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Rainbow smelt spawning population and habitat characteristics in a Missouri River reservoir

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ABSTRACT

Rainbow Smelt *Osmerus mordax* are the primary coldwater forage species in Lake Oahe, South Dakota, yet most aspects of their life history remain unknown. As Missouri River reservoirs present a novel habitat compared to elsewhere in the Rainbow Smelt's range, we investigated their spawning site use relative to available physical and thermal habitat from spring 2016 − 2018 using a mobile horizontal-beaming hydroacoustic survey. We mapped spawning habitat using side-scanning sonar to establish relationships with site bathymetry and thermal spawning conditions. From our site mapping, we determined the depth, slope, bottom hardness, and ruggedness of individual sites. We used a PCA to condense our physical habitat metrics, with PC1 representing 77% of cumulative variance. Peak abundance was linked to a physical habitat gradient, representing [steep slope, deep, soft bottom] to [low slope, shallow, hard bottom]. Peak Rainbow Smelt spawning aggregations were observed at $6.8 \pm 1.7\,^{\circ}C$ (Mean ± StDev). An information-theoretic regression analysis revealed an interactive effect of temperature and habitat, whereby shallower, warmer sites typically had a lower peak abundance. These results represent the first step toward understanding habitat use characteristics of spawning Rainbow Smelt in reservoir systems.

Introduction

Fish habitat encompasses all the physical and biological components of a system required to support fish growth, survival, and reproduction (Newcomb et al. 2007). More narrowly, the Magnuson-Stevens Act defines essential fish habitat as "those waters and substrates necessary to fish for spawning, breeding, feeding, or growth to maturity" (Magnuson-Stevens Act 2006). Thus, fish habitat encompasses all the attributes of a system wherein a species is successfully completing its life cycle, with some locations within the system more essential for specific life stages.

If a species demonstrates disproportionate use of a habitat type, it is inferred that selection has occurred for those habitat criteria (Krausman 1999). In practice, this inference is usually based on more observations or greater rates of occupancy for a given habitat type relative to alternatives. Proximate habitat selection is factor-based site selection of site attributes, whereas ultimate selection is based on outcomes such as reproductive success and survival (Hilden 1965). Cues for individual habitat use decisions are therefore the basis for eventual population outcomes. By extension, selection of spawning sites by adult fish should have consequences for the post-emergence offspring, and this in turn should have eventual population-level effects.

The concept of preferred spawning habitat is widely applied within fisheries, encompassing thermal and physical site attributes. Site selection varies widely by species, as does overall spawning strategy. Winemiller and Rose (1991) classified a variety of North American fishes based on a trilateral gradient of fecundity, juvenile survivorship, and age of maturity. Under this system, opportunistic species are typified by early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover. The opportunistic spawning strategy's success hinges on maximizing colonization across environments with frequent, stochastic change on relatively small spatial and temporal scales. Thus, it is expected that spawning site selection plays a relatively small role for these species. Conversely, periodic species are typified by delaying maturation to attain a larger adult size, increasing survival and producing larger clutches. Periodic species also exhibit synchronous spawning episodes, whereby movement into preferred spawning habitat or a favorable spawn timing (e.g., spring) is expected.

Rainbow Smelt *Osmerus mordax* represent an intermediate spawning strategy. They are a small bodied, relatively short-lived species with seasonal spawning, moderately large clutches, small eggs, and only a few spawning bouts per season (Winemiller and Rose 1991). Although Rainbow Smelt exhibit iteroparity and recurrent annual site use (Murawski et al. 1980) throughout their range, Lake Oahe, South Dakota represents a novel habitat as a large prairie reservoir. Rainbow Smelt have been present since the early 1970s and are the dominant forage species for Walleye *Sander vitreus,* the primary sport fish in the system (Fincel et al. 2014a, b). Although the importance of the species is well-documented, relatively little is known about the Lake Oahe Rainbow Smelt spawn timing, site selection, or spawning stock attributes. Additionally, Rainbow Smelt abundance is variable throughout Lake Oahe. It would therefore be beneficial to understand how reservoir habitat and spring conditions influence Rainbow Smelt spawning, as this would aid in predicting future trends of this important sportfish forage base. We therefore 1) estimated Rainbow Smelt spawning abundances across the reservoir to determine spatial patterns of spawning occurrence, 2) mapped the spawning sites to determine if bathymetric habitat features indicated site selection patterns, and 3) incorporated spring water warming patterns to evaluate how temperature mediates the Rainbow Smelt spawning-habitat relationship.

Methods

Study area – Lake Oahe is the second largest storage reservoir on the Missouri River, stretching 372 km from central North Dakota to central South Dakota (Figure 1). At normal pool, Lake Oahe's surface area measures 145,000 ha, with 3,623 km of shoreline. Three major tributary arms, along with myriad embayments, provide complex littoral habitats, with an overall shoreline development index of 27.4 (Nelson and Walburg 1977). The upper portion of Lake Oahe in South Dakota is mesotrophic and transitions to
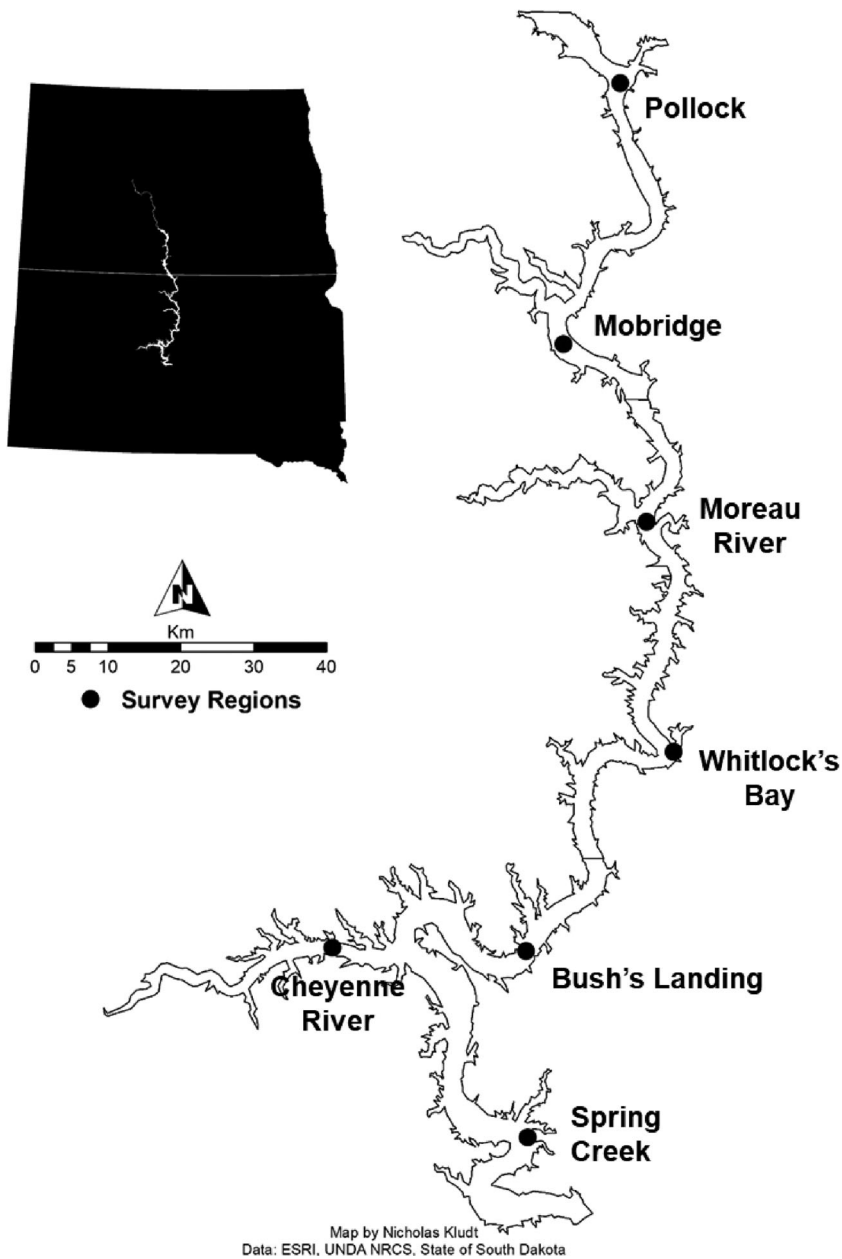
Figure 1. Spring hydroacoustic survey regions, 2016–2018, in Lake Oahe. Inset – Lake Oahe location in North and South Dakota.

oligotrophic downstream toward the dam (Fincel 2011). The lower 169 km of Lake Oahe, approximately 68,500 ha, annually stratify during the summer months (Burczynski et al. 1987) and supports a 2-tier fishery. Although Rainbow Smelt spatial distribution is constrained by thermal habitat during this period, temperature conditions following ice-out allow Rainbow Smelt access to the entire reservoir.

Rainbow Smelt were first detected in Lake Oahe in 1972, following a 1971 stocking by North Dakota Game and Fish in Lake Sakakawea, 165 km upstream of Lake Oahe. Before

the 2011 Missouri River flood and attendant Rainbow Smelt population crash (Fincel et al. 2016), a short-term spring recreational Rainbow Smelt dip net and seine fishery existed at most public access locations on the eastern shore of Lake Oahe (Robert Hanten, SDGFP, personal communication). These anecdotes represented a variety of potential spawning habitats across a 155 km latitudinal gradient and formed the basis for our sampling spatial and temporal frame.

Spawning survey and analysis – Due to the large spatial extent of our sampling frame, we favored complete spatial coverage over complete replication. We surveyed 32 sites, organized as 7 lake regions (Figure 1), within an incomplete design during the springs of 2016–2018, using "region" and "year" as blocking variables. Regions were designed to cover the entire longitudinal extent of the reservoir with roughly equidistant spacing. Each region was randomly assigned 2 survey springs and 1 excluded spring. Each spring consisted of 3 survey periods, with 7–10 days (weather dependent) between visits to a region. Within a region, each site was a 1 km transect with transects apportioned evenly between embayment and reef/point habitat types. Each region contained 4–6 sites, with a minimum of 2 km between sites. We randomized site visits and transect sampling order within each survey period to avoid systematic temporal bias. We used this design to maximize our spatial coverage of Lake Oahe, while still providing site replication through the spawning period following ice-out.

We used a mobile horizontal-beaming hydroacoustic survey to determine the abundance of Rainbow Smelt at each site. While this method did not actually observe Rainbow Smelt in the act of spawning, we assumed the hydroacoustic estimate of each transect represented a snapshot of spawning Rainbow Smelt abundance at a given site and time. Surveys commenced 30 minutes after sundown and were run in darkness with only running lights on the survey vessel, given the documented light avoidance of spawning Rainbow Smelt (McKenzie 1965). Hydroacoustic surveys were conducted using a Biosonics DT-X system with a 420 kHz split beam transducer. The transducer had a 6.9° circular beam and was mounted at a 4° angle below horizontal to avoid surface interference (Gangl and Whaley 2004). Survey settings were 5 pings/s with a pulse duration of 0.5 ms, with a −100 dB collection threshold. System calibration was periodically checked according to the manufacturer's instructions using a 17.5 mm tungsten carbide target sphere. Echogram creation used 40-log(R) time varied gain, 3 dB 1-way maximum gain compensation, and echo length 0.80–1.20 times the original pulse length, using Sonar5-Pro (Balk and Lindem 2015). We used the Sonar5-Pro cross-filter detector optimized for fish tracking to extract individual fish tracks from the echogram. The cross-filter detection method is based on 2-dimensional low-pass filters, advancing the image processing analysis approach (Balk and Lindem 2000), and is demonstrated in detail in Balk and Lindem (2002). To convert target strength (TS) to approximate fish length and subsequently assign a species identification, we used the TS equation developed at 420 kHz for horizontal Rainbow Trout *Oncorhynchus mykiss* from Kubecka and Duncan (1998), expressed in the general form of Love (1977):

$$TS = 27.48 * log_{10}(10 * TL) - 98.6$$

where *TS* is the target strength of an individual fish, and *TL* is the total length (cm) of the fish. This equation is very similar to the Kubecka and Duncan (1998) mixed stock 420 kHz equation; however, we used the Rainbow Trout TS-equation because both species have a physostomous swim bladder and are phylogenetically similar (Bentancur et al. 2013).

Hydroacoustics, when employed alone, cannot determine species composition. An additional sampling technique is necessary to generate length-frequencies of species present at the time of the hydroacoustic survey. We accomplished this using 9.5-mm mesh, 1.2×30.5 m monofilament gill nets (0.12-mm diameter), fished as short-term benthic sets while we conducted the hydroacoustic survey. Nets were oriented perpendicular to the shoreline at 2–3 m depth. Captured Rainbow Smelt were sexed and total length was recorded. All captured individuals were expressing gametes, regardless of sex. Lengths were also taken from any bycatch. These were examined for percent overlap in length-frequency distribution with Rainbow Smelt for length-based assignment of species identification, similar to Fincel et al. (2016).

A random subsample of Rainbow Smelt (n = 211) was retained for age-length analysis in 2018. The sagittal otoliths of these fish were mounted in epoxy (Buehler, EpoxiCure 2, Lake Bluff, Illinois), cross sectioned using a low speed isometric saw (Buehler, M11-1280-160, Lake Bluff, Illinois), and photographed under an Olympus SZX 16 dissecting microscope. Otolith images were then consensus aged using three readers (Quist and Isermann 2017), and a von Bertalanffy growth curve was fit using the least-squares method.

Habitat survey and summary – We developed explanatory habitat metrics for spawning Rainbow Smelt abundances. We recorded visit-specific thermal conditions by calculating the mean of a temperature profile at the centroid of each hydroacoustic transect, excluding the 1 m surface layer. We used site-specific variables to describe the bathymetry and bottom habitat attributes. We refer to this as physical habitat hereafter. To generate these spatial variables, we mapped all our sites in 2018 using a Lowrance HDS 7 unit with 200 kHz HDI transducer. Three mapping transects were laid out parallel to shore using 2018 TerraColor Landsat 8 aerial imagery mosaics (Earthstar Geographics 2018). The outermost transect was 50 m from shore, and the innermost was as reasonably close to the shoreline as could be accomplished safely. The middle transect was 25 m from shore, with occasional deviations to cover bathymetric features of interest (e.g., prominent reef). Transects were mapped at maximum 8 kmph and slowed depending on wave interference and real-time visual assessment of sonar performance. Although we acknowledge water levels are dynamic in reservoirs and actual wetted shoreline may have fluctuated inter-annually, we assumed our 2018 mapping data was representative of the habitat available at each site.

Post-processing was completed by BioBase (2018). Output was 2 D point cloud with depth, slope, and bottom hardness attributes, encompassing the shoreline along the 1 km hydroacoustic transects and extending 50 m offshore. The point cloud was subsequently rasterized, following recommendations from BioBase (2018) using the Feature to Raster tool in ArcGIS 10.4 (ESRI 2016). From this, we calculated the vector ruggedness measure (VRM), which measures terrain ruggedness as the variation of 3 D orientation in neighborhood cells, condensing slope and aspect variance into a single measure. This is scaled from 0 (no terrain variation) to 1 (complete variation), with typical ranges between 0–0.4 (Sappington et al. 2007). We applied this terrestrial metric as an index of bathymetric habitat complexity and favored it over other options because it is less correlated to slope as other derived ruggedness metrics (Sappington et al. 2007). We used mean values for site habitat variables to simplify analysis.

We then condensed the habitat variables into a single descriptive metric using a principle components analysis (PCA) in R (R Core Team 2018) using the "stats" package (R Core Team 2019) to minimize collinearity concerns for further analyses. We checked the data for normality using normal QQ-plots and assessed collinearity with Pearson's correlation tests. As expected, all habitat metrics were significantly collinear ($p < 0.05$). Despite

this, we included VRM, depth, slope, and bottom hardness in the PCA, and examined the component loadings. The first and second components included the same two variables and were biologically relevant. We therefore retained the first component as an independent variable describing a physical habitat gradient and reference this variable as PC1.

Other Statistical Analysis – We compared Rainbow Smelt spawning abundances, our dependent variable, to the PC1 habitat gradient, mean temperature, and the date of the survey. We used Pearson's correlation tests to explore relationships between the independent variables. As temperature and date were collinear, we only used temperature in the following analysis. We used an information theoretic multiple regression analysis to determine the nature of the temperature-habitat interaction on peak spawning abundance, and how that relationship changed throughout the spring warming period. We modelled the relationship as 2 simple linear regressions and 2 multiple regressions: 1 additive and 1 multiplicative interaction, because we were curious of the nature of the interaction, if any existed. Peak spawning abundance was defined as the log_{10}-transformed maximum abundance estimate of spawning Rainbow Smelt at each site across all survey periods and assumed that Rainbow Smelt abundance variation was responsive to changing habitat conditions. This was conducted with all peak abundances pooled using the R package "AICcmodavg" (Mazerolle 2019).

Results

Spawning surveys –Rainbow Smelt length-frequency distribution did not overlap with bycatch species in the gillnet data (Figure 2). This result was consistent for 2016, 2017, and 2018. Rainbow Smelt typically were between 105 and 155 mm. Bycatch species included Yellow Perch *Perca flavescens*, Spottail Shiner *Notropis hudsonius*, Walleye, and immediately post-stocked Chinook Salmon *Oncorhynchus tshawytscha*, but the percent overlap of these species with the Rainbow Smelt length-frequency distribution was minimal (Figure 2). We therefore were confident that any fish within the aforementioned size range was a Rainbow Smelt.

Rainbow Smelt spawning distributions, as detected by our hydroacoustic survey, varied widely between survey regions and years (Figure 3). We were unable to detect any consistent "hot spots" of Rainbow Smelt spawning abundance. Instead, we discovered widespread use of the reservoir for spawning activity. The exception to this was the Pollock region, where Rainbow Smelt abundances were consistently low to nonexistent.

From the 2018 subsample, the age structure of spawning Rainbow Smelt was dominated by age-3 fish (54%, Figure 4). Age-4 fish were the next most numerous (25%), followed by age-2 (11%), age-5 (8%), and age-6 (2%). Overall, the Rainbow Smelt spawning population is generally comprised of younger fish, which is not uncommon for prey species. We recorded mature, spawning age-2 females and males. No age-1 Rainbow Smelt were sampled. Rainbow Smelt growth was asymptotic (Figure 4), with a small increase in mean length-at-age between ages-2 and −3 (9 mm), and little growth occurring after age-3. This age and size structure is consistent with Rainbow Smelt sampled by SDGFP (South Dakota Department of Game, Fish, and Parks) over the preceding two decades (e.g., Lott et al. 1994, Johnson et al. 1995, Johnson et al. 1997, Adams et al. 2009, Longhenry et al. 2010, Potter et al. 2016).

The aging subsample was dominated by 79.6% male fish. The nearly 4:1 sex ratio (M:F) is not unexpected for Rainbow Smelt sampled during the spawn, as there is ample evidence that males generally spend more time at the spawning grounds than females (Rupp 1968, McKenzie 1964), with sex ratios in excess of 8:1 reported (Murawski et al.
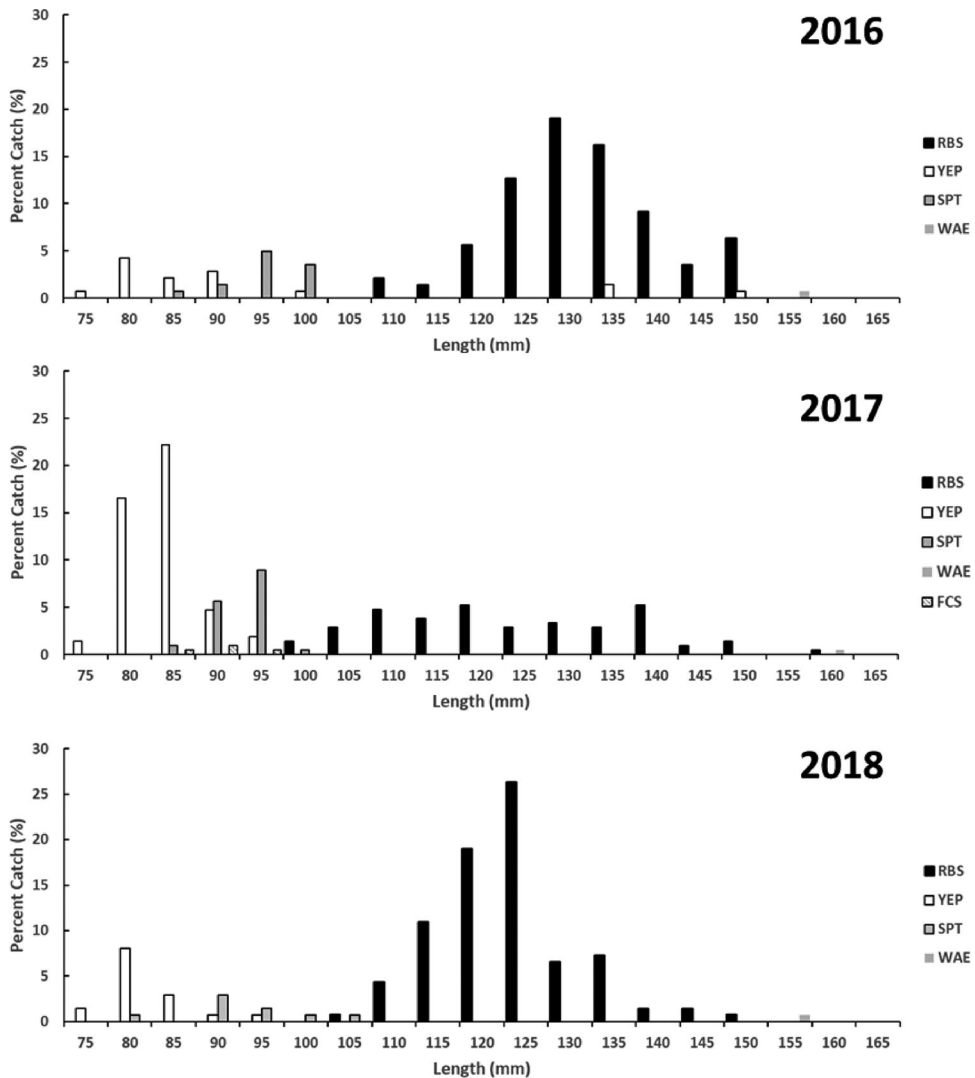
Figure 2. Length-frequency distribution of Rainbow Smelt and bycatch species by 5 mm length bin from short term gillnetting, 2016–2018, Lake Oahe, South Dakota. RBS – Rainbow Smelt, YEP – Yellow Perch, SPT – Spottail Shiner, WAE – Walleye, and FCS – Chinook Salmon.

1980). Repeat spawning bouts are observed in males and females, but males made spawning movements at 1.6–3.7 times the frequency of females (Enterline 2013). Our sample was therefore consistent with those reported elsewhere.

Habitat Survey and analysis - Peak abundances detected at sites varied by survey period (Figure 3), and we used temperature and date to examine this pattern. Peak abundances occurred in the water temperature range of 5–9 °C during 2016 and 2017 (Figure 5). Peak abundances were observed at higher temperatures compared to 2016 or 2017. The 2018 peak abundances occurred 2–4 weeks later (Figure 6), which led to a wider temperature range than previous years (Figure 7). The wider range of temperatures is due to differential warming rates across the large north-south extent of Lake Oahe, in addition to complex reservoir morphology. In the "normal" years, assuming 2018 to be abnormal, Rainbow Smelt spawning peaked approximately mid-April and was concluding near the first week of May.
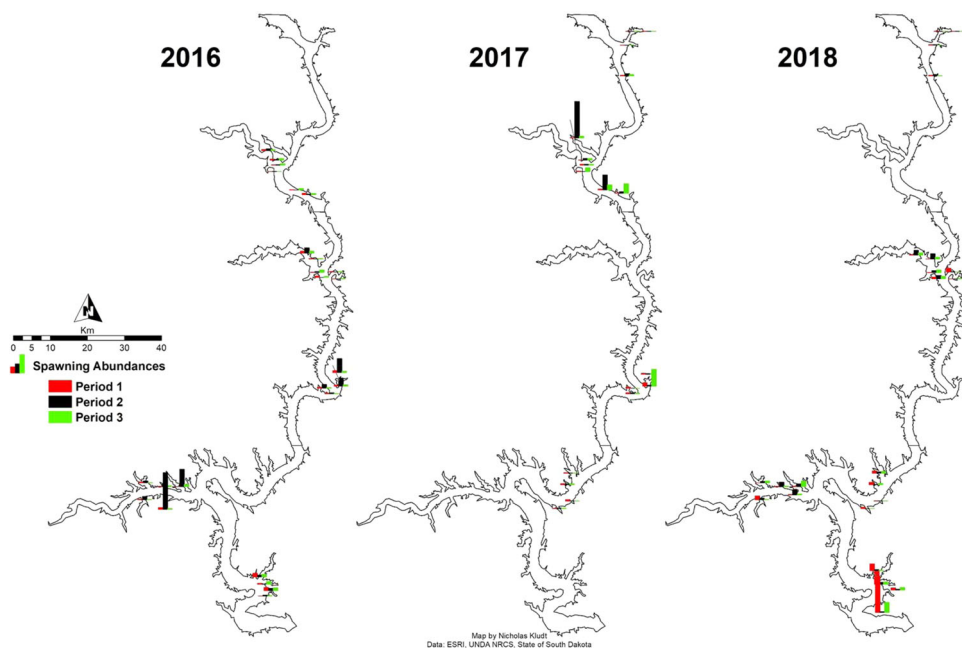
Figure 3. Rainbow Smelt spawning abundances by survey period, 2016–2018, Lake Oahe, South Dakota.
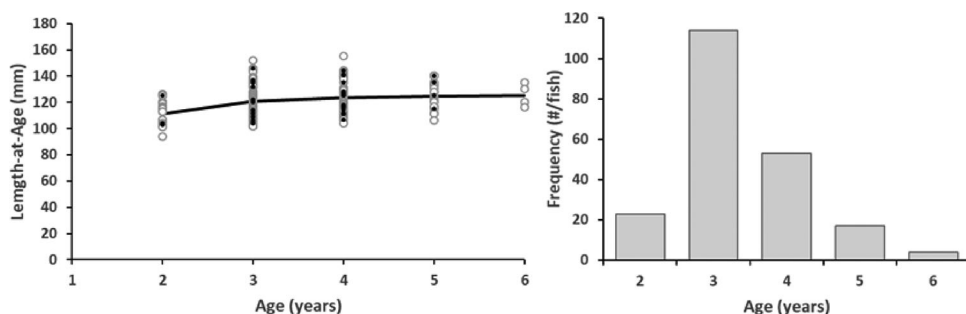

Figure 4. Von Bertalanffy growth model for spawning Rainbow Smelt mean length-at-age, 2018 (left), and age frequencies (right), Lake Oahe, South Dakota. Regression parameters: $L_\infty = 125.25$, $k = 1.10$, $t_0 = 0.025$, $r^2 = 0.99$. Female (black, n = 43), male (gray, n = 168), and estimated mean (black line) lengths shown for reference.

Although temperature plays a major role in Rainbow Smelt spawn timing, we also investigated the influence of physical habitat on the variable spawning Rainbow Smelt abundances. The loadings for the first 2 components of the PCA accounted for 99% of the variance, and the components contained the same 2 variables (Table 1). The first component's scores (PC1) were used as a predictor variable. Higher PC1 scores were correlated to deeper and high slope sites, while low PC1 scores described shallow sites with a low slope.

The information-theoretic regression related the PC1 habitat metric and mean site temperature to peak observed spawning abundance (Table 2). The two interaction models described the data well (ΣAICc $W = 0.56$), although it was evident from the single term models that temperature (AICc $W = 0.26$) independently was more influential than habitat
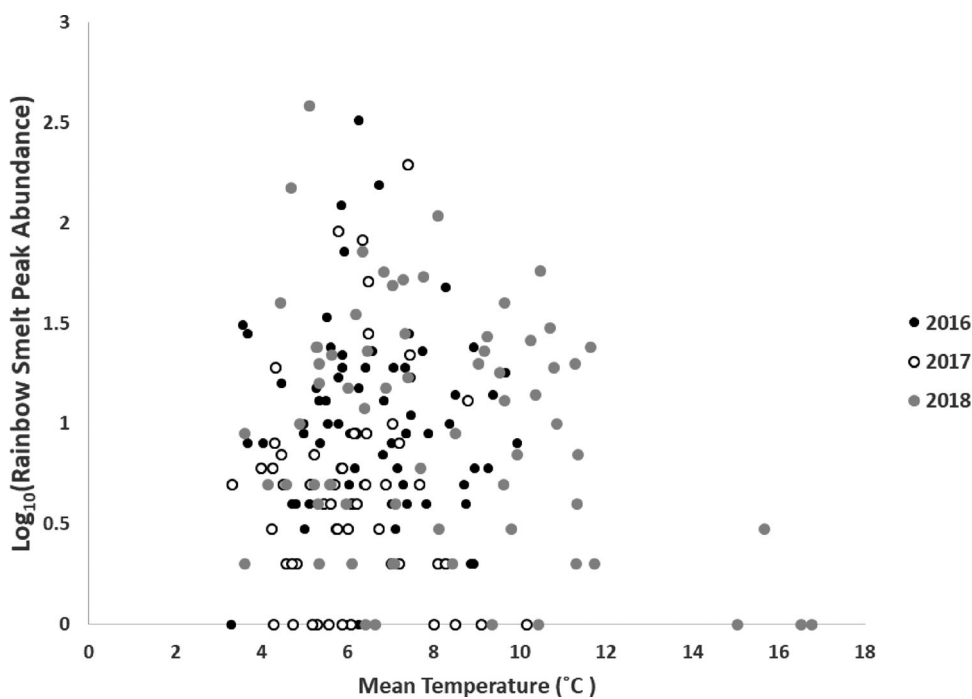
Figure 5. Rainbow Smelt site abundance estimates, 2016–2018, by mean site temperature, determined from a profile taken at the transect centroid, Lake Oahe, South Dakota. Mean temperature excludes 1 m surface layer.
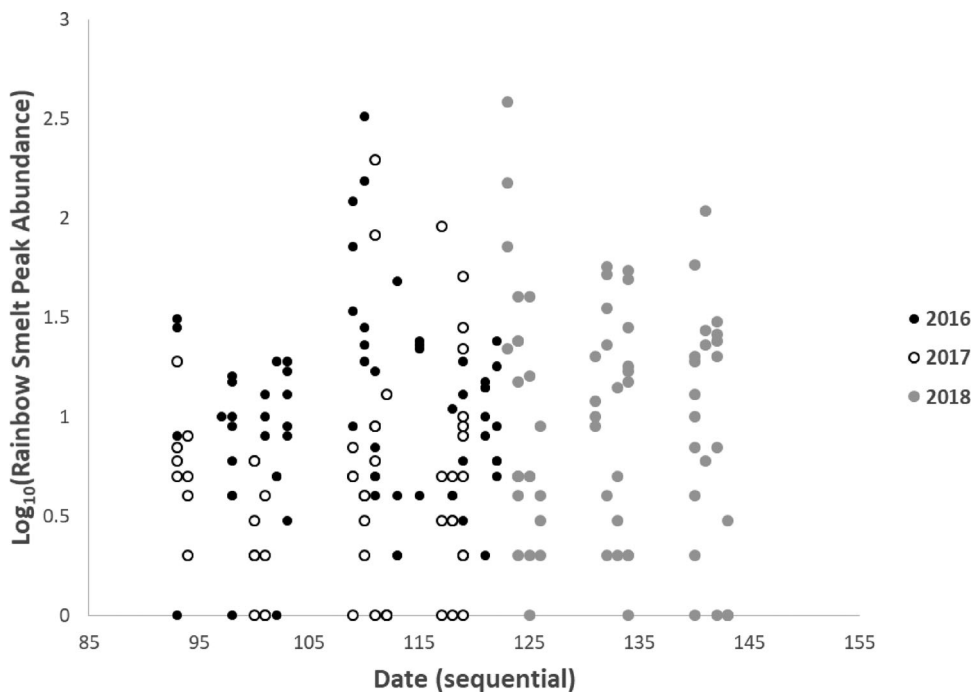

Figure 6. Peak Rainbow Smelt site abundance estimates, 2016–2018, by date, Lake Oahe, South Dakota. Sequential days start January 1 and include 2016 leap day.

Table 1. Principle components analysis results of physical habitat variables. PC1 values, retained for analysis, represent a gradient, with higher values indicating steeper and deeper sites.

	Comp. 1	Comp. 2
Standard Deviation	5.1167	2.754
Cumulative % Variance	0.779	0.999
Loadings:		
Mean VRM	−	−
Mean Depth	−0.832	0.555
Mean Slope	0.555	0.832
Mean Hardness	−	−

Table 2. Information theoretic multiple regression results of Rainbow Smelt abundance compared to habitat covariates.

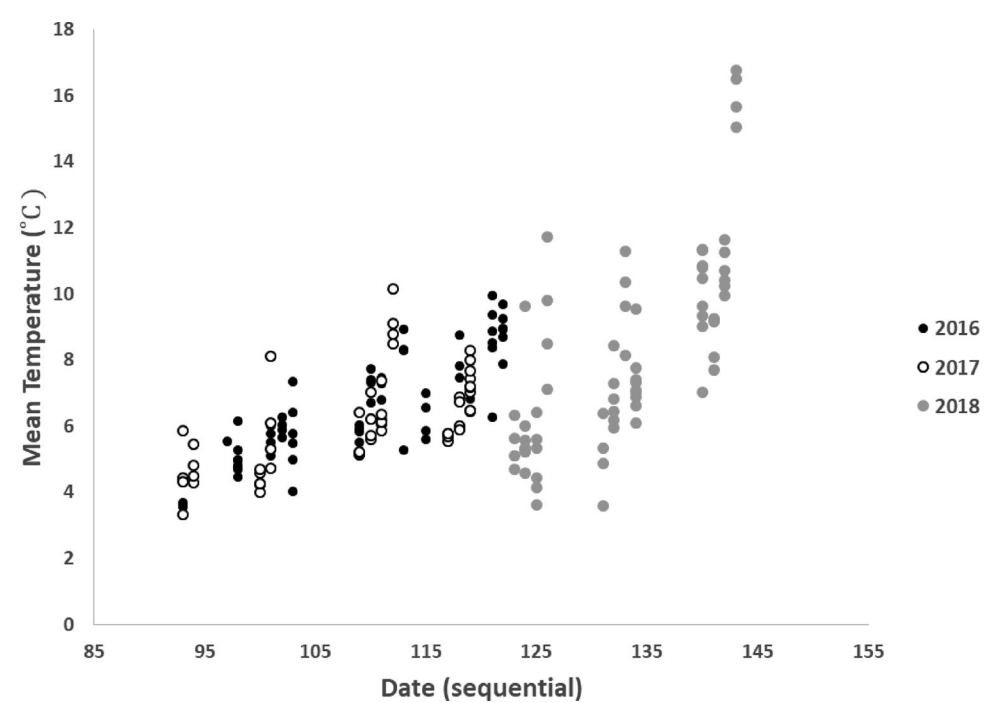| Model	k	ΔAICc	AICc W	P-value
Temp + Habitat + Temp * Habitat	5	0.00	0.39	0.006
Temp + Habitat	4	0.76	0.27	0.009
Temp	3	0.77	0.26	0.007
Habitat	3	3.70	0.06	0.035
Intercept	2	6.08	0.02	<0.001

Figure 7. Spring warming patterns, 2016–2018, Lake Oahe, South Dakota. Mean site temperature was determined from a profile taken at the transect centroid, excluding the 1 m surface layer. Sequential days start January 1 and include 2016 leap day.

(AICc $W = 0.06$). Overall, temperature (ΣAICc $W = 0.82$) had stronger support than habitat (ΣAICc $W = 0.62$), yet the top interaction model was separated from the habitat model by ΔAICc $= 3.70$. All biological models outperformed the intercept model (Table 2).

We used the top model, with the multiplicative interaction, to examine how temperature and habitat interacted with peak spawning abundances. To visualize how this

Figure 8. Top-ranked AICc multiple regression of Rainbow Smelt $\log_{10}$ - transformed peak abundance by PC1 habitat gradient and temperature, illustrating change in Rainbow Smelt interactions with physical habitat with increasing temperature throughout the spring spawning period. Temperature values in the regression (black line, shading $=$ 95% CI) were held constant at the (L to R) minimum, 1st quartile, median, 3rd quartile, and maximum site temperatures for visualization.

interaction changes through the spring, we used the minimum, 1st quartile (Q1), median, 3rd quartile (Q3), and maximum temperatures. At the minimum temperature, Rainbow Smelt displayed a weak affinity for shallower sites (Figure 8). As temperatures warmed into the Q1 and median ranges, where the highest peak abundances were observed ($5.8 - 6.8\,°C$, Figure 7), Rainbow Smelt spawning site abundances became more associated with deeper, steeper sites (Figure 8). The relationship between higher abundances and deeper, steeper habitat progressively became more pronounced at the upper end of the temperature range (Q3 and maximum, Figure 8).

Discussion

We observed a habitat preference for spawning Rainbow Smelt mediated by thermal conditions. Thermal influences on Rainbow Smelt spawn timing have been documented in Maine inland lakes (Rupp 1959), Lake Champlain (Simonin et al. 2016), and the Great Lakes region (Creaser 1925, O'Brien et al. 2012), with spawning taking place shortly after ice out. Lake Oahe peak abundances were generally recorded between $5–9\,°C$, with sampling occurring across a temperature range from $3.5\,°C$ to $17\,°C$. The thermal range of peak detections is like that of O'Brien et al. ($3–10\,°C$, 2012) in Lake Huron tributaries, and the stream ($4.5–7\,°C$) and Great Lakes ($2.2–14.5\,°C$) ranges from Carlander (1969). As our observations spanned a wide range of dates due to a late spring in 2018, Rainbow Smelt appeared to be more temperature-oriented than photoperiod-oriented on the gradient described by Winemiller and Rose (1991).

As water temperature increased, Rainbow Smelt used deeper and steeper habitats. Given the role of temperature cues in Rainbow Smelt spawning, access to deeper thermal refuges seemed to increase in importance as spring warming progressed. In the Great Bay and Piscataqua estuary system, NH, Rainbow Smelt visited multiple rivers during the spawning season, and retreated to the deeper waters of the estuary and near-coast between spawning bouts and after conclusion of spawning (Enterline 2013). As $15\,°C$ is generally when spawning ceases (Carlander 1969, Scott and Crossman 1973), the use of sites near deep thermal refuges may allow spawning to continue where the inshore temperature is at or near the maximum temperature threshold.

Our sampling incorporated a variety of embayments, the number and diversity of which are the defining feature of the Lake Oahe shoreline (Figure 3). Rainbow Smelt have been observed spawning on fine sand, boulders, mud, aquatic vegetation, brush, flooded grassland, concrete, and wooden sluiceways (Rupp 1959), with sand and gravel usually considered ideal (Scott and Crossman 1973). A diversity of spawning substrates is not unusual for broadcast spawning species; however, eggs spawned on a diversity of substrates do not survive at similar rates. On the preferred substrates, egg suffocation was not identified as major cause of mortality; instead, wave action was the primary cause of Rainbow Smelt egg mortality, with more exposed sites experiencing higher mortality (Rupp 1965). While silt-egg interactions were not explored in Rainbow Smelt, 2 mm of silt coverage is sufficient to cause 71% Walleye egg mortality, which are another lithophilic broadcast spawner (Gatch et al. 2020). Thus, we assume silt substrates would be less optimal for Rainbow Smelt egg survival, but locations may not be actively selected against by spawning adults.

At the rear of many Lake Oahe embayments are creeks and we reasoned these lotic habitats were not likely responsible for major annual reproductive contributions due to excessive sediment. Each of the major western tributaries of Lake Oahe contribute massive volumes of sediment per year to the reservoir: Grand (970,905 tons/year), Moreau

(1,431,475 tons/year), and Cheyenne Rivers (5,459,641 tons/year, USDA NRCS 2009). Creaser (1925) noted the spawning Rainbow Smelt is not a strong swimmer and does not ascend far upstream. Rainbow Smelt in streams deposit eggs across the full gradient of stream habitat available as one works upstream (Creaser 1925). In the case of Lake Oahe, such a gradient equates to tributary channels with accumulated clay silts that stretch for several river miles upstream. Rainbow Smelt preferred stream spawning habitat includes riffles with larger diameter substrate (10–20 cm, Chase 2006), or clean gravel and coarse sand (Scott and Crossman 1973). High turbidity causes cessation of Rainbow Smelt spawning (Murawski et al. 1980). Thus, we qualitatively judged the sediment impaired, low gradient stream habitat local to the reservoir, which is quite turbid during spring run-off, to be generally unsuitable for spawning runs of Rainbow Smelt. Although some stream spawning may occur given the behavioral plasticity of Rainbow Smelt, we believe the Lake Oahe population to be dominated by shore spawning.

Accordingly, we concentrated on Rainbow Smelt spawning on lake shorelines and reefs. Although stream spawning is common across the Rainbow Smelt range (Scott and Crossman 1973), lake spawning can sustain populations in the absence of suitable stream habitat (Rupp 1959). Lake spawning can also provide more consistent production, as seen in St. Martin Bay, Lake Ontario, where lake-contribution larva were moderate, yet less variable relative to stream production (Brown 1994). In Lake Oahe, lake spawning Rainbow Smelt site abundances were inconsistent between survey periods and years (Figure 3). Although recurrent stream site use is common elsewhere in the Rainbow Smelt range (Murawski et al. 1980), it appears our lake spawning population lack a reliable spatial pattern.

It appears that on the Winemiller and Rose (1991) gradient of photoperiod vs. temperature spawning cues, temperature is the more dominant factor driving the Lake Oahe Rainbow Smelt spawn timing. The unusually late spring ice-out in 2018 led to peak Rainbow Smelt spawning abundances observed over two weeks later than the preceding two years. Were photoperiod the dominant cue, we would expect to see a lower magnitude of peak spawning activity, with the peak occurring under the ice and before surveying commenced. Under ice spawning does occur (Rupp 1959, Carlander 1969), but peak activity is generally after ice out at slightly higher temperatures (Rupp 1959, Creaser 1925, O'Brien et al. 2012). It may be that Rainbow Smelt stage inconsistently throughout the reservoir and have spawning movements at various locations, cued by temperature. This is consistent with estuarine Rainbow Smelt spawning movements, where male and female fish visited multiple rivers within a coastal embayment in a single spawning season (Enterline 2013, Murawski et al. 1980).

The Lake Oahe Rainbow Smelt age and length distributions were skewed toward older and smaller individuals though consistent with Rainbow Smelt sampled by SDGFP over the preceding two decades (e.g., Lott et al. 1994, Johnson et al. 1995, Johnson et al. 1997, Adams et al. 2009, Longhenry et al. 2010, Potter et al. 2016). In Lake Oahe, length was asymptotic and little difference was observed between lengths at age for smelt 2–6 years old. Overall Lake Oahe mean length (120.7 ± 11.5 SD) was approximately 25 mm less than Gulf of Maine age-1 Rainbow Smelt (Enterline 2013). This is also smaller than the 178–203 mm average adult size reported by Scott and Crossman (1973). Lake Oahe Rainbow Smelt lengths were consistently below the range-wide length-at-age data from Carlander (1969), with average length-at-age smaller than the dwarf race of Rainbow Smelt reported from Lake Champlain and inland Atlantic Northeast lakes (mean = 157 mm, age-3). Size appears to be genetically plastic, as shown by anecdotes of transplantation experiments from dwarf Rainbow Smelt source populations (Carlander 1969).

Our population follows the trend of small, inland systems having smaller mean adult lengths (mean = 104 mm) than larger-bodied marine or Great Lakes populations (up to 356 mm, Scott and Crossman 1973), despite the large scale of Lake Oahe. Our sampled age distribution is probably the result of late maturation. Rainbow Smelt typically mature at ages 2–3 (Carlander 1969), yet a majority of our sample of actively spawning fish was comprised of individuals ≥ age-3.

The slow growth of Lake Oahe Rainbow Smelt, and possibly the resultant delayed maturation, may be diet related. Rainbow Smelt are usually zooplanktivorous as juveniles, transitioning to piscivory with increasing size (Carlander 1969). Yet, in a survey of adult Rainbow Smelt diets in Lake Oahe, fish occurred in diets with a frequency of 0.7%, with Chesson's selectivity values of nearly 0, which is below neutral selectivity levels (Karnitz 1992). A decade later, stable isotope analysis showed that Rainbow Smelt adults remained partially zooplanktivorous, roughly one trophic level below Walleye, a top-tier piscivore in Lake Oahe (Davis 2004). The dominance of zooplankton diets, and the incomplete piscivory of Lake Oahe Rainbow Smelt may explain their slow growth, as the energy density of invertebrates is less than fish (Karnitz 1992, Davis 2004). Rainbow Smelt diets in Horsetooth Reservoir, CO (755 ha), were similar and yielded similarly depressed adults size structure, despite the differences in system scale (Johnson and Goettl 1999). The exact cause of the small adult size structure in Lake Oahe, however, remains unknown.

Our survey and analysis did make some important assumptions. The use of the Kubecka and Duncan (1998) Rainbow Trout 420 kHz horizontal beaming TS-equation coefficients likely affected our *in-situ* length estimates, as species- and frequency-specific equations are generally preferable (Simmonds and MacLennan 2005). Despite the widely acknowledged concerns with generalized TS-equations (Simmonds and MacLennan 2005), these equations, notably Love (1977), continue to be used (e.g., Fincel et al. 2016). Additionally, the generalized use of Rainbow Trout equations for the pelagic fish community has demonstrated utility and precedent (Yule 2000). We also may not have observed all spawning Rainbow Smelt directly, as some spawn in waters ≤ 0.5 m (Rupp 1959, Rupp 1965), which is beyond the reach of horizontal beaming sonar. Instead, we likely observed fish spawning in slightly deeper water offshore, similar to Nellbring (1989) and Evans and Loftus (1987) or staging prior to inshore movement. If we hydroacoustically counted Rainbow Smelt at a given transect, we assumed that fish was spawning immediately inshore from its location or within the 0.5 km transect, as that was the inference scale. Given the propensity of males to remain on the spawning ground awaiting females, out of our detection ability, we may have scanned a disproportionate number of staging females, which would only serve to strengthen the importance of the deeper, steeper sites that seemed preferable.

Management implications

Presently, Lake Oahe water level management is conducted by the US Army Corps of Engineers, with recommendations by SDGFP to favor spring reservoir surface elevations remaining steady or rising. The goal, among others, was to prevent egg stranding from occurring on shallow, sandy flats, where Rainbow Smelt have been detected in the past with a combination of seines and mini-fyke nets (South Dakota Game, Fish and Parks, unpublished data). This recommendation also protects Rainbow Smelt eggs spawned along the shoreline of steeper sites, which we observed to be important. Subsequently, we suggest SDGFP continue recommending stable to rising reservoir surface elevations.

These results represent the first step toward understanding habitat use characteristics of spawning Rainbow Smelt in reservoir systems. We hoped to identify a spawning habitat niche for Rainbow Smelt that could be replicated over time around the reservoir to enhance the overall quantity of spawning habitat available. This proved to be elusive, as strong habitat correlations did not exist beyond general slope and depth metrics. Instead, Rainbow Smelt spawning occurs in indeterminate locations throughout the reservoir that meet general thermal criteria, attenuated by bathymetry throughout the spring warming period.

Disclosure statement

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