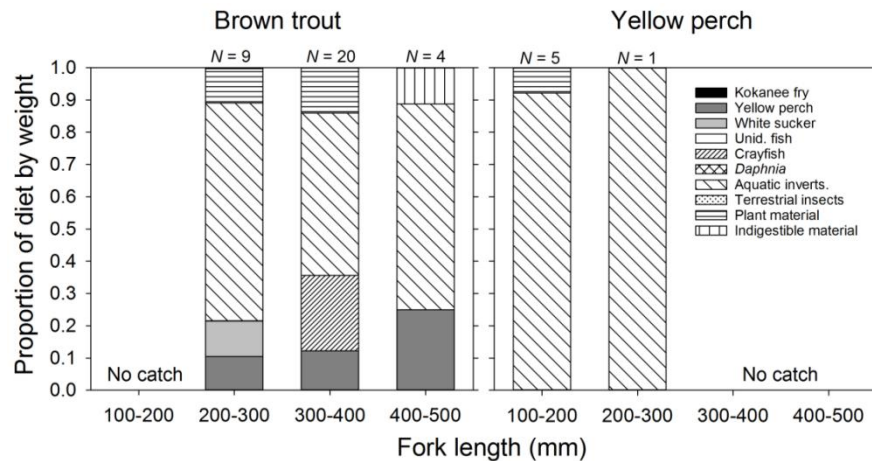


Figure 5. Diet composition (mean proportion by weight) of different size-classes of brown trout and yellow perch captured in short-term horizontal gill nets set at six standard sites within the inlet region of Blue Mesa Reservoir on the morning of 20 April 2016, one week after kokanee fry were released. Values denote the number of non-empty stomach samples analyzed.

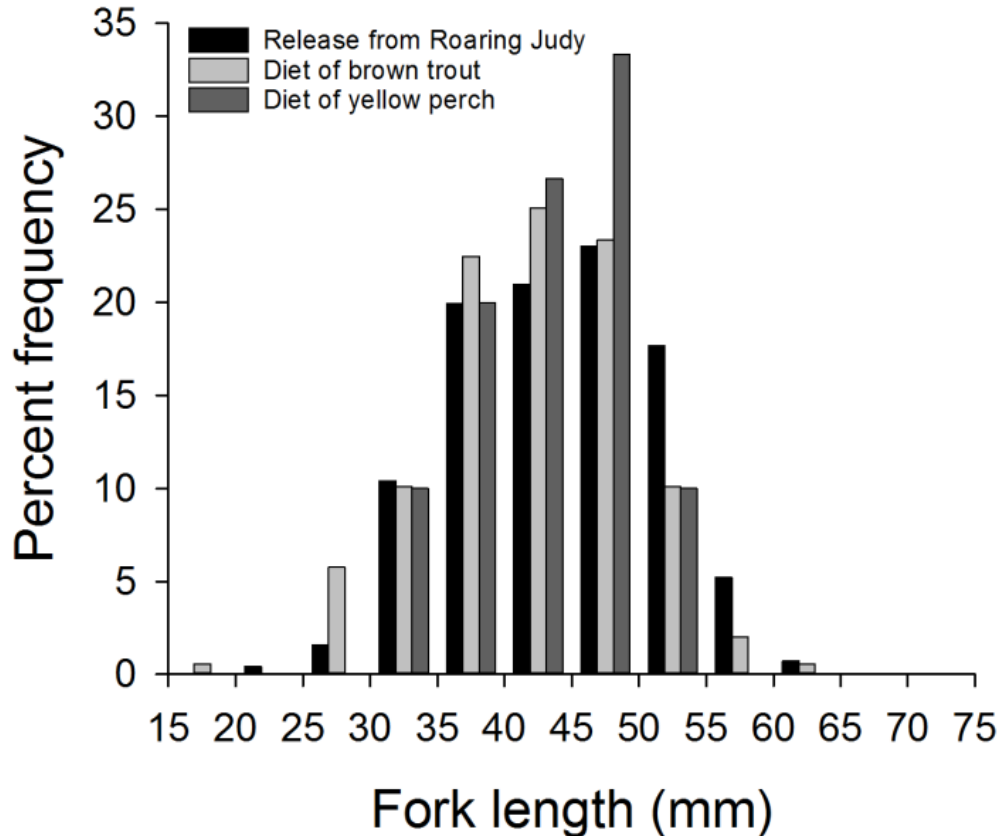


Figure 6. Length frequency distribution adjusted for differential egg lot size of kokanee fry ($N = 574$ measurements) released from Roaring Judy Fish Hatchery the evening of 12 April 2016 and of fry found in the diets of brown trout ($N = 347$) and yellow perch ($N = 30$) captured within the inlet region of Blue Mesa Reservoir on the morning of 13 April 2016. Conversion between fork length (FL) and total length (TL) for kokanee fry: $FL = 0.925 \cdot TL + 0.402$ ($N = 574$; $r^2 = 0.983$).

We detected a hyperphagic response (i.e., binge-feeding) to the pulse of kokanee fry from individual brown trout and yellow perch captured within the inlet region of BMR and from brown trout sampled from the Gunnison River during the release in 2010 (3,416,258 fry released in 2010 vs. 3,135,129 in 2016) as part of a riverine predation study (Pate et al. 2014; D. Brauch, *unpublished data*). Binge-feeding occurs when the daily consumption of prey by a fish exceeds its average daily capacity to digest that prey and enables fish to capitalize on ephemeral food resource pulses, but is mediated by stomach volume (Armstrong and Schindler 2011). Binge-feeding can have important consequences for the energy budgets of fish (Armstrong and Bond 2013; Armstrong et al. 2013) as well as acute predation impacts on prey (Furey et al. 2016).

The average daily consumption/digestive rate of fish expected under stable feeding conditions can be estimated with a species-specific bioenergetics model by computing the theoretical daily maximum consumption rate (C_{max} ; g/day) for a given body size of predator (WW; g) and water temperature ($^{\circ}C$) (Hanson et al. 1997). The degree of binge-feeding is calculated as the ratio of observed consumption reconstructed from gut content analysis (C ; g/day) to C_{max} where values exceeding 1.0 would indicate binge-feeding (Furey et al. 2016) (**Figure 7**).

The strongest hyperphagic responses observed by fish have occurred in low productivity, high latitude, anadromous salmon dominated systems where prey resources are scarce until adult salmon return to spawn allowing resident fishes to gorge on eggs or carcasses (Armstrong and Bond 2013) or when salmon smolts out-migrate (Lowery and Beauchamp 2015; Furey et al. 2016). In these types of systems, nearly the entire annual energy budget of resident fish may be supported by large temporary pulses of prey. Here, we demonstrate that fish can also exhibit short-term hyperphagic responses to pulses of stocked prey in low latitude, higher productivity systems where feeding opportunities are more stable throughout the year and large pulses of prey are less critical for growth, survival, and reproduction.

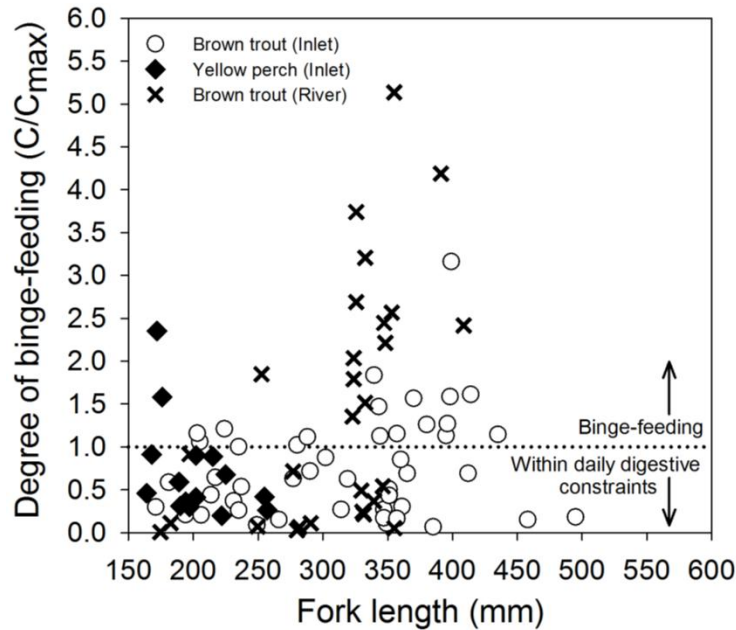


Figure 7. Estimated degree of binge-feeding as a function of fork length for individual piscivorous yellow perch ($N = 15$) sampled within the inlet region of Blue Mesa Reservoir on 13 April 2016 when kokanee fry funneled into the reservoir, and for individual piscivorous brown trout sampled in both the inlet (13 April 2016; $N = 48$) and in the Gunnison River ($N = 28$) during the 2010 kokanee fry release (D. Brauch, *unpublished data*). Observed consumption (C ; g/day) was calculated by reconstructing the length and weight of kokanee fry and other fish observed in the diet of each predator. The theoretical daily maximum consumption rate (C_{max} ; g/day) was computed using a bioenergetics model parameterized for each species (Kitchell et al. 1977; Dieterman et al. 2004) based on the body weight (WW ; g) of each predator and water temperature observed in the river (6.7°C) and inlet region (7.6°C).

Even though yellow perch were capable of exhibiting a hyperphagic response on the basis of prey mass eaten at observed water temperatures and body sizes, they consumed few fry numerically when compared to the larger more numerous brown trout (**Figures 8 & 9**). Each yellow perch stomach analyzed containing kokanee included less than 5 fry, whereas brown trout sampled within the inlet contained up to 40 fry. Brown trout sampled in the Gunnison River contained up to 86 fry. Results from the riverine predation study are not directly comparable to the inlet study since feeding conditions (e.g., duration of encounter with prey pulse and fry

density) were likely different between habitat types despite a similar number of fry released each year, but they help demonstrate how brown trout were more effective predators on kokanee fry than were yellow perch. In addition, brown trout greater than 325 mm FL in both the inlet and river were most effective at consuming fry, a size range not obtained by yellow perch in BMR (Figures 9 & 10). Overall, the predatory diagnostics presented here and comparisons to brown trout, the dominant predator within the inlet during spring, indicate that acute predation from yellow perch within the inlet region is not an important source of mortality for kokanee fry.

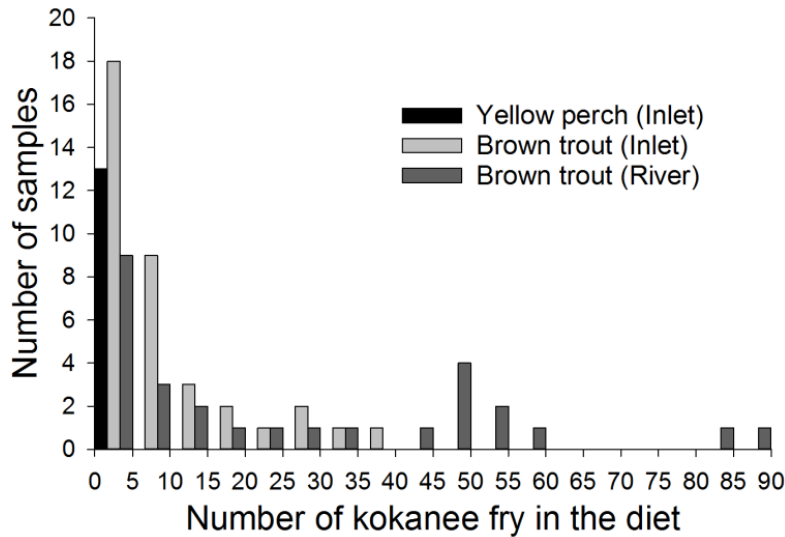


Figure 8. Frequency distribution for the number of kokanee fry observed in the diets of all size-classes of piscivorous yellow perch ($N = 13$) and brown trout ($N = 37$) sampled within the inlet region of Blue Mesa Reservoir on 13 April 2016 and brown trout ($N = 28$) sampled in the Gunnison River during the 2010 fry release.

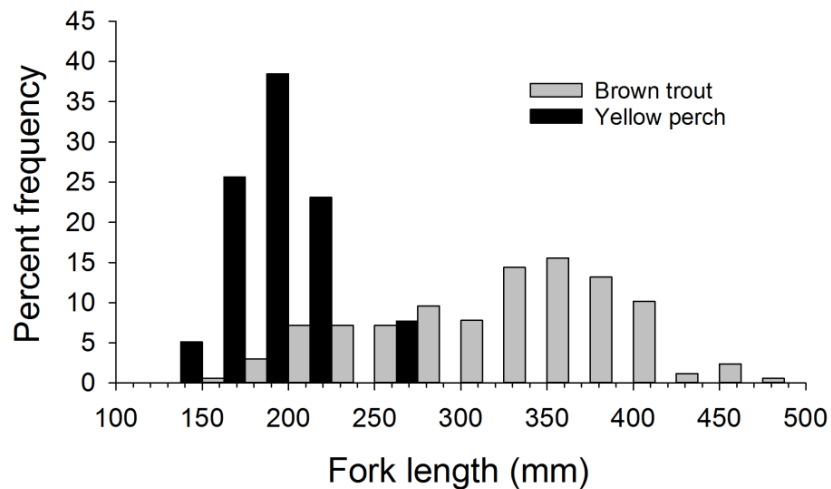


Figure 9. Size-distribution of yellow perch ($N = 39$) and brown trout ($N = 167$) sampled with short-term horizontal gill nets set at six standard sites within the inlet region of Blue Mesa Reservoir on 13 April and 20 April 2016. Size-distributions were not corrected for the relative size-selectivity of different mesh sizes. Effort was the same across mesh sizes.

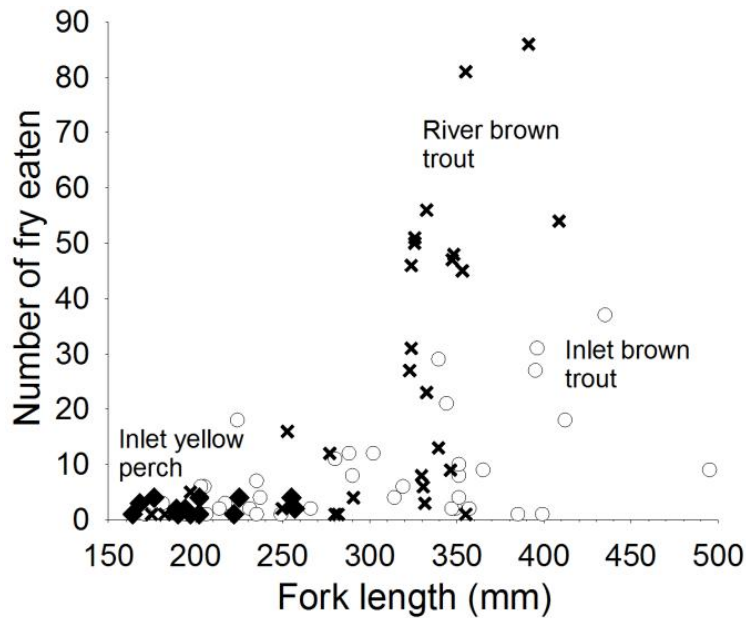


Figure 10. Number of kokanee fry observed in the diet as a function of fork length for individual piscivorous yellow perch ($N = 13$; filled diamonds) and brown trout ($N = 37$; open circles) sampled within the inlet region of Blue Mesa Reservoir on 13 April 2016 and brown trout ($N = 28$; \times symbols) sampled in the Gunnison River during the 2010 fry release.

Seasonal Distribution and Diet Composition

Because no notable differences in the depth-distribution or catch rate of different species of fish were observed in overnight horizontal gill net sets among basins, we pooled catch from nets across basins to characterize the seasonal nearshore distribution of brown trout and yellow perch. The depth-distribution and overall catch rate of brown trout were similar across seasons. Conversely, catch rates of yellow perch were greatest and increased considerably in 0-10 m depths during summer which corresponded to the warm epilimnion (**Figure 11**).

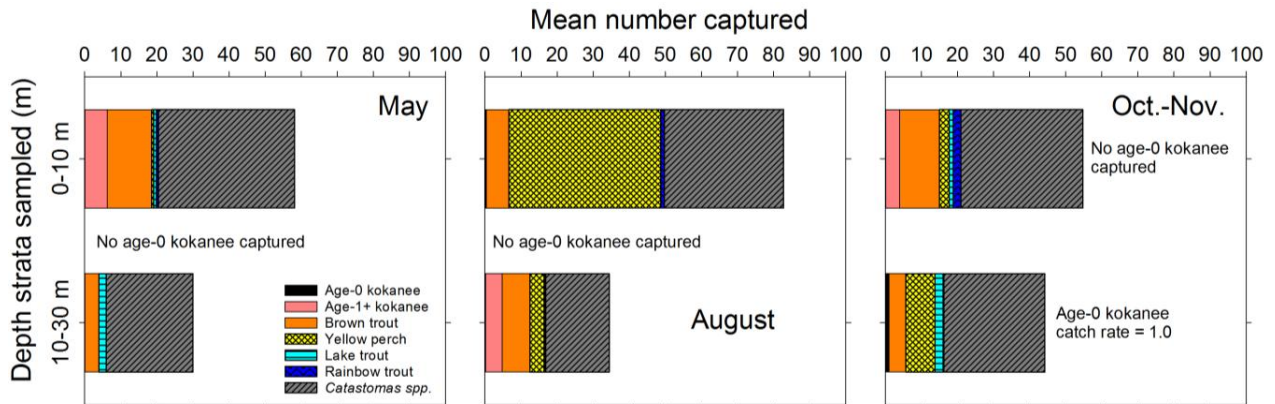


Figure 11. Seasonal nearshore depth-distribution of different species of fish in Blue Mesa Reservoir. Bars represent the mean number of fish captured per overnight horizontal gill net set at standard locations in each basin of Blue Mesa Reservoir.

We did not detect any overlap between brown trout or yellow perch and age-0 kokanee in standard horizontal gill nets until Autumn (October-November) in 10-30 m depths. However, age-0 kokanee captured during Autumn had outgrown (Figure 12) the gape limitation (Figure 13) of most piscivorous yellow perch within the population (Figure 14). Yellow perch consumed prey up to 40-50% of their own body length. Age-0 kokanee were however, still vulnerable to larger-bodied brown trout which comprised ~20% of the population at that time and consumed prey up to 40% of their own body length (Figure 13).

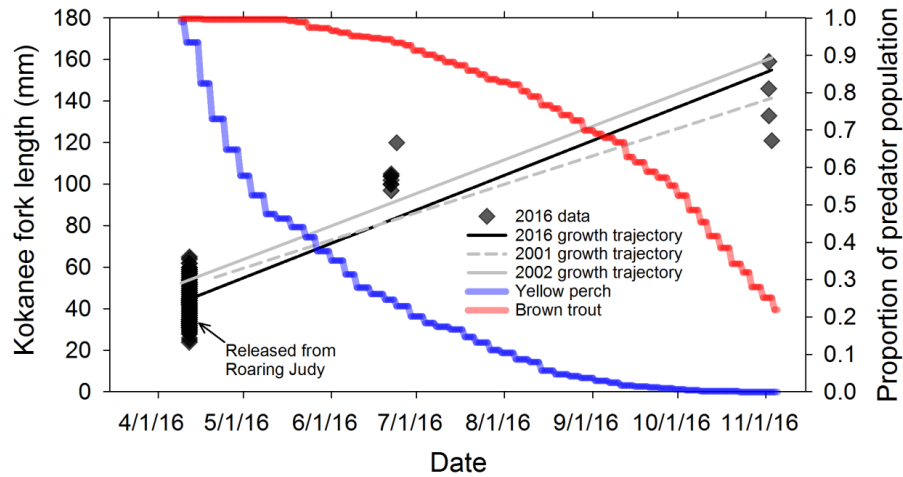


Figure 12. Mean growth trajectories of age-0 kokanee (confirmed with otoliths) in Blue Mesa Reservoir during 2016 (present study) and during 2001 and 2002 (Johnson and Koski 2005). Colored lines represent the estimated proportion of the yellow perch and brown trout population that could effectively consume an averaged sized age-0 kokanee after accounting for growth over time based on the observed gape limit (50% body length for yellow perch and 40% for brown trout; Figure 13) and relative size-structure of each predator species (Figure 14).

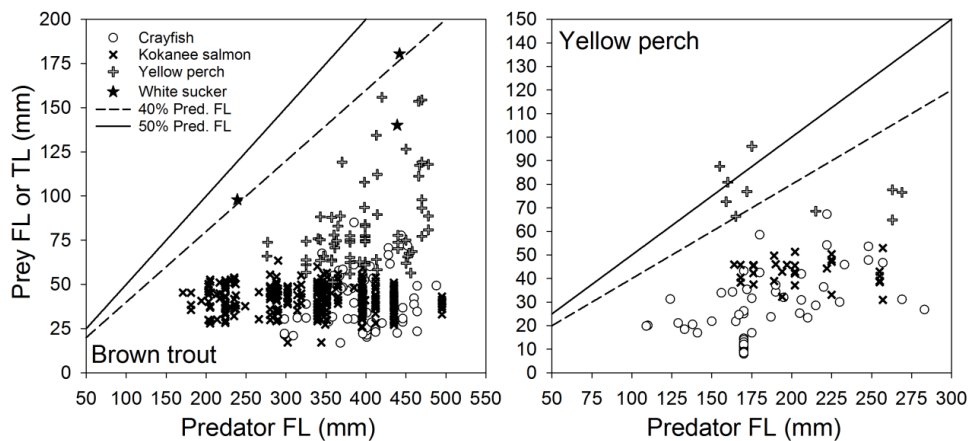


Figure 13. Relationship between the fork length (FL) of brown trout and yellow perch and the FLs of ingested prey fish and total lengths (TL) of ingested crayfish ($N = 451$ for brown trout and $N = 105$ for yellow perch). Conversion between FL and TL for brown trout: $FL = 0.975 \cdot TL - 7.716$ ($N = 334$; $r^2 = 0.998$). Conversion between FL and TL for yellow perch: $FL = 0.961 \cdot TL - 1.162$ ($N = 547$; $r^2 = 0.998$).

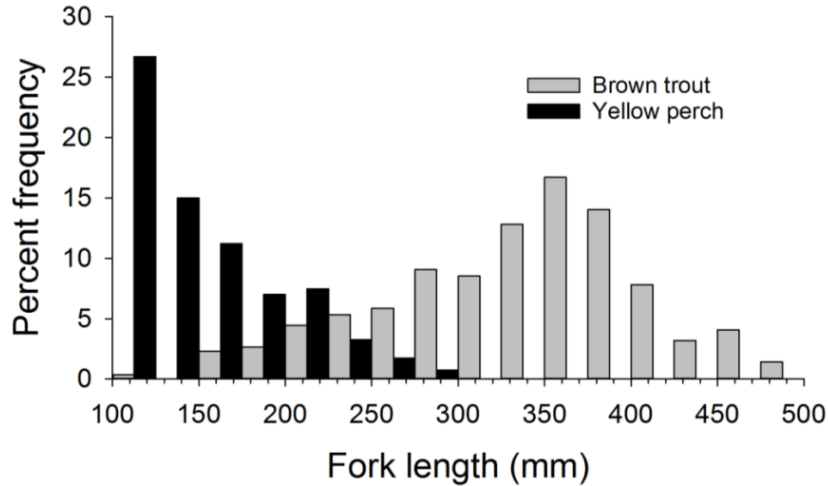


Figure 14. Size-distribution of yellow perch ($N = 401$) and brown trout ($N = 563$) sampled with standard nearshore horizontal gill nets set (short-term and overnight) at standard and exploratory locations across all regions of Blue Mesa Reservoir. Size-distributions were not corrected for the relative size-selectivity of different mesh sizes. Effort was the same across mesh sizes.

During spring (April-June) and summer (July-August), when an average age-0 kokanee was still vulnerable to predation from meaningful fractions of the yellow perch population (**Figure 12**), they were likely too small to be caught effectively in our horizontal experimental gill nets. We did capture a few individuals in one short-term daylight set in Iola during late June, but these fish likely only represented the largest individuals from the 2016 cohort. Therefore, it is possible that age-0 kokanee overlapped with brown trout and yellow perch nearshore more than what was indicated by catch in our standard horizontal gill nets during these seasons. However, no kokanee were observed in the nearshore diets of brown trout or yellow perch during any season indicating that encounters were rare (**Figures 15 & 16**). Overall, fish were rare in the diet of both predator species and they relied predominately on crayfish or other invertebrates.

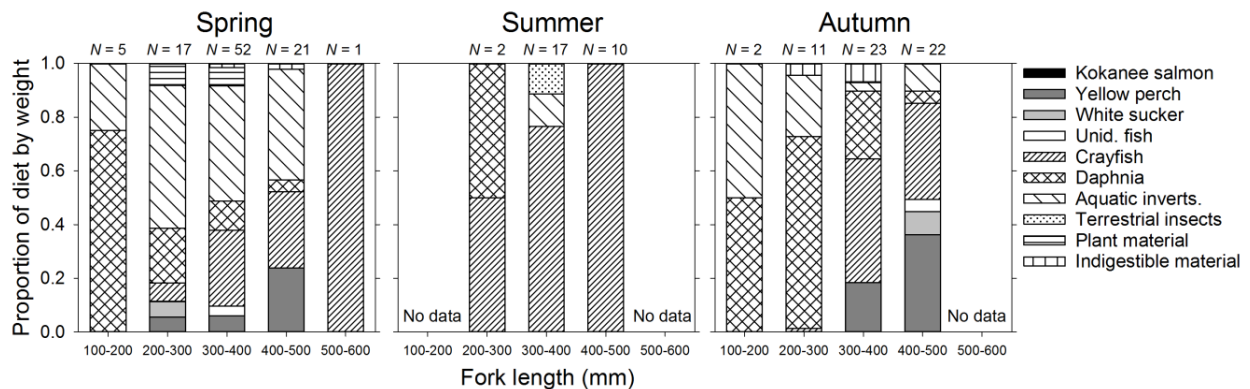


Figure 15. Seasonal nearshore diet composition (mean proportion by weight) of different size-classes of brown trout pooled across each basin of Blue Mesa Reservoir. Values denote the number of non-empty stomach samples analyzed. Spring incorporates the diets of fish sampled in April (excluding fry release on 13 April 2016), May, and June. Summer incorporates samples from July and August. Autumn incorporates samples from October and November.

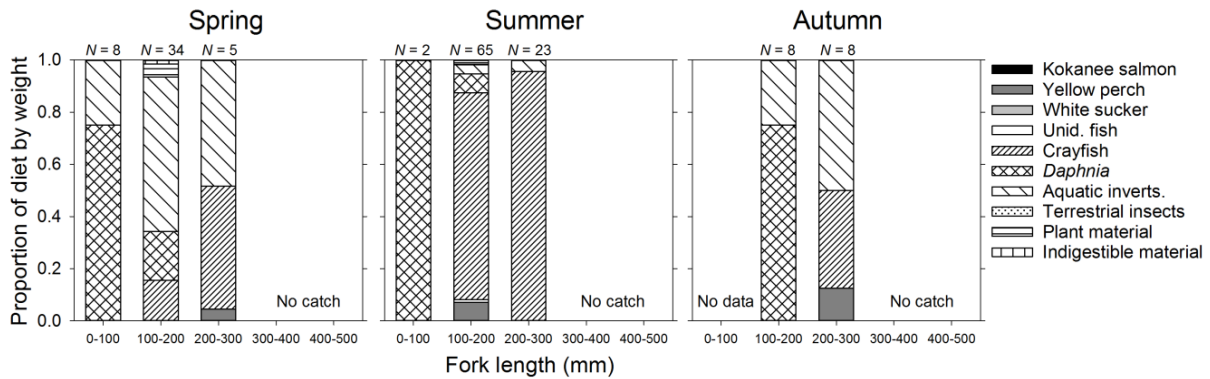


Figure 16. Seasonal nearshore diet composition (mean proportion by weight) of different size-classes of yellow perch pooled across each basin of Blue Mesa Reservoir. Values denote the number of non-empty stomach samples analyzed. Spring incorporates the diets of fish sampled in April (excluding fry release on 13 April 2016), May, and June. Summer incorporates samples from July and August. Autumn incorporates samples from October and November.

Furthermore, hydroacoustics surveys indicated that age-0 kokanee typically occupy deeper, darker offshore depths greater than 40 m during daylight in May and June (Hardiman et al. 2004; Johnson and Koski 2005) where no yellow perch or brown trout were captured in standard offshore vertical gill nets during May (**Figure 17**).

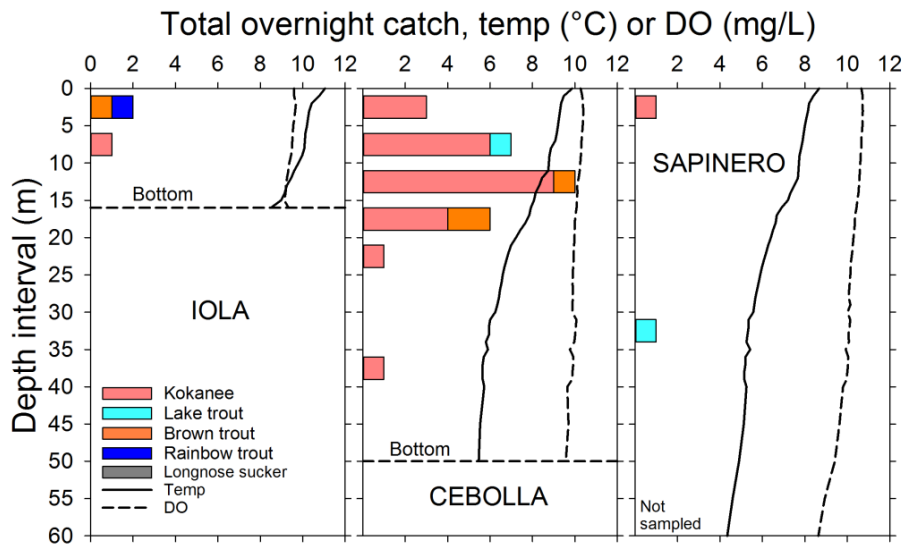


Figure 17. Vertical distribution of fish (bars) in relation to temperature and dissolved oxygen (DO) conditions (lines) captured in a standard suite of three vertical gill nets set at an offshore station overnight in each basin during May 2016. Because of the low catch, we doubled effort in August by increasing the number of nets fished within each basin from three to six.

During August, offshore depths utilized by age-0 kokanee were generally shallower than during May or June based on hydroacoustics (Hardiman et al. 2004; Johnson and Koski 2005), but were still within the cooler thermocline (10-30 m) and largely segregated from the nearshore concentration of yellow perch in 0-10 m depths (**Figure 11**). These shallower depths

corresponded to the warm epilimnion thereby creating a thermal refuge for age-0 kokanee from yellow perch during summer. All age-classes of kokanee captured in standard offshore vertical gill nets (only age-1+ fish) during August occupied cooler water temperatures at depths within the thermocline (**Figure 18**). A high fraction of kokanee sampled within Cebolla and Iola basins were pre-spawn adults (**Figure 19**).

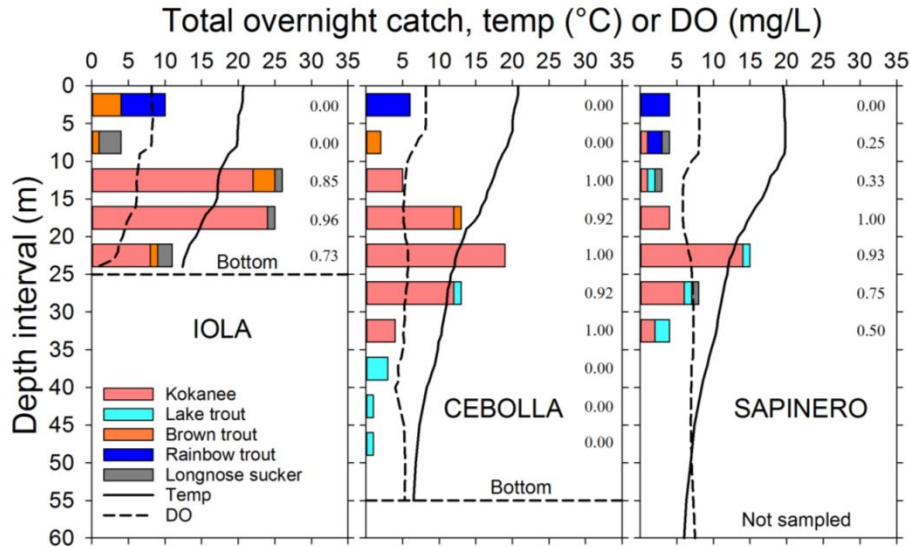


Figure 18. Vertical distribution of fish (bars) in relation to temperature and dissolved oxygen (DO) conditions (lines) captured in a standard suite of six vertical gill nets set at an offshore station overnight in each basin during August 2016. Values indicate the proportion of catch within each depth interval that was kokanee.

Conclusions

Reservoir predator-prey interactions are mediated by seasonal shifts in environmental conditions (e.g., vertical gradients in temperature and oxygen) and corresponding shifts in the distribution, growth, and size-structure of predator and prey populations. In order for predation to occur, predators and prey must first overlap in time and space. During the kokanee fry release, overlap with yellow perch within the inlet region of Blue Mesa Reservoir was brief. Acute predation from yellow perch during this period was negligible when compared to the more abundant, larger-bodied brown trout based on a series of predatory diagnostics. Brown trout have been present in Blue Mesa for a much longer period and have always exerted some level of predation mortality on kokanee fry.

After the release, minimal spatial overlap was observed between yellow perch and age-0 kokanee across seasons, particularly during summer when a thermal refuge from yellow perch formed. Yellow perch occupied warm epilimnetic depths nearshore at this time while age-0 kokanee occupied deeper depths offshore within the thermocline or hypolimnion (based on previous hydroacoustics surveys). Yellow perch were never captured offshore. In addition, the growth rate of age-0 kokanee indicated that they could outgrow approximately 80% of piscivorous sized yellow perch by July, limiting the potential for persistent or chronic levels of predation mortality throughout the growing season.

Further, outside of the fry release period, no kokanee and few fish in general were observed in the diets of yellow perch and brown trout across seasons. Only yellow perch and white sucker were consumed. Lastly, smaller size-classes of brown trout and yellow perch ate notable fractions of *Daphnia* during each season. However, relatively high densities of large-bodied *Daphnia* were present during each month sampled (see *Physical Limnology, Zooplankton and Mysis* section above) indicating that the contemporary food supply can support all reservoir consumers at current population sizes. Monitoring will continue and the indirect effects of yellow perch within the BMR food web will be investigated further if warranted.

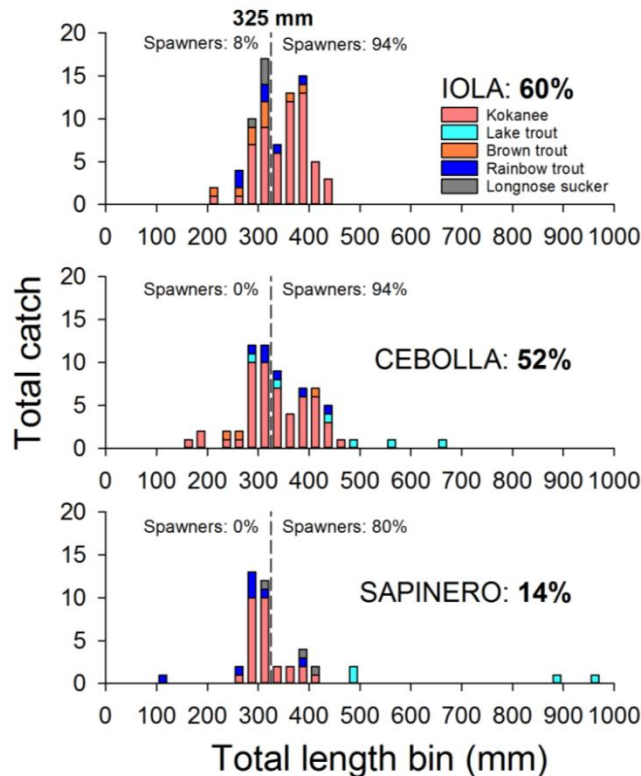


Figure 19. Length-frequency distribution of fish captured in standard offshore vertical gill nets set overnight during August 2016 in each Basin of Blue Mesa Reservoir. Values in bold indicate the total percent of kokanee caught that were pre-spawning adults. The percent of kokanee caught that were pre-spawners is also indicated for two relevant size-classes of fish observed (those < 325 mm total length and those ≥ 325 mm total length).

Acknowledgments

This research project was conducted in collaboration with Dan Brauch, Area Aquatic Biologist. I'd like to thank Ashley Hillard for helping create the map of Blue Mesa Reservoir.

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Project B. Tiger trout as a biological control agent

Status: Ongoing

Purpose and Objectives: Many of Colorado's coldwater lakes contain fish species, such as suckers and minnows, which can achieve high densities (**Figure 1**), provide little value to anglers, compete with managed sport fish, and have the potential to reduce water quality. However, these undesirable fish may be valuable prey items. Sterile fish that have the ability to grow to predatory size quickly and eat the unwanted fish could act as a biological control agent and provide a unique fishing opportunity. Being unable to reproduce, sterile fish can be closely managed through stocking and harvest regulations. Tiger trout, a sterile hybrid between male brook trout (*Salvelinus fontinalis*) and female brown trout (*Salmo trutta*), have the potential to fill this role. Tiger trout have already been stocked in some Colorado lakes. Our understanding of what tiger trout eat and how well they grow and survive in lakes with different species of undesirable fish remains limited, and should be fully investigated as a management tool.



Figure 1. Micro-mesh gill net full of fathead minnows.

Factors such as the number of tiger trout stocked per acre of lake and the presence of small-bodied minnows versus larger-bodied suckers may affect the ability of tiger trout to grow quickly enough and survive long enough to eat and suppress the population of undesirable fish. The objective of this research is to quantify the feeding, growth and survival of tiger trout stocked into lakes with different species of undesirable fish. Results will help CPW prioritize which lakes receive tiger trout, inform appropriate numbers to stock, and calibrate expectations on the effectiveness of tiger trout as a biological control agent. Informed stocking translates into (1) efficient use of the limited number of tiger trout produced by our hatchery system, (2) a greater chance tiger trout will perform well at the onset of stocking, and (3) more rapid development of a quality fishing opportunity for anglers.

Methods

Study area.—The Grand Mesa is an ideal location to conduct this research project. First, there is a relatively high concentration of lakes that have been stocked with tiger trout. Second, all study lakes are in close proximity, and the habitat features of the lakes are similar. For observational studies such as this one, the latter should help us quantify the effects of stocking density and fish species composition on tiger trout feeding and growth more effectively.

General sampling protocol.—Over a 3 week period between 6/28/2017 and 7/13/2017, we sampled 8 lakes on the Grand Mesa previously stocked with tiger trout. The study lakes contained different species of undesirable fish, either stunted brook trout ($N = 2$), fathead minnows ($N = 5$), or white suckers ($N = 1$), and were stocked at variable densities with tiger trout (**Table 1**). Tiger trout were present in all lakes sampled except Main Griffith (despite being stocked once in 2014), which contained only fathead minnows (*Pimephales promelas*) and therefore is serving as a reference lake for the relative abundance and size-structure of fathead minnows we'd expect in the absence of tiger trout. Reference lakes for brook trout and white suckers (*Catostomus commersonii*) will be sampled in 2018.

Table 1. Study lakes sampled during summer 2017 on the Grand Mesa and associated tiger trout stocking history. The species codes BKT, FHM, and WHS stand for brook trout, fathead minnow, and white sucker.

Lake	Water code	Elevation (ft)	Surface area (acres)	Max observed depth (m)	Year stocked	Date stocked	Mean size (in)	Number	Rate (#/ha)	Biological control for:
Big Battlement	88460	10,080	41.00	13	2016	21-Jun	3.44	476	11.61	Stunted BKT
Cottonwood Lake #4	66008	10,205	37.69	12	2014	22-Jul	4.26	2,100	55.71	FHM
					2016	21-Jun	3.44	1,653	43.86	
					2016	27-Jul	3.97	1,500	39.80	
Deep Slough Lake	89462	10,018	45.09	4	2007	17-Jul	2.85	376	8.34	WHS
					2008	26-Jun	4.00	4,376	97.05	
					2011	11-Jul	3.51	1,000	22.18	
					2012	14-Jun	2.88	2,400	53.23	
					2014	25-Jun	3.76	3,000	66.54	
					2016	21-Jun	3.44	1,505	33.38	
Granby Reservoir #2	90150	10,060	18.30	6	2016	21-Jun	3.44	404	22.08	FHM
Granby Reservoir #12	90201	10,000	48.40	7	2016	21-Jun	3.44	238	4.92	FHM
Main Griffith Lake	67048	10,050	62.61	11	2014	25-Jun	3.76	1,000	15.97	FHM
Middle Griffith Lake ^a	67050	10,025	33.85	16	2014	25-Jun	3.76	1,000	29.54	FHM
Sackett Reservoir	92116	10,460	9.40	7	2011	25-Aug	4.29	1,500	159.57	Stunted BKT
					2014	25-Jun	3.76	2,000	212.77	
					2016	21-Jun	3.44	303	32.23	

^aNo tiger trout were detected and is now serving as a reference lake.

Field sampling.—Our field sampling protocol was similar to other standard high mountains lakes sampling procedures (CA Dept. of Fish and Wildlife 2009) and was designed to characterize the (1) physical limnology (temperature, dissolved oxygen, and Secchi disk depth), (2) zooplankton

density, size-structure, and community composition, and (3) the relative abundance and size-structure of undesirable fish and tiger trout in each study lake.

Physical limnology and zooplankton.—Three equally dispersed offshore stations along the longitudinal axis of each lake were sampled for limnology and zooplankton. One of the stations was located in the deepest region of each lake. Vertical temperature and dissolved oxygen profiles were measured with a YSI Pro-DO meter and DataSonde from the surface to the bottom at 1-m intervals. We collected zooplankton for estimation of density, size-structure, and community-composition from a single vertical tow with a 153- μm Wisconsin style zooplankton net from the lake bottom to the surface at each station and preserved the samples in 4% sugared formalin (buffered). Standard zooplankton samples are currently being analyzed following the same procedures outlined in Section I. We also collected bulk zooplankton for stable isotope analysis. The Secchi depth was recorded at each station and averaged across stations.

Fish sampling.—We used a suite of sampling gears to characterize the relative abundance (number captured per hour of soak time or “catch rate”) and size-structure of fish in each lake. Fishing multiple gears reduced the size-selective bias of any one gear and ensured sufficient capture of small-bodied minnows. Sampling equipment included two 50' long \times 5' deep micro-mesh gill nets with five randomly positioned mesh panels (1/2"; 1/4"; 3/4"; 3/8"; 5/8" bar measure), two 80' long \times 6' deep experimental gill nets with eight randomly positioned mesh panels (1-1/2"; 2-1/4"; 1"; 1-3/4"; 3/4"; 2-1/2"; 1-1/4"; 2" bar measure; Bonar et al. 2009), and two 3/8" knotless mesh, mini-trap nets with a 2' \times 3' box frame and 25' lead (from Duluth Nets).

Micro-mesh and experimental gill nets were set for short periods (30 min to 1.5 hours depending on fish density in order to avoid gear saturation and undue mortality in tiger trout) during daylight in a paired fashion. Because the lakes were already thermally stratified, the first net was attached to and set perpendicular to the shoreline within warmer epilimnetic depths (generally 0-2 m and ranged from 17-19°C across lakes during the sampling period) and the second net was set along the same axis but in deeper offshore water at depths within the cooler thermocline (generally 2-6 m and ranged from 5-17°C). We attempted to complete three independent paired short-term sets with each gill net type in each lake. Set locations were dispersed across each lake and selected to capture the range of variability in observed habitat types (typically steeper shoreline with rocky/wooded substrate versus more gradually sloped shoreline with vegetated substrate). Lastly, each mini-trap net was attached to and fished perpendicular to the shoreline in different habitat types. One was placed at a suitable location near the inlet of each lake if possible. Trap nets were set first and pulled after all other sampling was completed.

Biological samples.—All fish captured were counted and measured for fork (FL) and total length (TL) in mm and weighed to the nearest 0.1 gram. We then collected caudal fin tissue for stable isotope analysis (Sanderson et al. 2009), stomach contents via gastric lavage for diet analysis, and otoliths (from mortalities) or scales for age-and-growth analysis from all or a systematic-random subsample of fish depending on catch rates in nets. Lastly, we collected benthic invertebrates, periphyton, and rooted macrophytes from three locations spread across each lake for stable isotope analysis. These samples, combined with the bulk zooplankton, will determine baseline $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for characterizing the food web structure of each lake.

Collectively, biological samples will inform the trophic position of and dominant prey supporting different size- or age-classes of tiger trout as well as their growth and survival. Biological samples are currently being analyzed in the laboratory.

Results and Discussion

We found evidence that relatively high densities of undesirable fish, particularly of large-bodied suckers, may have a detrimental effect on water clarity through processes related to nutrient recycling or other food web interactions in lakes on the Grand Mesa. Mean Secchi disk depth varied five-fold across study lakes and was negatively associated (linear regression; $R^2 = 0.65$; $P = 0.016$; $N = 8$) with the mean catch rate of undesirable fish pooled across all sampling gears (Figure 2).

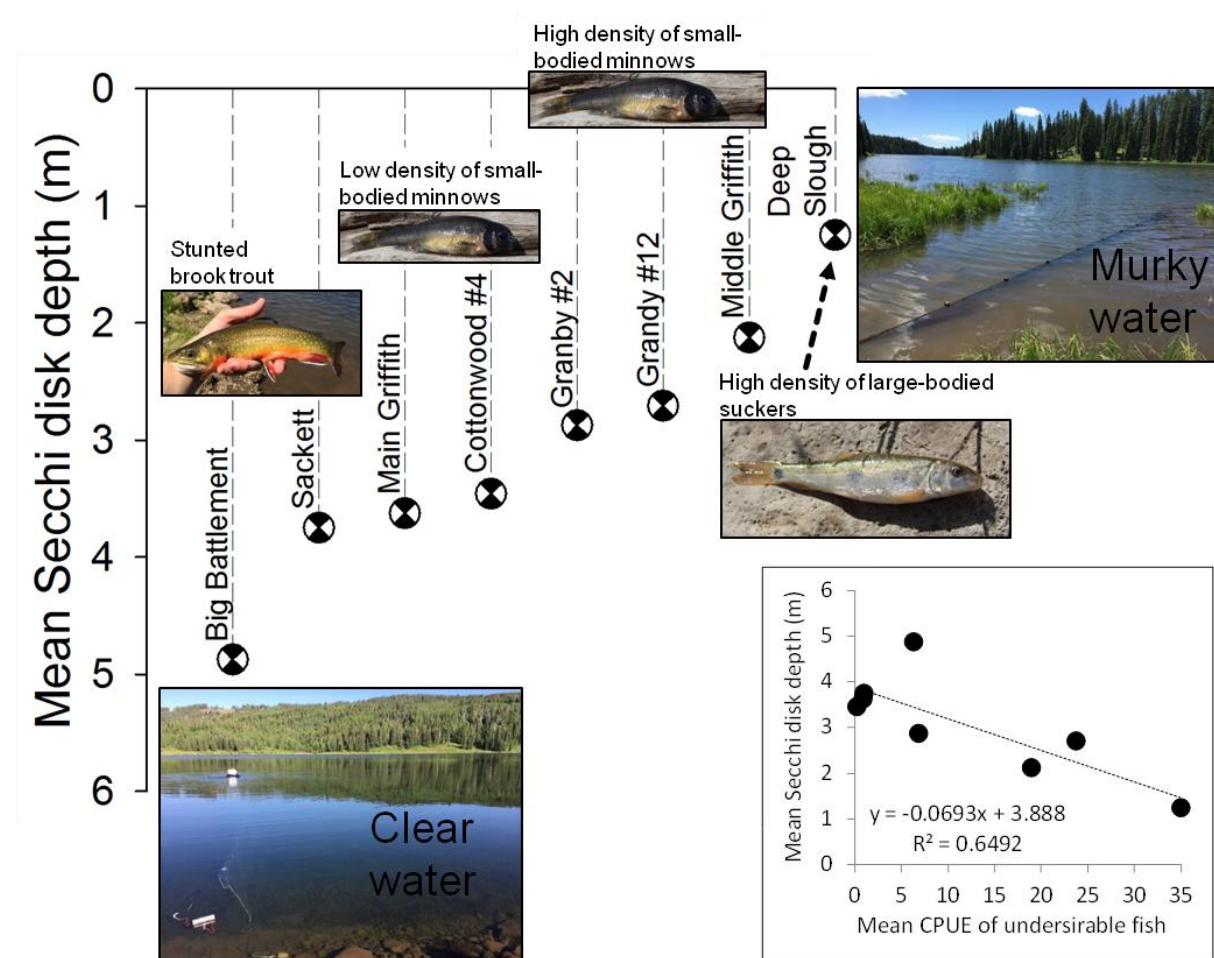


Figure 2. Mean Secchi disk depth estimated for each study lake from three offshore limnological and zooplankton sampling stations. The inset panel describes the relationship between mean Secchi disk depth and the mean catch rate of undesirable fish.

The catch rates and size-structures of undesirable fish and tiger trout also varied across study lakes (Table 2; Figure 3). As expected from stocking records and based on length-frequency

distributions, multiple age-classes of tiger trout were present in Cottonwood Lake #4 (ages 1 and 3; fathead minnows present), Deep Slough Lake (ages 1, 3, and possibly 5-6; white suckers), and Sackett Reservoir (ages 1, 3, and possibly 6; brook trout). The remaining lakes only contained either age-1 tiger trout stocked in 2016 (Big Battlement with brook trout, Granby Reservoir #2 with fathead minnows, and Granby Reservoir #12 with fathead minnows) or age-3 tiger trout stocked in 2014 (Main Griffith with fathead minnows). The study lakes will continue to be stocked with tiger trout every two years at the same density as in previous years and we will revisit each lake in 2019 to evaluate the growth and survival of different cohorts of tiger trout and assess for potential changes in the relative abundance and size-structure of undesirable fish.

Table 2. Mean catch rates (number/hour) of tiger trout and undesirable fish from each sampling gear (micro-mesh gill nets, experimental gill nets, and mini-trap nets) set in each of the eight study lakes.

Lake	Species	Mean catch per hour in each sampling gear					
		Micro-mesh		Experimental		Trap	
		Mean	SD	Mean	SD	Mean	SD
Big Battlement	Tiger trout	0.98	1.18	0.36	0.55	0.00	0.00
	Brook trout	5.00	3.47	9.29	5.29	0.00	0.00
Cottonwood Lake #4	Tiger trout	1.32	1.16	6.03	4.62	0.00	0.00
	Fathead minnows	0.17	0.41	0.00	0.00	3.68	3.92
Deep Slough Lake	Tiger trout	0.00	-	3.42	2.76	0.00	0.00
	White suckers	44.00	-	44.25	22.50	2.75	3.89
Granby Reservoir #2	Tiger trout	0.75	1.85	0.45	1.11	0.00	0.00
	Fathead minnows	13.69	19.92	0.00	0.00	Not fished	
Granby Reservoir #12	Tiger trout	0.00	0.00	0.22	0.47	0.00	0.00
	Fathead minnows	91.03	101.97	0.00	0.00	7.92	6.08
Main Griffith Lake	Tiger trout	0.29	0.72	2.21	1.97	0.00	0.00
	Fathead minnows	1.98	3.30	0.00	0.00	0.23	0.00
Middle Griffith Lake	Tiger trout	0.00	0.00	0.00	0.00	0.00	0.00
	Fathead minnows	29.03	50.47	0.00	0.00	45.62	29.00
Sackett Reservoir	Tiger trout	4.14	0.30	3.52	2.80	0.00	0.00
	Brook trout	1.47	1.30	0.98	1.13	0.00	0.00

Initial observations suggest that tiger trout grow well and can suppress populations of undesirable fish in lakes containing small-bodied minnows by upwards of 97% (**Figure 4**). For example, based on catch rates in nets, fathead minnows were much more numerous in the three lakes where tiger trout were either absent (Middle Griffith) or only present for one year (Granby #2 and Granby #12) compared with the two lakes where tiger trout were present for 3 years (Cottonwood Lake #4 and Main Griffith). In addition, tiger trout grew from an average of 3.76 inches at time of stocking to 19.2 inches after 3 years in Main Griffith. Continued study and monitoring is needed to validate this apparent strong influence of tiger trout.

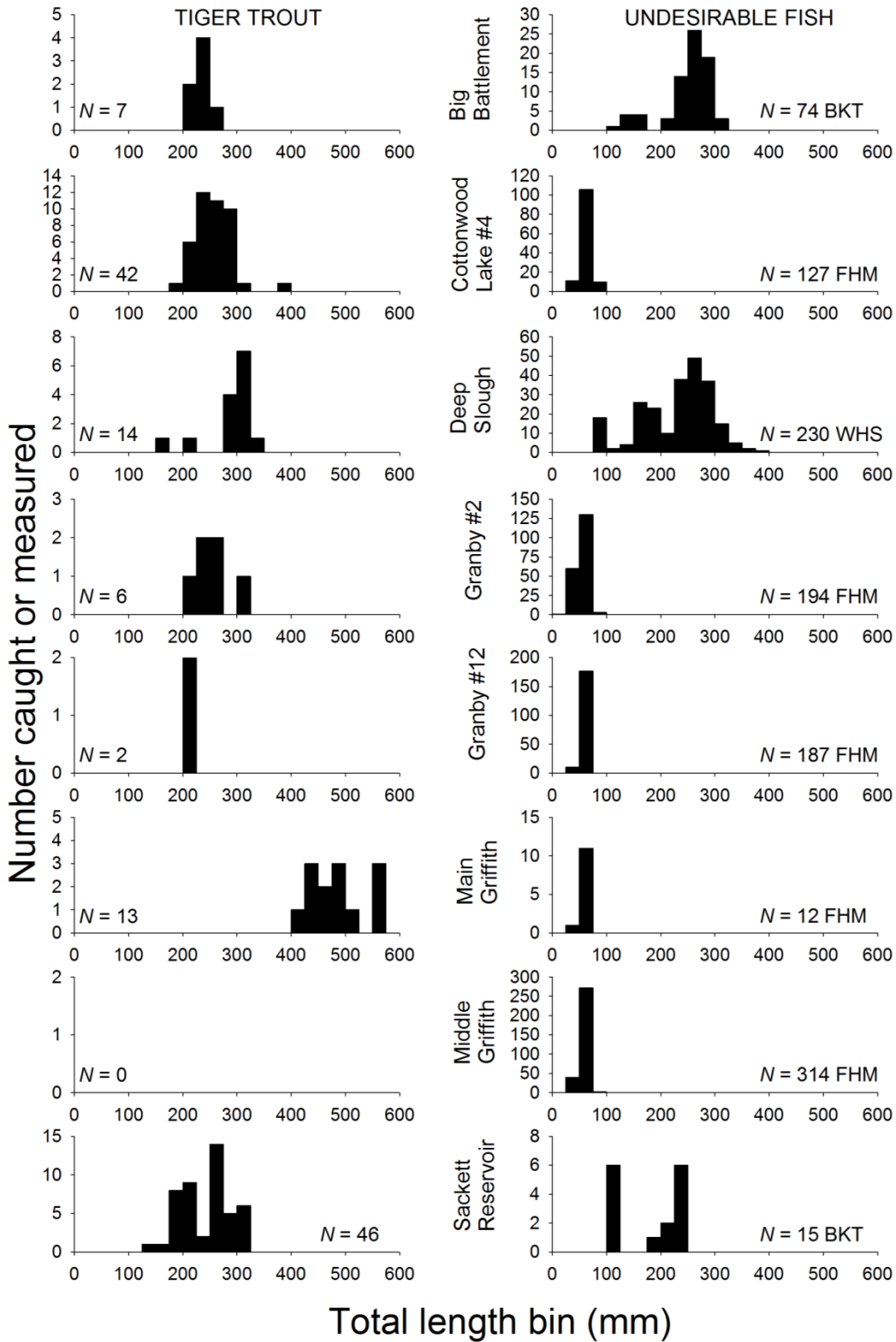


Figure 3. Length-frequency distributions of tiger trout and undesirable fish captured and measured in each study lake. For the undesirable fish, sample size numbers do not necessarily reflect the total catch as subsampling was required in some lakes. Note that the y-axes differ.

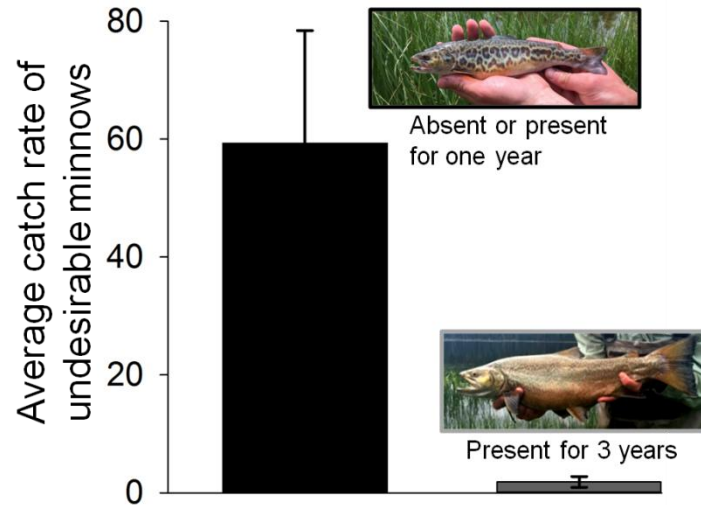


Figure 4. Mean catch rate (number/hour) of undesirable fathead minnows across all sampling gear types in lakes where tiger trout were either absent or present for one year ($N = 3$) versus those where tiger trout were present for 3 years ($N = 2$).

Acknowledgments

This research project is being conducted in collaboration with Eric Gardunio and Ben Felt, Area Aquatic Biologists.

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Project C. Population assessment of walleye and rainbow smelt in Horsetooth Reservoir

Status: Ongoing

Purpose and Objectives: Walleye (*Sander vitreus*) are popular sport and food fish in Colorado. The Colorado Department of Public Health and Environment has characterized the risk associated with consuming walleye or other sport fish contaminated with mercury (Hg) in waters of the state. In Horsetooth Reservoir, walleye Hg concentrations are dependent on the assemblage of prey eaten by walleye. Hg concentrations are reduced below consumption advisory levels (0.3 ug/g wet mass) for certain size or age-classes of walleye when more energy dense (4,868 J/g), low Hg prey fish like rainbow smelt (*Osmerus mordax*)—a naturally reproducing forage fish in the reservoir—represent high fractions of the diet and less energy dense (2,942 J/g), high Hg invertebrate prey like crayfish are largely excluded from the diet (Johnson et al. 2015).

Rainbow smelt were first introduced into Horsetooth Reservoir in 1983 to support a forage base for walleye. Their numbers expanded and walleye growth and condition improved greatly (Jones et al. 1994). However, the density of rainbow smelt started to decline in 1995 and smelt appeared extirpated by 2000. The body condition of walleye also declined over this period (Johnson and Goettl 1999) and remained low ultimately resulting in the establishment of a consumption advisory for walleye in 2007. Sometime after 2008, the rainbow smelt population rebounded and is now at relatively high abundance (Johnson et al. 2015). Our understanding of what is driving the volatile population dynamics of rainbow smelt in Horsetooth Reservoir is poor, and there is currently no dedicated standard monitoring program for rainbow smelt despite their importance to maintaining high feeding and growth in walleye and keeping walleye Hg concentrations at relatively low levels.

The primary objectives of this project are to (1) establish a standard monitoring program for rainbow smelt in Horsetooth Reservoir using a combination of pelagic gill netting and hydroacoustics surveys, (2) collect additional biological information from both walleye and rainbow smelt (i.e., diet, stable isotope, age-and-growth, energy density, and Hg information) to bolster existing datasets and use these data to assess how the populations respond to fluctuations in smelt abundance, (3) reinstate a zooplankton, *Mysis*, and temp-DO monitoring program on the reservoir, and (4) compare contemporary data to past data to try and diagnose potential food-web related factors influencing the dynamics of rainbow smelt.

Methods

Biological samples (diet, muscle tissue, otoliths, and some whole bodies for energy density estimation) were collected from walleye in May 2017 during the annual spring nearshore horizontal gill netting survey conducted by Kyle Battige, Area Aquatic Biologist. We conducted a standard depth-stratified pelagic gill netting survey for rainbow smelt and other larger pelagic oriented fish during August 2017 when the reservoir was thermally stratified. The primary goal of this netting survey was to characterize the distribution of different species of fish in different regions of the reservoir to inform the nocturnal hydroacoustics survey conducted during the same period, but to also collect biological samples of rainbow smelt for diet, Hg, and age-and-growth

analysis. The hydroacoustics survey followed similar methods as described by Johnson and Goettl (1999) and those data are currently being analyzed.

During the pelagic gill netting survey, we fished a series of three curtain-style experimental gill nets custom built to capture smelt and a series of three standard vertical gill nets to capture larger fish (mesh sizes ranged from 1/2" to 2" bar measure) at a standard sampling station in each of three basins in Horsetooth Reservoir (Soldier, Dixon, and Spring Canyon) (**Figure 1**). Net sets in Soldier and Dixon Canyon were overnight, whereas nets in Spring Canyon were set for short periods (2 hours) over a single day-dusk-night sequence to collect fresh biological samples. The curtain nets were 100' long × 17' deep and consisted of four 25' long randomized micro-mesh panels [1/4" (0.10 mm); 3/8" (0.12 mm); 1/2" (0.15 mm); 5/8" (0.20 mm) bar measure]. Based on vertical temperature profiles, we suspended one curtain net within the epilimnion (sampled 2-7 m depths), thermocline (12-17 m depths), and hypolimnion (25-30 m depths) in each basin. The vertical gillnets extended from the surface to the bottom. Captured fish were measured for fork (FL) and total length (TL) in mm and weighed to the nearest 0.1 gram. A systematic subsample of rainbow smelt was collected from each basin and depth-strata for laboratory analysis.



Figure 1. Picture of curtain net (left) and standard vertical gill net (right) used to sample rainbow smelt and other larger pelagic oriented fish in Horsetooth Reservoir during August 2017.

Results and Discussion

Biological samples are currently being processed in the laboratory. Walleye otoliths and zooplankton samples are being analyzed by Dr. Brett Johnson in the Department of Fish, Wildlife, and Conservation at Colorado State University. Andy Treble, Aquatic Research Scientist, is analyzing the hydroacoustics data with the assistance of Pat Neilson at Hydroacoustic Technology, Inc. I focus reporting here on fish distribution patterns observed during the August 2017 netting efforts to inform the hydroacoustics analysis.

Catch in Curtain Nets

Rainbow smelt dominated the catch in curtain nets in each depth-strata and basin sampled, and were largely concentrated within the thermocline (10-20 m depths) where temperatures ranged

from 10-18°C and dissolved oxygen concentrations ranged from 4-5 mg/L (**Figure 2**). In the epilimnion (0-10 m depths), temperatures ranged from 20-22°C and dissolved oxygen levels ranged from 7-8 mg/L. Temperatures in the hypolimnion (>20 m depths) were 8-10°C and dissolved oxygen remained slightly above 5 mg/L at all depths. In each basin, 100% of the catch in the thermocline and hypolimnion was rainbow smelt, whereas gizzard shad (*Dorosoma cepedianum*) appeared at measurable levels (10-29% of catch) in the epilimnion in Dixon and Spring Canyon.

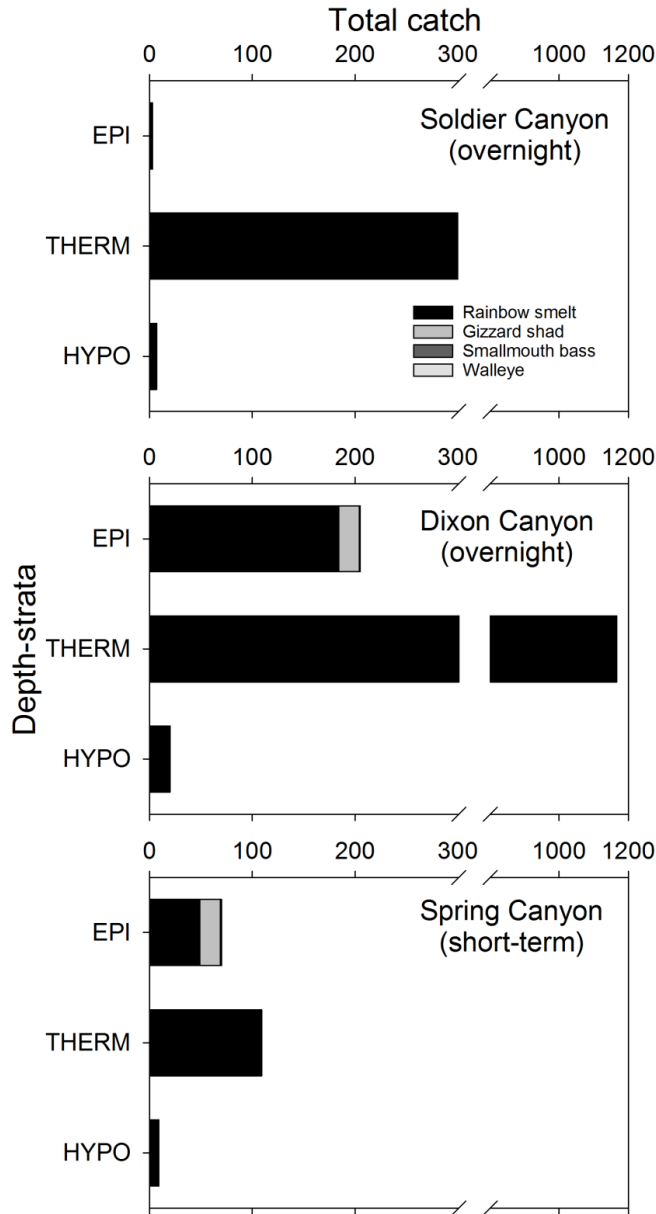


Figure 2. Summary of catch in curtain nets fished within different depth strata [EPI = epilimnion (sampled 2-7 m depths), THERM = thermocline (12-17 m depths), and HYPO = hypolimnion (25-30 m depths)]. Curtain nets were set overnight in Soldier and Dixon Canyon, but for only 2 hours over a single day-dusk-night sequence in Spring Canyon.

Catch in Vertical Gill Nets

Overnight catch in vertical gill nets was low, and most fish were captured at depths within the warm epilimnion (0-10 m) (**Figure 3**), and thus, largely segregated from the concentration of rainbow smelt within the thermocline (10-20 m depths). The catch was dominated by smallmouth bass (*Micropterus dolomieu*) and walleye, but one rainbow smelt was captured in Soldier Canyon and five white bass (*Morone chrysops*) were captured in Spring Canyon.

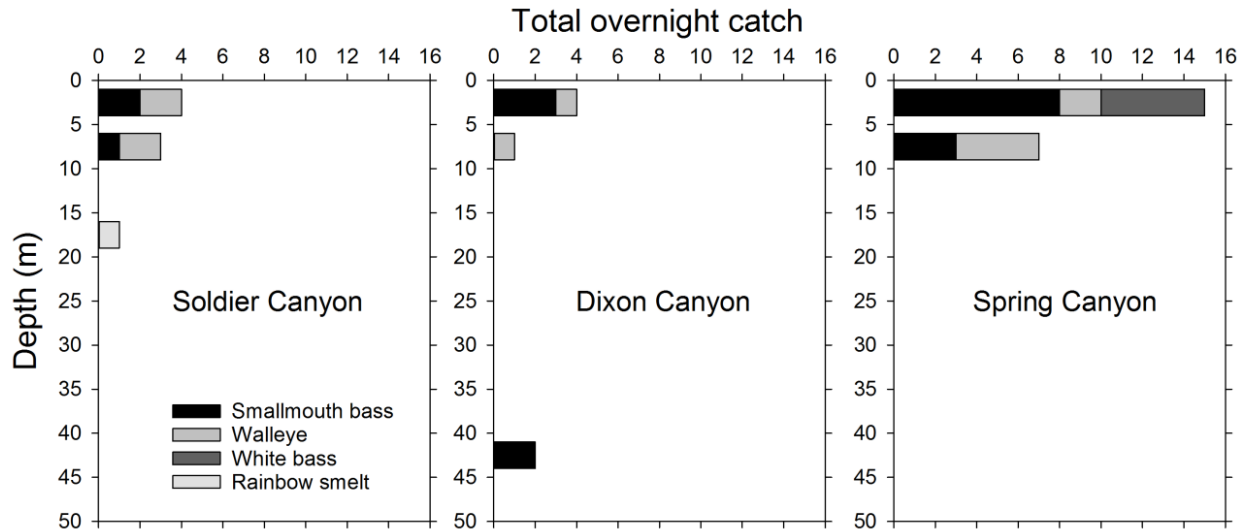


Figure 3. Summary of total catch in a standard suite of three vertical gill nets set overnight in each basin of Horsetooth Reservoir in August 2017.

Implications for Estimation of Rainbow Smelt Density from Hydroacoustics

Catch in nets during peak thermal stratification indicated that fish below 10 m in depth and suspended within the water column at depths down to 35-40 m were predominately rainbow smelt. Thus, hydroacoustic backscatter from those depths could be attributed entirely to rainbow smelt. Catch in the warm epilimnion (depths <10m) however, was mixed, but included reasonable fractions of rainbow smelt, particularly in Spring and Dixon Canyon. With the exception of gizzard shad however, non-target species present offshore in the epilimnion were segregated from rainbow smelt by size. Non-target fish like smallmouth bass and walleye were mostly >200 mm TL, whereas fish <200 mm TL were either rainbow smelt or gizzard shad (**Figure 4**).

This length cutoff could be used to filter out larger dispersed single targets from epilimnetic depths or depths below 10 m prior to quantifying the backscatter from rainbow smelt through echo integration. Backscatter from the epilimnion could then be adjusted for the estimated fraction of gizzard shad present, given their overlapping size with rainbow smelt. In order to (1) streamline hydroacoustics data analyses for long-term monitoring purposes, (2) avoid the potential erroneous inflation of estimated fish densities at depths <10m from a narrower acoustic beam and reduced sample volumes at those depths, and (3) limit the inclusion of gizzard shad into echo integrals, restricting the analysis to depths ≥ 10 m where rainbow smelt predominate

and are concentrated may be the most standard and efficient method for monitoring changes in their abundance over time in Horsetooth Reservoir.

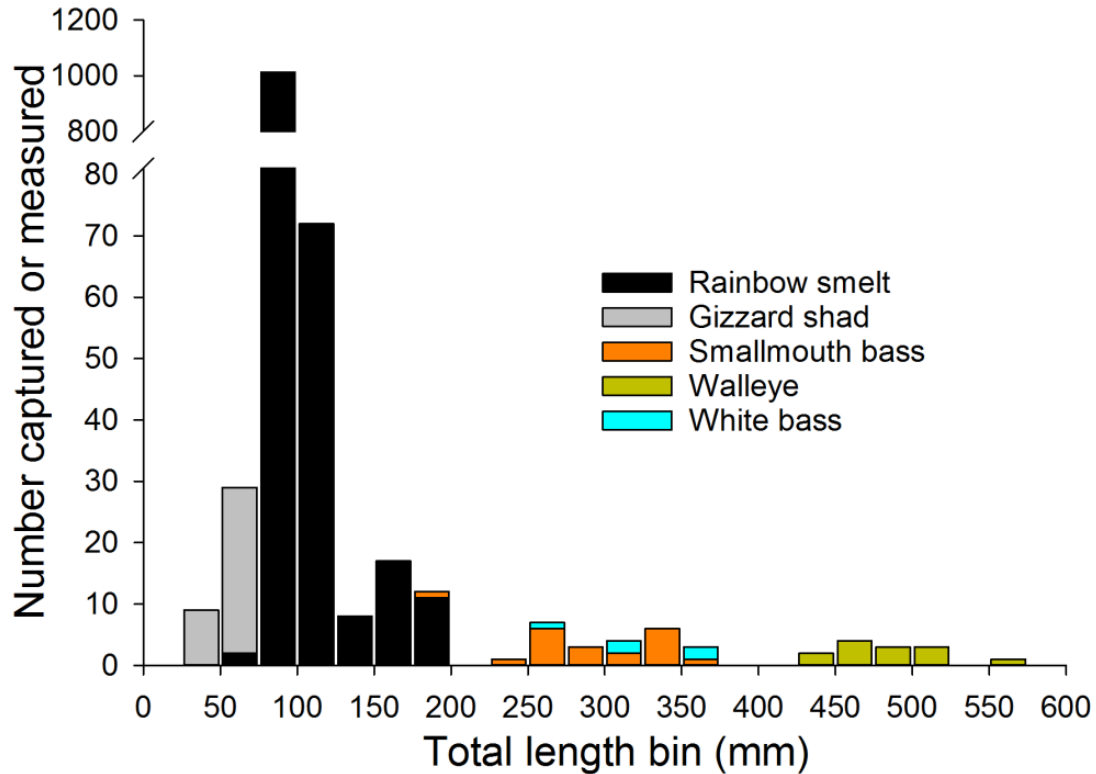


Figure 3. Length-frequency distributions of different species of fish captured in curtain nets and vertical gill nets pooled across each basin sampled in Horsetooth Reservoir during August 2017.

Acknowledgments

This research project is being conducted in collaboration with Kyle Battige—Area Aquatic Biologist, Andrew Treble—Aquatic Research Scientist, and Dr. Brett Johnson and Bill Pate at Colorado State University.

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III. Sport Fish Population Dynamics

Project A. Summer profundal index netting for tracking trends in the abundance of lake trout in coldwater lakes and reservoirs of Colorado: results from 2016

Status: Ongoing

Introduction

Summer profundal index netting (SPIN) is a quantitative method for rapidly estimating the population size of lake trout (Sandstrom and Lester 2009). Previous investigations by Colorado Parks and Wildlife concluded that SPIN is a viable alternative to more intensive methods (e.g., mark-recapture) for estimating and tracking trends in the abundance of lake trout in key coldwater lakes and reservoirs of Colorado to help guide management (Lepak 2011; Lepak 2013). Currently, four water bodies are sampled using SPIN methodology: Taylor Park Reservoir (surveyed in 2013), Lake Granby (2014), Grand Lake (2013, 2016), and Blue Mesa Reservoir (2011, 2014, 2016). Each reservoir is on either a two or three year survey rotation. During the 2016 field season, SPIN was conducted in Grand Lake (in collaboration with aquatic biologist Jon Ewert) and in Blue Mesa Reservoir (in collaboration with aquatic biologist Dan Brauch) to obtain lake trout population estimates. Results from these two surveys are reported here.

Methods

Summer profundal index netting methodology was developed by the Ontario Ministry of Natural Resources. For a detailed description of SPIN see Sandstrom and Lester (2009). In brief, this method uses suites of standardized gill nets (three 1.8×64 m nets consisting of eight panels with stretch mesh sizes of 57, 64, 70, 76, 89, 102, 114 and 127 mm placed in random order) to capture lake trout in such a way that allows us to estimate the density of lake trout directly (i.e., number per ha). These estimates of density are then scaled up to a total abundance based on the area of the lake or reservoir that was surveyed.

Catch rates of lake trout in gill nets (i.e., number caught per gill net set) fished in Colorado reservoirs are compared to catch rates of lake trout in the same type of gill nets in 700-800 other water bodies where concurrent estimates of lake trout density were also available. The catch is adjusted for the size-selectivity of the gill nets. Nets are set along the bottom in random orientation. Set locations are selected at random and stratified by depth (2-10 m, 10-20 m, 20-30 m, 30-40 m, 40-60 m, 60-80 m, and >80 m). Sampling is also stratified by different regions within the lake or reservoir if necessary, to account for potential differences in lake trout habitat. Sampling is conducted when surface temperatures exceed 18°C and the nets are set for two hours during daylight. Netting for surveys in 2016 was conducted from 19 to 20 July, 2011 in Grand Lake (**Figure 1**) and from 8 to 11 August, 2016 in Blue Mesa Reservoir (**Figure 2**). The power of this particular method is the use of data from hundreds of systems as a calibration tool to quantify lake trout densities in Colorado that can be used to estimate total abundance, versus techniques that just provide estimates of relative abundance through time and across systems.

Results and Discussion

Grand Lake

Sampling was completed over the course of two days, during which 36 nets were set capturing a total of 109 lake trout ranging in size from 260 mm to 900 mm fork length (FL; mean = 396 mm \pm 135 mm S.D.). Lake trout were most prevalent in the 10-20 m depth strata in 2016. In 2013, they were more distributed across 10-40 m depths. The depth distribution, size structure, and extent of the catch in 2016 produced a total lake trout abundance estimate of 3,131 lake trout \geq 260 mm FL [lower 68% confidence limit (LCL) = 2,561; upper 68% confidence limit (UCL) = 3,783], slightly above that estimated in 2013 (2,452; LCL = 1,974; UCL = 2,996; Lepak 2013; **Table 1**). The 68% confidence intervals bounding estimates from 2013 and 2016 overlap, so we cannot say with any degree of certainty that lake trout abundance increased between these two sampling events.

We did not detect a significant difference between the size structure of lake trout captured in 2013 versus those captured in 2016 (Kruskal-Wallis Test; $X^2 < 0.01$; $P > 0.9$). A number of notable fish $>$ 800 mm total length (TL) were captured in Grand Lake during the 2016 survey: 805 mm / 5.4 kg; 875 mm; 930 mm; 980 mm / 11.15 kg; 980 mm / 10.5 kg.

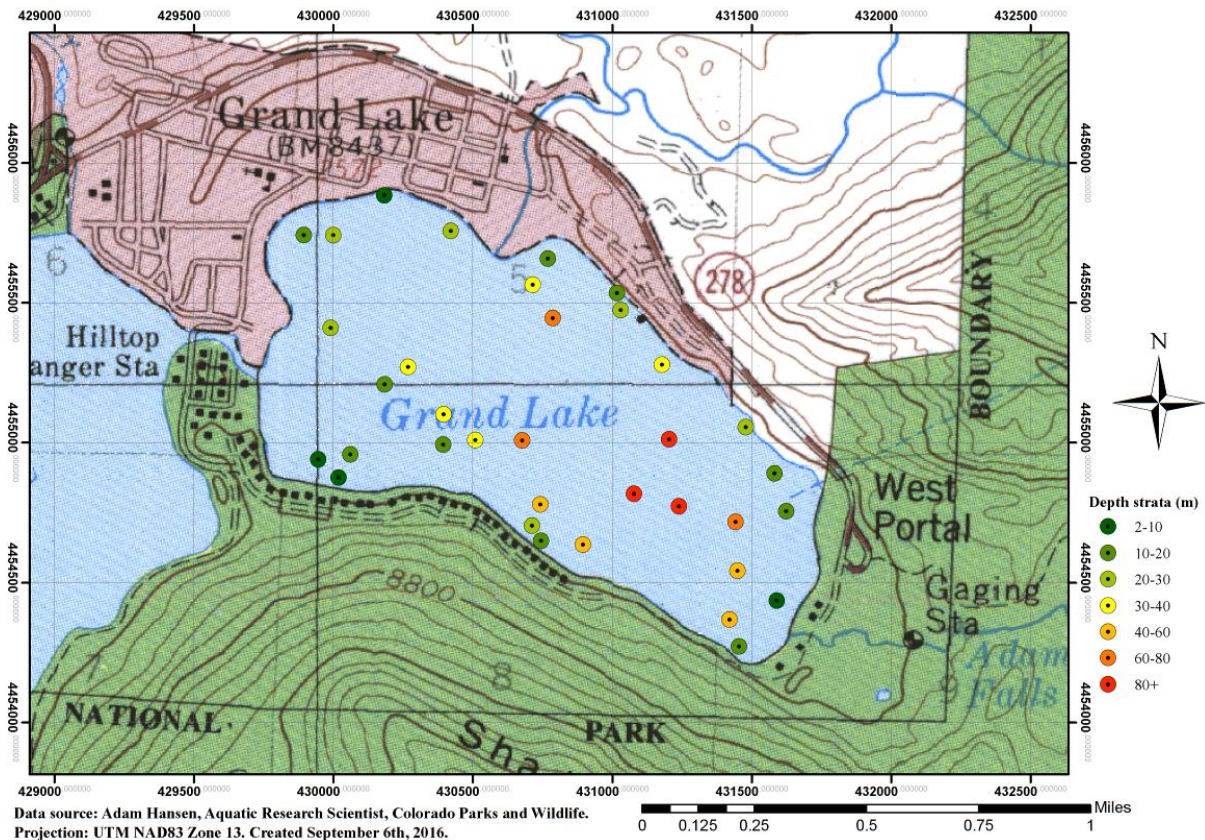


Figure 1. Map of Grand Lake, Colorado showing gill net set locations ($N = 36$; dots) and the associated depth strata sampled (colors).

Blue Mesa Reservoir

Sampling was completed over the course of four days, during which 83 nets were set capturing a total of 180 lake trout ranging in size from 180 mm to 900 mm FL (mean = 398 mm \pm 105 mm S.D.). Lake trout were most prevalent in 20-40 m depths across Iola, Cebolla, and Sapinero Basins. The depth distribution of lake trout captured in 2016 was similar to those captured in 2011, whereas fish captured in 2014 were more prevalent in the 30-40 m and 40-60 m depth strata. The depth distribution, size structure, and extent of the catch in 2016 produced a total lake trout abundance estimate of 24,368 lake trout \geq 180 mm FL (LCL = 16,538; UCL = 30,948). The catch of lake trout $<$ 250 mm FL was incidental (3% of catch). This abundance estimate best reflects that of fish \geq 250 mm FL as in previous surveys (Sandstrom and Lester 2009; **Table 1**). The abundance estimate from 2016 was lower, but on par with the 2014 estimate, suggesting that the population size of lake trout in Blue Mesa Reservoir has changed little over this two year period (**Figure 3**).

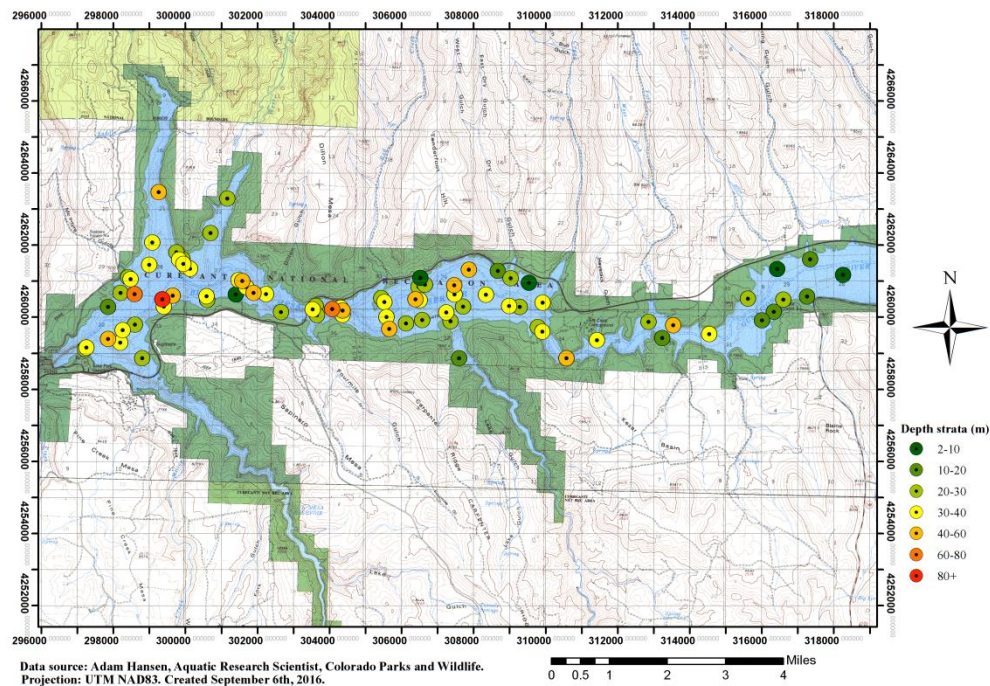


Figure 2. Map of Blue Mesa Reservoir, Colorado showing gill net set locations ($N = 83$; dots) and the associated depth strata sampled (colors).

We examined whether there has been a disproportionate change in the estimated abundance of lake trout \geq 363 mm FL or 400 mm TL when compared to all fish vulnerable to the gear in Blue Mesa Reservoir over the period of record. In general, this length cutoff encompasses the most piscivorous fraction of the lake trout population, and those most vulnerable to anglers and ongoing removal efforts (Lepak 2011; Pate et al. 2014). Abundance estimates for this separate size group of fish were lower, but exhibited a similar temporal pattern as those incorporating all sizes of lake trout. This indicates that there has not been a disproportionate change in the abundance of this secondary size group when compared to all sizes of fish over the period of record (**Figure 3**). The large deviation between estimates for each size group within each year

indicates that there is a healthy number of smaller, presumably younger fish available to recruit into the larger more piscivorous size class as would be expected from a naturally reproducing population of lake trout.

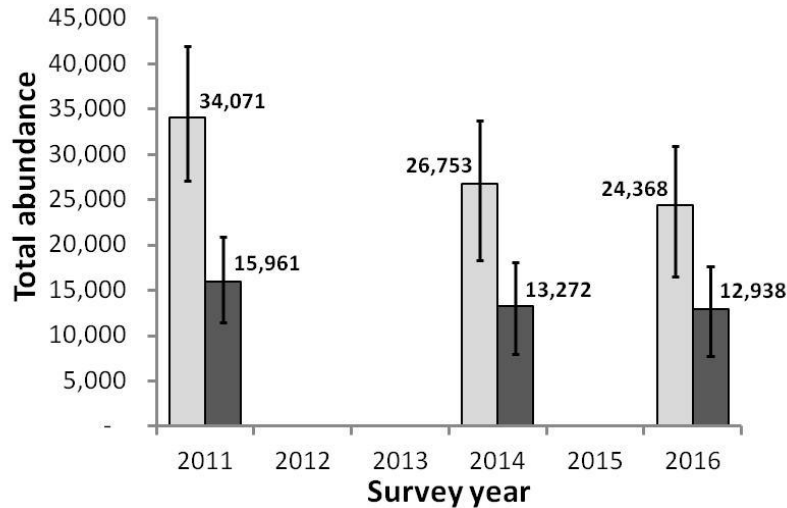


Figure 3. Abundance estimates for all lake trout vulnerable to the sampling gear (generally those ≥ 250 mm FL or 275 mm TL) in Blue Mesa Reservoir (light gray bars) and just those ≥ 363 mm FL or 400 mm TL (dark gray bars) from all SPIN surveys conducted in this reservoir to date. Error bars represent 68% confidence intervals.

Table 1. Summary data from each SPIN survey conducted in each lake and reservoir to date. Abundance estimates are for all lake trout vulnerable to the sampling gear (generally those ≥ 250 mm FL or 275 mm TL). The acronym LCL stands for lower 68% confidence limit, and UCL stands for upper 68% confidence limit for the abundance estimate. Adjusted CUE is the area-weighted (area of different depth strata) catch of lake trout per gill net set, after correcting the catch for size-selectivity. Asterisks indicate the presence of *Mysis diluviana*.

Survey year	Lake or reservoir	Number of sets	Number of lake trout caught	Mean TL (mm)	S.D. of TL (mm)	Adjusted CUE	Density (fish/ha)	Total area surveyed (ha)	Abundance estimate	LCL	UCL
2011	Blue Mesa	81	129	437	110	2.29	11.14	3,059	34,071	27,144	41,929
2013	Grand Lake*	36	87	419	107	2.61	12.71	193	2,452	1,974	2,996
	Taylor Park*	36	271	416	94	4.03	19.61	610	11,950	9,871	14,341
2014	Blue Mesa	81	211	425	97	1.61	7.85	3,409	26,753	18,383	33,716
	^a Lake Granby*	71	501	417	79	11.78	57.26	2,780	159,193	135,533	186,844
2016	Blue Mesa	83	180	438	114	1.47	7.15	3,409	24,368	16,538	30,948
	Grand Lake*	36	109	436	147	3.34	16.22	193	3,131	2,561	3,783

^aEstimates for Lake Granby are subject to change. Food web interactions could make lake trout more vulnerable to the sampling gear causing the SPIN method to overestimate their abundance. This is currently being evaluated.

Lastly, we did not detect any significant differences in the size structure of lake trout captured during SPIN in 2011, 2014, and 2016 (Kruskal-Wallis Test; $\chi^2 = 3.21$; $P = 0.20$) (**Figure 4**). A number of notable fish >800 mm TL were captured in Blue Mesa Reservoir during the 2016 survey: 818 mm / 5.78 kg; 859 mm / 7.70 kg; 860 mm; 872 mm / 9.25 kg; 902 mm / 9.73 kg; 972 mm. All were released successfully.

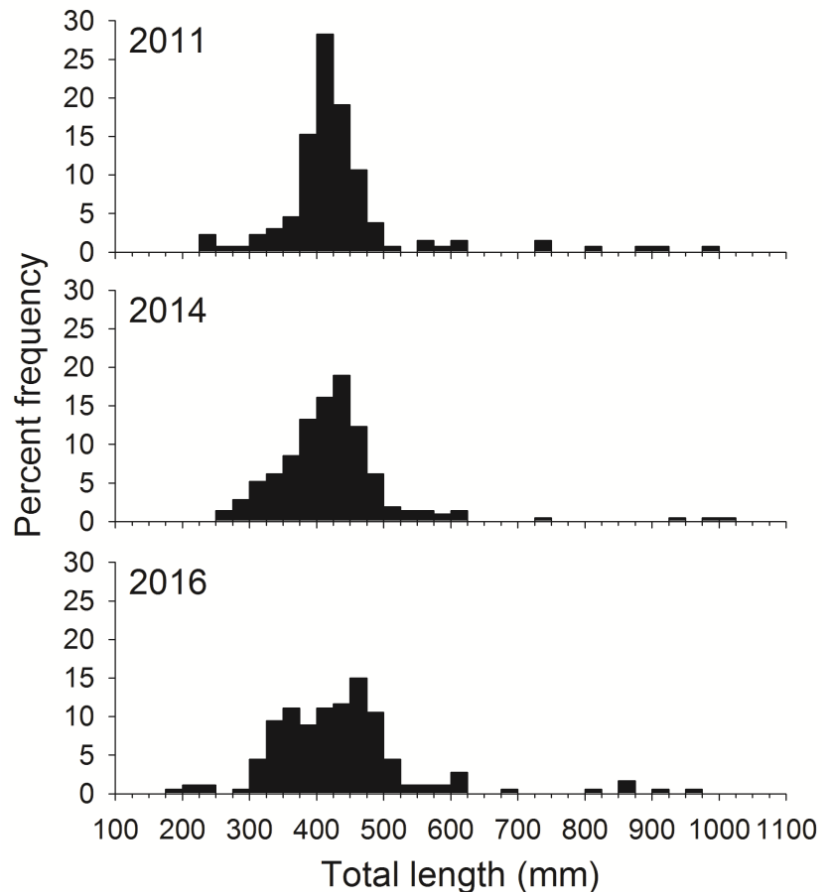


Figure 4. Length-frequency distributions of lake trout captured during consecutive SPIN surveys on Blue Mesa Reservoir.

Acknowledgments

I would like to thank Dan Brauch and Jon Ewert for providing equipment and support in the field. I also thank Chris Hill, John Kesler, Sirena Mares, Griffin Pinkus, Katie Rohwer, Jedidiah Thompson, Estevan Vigil and Ben Wasserstein for their assistance with these surveys and contributing long hours in the field. Ben Wasserstein created the maps.

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Project B. Model evaluation of a reduced maximum length limit for lake trout suppression in Blue Mesa Reservoir

Status: Complete

Purpose and Objectives: Inform ongoing management efforts aimed at recovering the kokanee salmon population while maintaining a trophy lake trout fishery in Blue Mesa Reservoir. Specific objectives were to (1) apply existing models to evaluate the effect of a reduced maximum length limit for lake trout suppression on Blue Mesa Reservoir (reducing from 800 mm TL to 700 mm TL) on (a) the equilibrium abundance of lake trout and (b) the extent of predation on kokanee under contemporary levels of harvest from both anglers and CPW autumn gill netting efforts; (2) apply a yield-per-recruit model to identify the long-term sustainable harvest levels of lake trout under both the contemporary (800 mm) and proposed (700 mm) length limits to see if there is a notable difference.

Approach

Objective 1.—I first adapt the baseline lake trout population model of Pate et al. (2014) to reflect contemporary removal efforts (maximum length limit = 800 mm TL) and then to reflect the reduced maximum length limit (700 mm TL). The baseline model of Pate et al. (2014) applied a conditional fishing mortality rate ($f_m = 0.2307$) in addition to a conditional natural mortality rate ($c_m = 0.3589$) to age-4 through age-9 lake trout as these age-classes are currently either targeted for removal or are most vulnerable to harvest by anglers. Only conditional natural mortality rate was applied to the other age-classes (maximum age modeled = 25).

Based on length-at-age data, a von Bertalanffy growth function (vBGF), and an age-length key (Pate et al. 2014), the 700-800 mm size bin includes age-8 (estimated length from vBGF = 650 mm) through age-11 (779 mm) lake trout, although most age-8 and age-9 lake trout sampled were below 700 mm. To estimate the equilibrium abundance of different age-classes of lake trout and their associated predation on kokanee under a maximum length limit of 800 mm for removal, I applied the same conditional fishing and natural mortality rates estimated above to age-4 through age-11 lake trout in the baseline population model. I then sequentially removed fishing mortality (leaving only natural mortality) from subsequent age-classes, starting with age-11 and ending with age-8 lake trout to reflect the switch in the length limit from 800 mm to 700 mm.

Simulations were run assuming two natural survival rates for lake trout age-10 and older: (1) annual survival = 64%, and (2) annual survival = 88% (Pate et al. 2014). Catch curve analysis from Pate et al. (2014) suggested that the annual survival rate of age-10 and older lake trout was higher than 64%, but hard to estimate given uncertainty in catch-at-age numbers for older fish. These two annual survival rates bracket the minimum and maximum rates we would expect for older lake trout in Blue Mesa Reservoir. For each simulation, the total number of lake trout \geq age-10 and total predation on kokanee (based on age-specific estimates of predation from Pate et al. 2014) were calculated and compared.

Objective 2.—The analysis above was meant to mirror the approach of Pate et al. (2014). For the second objective, I incorporate two new components into the population model of Pate et al. (2014) to estimate the long-term sustainable harvest levels of lake trout under each maximum

length limit: (1) a Beverton-Holt stock-recruitment function with steepness parameterization, and (2) a curve describing the relative vulnerability of different age-classes of lake trout to harvest by anglers and CPW netting efforts.

The Beverton-Holt stock-recruitment function with steepness parameterization describes in relative terms the relationship between maximum recruitment (58,500 age-0 lake trout; Pate et al. 2014) and spawning stock biomass. The steepness parameter (h), describes how quickly maximum recruitment is achieved at low levels of spawning stock biomass. The time series of SPIN estimates for the population size of harvestable lake trout in Blue Mesa Reservoir (~28,300 on average between 2011 and 2016; Hansen 2016) and of the estimated number of lake trout harvested by anglers and removed by CPW (~5,200 annually on average) suggests that the lake trout population is at equilibrium and subject to a sustainable exploitation rate (u) of about 0.18. Therefore, I iteratively fit the steepness parameter such that predictions for the equilibrium abundance of harvestable lake trout and the sustainable yield of lake trout at $u = 0.18$ from the population model matched 28,300 and 5,200, respectively. The estimate for the steepness parameter was $h = 0.64$, on par with what we would expect for salmonids (Meyers et al 1999).

Vulnerability curves help account for the accidental removal of smaller than average, older fish in the age-structured population model given the observed variation in length-at-age for Blue Mesa Reservoir lake trout. Different vulnerability curves were generated to reflect the different maximum length limits: (1) age-4 to age-11 lake trout most vulnerable to harvest (reflective of the current limit of 800 mm); (2) age-4 to age-9 lake trout most vulnerable (reflective of the proposed 700 mm limit); (3) age-4 to age-7 lake trout most vulnerable (most extreme representation of the reduced limit) (**Figure 1**). Vulnerability curves were generated by fitting Gaussian functions to age-specific estimates of exploitation rate developed by Pate et al. (2014).

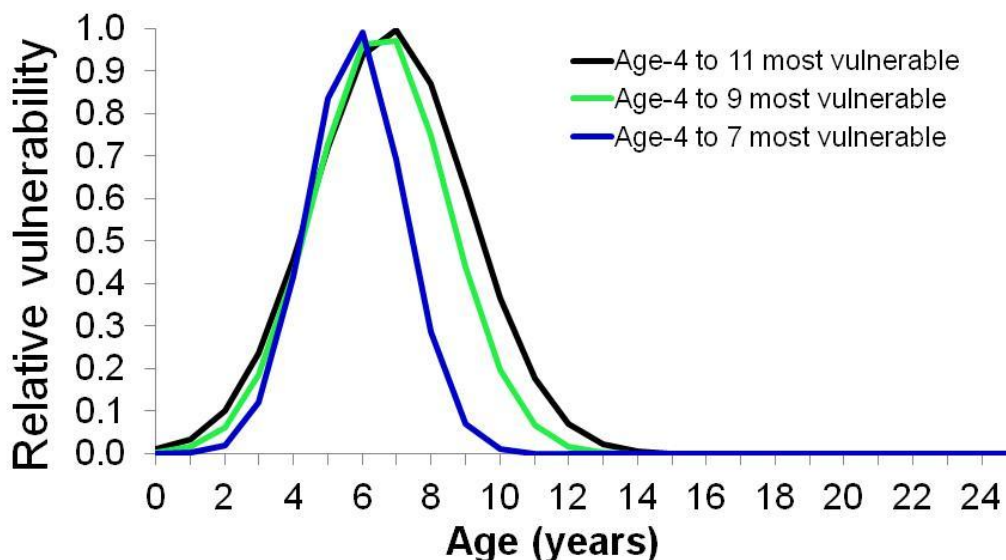


Figure 1. Relative vulnerability of different age-classes of lake trout to harvest by anglers and CPW removal efforts under the current maximum length limit for removal (800 mm TL; black curve and used as the baseline for comparison), under the new proposed limit (700 mm TL; green curve), and under the most extreme representation of the reduced limit (blue curve).

Results and Discussion

Objective 1

Model simulations indicated that reducing the maximum length limit for lake trout removal from 800 mm to 700 mm (by consecutively removing fishing mortality from age-11 through age-8 lake trout in the model) could lead to notable increases in the abundance of fish \geq age-10, with minor increases in expected predation on kokanee. However, the magnitude of the predicted increase for abundance and predation was highly sensitive to the assumed annual survival rate of fish \geq age-10 (64% vs. 88%; **Table 1**).

It is important to note that: (1) I adapted the baseline model of Pate et al. (2014) by applying fishing mortality to age-10 and age-11 lake trout (given their average length in relation to the 800 mm limit). The fishing mortality rate applied ($fm = 0.2307$) was also likely an overestimate for these two age-classes. Therefore, the estimated percent increases in abundance and predation generated from the reduced length limit reflect maximum expectations under current equilibrium conditions; (2) the scenario where fishing mortality was removed from age-8 and age-9 in addition to age-10 and age-11 lake trout was designed to represent the most extreme case in that all individuals from these age-classes captured are released. Even though a proportion of age-8 and age-9 fish fall within the 700-800 mm size bin, this scenario still provides maximum expectations for potential increases in predation on kokanee since fish from both of these age-classes are on average <700 mm and will still be removed regardless of the reduced limit. Overall, results from model simulations using the first approach described above support the reduced maximum length limit of 700 mm for lake trout removal in Blue Mesa Reservoir.

Table 1. Results from model simulations using the approach described under objective 1 above. Simulations were conducted assuming two annual survival rates for fish \geq age-10 as indicated by light and dark shading. Fishing mortality was applied to the different sets of age-classes indicated under the “Age-group fished” column. Age-4 to 11 reflects the 800 mm TL maximum length limit and was used as the baseline simulation for calculating percent changes in lake trout abundance and predation on kokanee for simulations reflecting the reduced length limit; Age-4 to 9 reflects the 700 mm limit; Age-4 to 7 reflects the most extreme case.

Age-group fished	Annual survival (\geq age-10)	Equilibrium abundance (\geq age-4)	Equilibrium abundance (\geq age-10)	Predation on kokanee (number)	Percent change in abundance (\geq age-4)	Percent change in abundance (\geq age-10)	Percent change in predation
Age-4 to 11	88%	19,669	450	1,473,209	-	-	-
Age-4 to 9	88%	20,240	1,021	1,490,673	+2.9 %	+126.8 %	+1.2 %
Age-4 to 7	88%	21,030	1,725	1,516,457	+6.9 %	+283.2 %	+2.9 %
Age-4 to 11	64%	19,527	309	1,469,159	-	-	-
Age-4 to 9	64%	19,615	396	1,472,047	+0.4 %	+28.3 %	+0.2 %
Age-4 to 7	64%	19,974	669	1,484,984	+2.3 %	+116.8 %	+1.1 %

Objective 2

Reducing the maximum length limit from 800 mm to 700 mm would allow more large fish to spawn, thus adding more biomass to the spawning stock, which could alter the sustainable harvest of lake trout from the population and increase the exploitation rate required to maintain the same equilibrium abundance of fish in the system (whatever the target abundance may be). The second modeling approach described above was once again designed to evaluate maximum potential changes in these two factors.

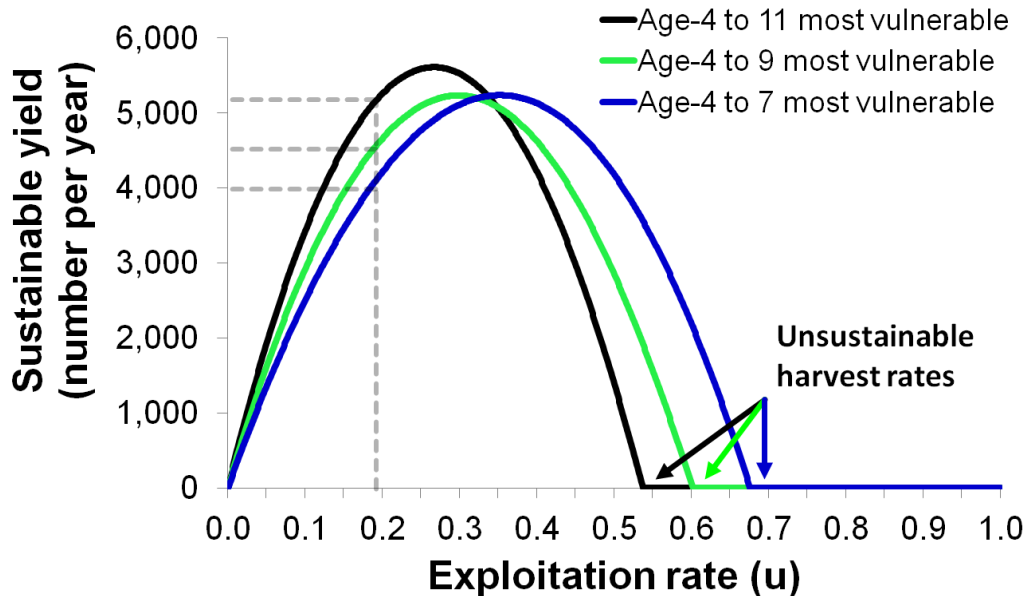


Figure 2. Estimated sustainable yield of lake trout (i.e., equilibrium number that can be harvested or removed every year) as a function of exploitation rate under the current maximum length limit for removal (800 mm TL; black curve and used as the baseline for comparison), under the new proposed limit (700 mm TL; green curve), and under the most extreme representation of the reduced limit (blue curve). The dashed gray lines denote the current, estimated exploitation rate of lake trout in Blue Mesa Reservoir and the associated sustainable yield corresponding to each length limit scenario.

Model simulations using the second approach indicated that (1) reducing the length limit from 800 mm to 700 mm would increase the range of sustainable harvest rates for lake trout in Blue Mesa Reservoir, but decrease the maximum sustainable yield from the population under equilibrium conditions (black vs. green curves; **Figure 2**), and (2) harvest rate would need to increase by approximately 12-14% under the reduced length limit to maintain the same equilibrium abundance as that estimated for the current length limit (black vs. green curves; **Figure 3**).

While operating under the reduced length limit in the model, the harvest rate required to maintain the same equilibrium abundance of lake trout increased because removal was more concentrated on a reduced subset of age-classes (age-4 to age-9 instead of age-4 to age-11). Since removal was no longer dispersed over a broader range of age-classes and more large fish were

contributing to the spawning stock, maximum sustainable yield declined slightly, but the range of sustainable harvest rates expanded slightly.

Overall, these shifts appear relatively minor, particularly considering that they represent maximum expectations. Between 2009 and 2015, an average of only 31 lake trout (range: 11-64) within the 700-800 mm size bin were removed by CPW netting efforts while operating under the 800 mm limit. Under contemporary conditions estimated for Blue Mesa Reservoir (equilibrium abundance of ~28,300 harvestable lake trout and a harvest rate of ~0.18), the model predicted that 161-368 lake trout within age-classes representing the 700-800 mm length bin would be released and allowed to recruit to the spawning stock if the 700 mm limit was implemented. Collectively, results from both modeling approaches used in this analysis support reducing the maximum length limit for lake trout removal in Blue Mesa Reservoir from 800 mm to 700 mm.

When interpreting the results from the model simulations above, it is important to acknowledge key assumptions: (1) the number of harvestable lake trout in Blue Mesa Reservoir estimated from SPIN represents their true abundance; (2) the lake trout population is currently at equilibrium, as suggested by SPIN and average estimates of lake trout harvest from previous creel surveys and CPW netting efforts; (3) the estimated steepness parameter describing the stock-recruitment relationship for lake trout in Blue Mesa Reservoir is correct. As more information is gathered, it will be important to continuously update the models presented above and adapt management as necessary.

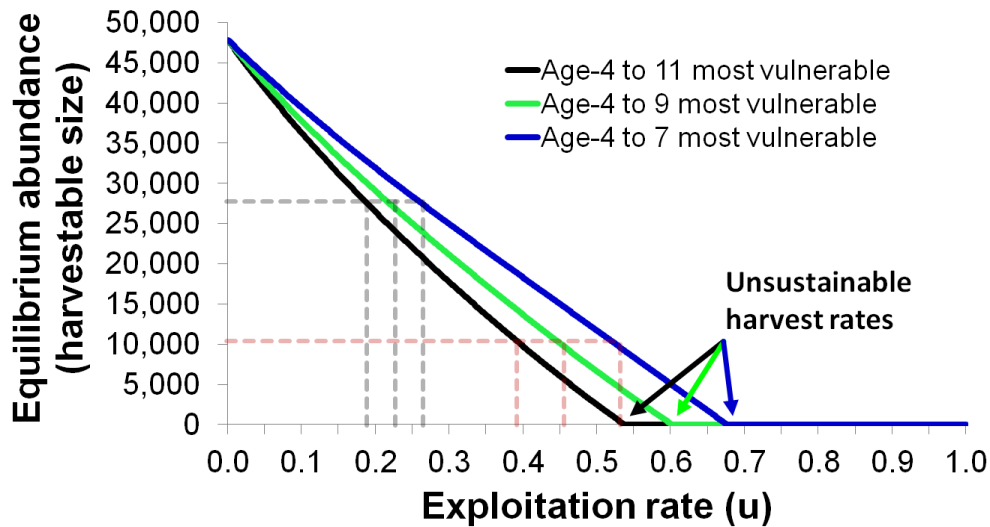


Figure 3. Estimated equilibrium abundance of harvestable lake trout as a function of exploitation rate under the current maximum length limit for removal (800 mm TL; black curve and used as the baseline for comparison), under the new proposed limit (700 mm TL; green curve), and under the most extreme representation of the reduced limit (blue curve). The dashed gray lines denote the current, estimated equilibrium abundance of lake trout in Blue Mesa Reservoir and the corresponding exploitation rates associated with the different length limit scenarios. The dashed red line denoting an abundance of 10,000 lake trout is reflective of the population size of lake trout in the early 2000's and is meant for comparative purposes only.

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Project C. Biological effectiveness of incentive-based harvest tournaments for suppressing nonnative piscivores in fluctuating coldwater reservoirs

Status: Ongoing

Introduction

The effects of dams on river ecosystems are well documented (Petts 1984; Ligon et al. 1995; Poff et al. 1997; Stanley and Doyle 2003). In some regions, reservoirs created by dams allow for entrainment of nonnative piscivores that were once stocked by agencies or transplanted illegally to supplement sport fisheries (Martinez et al. 1994; Falke and Gido 2006; Wolff et al. 2012; Janac et al. 2013). Nonnative piscivores often have substantial negative effects on native fish and their natural or assisted dispersal from reservoirs can undermine efforts to recover endangered species (Tyus and Saunders 2000; Johnson et al. 2009; Breton et al. 2013; Zelasko et al. 2016). Conflict with anglers can arise if agency programs curtail the threat of nonnative sport fish in reservoirs; particularly if such programs exclude anglers and reduce fishing opportunity. Lack of cooperation may perpetuate conflict, which could undermine long-term conservation efforts. Therefore, it is important to evaluate alternative solutions that harmonize conservation efforts and sport fisheries by incorporating anglers (Mueller 2005; Cowx et al. 2010).

The Upper Colorado River Basin (UCRB), USA, is at the forefront of this issue. The UCRB contains critical habitat for the endemic Colorado pikeminnow *Ptychocheilus lucius*, humpback chub *Gila cypha*, bonytail chub *Gila elegans*, and razorback sucker *Xyrauchen texanus*. The basin is heavily impounded and most reservoirs contain nonnative piscivores, many originating from illicit introductions (Johnson et al. 2009; Wolff et al. 2012). The most prevalent species are northern pike *Esox lucius*, smallmouth bass *Micropterus dolomieu*, and walleye *Sander vitreus*. Channelization, blocked migration, altered flow and temperature, and establishment of nonnative piscivores that dispersed from reservoirs contributed to the imperilment of fish endemic to the basin and now inhibit recovery (Martinez et al. 1994; Stanford 1994; Tyus and Saunders 2000; Valdez and Muth 2005). Control of nonnative piscivores is a major objective for native fish recovery in the UCRB. Approximately US\$1 million is spent annually on removal of nonnatives from critical habitat (Johnson et al. 2009). Programs that mitigate the threat of nonnative piscivores in reservoirs while fostering education and cooperation could benefit recovery.

Invasive smallmouth bass are considered particularly problematic because of their ability to exert high levels of predation on native fish communities (Vander Zanden et al. 2004; Johnson et al. 2008). Aside from mechanical removal (Weidel et al. 2007; Breton et al. 2015), options for controlling nonnative piscivores often involve mandatory retention policies, cash incentives to anglers, or liberalized harvest. The efficacy of these approaches depends on fishing pressure, angler mentality, control program goals, and size of the water body (Beamesderfer et al. 1996; Martinez et al. 2009; Carey et al. 2011; Lopponow et al. 2013). For example, the growing contingent of sport anglers for invasive smallmouth bass in Washington State are against destroying individuals, so mandatory retention is not viable (Aday et al. 2009; Carey et al. 2011). Cash incentives boosted angler participation in suppressing nonnative lake trout in Lake Pend Oreille, Idaho. Here, anglers maintained heavy exploitation on lake trout during the onset of suppression while commercial netters worked to improve efficiency. Both approaches were

needed to suppress lake trout at the large scale of Lake Pend Oreille (Hansen et al. 2010; Wahl et al. 2015). However, paying anglers on a per fish basis while fronting the cost of mechanical removal can be prohibitively costly, even on small systems. Liberalizing harvest, with no additional incentive for anglers, has been dismissed as a viable control strategy for invasive smallmouth bass (Boucher 2005; Gomez and Wilkinson 2008; Lopponow et al. 2013).

Exploitation can cause a compensatory response in population metrics (e.g., fecundity and size-at-maturity) if reductions in abundance reduce density dependence. These responses increase the resilience of populations to overharvest (Rose et al. 2001; Zipkin et al. 2009; Syslo et al. 2011). Removal of invasive smallmouth bass from Little Moose Lake, New York, reduced the CPUE of adult piscivorous bass by 90% after 2 years. The native littoral fish community and the lakes food web recovered rapidly (Lepak et al. 2006; Weidel et al. 2007). However, during the 7 years of removal, strong year-classes of smallmouth bass were produced, and the overall CPUE of bass increased, primarily from a greater number of juvenile fish. A stage-structured model indicated that harvest likely reduced competition among reproductive bass, since a high per-capita recruitment rate (expected at low spawner density; Ricker 1975) along with high survival or maturation of juvenile fish was needed to generate overcompensation (Zipkin et al. 2008). Spawning and recruitment by smallmouth bass is complex (Ridgway et al. 1991; Gross and Kapuscinski 1997; Ridgway et al. 2002). The scarcity of empirical removal studies makes it difficult to generalize how other populations will respond to harvest (Zipkin et al. 2009; Lopponow and Venturelli 2014).

There are no documented attempts to suppress invasive smallmouth bass using a cost effective angler incentive program. Yet, this approach allows anglers to support management and could be effective in small systems alone or in conjunction with other methods. Anglers could limit recently introduced populations for which density-dependent recruitment might differ from more established populations (Shuter et al. 1987; Zipkin et al. 2008; Lopponow and Venturelli 2014). Smallmouth bass were present in Little Moose Lake for over 5 decades before removal started (Weidel et al. 2007). The primary objective of this study was to evaluate the efficacy of this approach at the onset of a removal program to inform future efforts and calibrate expectations for the UCRB and elsewhere. We quantified the harvest dynamics of anglers during a series of incentive-based fishing tournaments designed to suppress a population of smallmouth bass illegally introduced (within 15 years) into an oligotrophic UCRB reservoir. The tournaments occurred annually, and varied in duration (9 days vs. 24 days) and timing (pre-spawn vs. mostly post-spawn), so we were able to estimate angler effectiveness (represented by the age-specific catchability of bass) and quantify exploitation under alternative physical and biological conditions and logistically feasible tournament structures. We used field data collected during the tournaments to parameterize an age-structured population model to simulate the short- and long-term dynamics of smallmouth bass under alternative scenarios related to (1) angler effectiveness and effort level, (2) density-dependent recruitment (deterministic vs. stochastic), and (3) compensation in juvenile survival and maturity.

Methods

Study site.—Ridgway Reservoir is an oligotrophic 392 ha impoundment at 2,094 m elevation on

the Uncompahgre River in southwestern Colorado. The reservoir thermally stratifies by late June, and epilimnetic temperatures reach 18-22°C over summer. The fishery is managed for naturally reproducing brown trout *Salmo trutta* and stocked rainbow trout *Oncorhynchus mykiss*, but native longnose sucker *Catostomus catostomus*, stocked kokanee *O. nerka*, and illicitly introduced yellow perch *Perca flavescens* are present. Splake (male brook trout *Salvelinus fontinalis* × female lake trout *Salvelinus namaycush*) are stocked periodically to diversify the fishery.

Smallmouth bass were first confirmed in the reservoir in 2013, but anglers reported their presence 5 years prior. Three strategies were examined to suppress the growing population and limit escapement: eradication via rotenone, containment, and angler harvest. Eradication was not feasible given the volume of the reservoir. Containment efforts include construction of a net to block escapement over the spillway, but entrainment through the dam's outlet is still possible. An angler harvest program in the form of an incentive-based fishing tournament was selected as cost-effective approach to (1) exploit and suppress the population, (2) study population dynamics, and (3) assess the susceptibility or resilience of invasive smallmouth bass to harvest.

Tournament structure.—Tournaments were conducted 11-19 July 2015, 4-12 June 2016, and 7-30 July 2017. A set of prizes, one grand prize (Guide V-14 Tracker boat and trailer with 5-hp, four-stroke Mercury outboard; value = US\$4,500), and ten secondary prize packages each valuing US\$300, was the incentive. A fish tagging and raffle system was used for prize giveaway. To enter, licensed anglers had to euthanize and present their catch to representatives at a check station for processing. At first check-in, each angler provided contact information, received an identification number, and was given one raffle ticket per fish removed, regardless of size. Prior to the 2017 tournament, ten smallmouth bass independent of size were captured and released with a unique internal Passive Integrated Transponder (12 mm HDX PIT tags from Oregon RFID) that could not be detected by anglers. Of these ten, one was randomly selected as the grand prize fish and unveiled at tournament end. An angler won the boat outright if returned. Anglers won secondary prizes outright for returning the other PIT tagged fish. If no or not all PIT tags were returned, a raffle determined prize winners. In 2017, prize giveaway was entirely raffle based and fish were not PIT tagged. Prize structure encouraged anglers to remove all fish captured independent of size.

Angler creel.—We conducted a creel survey from 1 April to 30 September 2016 to determine if smallmouth bass were harvested outside the tournament. The survey used a stratified random design with instantaneous counts of anglers and access point interviews (Nuhold and Lu 1957; Schisler and Bowden 2012). We interviewed 1,594 anglers, 29% of the total number estimated to visit the reservoir during the count period. Over this period, 1,940 (SE = 771) smallmouth bass were caught and 1,496 (SE = 781) harvested. The majority of estimated catch (80%) and harvest (92%) occurred in June, the month of the tournament. During the 9-day contest, 1,140 smallmouth bass were known removals. Thus, creel estimates indicated that harvest was low and release rates were high (~53% in 2016) without an incentive. Additionally, less than 20% of the anglers interviewed before and after the tournament preferred to catch smallmouth bass. Therefore, we only used the known number of fish removed during the tournaments to quantify contemporary harvest rates for the population model.

Pre-tournament data collection.—Smallmouth bass were sampled with a Smith-Root 2.5 GPP boat electrofisher within a 2 week period during May-June (Weidel et al. 2007) prior to each tournament to characterize population size structure and tag fish for mark-recapture analysis. Captured fish were sexed, weighed (wet weight in g), measured (total length in mm; TL), and marked with a year-specific fin clip. The 2015 contest was a pilot study to assess tournament potential and estimate adult abundance. Therefore, sampling effort was reduced and only fish ≥ 150 mm TL were marked because these were considered most vulnerable to angling (Beamesderfer and Rieman 1988). We increased effort after 2015 to boost numbers of marked fish, strengthen estimates of size structure, and systematically sample shoreline in every region of the reservoir. After 2015, all fish independent of size were marked; fish ≥ 150 mm TL were given a unique Visible Implant Alpha tag (VI Alpha; Northwest Marine Technology, Inc.) to track growth and survival. On two occasions in 2016 and in 2017, 18-24 VI Alpha tagged fish were held in live pens for 24 hours to assess short-term handling mortality. No mortality was observed. Fish were released in the same region of capture.

Tournament data collection.—Fish from each angler or group of anglers for which catch had been combined at the check station were measured for TL, inspected for a mark and VI Alpha tag, and counted. Total effort (sum of person-hours fished since previous check-in) it took for each angler group to obtain the submitted catch was recorded in 2016 and 2017 to estimate angler catch·hour⁻¹ and quantify cumulative effort. After 2015, anglers could donate their catch for research. Most fish in 2016 and 2017 ($\geq 90\%$) were donated. These fish were placed on ice and later frozen at -20°C until processed for biological samples.

Biological samples.—We extracted and sectioned left sagittal otoliths ($n = 637$ between 2016 and 2017) for age-and-growth analysis, ovaries for fecundity assessment ($n = 42$ in 2016 only), and evaluated the maturity status of male ($n = 1,192$) and female ($n = 1,530$) smallmouth bass from systematic random subsamples taken from donated fish. Otoliths were aged by two readers. We compared population metrics from Ridgway to literature values to (1) assess for possible differences between a recent introduction and more established populations and (2) gauge the potential for compensatory responses.

Growth was expressed using a von Bertalanffy growth function (vBGF) fit to mean length-at-age using maximum likelihood estimation in R 3.3.2 (R Development Core Team 2016):

$$L_a = L_{\infty} \cdot (1 - e^{-K \cdot (a - t_0)}), \quad (1)$$

where L_a is TL at age a , L_{∞} is the asymptotic average TL, K is a growth rate coefficient, and t_0 is the hypothetical age at which a fish has zero length (Quinn and Deriso 1999). A single model ($\Delta\text{AIC}_c = 0.00$) instead of separate models ($\Delta\text{AIC}_c = 2.85$) was sufficient to describe length-at-age for both sexes, so data were combined for estimating means (**Figure 1**). Fecundity was estimated gravimetrically for pre-spawning mature females (Murua et al. 2003; Syslo 2010). We counted viable eggs (large, clear, defined yolk and oil globule) separately from what appeared as unviable eggs (small, dark, no distinct internal structure) (**Figure 2**). We estimated the length-dependent probability of maturity of male and female smallmouth bass using logistic regression fit to the binary response data in R (**Figure 3**):

$$P_{male \text{ or } P_{female}} = \frac{\exp(-\beta_0 + \beta_1 \cdot TL)}{1 + \exp(-\beta_0 + \beta_1 \cdot TL)}, \quad (2)$$

where β_0 and β_1 are fitted parameters for each sex (**Table 1**). Logistic regression models and the fitted vBGF were used to estimate sex- and age-dependent probabilities of maturity for the population model.

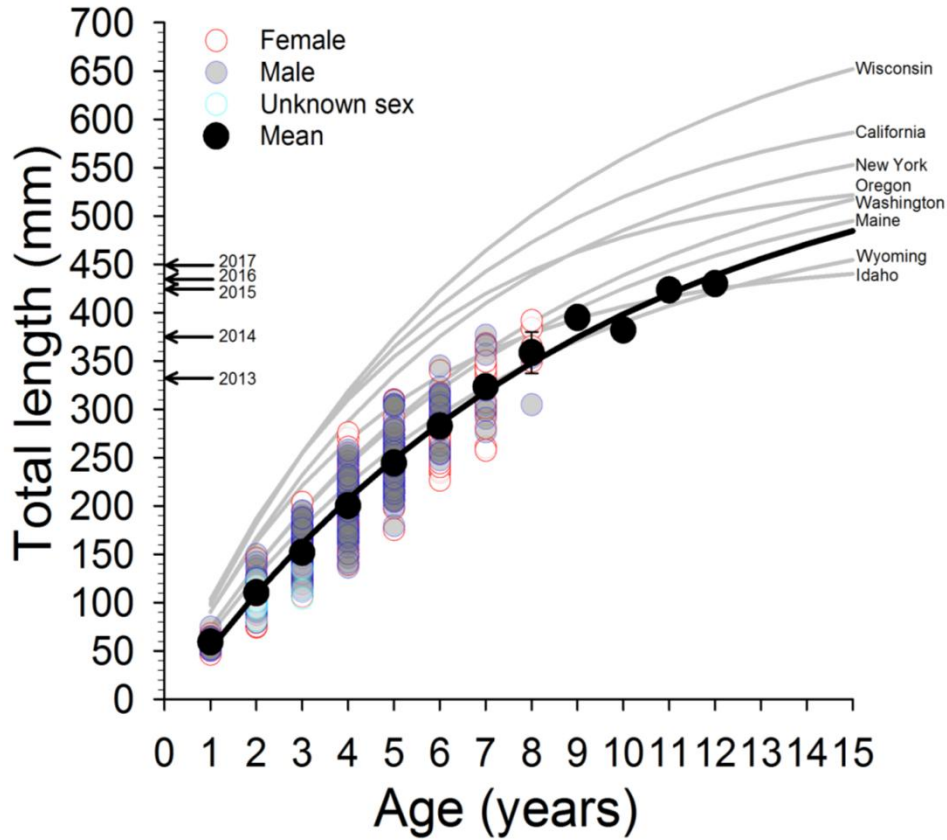


Figure 1. Mean length-at-age (± 2 SE) and individual length-at-age estimated for male and female smallmouth bass collected during the 2016 and 2017 fishing tournaments held on Ridgway Reservoir, Colorado. The black line represents the von Bertalanffy growth function fit to mean length-at-age. Gray lines denote von Bertalanffy growth curves representing the average growth of multiple populations ($N = 2$ to 43) found within other states for comparison (data from Beamesderfer and North 1995). Numbers and arrows on the y-axis indicate the maximum observed length of smallmouth bass in each year.

Smallmouth bass abundance and age-structure.—Year-specific starting numbers-at-age ($N_{a,t}$) were specified as inputs to the population model (**Table 1**). First, we estimated the annual pre-tournament abundance (\hat{N}) of smallmouth bass using Chapman’s estimator (Seber 1982; Hayes et al. 2007):

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1, \quad (3)$$

where n_1 = the number marked from boat electrofishing, n_2 = the number captured by anglers during the tournament, and m_2 = the number of marked fish captured by anglers. Variance was approximated as:

$$V(\hat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)} - 1, \quad (4)$$

and 95% confidence intervals ($\alpha = 0.05$; $Z_{\alpha/2} = 1.96$) as:

$$\hat{N} \pm Z_{\alpha/2} \sqrt{V(\hat{N})}. \quad (5)$$

We partitioned \hat{N} into 25 mm length bins based on the year-specific length-frequency of fish sampled boat electrofishing. Numbers-at-age were estimated by applying age-frequencies tabulated from year-specific age-length-keys to the abundances partitioned by length (Ricker 1975; Isley and Grabowski 2007). We explored correcting length-frequency distributions for the size-dependent capture efficiency of boat electrofishing (Beamesderfer and Rieman 1988; Bayley and Austin 2002). However, these corrections resulted in an apparent underrepresentation of larger fish, based on the known number removed. Therefore, we assumed the uncorrected catch was representative of the population vulnerable to anglers.

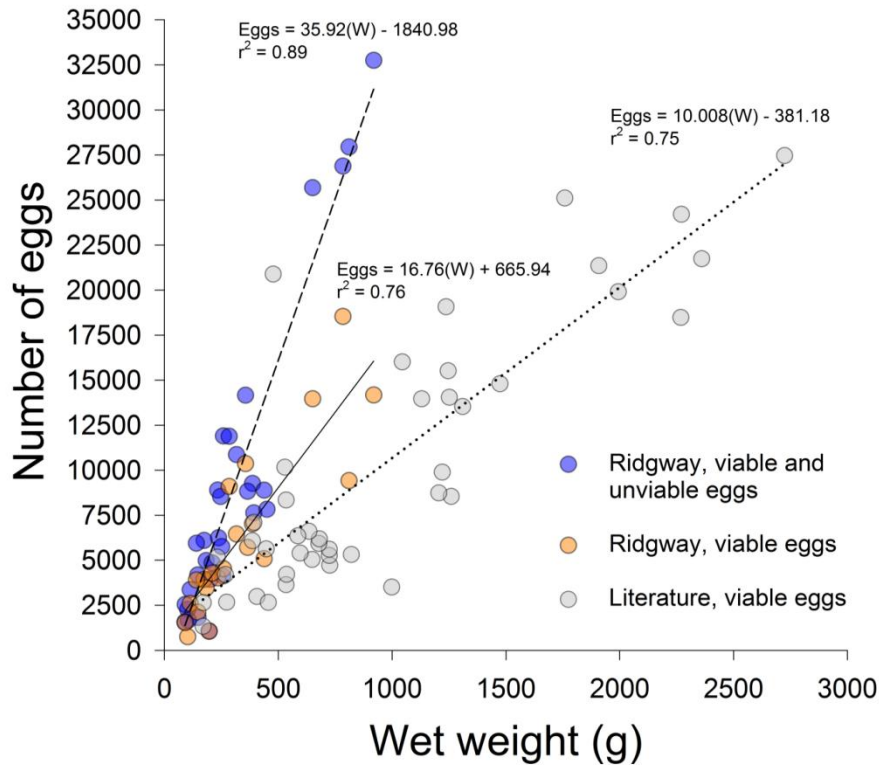


Figure 2. Estimates of mass-dependent fecundity from pre-spawning mature female smallmouth bass in Ridgway Reservoir, Colorado in comparison to conspecifics reported in the literature (Chu 2001). Lines and equations represent fitted linear regression models.

Mark-recapture estimates were computed for two size-classes of smallmouth bass prior to partitioning abundance into different length bins and applying age-length-keys to minimize bias associated with slight differences observed in the size-selectivity of boat electrofishing (used to mark fish) versus angling (used to recapture fish) (Ricker 1975). Abundance was estimated for fish 75-125 mm TL which corresponded predominately to age-2 separately from fish ≥ 125 mm TL which corresponded predominately to age-3 when smallmouth bass were fully recruited to both sampling gears.

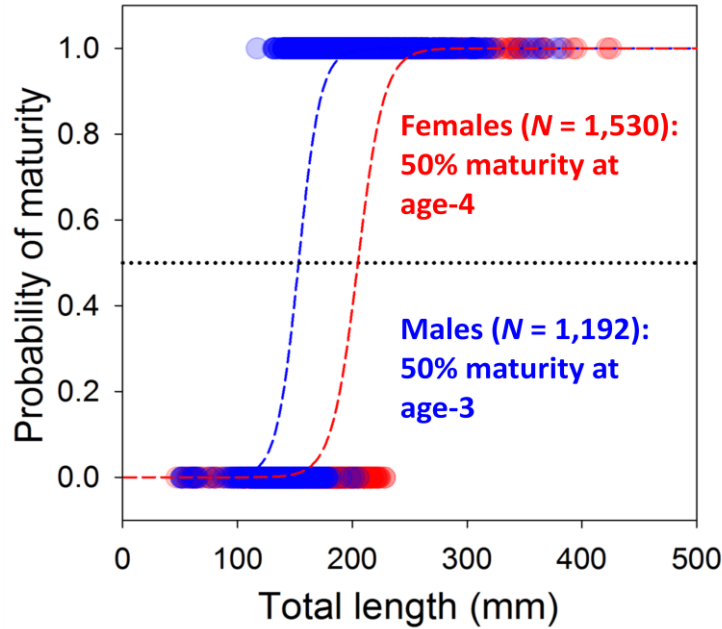


Figure 3. Probability of maturity as a function of length for male (blue) and female (red) smallmouth bass in Ridgway Reservoir. Lines represent the fitted logistic regression models.

Harvest, exploitation, and catchability.—Harvest-at-age ($h_{a,t}$) was estimated by applying year-specific age-length-keys to the number and length-frequency of smallmouth bass caught by anglers. Age-specific exploitation rates ($\mu_{a,t}$) were calculated by dividing $h_{a,t}$ by $N_{a,t}$. Because we wanted to simulate population dynamics over varying levels of fishing effort, we linked fishing effort to exploitation rate using a catchability coefficient ($q_{a,t}$; proportion of an age-class harvested after one unit of fishing effort). Catchability-at-age was estimated as:

$$q_{a,t} = h_{a,t}/E_t \cdot N_{a,t}, \quad (6)$$

where E_t is the total cumulative fishing effort in hours from the fishing tournament in year t . We characterized catchability-at-age with a double logistic function fit using nonlinear least squares (**Figure 4**):

$$q_{a,t} = \frac{1}{1 + e^{-b_2(a-b_1)}} \times \left[1 - \frac{1}{1 + e^{-b_4(a-b_3)}} \right], \quad (7)$$

where b_1 through b_4 are fitted parameters for each tournament year (**Table 1**).

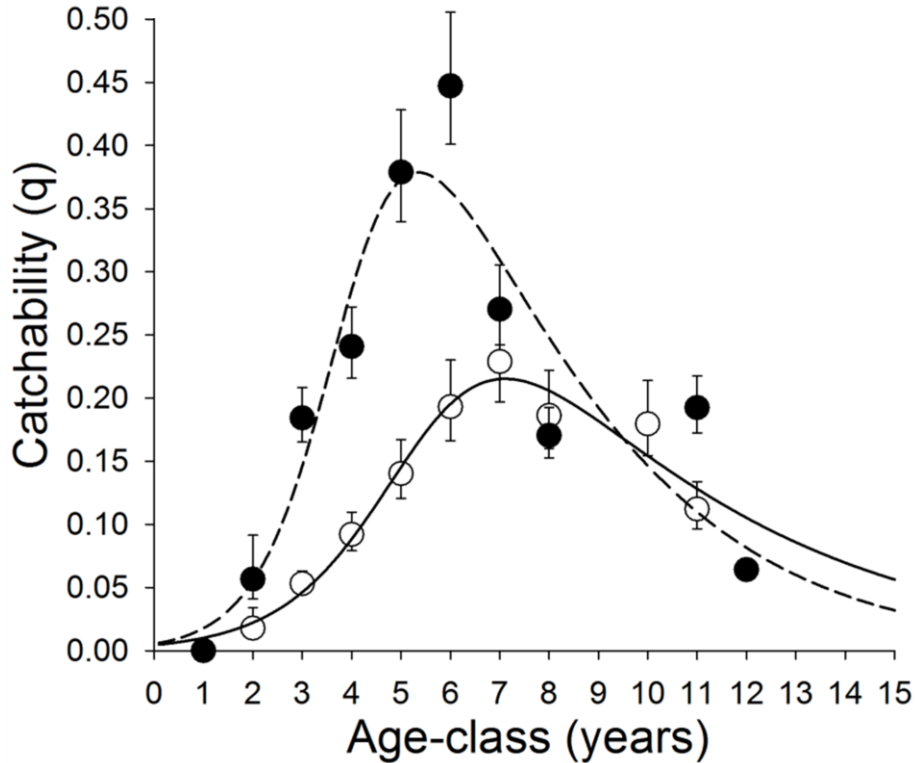


Figure 4. Catchability-at-age (represented here as the proportion of each age-class harvested after 1,000 hours of fishing effort) estimated for smallmouth bass in Ridgway Reservoir during the fishing tournament conducted in June 2016 (open circles and solid line) versus July 2017 (closed circles and dashed line). Lines represent the fitted double logistic functions.

Catchability can vary inversely with abundance (Peterman and Steer 1981; Shuter et al. 1998). Whether a similar relationship exists for smallmouth bass has not been evaluated, but could have important implications for an angler-based suppression program. We used a 47 year time series of catchability and abundance data derived for smallmouth bass most vulnerable to catch and harvest by anglers (those \geq age-5) in Lake Opeongo, Ontario (Shuter et al. 1987) to develop our own empirical relationship ($R^2 = 0.73$) for this species:

$$q_{opeongo} = 0.507e^{-0.000248 \cdot N_{vuln}}, \quad (8)$$

where N_{vuln} is the number of smallmouth bass vulnerable to anglers in the population. Data were adjusted for temporal changes in creel survey effectiveness and nature of the fishery (harvest vs. catch and release) over the study period following the methods of Shuter et al. (1987) prior to fitting the exponential relationship. Because N_{vuln} is represented by fish \geq age-3 not \geq age-5 in Ridgway Reservoir, we used the empirical relationship developed for Lake Opeongo to generate relative scaling factors for adjusting our direct estimates of catchability-at-age based on the corresponding abundance of fish \geq age-3 in the population during the 2017 tournament (**Figure 5**). In addition to running simulations where catchability-at-age was fixed (i.e., did not vary inversely with abundance), we used these scaling factors to run simulations under the assumption that catchability is inversely related to abundance with the population model.

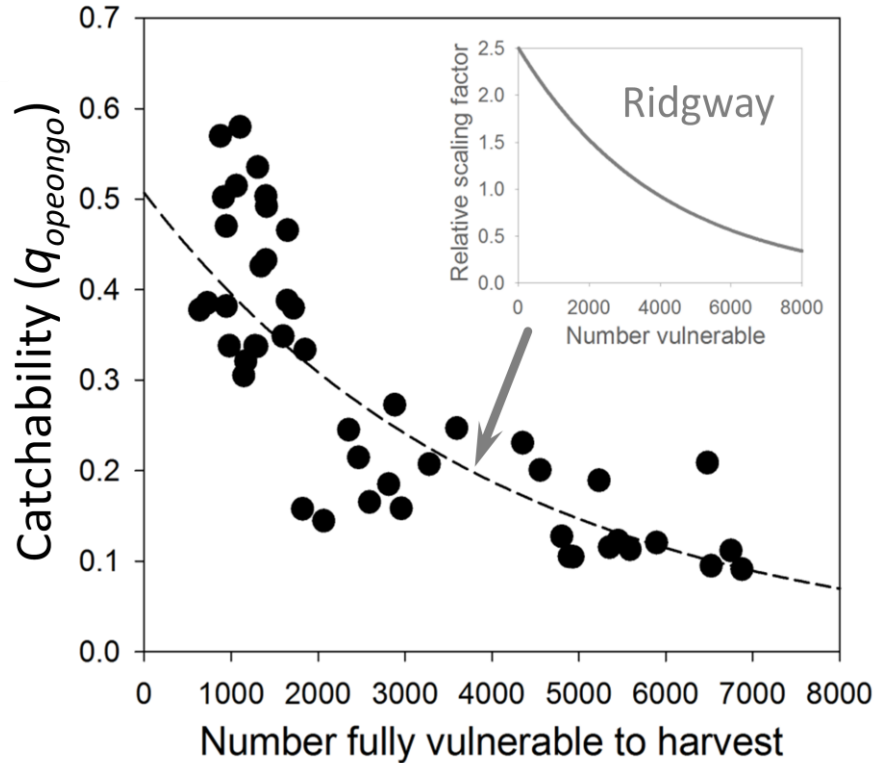


Figure 5. Empirical relationship between the catchability and the abundance of smallmouth bass most vulnerable to anglers (those \geq age-5) in Lake Opeongo, Ontario between 1936 and 1983. Data are from Shuter et al. (1987). The inset panel shows the relative scaling factors generated for application to the catchability of each age-class of smallmouth bass in Ridgway Reservoir based on the corresponding number of fish \geq age-3 present prior to the July 2017 fishing tournament in Ridgway Reservoir.

Natural mortality.—We estimated the natural mortality rate of smallmouth bass using three methods. First, we estimated an instantaneous natural mortality rate ($M = 0.454$) and converted it to an annual survival rate ($S = 0.635$, where $S = \exp(-M)$) with the equation of Pauly (1980):

$$\log(M) = -0.0066 - 0.279 \cdot \log_{10}(L_{\infty}) + 0.6543 \cdot \log_{10}(K) + 0.4634 \cdot \log_{10}(T), \quad (9)$$

where L_{∞} and K are parameters of the fitted vBGF and T is the mean annual thermal experience of smallmouth bass in Ridgway Reservoir (12.36°C). Next, we estimated M (0.384) and S (0.681) based on the maximum observed age of smallmouth bass (age-12) in the population following the equation of Quinn and Deriso (1999):

$$M = \ln(0.01)/\text{max age}. \quad (10)$$

Lastly, we used weighted catch curve regression for smallmouth bass age-3 and older sampled in 2016 with boat electrofishing to estimate S (0.716, where $S = 1 - v$) based on relationships among total instantaneous mortality rate ($Z = 1.048$; slope of weighted catch curve; $n = 9$; $R^2 = 0.95$; P

<0.001), total annual mortality rate ($A = 0.649$, where $A = 1 - e^{-Z}$), the observed exploitation rate of fish age-3 and older during the first tournament in 2015 ($\mu = 0.365$), and the expectation of natural death ($v = 0.284$, where $v = A - \mu$) (Miranda and Bettoli 2007; Splike and Maceina 2013). Even though increasing or variable recruitment from an expanding population of smallmouth bass can bias catch curve estimates of mortality, congruency among all three methods used for determining the natural survival rate strengthened support for our estimates of this parameter. Therefore, we averaged all three natural survival rates (mean $S = 0.677$, SD = 0.040) and applied this value to each age-class in the population model.

Recruitment.—The number of age-1 smallmouth bass recruits ($N_{l,t+1}$) entering the population the year following the fishing tournament was calculated as a function of the number of mature male and female spawners at large ($N_{s,t}$) after the present year's tournament if conducted in June or prior to the tournament if conducted in July (based on temporal patterns in the gonadal somatic index of female smallmouth bass) using the Ricker stock-recruitment function (Ricker 1975; Zipkin et al. 2008):

$$N_{l,t+1} = \alpha N_{s,t} \cdot (e^{-\beta N_{s,t}}) \cdot e^{\varepsilon} \text{ where } N_{l,t+1} \nlessgtr N_{l,max}. \quad (11)$$

In this model, the parameter α represents the maximum number of recruits per spawner, β represents the instantaneous rate at which recruits per spawner declines as the number of spawning adults increases, and the term e^{ε} represents multiplicative process error which we used to create random lognormal deviates around the underlying deterministic stock-recruitment relationship. We assumed ε was normally distributed with a mean = 0 and a SD = 0.38 estimated from variation in the catch rate of age-1 fish during pre-tournament boat electrofishing surveys conducted 2015-2017.

We approximated α and β (**Table 1**) by assuming the smallmouth bass population in Ridgway Reservoir was at an intermediate stock size where density-dependent recruitment is near its peak (Ricker 1975; Hansen et al. 2010). This assumption was supported by our age-and-growth and fecundity assessments (see results below) and similarity in the abundance of at least 50% mature smallmouth bass (fish age-3+) observed in Ridgway Reservoir versus the abundance of at least 50% mature smallmouth bass (fish age-5+) where peak recruitment levels were observed in Lake Opeongo (Shuter and Ridgway 2002). We estimated the peak of the stock-recruitment curve and associated parameter values ($N_s = 1/\beta$, $N_l = \alpha/\beta e$; Ricker 1975) based on the estimated number of male and female spawners in 2015 ($\beta = 1/2,392$) and the estimated number of age-1 recruits in 2016 ($\alpha = 2,451/2,392e$) back-calculated using our mean annual natural survival rate from the number of age-2 fish present in 2017 ($N_{2,2017} = 1,660$) estimated via mark-recapture. We developed a maximum recruitment level ($N_{l,max} = 8,596$) based on the abundance of the largest year-class of smallmouth bass ($N_{3,2016} = 3,945$) observed over the study period using the same back-calculation procedures.

Population model.—We developed a stochastic age-structured population model to simulate the short- and long-term dynamics of smallmouth bass under different incentive-based fishing tournament designs and effort levels. The core model tracked numbers-at-age over consecutive years t and followed a sequence reflective of a type I fishery whereby the population is first

subject to a non-continuous period of fishing mortality from the tournament ($q_{a,t} \cdot E_t$ term) and survivors are then subject to natural mortality (S_t):

$$N_{a+1,t+1} = (1 - q_{a,t} \cdot E_t) \cdot N_{a,t} \cdot S_t \quad \text{for } 1 < a < n, \quad (12)$$

where $q_{a,t}$ is specific to estimates from the June 2016 versus July 2017 tournament (**Figure 4**) and n was set to a maximum age of 15 (Beamesderfer and North 1995). The number of age-1 recruits in year $t+1$ ($N_{1,t+1}$) was computed using equ. (11) and the corresponding number of male and female spawners ($N_{s,t}$) was calculated as (equ. 13):

$$N_{s,t} = \sum_{a=1}^n [(1 - q_{a,t} \cdot E_t) \cdot N_{a,t} \cdot Prop_m \cdot P_{male,a}] \\ + \sum_{a=1}^n [(1 - q_{a,t} \cdot E_t) \cdot N_{a,t} \cdot Prop_f \cdot P_{female,a}]$$

if a June tournament in year t (i.e., spawning occurs after the tournament), or (equ. 14):

$$N_{s,t} = \sum_{a=1}^n [(1 - q_{a,t-1} \cdot E_{t-1}) \cdot N_{a,t-1} \cdot S_{t-1} \cdot Prop_m \cdot P_{male,a}] \\ + \sum_{a=1}^n [(1 - q_{a,t-1} \cdot E_{t-1}) \cdot N_{a,t-1} \cdot S_{t-1} \cdot Prop_f \cdot P_{female,a}]$$

if a July tournament in year t (i.e., spawning occurs prior to tournament) where $Prop_m$ and $Prop_f$ represent the proportion of the population that is male versus female, respectively (**Table 1**).

Model simulations.—Analysis is ongoing. For this report, we evaluated short-term dynamics by simulating the population model 10,000 times with each projection extending for 30 years. We simulated the scenario in which (1) catchability-at-age corresponded to what was observed during the July 2017 tournament each year (**Figure 4**), (2) angler interest and effort level would equal that observed during July 2017 (1,937 hrs) and vary little year-after-year, and (3) no compensation in the demographics of smallmouth bass.

In addition, we repeated simulations assuming catchability-at-age was fixed versus varied inversely with abundance (**Figure 5**). For each set of simulations, we incorporated random normal error into the process of natural mortality [$S_t \sim N(\mu = 0.677, \sigma = 0.040)$], lognormal error into the process of recruitment [see equ. (11)], and normal error into the fishing process by varying effort level [$E_t \sim N(\mu = 1,937 \text{ hrs}, \sigma = 181.73 \text{ hrs})$].

For each set of 10,000 simulations, we computed the mean abundance trajectory of fish \geq age-1 and fish \geq age-3 (most reflective of the spawning stock) and calculated the corresponding percent

change in abundance at simulation year 10. Confidence intervals (95%) were approximated using the 2.5 and 97.5 percentiles of simulated abundances in each simulation year. We seeded the model with numbers-at-age available to anglers during the July 2017 tournament (**Table 1**).

Results and Discussion

Smallmouth Bass Demographics

The maximum length observed in the smallmouth bass population progressively increased from 2013 to 2017 (**Figure 1**). Latter values corresponded to age 10-12 fish based on the fitted vBGF. Age-15 is a typical maximum for smallmouth bass (Beamesderfer and North 1995), so our population was likely still moderately young at the onset of removal in 2015.

The rate at which viable eggs increased with mass was higher than that from populations reported in the literature (three invasive and two native assembled by Chu 2001), as indicated by a significant interaction term ($F_{[1,64]} = 5.286$; $P = 0.025$) in a fitted ANCOVA model with population (reservoir vs. literature) as the main factor and weight as the covariate (**Figure 2**). Literature values were combined because published studies reporting mass-dependent fecundity were sparse, and no prominent differences were observed among populations (Neves 1975; Hurbert 1976; Carlander 1977; Serns 1984) assembled by Chu (2001).

The high apparent egg deposition potential for the heaviest fish in Ridgway Reservoir compared to conspecifics in the literature could reflect the importance of elevated reproductive output in an establishing population (Healy 1978; Trippel 1995; Ferreri and Taylor 1996). A large number of unviable eggs were observed (2-66% of total eggs). Our estimates for total fecundity (viable plus unviable) may reflect maximum egg deposition when spawner density is low and resources for reproductive investment are not limiting (**Figure 2**).

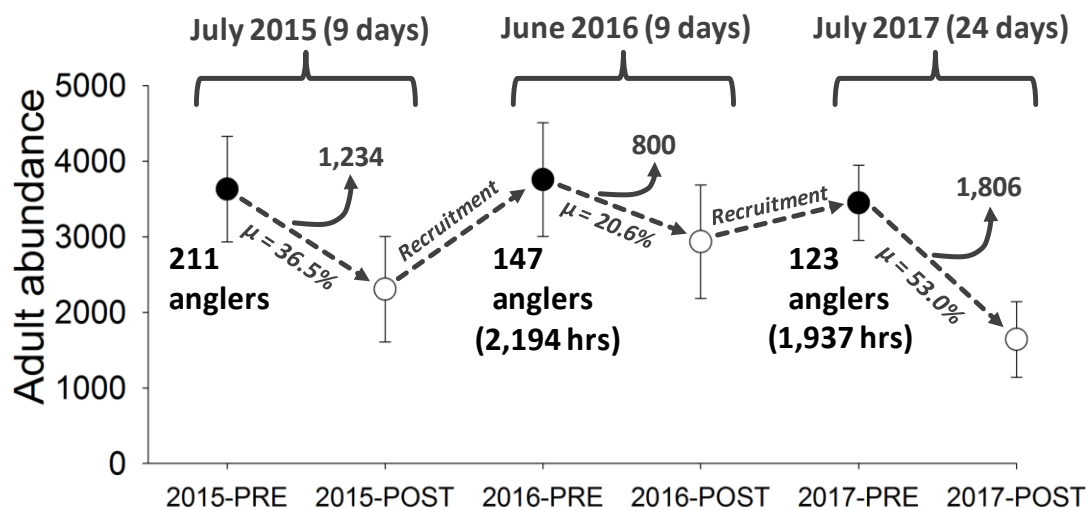


Figure 6. Time series of pre- and post-tournament mark-recapture abundance estimates for adult smallmouth bass ≥ 150 mm TL in Ridgway Reservoir and the associated number of adult fish harvested during each consecutive tournament (numbers above curved solid arrows).

Catchability-at-age Under Different Tournament Designs

The estimated catchability of smallmouth bass was considerably higher for intermediate age-classes of fish in July 2017 compared to June 2016 (**Figure 4**). We could not attribute this disparity to a difference in the abundance of smallmouth bass because 95% confidence intervals associated with the pre-tournament mark-recapture estimate of adult fish ≥ 150 mm TL overlapped and population size-structure was similar between years (**Figure 6**).

Table 1. Starting numbers-at-age and parameter values used for simulating the population dynamics of smallmouth bass in Ridgway Reservoir.

Parameter	Estimate	Error ($\pm 95\%$ CI or SD)
Starting numbers-at-age ($N_{a,2017}$)		
Age-1	2,451	932
Age-2	1,660	631
Age-3	2,649	306
Age-4	1,613	186
Age-5	435	50
Age-6	105	12
Age-7	76	9
Age-8	13	2
Age-9	0	-
Age-10	0	-
Age-11	8	1
Age-12	8	1
Age-13	0	-
Age-14	0	-
Age-15	0	-
Fishing effort (E)		
2015	211 anglers (effort not recorded)	-
2016	147 anglers and 2,194 hours	-
2017	123 anglers and 1,937 hours	181.73
von Bertalanffy growth parameters (mm)		
L_{∞}	601.04	-
K	0.11	-
t_0	0.18	-
Length-dependent probability of maturity (P_{male} and P_{female})		
β_0 (female)	18.057	-
β_1 (female)	0.088	-
β_0 (male)	16.124	-
β_1 (male)	0.105	-
Population sex-ratio		
$Prop_f$	0.562	-
$Prop_m$	0.438	-
Catchability-at-age (q_a; scaled to 1,000 hours of effort)		
b_1 (June 2016)	5.467	-
b_2 (June 2016)	0.904	-
b_3 (June 2016)	2.601	-
b_4 (June 2016)	0.227	-
b_1 (July 2017)	3.949	-
b_2 (July 2017)	1.266	-
b_3 (July 2017)	4.654	-
b_4 (July 2017)	0.330	-
Mortality rates		
M and S (Pauly 1980)	0.454, 0.635	-
M and S (Quinn and Deriso 1999)	0.384, 0.681	-
Z (catch curve)	1.048	-
A (catch curve)	0.649	-
μ (age-3+ in 2015)	0.365	-
v (catch curve)	0.284	-
S (catch curve)	0.716	-
Mean S	0.677	0.040
Ricker stock-recruitment		
α	2.786	-
β	0.000418	-
ϵ	0.38	-
$N_{L,max}$	8,596	-

Alternatively, the observed differences in catchability-at-age between years could be associated with spawning behavior and dynamic reservoir conditions (**Figure 7**). During June, fluctuations in reservoir surface elevation were greatest, reservoir inflows were at their peak, and surface water temperatures were closely linked with the range associated with smallmouth bass nesting, spawning, and egg incubation (Armour 1993). Reservoir conditions were generally more stable in July.

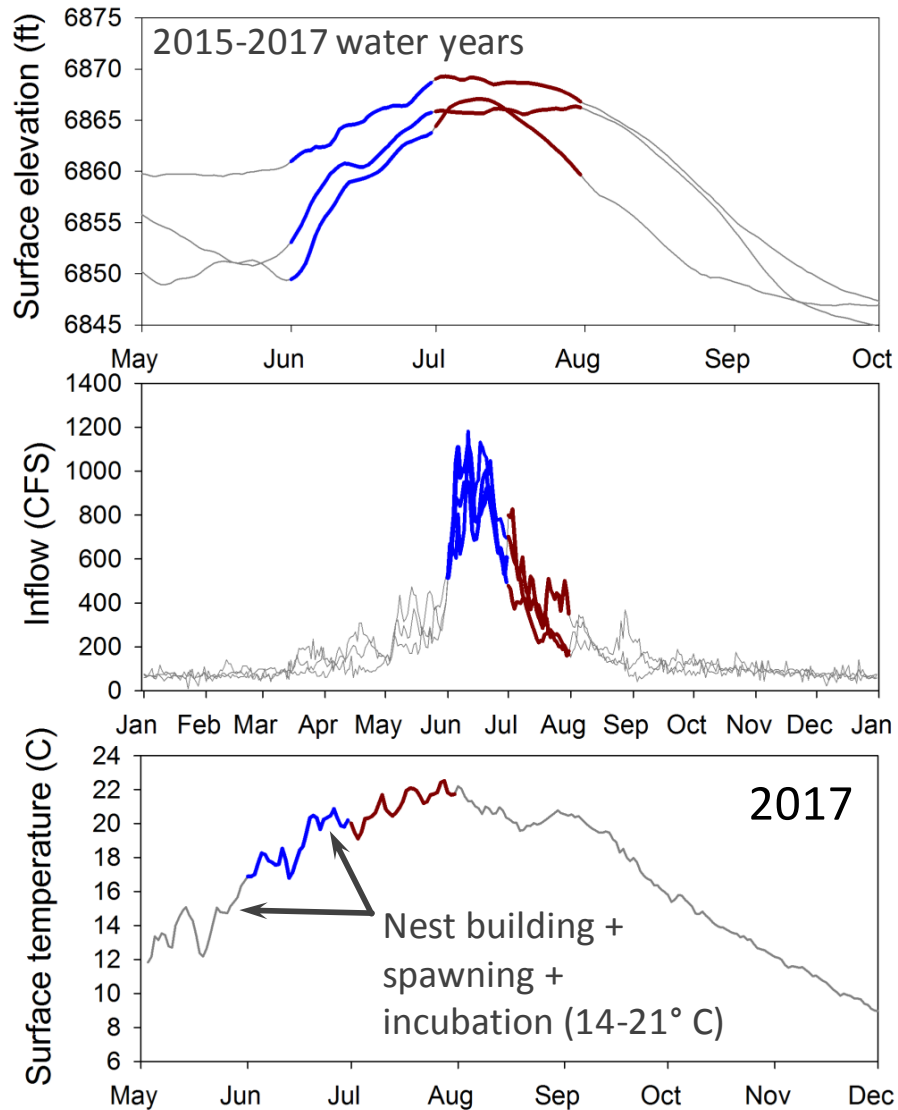


Figure 7. Conditions during the 2015-2017 water years in Ridgway Reservoir. Blue lines outline conditions associated with June while the red lines outline conditions associated with July. Mean surface water temperatures were only measured in 2017.

Short-term Population Projections

Results from the population modeling simulations indicated that harvest and fishing effort levels observed during the July 2017 tournament were sufficient to cause measurable decline in the abundance of fish \geq age-1 and fish \geq age-3 over a ten year period under both the fixed and

variable catchability scenarios (**Figure 8**). Under fixed catchability, model simulations predicted a 62% decline in the abundance of fish \geq age-1 and a 78% reduction in the abundance of fish \geq age-3 on average in 10 years. This outlook improved considerably under the variable catchability scenario whereby model simulations predicted a 90% and 95% reduction in the abundance of each set of age-classes, respectively (**Figure 8**). Contrary to the literature (Zipkin et al. 2008, 2009; Loppnow et al. 2013; Lopponow and Venturelli 2014), model results indicate that a cost-effective angler incentive program can be effective at suppressing invasive smallmouth bass alone or in conjunction with other methods in fluctuating coldwater reservoirs depending on management targets.

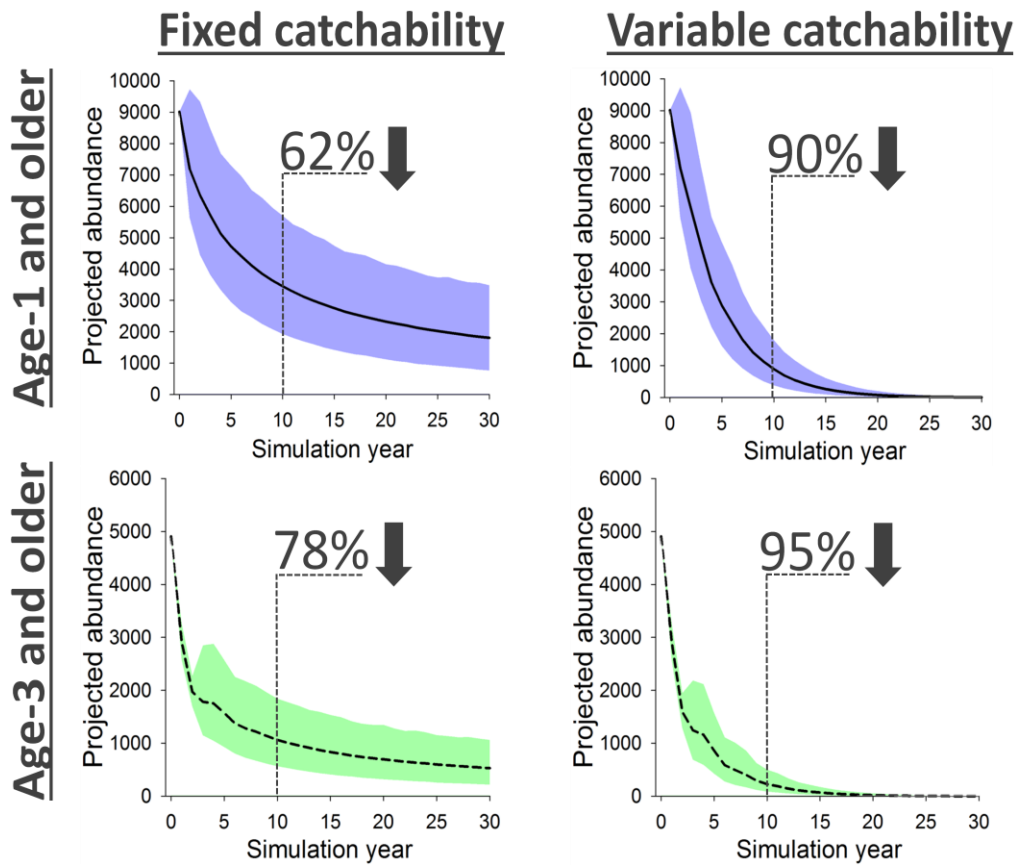


Figure 8. Average population projections (lines) and corresponding 95% confidence intervals (shaded regions) for smallmouth bass \geq age-1 and \geq age-3 in Ridgway Reservoir assuming both fixed and variable catchability-at-age. Values indicate the percent decline predicted for each set of age-classes under each catchability scenario over a 10 year period.

Acknowledgments

This research is being conducted in collaboration with Eric Gardunio on Ridgway Reservoir and Tory Eyre on Elkhead Reservoir, Area Aquatic Biologists. Similar population models and data sets are currently being developed for northern pike and smallmouth bass in Elkhead Reservoir and will be reported on during the next cycle.

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Zelasko, K.A., K.R. Bestgen, J.A. Hawkins, and G.C. White. 2016. Evaluation of a long-term predator removal program: abundance and population dynamics of invasive northern pike in the Yampa River, Colorado. *Transactions of the American Fisheries Society* 145:1153-1170.

Zipkin, E.F., C.E. Kraft, E.G. Cooch, and P.J. Sullivan. 2009. When can efforts to control nuisance and invasive species backfire? *Ecological Applications* 19:1585-1595.

Zipkin, E.F., P.J. Sullivan, E.G. Cooch, C.E. Kraft, B.J. Shuter, and B.C. Weidel. 2008. Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition? *Canadian Journal of Fisheries and Aquatic Sciences* 65:2279-2292.

IV. Research Communication and Collaboration

A. Peer-reviewed publications (2016-2018)

2018

- Spanjer, A.R., P.W. Moran, K.A. Larsen, L.A. Wetzel, **A.G. Hansen**, and D.A. Beauchamp. 2018. Juvenile coho salmon growth and health in streams across an urbanization gradient. *Science of the Total Environment* 625:1003-1012.

Abstract.—Expanding human population and urbanization alters freshwater systems through structural changes to habitat, temperature effects from increased runoff and reduced canopy cover, altered flows, and increased toxicants. Current stream assessments stop short of measuring health or condition of species utilizing these freshwater habitats and fail to link specific stressors mechanistically to the health of organisms in the stream. Juvenile fish growth integrates both external and internal conditions providing a useful indicator of habitat quality and ecosystem health. Thus, there is a need to account for ecological and environmental influences on fish growth accurately. Bioenergetics models can simulate changes in growth and consumption in response to environmental conditions and food availability to account for interactions between an organism's environmental experience and utilization of available resources. The bioenergetics approach accounts for how thermal regime, food supply, and food quality affect fish growth. This study used a bioenergetics modeling approach to evaluate the environmental factors influencing juvenile coho salmon growth among ten Pacific Northwest streams spanning an urban gradient. Urban streams tended to be warmer, have earlier emergence dates and stronger early season growth. However, fish in urban streams experienced increased stress through lower growth efficiencies, especially later in the summer as temperatures warmed, with as much as a 16.6% reduction when compared to fish from other streams. Bioenergetics modeling successfully characterized salmonid growth in small perennial streams as part of a more extensive monitoring program and provides a powerful assessment tool for characterizing mixed life-stage specific responses in urban streams.

2017

- Johnson, B.M., W.M. Pate, and **A.G. Hansen**. 2017. Energy density and dry matter content in fish: new observations and an evaluation of some empirical models. *Transactions of the American Fisheries Society* 146:1262-1278.

Abstract.—Energy density (ED) is an indicator of fish nutritional status, physiological status, and fitness. Estimates of ED of predators and prey are also needed for bioenergetics modeling, but direct measurements of ED are difficult to obtain. Hence, investigators often borrow published values from the same species or related species. Alternatively, models have been developed that predict ED from dry matter content (DM). The scarcity of published ED values makes data borrowing and the generality of predictive modeling difficult to evaluate. We report new ED measurements derived from bomb calorimetry for six freshwater fish species (Arctic Char *Salvelinus alpinus*, Brown Trout *Salmo trutta*, kokanee *Oncorhynchus nerka*, Lake Trout *Salvelinus namaycush*, Rainbow Trout *O. mykiss*, and White Sucker *Catostomus commersonii*) and compared them to previously published data. We used our data to validate existing ED:DM

models and to fit new ones. We also quantified bias that could result from borrowing inappropriate ED values for bioenergetics modeling. We collected a range of fish sizes from two reservoirs of differing productivity and measured whole-body ED (wet-mass basis) and DM. Our data substantially increase the range of ED data for Arctic Char, kokanee, and White Suckers. Two multispecies ED:DM models predicted the ED of our samples accurately (mean root mean square error [RMSE] < 500 J/g), even at the extremes for the range of prediction where data used for model development were limited. Taxon-specific models performed less well (mean RMSE = 775 J/g), and some appeared highly biased (RMSE 956–1,900 J/g). Bioenergetics model simulations showed that Lake Trout prey consumption could be overestimated by as much as 22% when using borrowed EDs for Lake Trout and their prey, but prey consumption estimates fell within $\pm 2\%$ of observed when ED was predicted from DM. When direct measures of ED are unattainable, measurement of DM and prediction of ED from one of the published multispecies models offer a practical and accurate method for bioenergetics modeling and other studies requiring information on fish energy content.

- Borin, J.M., M.L. Moser, **A.G. Hansen**, C. Donoghue, D.A. Beauchamp, C. Pruitt, S.C. Corbett, J.L. Ruesink, and B. Dumbauld. 2017. Energetic requirements of the North American green sturgeon (*Acipenser medirostris*) feeding on burrowing shrimp (*Neotrypaea californiensis*) in estuaries: importance of temperature, reproductive investment, and residence time. *Environmental Biology of Fishes* 100:1561-1573.

Abstract.—Habitat use can be complex, as tradeoffs among physiology, resource abundance, and predator avoidance affect the suitability of different environments for different species. Green sturgeon (*Acipenser medirostris*), an imperiled species along the west coast of North America, undertake extensive coastal migrations and occupy estuaries during the summer and early fall. Warm water and abundant prey in estuaries may afford a growth opportunity. We applied a bioenergetics model to investigate how variation in estuarine temperature, spawning frequency, and duration of estuarine residence affect consumption and growth potential for individual green sturgeon. We assumed that green sturgeon achieve observed annual growth by feeding solely in conditions represented by Willapa Bay, Washington, an estuary annually frequented by green sturgeon and containing extensive tidal flats that harbor a major prey source (burrowing shrimp, *Neotrypaea californiensis*). Modeled consumption rates increased little with reproductive investment (<0.4%), but responded strongly (10–50%) to water temperature and duration of residence, as higher temperatures and longer residence required greater consumption to achieve equivalent growth. Accordingly, although green sturgeon occupy Willapa Bay from May through September, acoustically-tagged individuals are observed over much shorter durations (34 d + 41 d SD, N = 89). Simulations of <34 d estuarine residence required unrealistically high consumption rates to achieve observed growth, whereas longer durations required sustained feeding, and therefore higher total intake, to compensate for prolonged exposure to warm temperatures. Model results provide a range of per capita consumption rates by green sturgeon feeding in estuaries to inform management decisions regarding resource and habitat protection for this protected species.

2016

- **Hansen, A.G.**, J.G. Gardner, D.A. Beauchamp, R. Paradis, T.P. Quinn. 2016. Recovery of sockeye salmon in the Elwha River, Washington, after dam removal: dependence of smolt production on the resumption of anadromy by landlocked kokanee. *Transactions of the American Fisheries Society* 145:1303-1317.

Abstract.—Pacific salmon *Oncorhynchus* spp. are adept at colonizing habitat that has been reopened to anadromous passage. Sockeye Salmon *O. nerka* are unique in that most populations require lakes to fulfill their life history. Thus, for Sockeye Salmon to colonize a system, projects like dam removals must provide access to lakes. However, if the lakes contain landlocked kokanee (lacustrine Sockeye Salmon), the recovery of Sockeye Salmon could be mediated by interactions between the two life history forms and the processes associated with the resumption of anadromy. Our objective was to evaluate the extent to which estimates of Sockeye Salmon smolt production and recovery are sensitive to the resumption of anadromy by kokanee after dam removal. We informed the analysis based on the abiotic and biotic features of Lake Sutherland, which was recently opened to passage after dam removal on the Elwha River, Washington. We first developed maximum expectations for the smolt-producing capacity of Lake Sutherland by using two predictive models developed from Sockeye Salmon populations in Alaska and British Columbia: one model was based on the mean seasonal biomass of macrozooplankton, and the other was based on the euphotic zone volume of the lake. We then constructed a bioenergetics-based simulation model to evaluate how the capacity of Lake Sutherland to rear yearling smolts could change with varying degrees of anadromy among *O. nerka* fry. We demonstrated that (1) the smolt-producing capacity of a nursery lake for juvenile Sockeye Salmon changes in nonlinear ways with changes in smolt growth, mortality, and the extent to which kokanee resume anadromy after dam removal; (2) kokanee populations may be robust to changes in abundance after dam removal, particularly if lakes are located higher in the watershed on tributaries separate from where dams were removed; and (3) the productivity of newly establishing Sockeye Salmon can vary considerably depending on whether the population becomes rearing limited or is recruitment limited and depending on how adult escapement is managed.

- Sorel, M.H., **A.G. Hansen**, K.A. Connelly, and D.A. Beauchamp. 2016. Trophic feasibility of reintroducing anadromous salmonids in three reservoirs on the North Fork Lewis River, Washington: prey supply and consumption demand of resident fishes. *Transactions of the American Fisheries Society* 145:1331-1347.

Abstract.—The reintroduction of anadromous salmonids in reservoirs is being proposed with increasing frequency, requiring baseline studies to evaluate feasibility and estimate the capacity of reservoir food webs to support reintroduced populations. Using three reservoirs on the North Fork Lewis River as a case study, we demonstrate a method to determine juvenile salmonid smolt rearing capacities for lakes and reservoirs. To determine if the Lewis River reservoirs can support reintroduced populations of juvenile stream-type Chinook Salmon *Oncorhynchus tshawytscha*, we evaluated the monthly production of *Daphnia* spp. (the primary zooplankton consumed by resident salmonids in the system) and used bioenergetics to model the consumption demand of resident fishes in each reservoir. To estimate the surplus of *Daphnia* prey available for reintroduced salmonids, we assumed a maximum sustainable exploitation rate and accounted

for the consumption demand of resident fishes. The number of smolts that could have been supported was estimated by dividing any surplus *Daphnia* production by the simulated consumption demand of an individual Chinook Salmon fry rearing in the reservoir to successful smolt size. In all three reservoirs, densities of *Daphnia* were highest in the epilimnion, but warm epilimnetic temperatures and the vertical distribution of planktivores suggested that access to abundant epilimnetic prey was limited. By comparing accessible prey supply and demand on a monthly basis, we were able to identify potential prey supply bottlenecks that could limit smolt production and growth. These results demonstrate that a bioenergetics approach can be a valuable method of examining constraints on lake and reservoir rearing capacity, such as thermal structure and temporal food supply. This method enables numerical estimation of rearing capacity, which is a useful metric for managers evaluating the feasibility of reintroducing Pacific salmon *Oncorhynchus* spp. in lentic systems.

- Sorel, M.H., **A.G. Hansen**, K.A. Connelly, A.C. Wilson, E.D. Lowery, and D.A. Beauchamp. 2016. Predation by northern pikeminnow and tiger muskellunge on juvenile salmonids in a high-head reservoir: implications for anadromous fish reintroductions. *Transactions of the American Fisheries Society* 145:521-536.

Abstract.—The feasibility of reintroducing anadromous salmonids into reservoirs above high-head dams is affected by the suitability of the reservoir habitat for rearing and the interactions of the resident fish with introduced fish. We evaluated the predation risk to anadromous salmonids considered for reintroduction in Merwin Reservoir on the North Fork Lewis River in Washington State for two reservoir use-scenarios: year-round rearing and smolt migration. We characterized the role of the primary predators, Northern Pikeminnow *Ptychocheilus oregonensis* and tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*), by using stable isotopes and stomach content analysis, quantified seasonal, per capita predation using bioenergetics modeling, and evaluated the size and age structures of the populations. We then combined these inputs to estimate predation rates of size-structured population units. Northern Pikeminnow of FL ≥ 300 mm were highly cannibalistic and exhibited modest, seasonal, per capita predation on salmonids, but they were disproportionately much less abundant than smaller, less piscivorous, conspecifics. The annual predation on kokanee *Oncorhynchus nerka* (in biomass) by a size-structured unit of 1,000 Northern Pikeminnow having a FL ≥ 300 mm was analogous to 16,000–40,000 age-0 spring Chinook Salmon *O. tshawytscha* rearing year-round, or 400–1,000 age-1 smolts migrating April–June. The per capita consumption of salmonids by Northern Pikeminnow having a FL ≥ 200 mm was relatively low, due in large part to spatial segregation during the summer and the skewed size distribution of the predator population. Tiger muskellunge fed heavily on Northern Pikeminnow, other non salmonids, and minimally on salmonids. In addition to cannibalism within the Northern Pikeminnow population, predation by tiger muskellunge likely contributed to the low recruitment of larger (more piscivorous) Northern Pikeminnow, thereby decreasing the risk of predation to salmonids. This study highlights the importance of evaluating trophic interactions within reservoirs slated for reintroduction with anadromous salmonids, as they can be functional migration corridors and may offer profitable juvenile-rearing habitats despite hosting abundant predator populations.

B. Publications in press or under review

- **Hansen, A.G.**, J.R. Gardner, K.A. Connelly, M. Polacek, and D.A. Beauchamp. *Under Review*. Trophic compression of lake food webs under hydrologic disturbance. *Ecosphere*.

Abstract.—The need to protect biostructure is increasingly recognized, yet empirical studies of how human exploits affect ecological networks are rare. Studying the effects of variation in human disturbance intensity from decades past can help us understand and anticipate ecosystem change under alleviated or amplified disturbance over decades to come. Here, we use stable isotopes and an innovative analytical approach to compare the food webs of two akin lake ecosystems subject to disparate water use regimes, a pervasive, yet unappreciated stressor. We show that intensive water use (persistent, early season, rapid lake-level drawdown) can compress trophic diversity by 46%, necessitating reorganization of biostructural elements configuring lake food webs. Compression occurred over the $\delta^{13}\text{C}$ axis indicating erosion of diversity stemming from basal carbon resources, but food chain length remained intact over the period and intensity of disturbance examined. This study demonstrates (1) how water use, like other disturbances (warming and eutrophication), can mute opportunity for benthic-pelagic coupling and benefits to organisms, food webs, and lake productivity, and (2) the inherent capacity of lake ecosystems to adapt to stress. Trophically compressed lakes may be less able to adapt to intensified water use.

- Litz, M.N.C., J.A. Miller, R.D. Brodeur, E.A. Daly, L.A. Weitkamp, and **A.G. Hansen**. *Under Review*. Energy dynamics of subyearling Chinook salmon reveal the importance of piscivory to short term growth during early marine residence. *Fisheries Oceanography*.

Abstract.—Variation in prey quantity and quality can influence growth and survival of marine predators, including anadromous fish that migrate from freshwater systems. The objective of this study was to quantify the relative importance of prey quantity, prey quality, and temperature to variation in seasonal growth rates of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) following freshwater emigration. To address this objective, a population of Chinook salmon and their prey were repeatedly sampled from June–September over two years in coastal waters off Oregon and Washington. Subyearlings from the same population were also reared under laboratory conditions. Using a bioenergetics model evaluated in the laboratory, we found that growth rate variability in the field was associated more with differences in northern anchovy (*Engraulis mordax*) consumption and less with variation in diet energy density or ocean temperature. Highest growth rates (2.43–3.22% body weight d^{-1}) occurred in months when anchovy biomass peaked, and the timing of peak anchovy biomass varied by year. Our results confirm a general pattern among juvenile Chinook salmon occurring from Alaska to California that feeding rates contribute most to growth rate variability during early marine residence, although dominant prey types can differ seasonally, annually, or by ecosystem. In the northern California Current, faster growth appears to be associated with the availability of age-0 anchovy. Identifying factors that influence the seasonal development of the prey field and regulate prey quantity and quality will improve understanding of salmon growth and survival during early marine residence.

C. Special reports and white papers

- **Hansen, A.G.** 2017. Fish Bioenergetics Research. Colorado Parks and Wildlife Fact Sheet. Fort Collins, Colorado.
- **Hansen, A.G.** 2017. Tiger Trout Research. Colorado Parks and Wildlife Fact Sheet. Fort Collins, Colorado.
- **Hansen, A.G.,** M. Polacek, K.A. Connelly, J.R. Gardner, and D.A. Beauchamp. 2017. Food web interactions in Kachess and Keechelus Reservoirs, Washington: implications for threatened adfluvial bull trout and management of water storage. Final report to Washington Department of Ecology. 67 pages.
- Clark, C.P., S. Ball, S. Burgess, **A.G. Hansen,** and D.A. Beauchamp. 2017. Growth, distribution, and abundance of pelagic fishes in Lake Washington: March and October 2016. Final report to Seattle Public Utilities. 39 pages.
- **Hansen, A.G.** 2016. Summer profundal index netting for tracking trends in the abundance of lake trout in coldwater lakes and reservoirs of Colorado: results from 2016. Summary report, Colorado Parks and Wildlife, Lake and Reservoir Research. 6 pages.
- **Hansen, A.G.** 2016. Model evaluation of a reduced maximum length limit for lake trout removal in Blue Mesa Reservoir, Colorado. Summary report, Colorado Parks and Wildlife, Lake and Reservoir Research. 6 pages.

D. Internal presentations

- **Hansen, A.G.,** and E.I. Gardunio. Biological effectiveness of incentive-based harvest tournament for smallmouth bass in Ridgway Reservoir, Colorado. Aquatic Biologist Meeting, Gunnison, Colorado. January 2018.
- **Hansen, A.G.** Model evaluation of an incentive-based fishing tournament for smallmouth bass in Ridgway Reservoir, Colorado. Presentation to Area 18 CPW representatives. Montrose, Colorado. February 2017.

E. External presentations

- M. Miller, E. Cristan, K. Paik, A. Smith, J. Wyer, K. Hall, C.A. Myrick, and **A.G. Hansen.** What is limiting the growth of northern pike *Esox lucius* in College Lake? A bioenergetics approach. **Poster submission** for Colorado-Wyoming Chapter of the America Fisheries Society Annual Meeting, Laramie, Wyoming. February 2018.
- Brauch, D, and **A.G. Hansen.** Riding a salmon “high”: factors contributing to a rebound of

Colorado's premier kokanee salmon fishery. Colorado-Wyoming Chapter of the American Fisheries Society Annual Meeting, Laramie, Wyoming. February 2018.

- **Hansen, A.G.**, E. I. Gardunio, and T. Eyre. Biological effectiveness of incentive-based harvest tournaments for controlling nonnative piscivores in fluctuating coldwater reservoirs. Upper Colorado River Basin Recovery Team Annual Researchers Meeting, Vernal, Utah. January 2018.
- **Hansen, A.G.** How will altered or more demanding water use regimes affect reservoir food webs and fisheries? North American Lake Management Society Conference, Westminster, Colorado. November 2017.
- **Hansen, A.G.** CPW sponsored harvest tournaments: collaborating with anglers to reconcile native fish conservation and warm water sport fishing in western Colorado. Invited speaker for Colorado State University student subunit of the American Fisheries Society, Fort Collins, Colorado. October 2017.
- **Hansen, A.G.**, J.G. Gardner, K.A. Connelly, M. Polacek, and D.A. Beauchamp. A bioenergetic-based food web evaluation of factors affecting bull trout and kokanee production in Kachess and Keechelus Reservoirs. Yakima Basin Science and Management Conference, Ellensburg, Washington. June 2017.
- Litz, M.N.C., J.A. Miller, R.D. Brodeur, E.A. Daly, L.A. Weitkamp, and **A.G. Hansen**. Energy dynamics and growth of juvenile Chinook salmon reveal the importance of piscivory during early marine residence. 3rd PICES/ICES Early Career Scientist Conference, Busan, Korea. May 2017.
- **Hansen, A.G.**, J.G. Gardner, K.A. Connelly, M. Polacek, and D.A. Beauchamp. Baseline food web interactions in Lake Kachess: seasonal predation by northern pikeminnow and burbot on prey important for bull trout. Yakima Basin Science and Management Conference. Ellensburg, Washington. Invited by Yakama Tribe, Washington Department of Fish and Wildlife, and US Fish and Wildlife Service. June 2016.

F. Involvement with Colorado State University

- Co-instructor with Dr. Chris Myrick for FW496 (spring 2017, fall 2017, and spring 2018 semesters): "***Independent study in fishery biology***" within the Department of Fish, Wildlife, and Conservation Biology (affiliate faculty status granted spring 2017). Course is focused on the field application and interpretation of fishery science principles. The study system is College Lake on the Foothills Research Campus.
- Collaborator with Dr. Brett Johnson and Dr. Chris Myrick in the Department of Fish, Wildlife, and Conservation Biology on a new masters student project (timeline: spring 2018-spring 2020) titled: "***Triploid walleye: a new frontier for managing coolwater predators in the West.***"