ICHTHYOPLANKTON DENSITY AND SHOVELNOSE STURGEON SPAWNING
IN RELATION TO VARYING DISCHARGE TREATMENTS

by

Benjamin Joseph Goodman

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2009
APPROVAL

of a thesis submitted by

Benjamin Joseph Goodman

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

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Dr. Carl A. Fox
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Benjamin Joseph Goodman

July 2009
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# TABLE OF CONTENTS

1. INTRODUCTION ..........................................................................................................1

2. STUDY AREA ...............................................................................................................6

3. METHODS ...................................................................................................................11
   Hydrograph Treatments .............................................................................................11
   Site Selection ..............................................................................................................13
   Embryonic and Larval Fish Collection and Identification ............................................15
   Estimation of Shovelnose Sturgeon Spawning Dates ...................................................17
   Data Analysis .............................................................................................................19

4. RESULTS .....................................................................................................................21
   Hydrograph Treatments .............................................................................................21
   Ichthyoplankton Assemblage .....................................................................................27
   Effects of Hydrograph Treatments on Shovelnose Sturgeon ........................................28
      Larval Density ........................................................................................................28
      Timing of Spawning ...............................................................................................33
      Spawning Conditions .............................................................................................40
      Spawning Locations ...............................................................................................41
   Effects of Hydrograph Treatments on Ichthyoplankton Bycatch ..................................43
      Overall Bycatch Density .......................................................................................43
      Larval Catostomid Density ....................................................................................44
      Larval Cyprinid Density .........................................................................................47

5. DISCUSSION ...............................................................................................................52
   Effects of Hydrograph Treatments on Shovelnose Sturgeon ........................................52
   Effects of Hydrograph Treatments on Ichthyoplankton Bycatch ..................................58
   Management Implications .........................................................................................61

LITERATURE CITED ......................................................................................................64

APPENDICES ...................................................................................................................73

   APPENDIX A: Photographs of Shovelnose Sturgeon
      Embryos with Notes on Developmental Stage .......................................................74
   APPENDIX B: Photographs Representing the Families of Larval Fish Sampled.............78
LIST OF TABLES

Table | Page
--- | ---
1. Fish species of the lower Marias and upper Missouri rivers (Berg 1981; Gardner 1997) with present status in Montana (MTFWP 2009). Species non-native to the upper Missouri River basin are denoted by an asterisk | 10
2. Estimates of fertilization timing for shovelnose sturgeon embryos and larvae collected in the Marias River, Missouri River, and Teton River, Montana, in 2006, 2007, and 2008. Developmental stages of embryos and larvae were estimated using information from Dettlaff et al. (1993) and Colombo et al. (2007). Number of hours post-fertilization for each embryo and larva was estimated using development rates from K. M. Kappenman and M. A. H. Webb (USFWS, personal communication) and Colombo et al. (2007) | 34
3. Mean bycatch density (larvae/m³, with minimum and maximum densities in parentheses) by family of larval fish sampled in the Marias and Missouri rivers in 2006 and 2007. Density data are not available for the Teton River in 2006 and 2007 because of low water velocity | 45
LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Map of the upper Missouri River, lower Marias River, lower Teton River, and the study area (denoted by the red line) .......................................................... 7</td>
</tr>
<tr>
<td>2.</td>
<td>Comparison of peak annual discharge (m³/s) in the Marias River upstream (USGS gauging station at Shelby, Montana) and downstream (USGS gauging station at Chester, Montana) of Tiber Dam from 1956 to 2005 ........................................ 8</td>
</tr>
<tr>
<td>5.</td>
<td>Map of study area with sampling locations (denoted by black bars) in the Marias, Missouri, and Teton rivers, and locations of hypothesized shovelnose sturgeon spawning habitat (i.e., large riffles) .......................................................... 14</td>
</tr>
<tr>
<td>6.</td>
<td>Mean daily discharge (top) and water temperature (bottom) in the Marias River at Loma, Montana (rkm 2), from 29 May to 17 July in 2006, 2007, and 2008. Optimal and suitable shovelnose sturgeon spawning temperature ranges are denoted by the dotted lines (optimal) and dashed lines (suitable) ............ 22</td>
</tr>
<tr>
<td>7.</td>
<td>Mean daily discharge (top; Fort Benton, Montana; rkm 3,337) and water temperature (bottom; rkm 3,303) in the Missouri River from 22 May to 17 July in 2006, 2007, and 2008. Optimal and suitable shovelnose sturgeon spawning temperature ranges are denoted by the dotted lines (optimal) and dashed lines (suitable) .......................................................... 24</td>
</tr>
<tr>
<td>8.</td>
<td>Mean daily discharge (top) and water temperature (bottom) in the Teton River at Loma, Montana (rkm 0.7), from 22 May to 17 July in 2006, 2007, and 2008. Optimal and suitable shovelnose sturgeon spawning temperature ranges are denoted by the dotted lines (optimal) and dashed lines (suitable) ............ 26</td>
</tr>
<tr>
<td>9.</td>
<td>Density of larval shovelnose sturgeon by sampling date and location in the Marias River in 2006 (top), 2007 (middle), and 2008 (bottom). Black squares represent overall mean density (Marias River sites combined) of larval shovelnose sturgeon by date .......................................................... 29</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>10</td>
<td>Density of larval shovelnose sturgeon by sampling date and location in the Missouri River in 2006 (top) and 2007 (bottom). Black squares represent overall mean density (Missouri River sites combined) of larval shovelnose sturgeon by date.</td>
</tr>
<tr>
<td>11</td>
<td>Density of larval shovelnose sturgeon by sampling date in the Teton River in 2008.</td>
</tr>
<tr>
<td>12</td>
<td>Mean daily discharge and water temperature in the Marias River at Loma, Montana (rkm 2), in 2006. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae.</td>
</tr>
<tr>
<td>13</td>
<td>Mean daily discharge and water temperature in the Marias River at Loma, Montana (rkm 2), from 29 May to 17 July in 2008. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae.</td>
</tr>
<tr>
<td>14</td>
<td>Mean daily discharge and water temperature for the Missouri River (rkm 3,337 for discharge and rkm 3,303 for water temperature) from 29 May to 17 July in 2006. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos.</td>
</tr>
<tr>
<td>15</td>
<td>Mean daily discharge and water temperature for the Missouri River (rkm 3,337 for discharge and rkm 3,303 for water temperature) from 29 May to 17 July in 2007. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae.</td>
</tr>
<tr>
<td>16</td>
<td>Mean daily discharge and water temperature in the Teton River (rkm 0.7) from 29 May to 10 July in 2006. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon larvae.</td>
</tr>
<tr>
<td>17</td>
<td>Mean daily discharge and water temperature in the Teton River (rkm 0.7) from 22 May to 10 July in 2008. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon larvae.</td>
</tr>
</tbody>
</table>
LIST OF FIGURES—CONTINUED

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>18. Mean daily larval shovelnose sturgeon density in the Marias River (all years) as a function of mean discharge and water temperature. Means of discharge and water temperature are from the period 3 to 9 days prior to each sampling day</td>
<td>42</td>
</tr>
<tr>
<td>19. Mean density (SE) of larval shovelnose sturgeon by site in the Marias River (top) and Missouri River (bottom) in 2006 and 2007</td>
<td>43</td>
</tr>
<tr>
<td>20. Density of larval catostomids by sampling date and location in the Marias River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Marias River sites combined) of larval catostomids by date</td>
<td>46</td>
</tr>
<tr>
<td>21. Density of larval catostomids by sampling date and location in the Missouri River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Missouri River sites combined) of larval catostomids by date</td>
<td>48</td>
</tr>
<tr>
<td>22. Density of larval cyprinids by sampling date and location in the Marias River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Marias River sites combined) of larval cyprinids by date</td>
<td>49</td>
</tr>
<tr>
<td>23. Density of larval cyprinids by sampling date and location in the Missouri River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Missouri River sites combined) of larval cyprinids by date</td>
<td>51</td>
</tr>
<tr>
<td>24. Shovelnose sturgeon embryo collected on 14 June 2006 in the lower Marias River (site three) estimated to be at developmental stage 11 or 12 (early to late blastula) (Dettlaff et al. 1993; Colombo et al. 2007)</td>
<td>75</td>
</tr>
<tr>
<td>25. Shovelnose sturgeon embryo collected on 14 June 2006 in the upper Missouri River (site one) estimated to be at developmental stage 12 (late blastula) (Dettlaff et al. 1993; Colombo et al. 2007)</td>
<td>75</td>
</tr>
<tr>
<td>26. Shovelnose sturgeon embryo collected on 14 June 2006 in the lower Marias River (site three) estimated to be at developmental stage 14 (formation of dorsal blastopore lip) (Dettlaff et al. 1993; Colombo et al. 2007)</td>
<td>76</td>
</tr>
<tr>
<td>27. Shovelnose sturgeon embryo collected on 15 June 2006 in the lower Marias River (site five) estimated to be at developmental stage 17 (small yolk plug visible) (Dettlaff et al. 1993; Colombo et al. 2007)</td>
<td>76</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>28.</td>
<td>Shovelnose sturgeon embryo collected on 18 June 2006 in the lower Marias River (site five) estimated to be at a stage of development from 27 to 29 (heart rudiment is present and is slightly s-shaped) (Dettlaff et al. 1993; Colombo et al. 2007)</td>
</tr>
<tr>
<td>29.</td>
<td>Shovelnose sturgeon embryo collected on 3 July 2008 in the lower Marias River (site two) estimated to be at a stage of development from 32 to 35 (tail extends past head) (Dettlaff et al. 1993; Colombo et al. 2007)</td>
</tr>
<tr>
<td>30.</td>
<td>Shovelnose sturgeon protolarvae: protolarval shovelnose sturgeon (0 to 24 hours post hatch) obtained from the hatchery for reference (top) and a protolarval shovelnose sturgeon sampled in the lower Marias River on 23 June 2006 (bottom)</td>
</tr>
<tr>
<td>31.</td>
<td>Larval representative of the family Catostomidae sampled in the lower Marias River</td>
</tr>
<tr>
<td>32.</td>
<td>Larval representative of the family Cottidae sampled in the lower Marias River</td>
</tr>
<tr>
<td>33.</td>
<td>Larval representative of the family Cyprinidae sampled in the lower Marias River</td>
</tr>
<tr>
<td>34.</td>
<td>Common carp larva (family Cyprinidae) sampled in the lower Marias River</td>
</tr>
<tr>
<td>35.</td>
<td>Goldeye larva (family Hiodontidae) sampled in the lower Marias River</td>
</tr>
<tr>
<td>36.</td>
<td>Larval representative of the family Ictaluridae sampled in the lower Marias River</td>
</tr>
</tbody>
</table>
ABSTRACT

Many lotic fish species use natural patterns of variation in discharge and water temperature as spawning cues and these natural patterns are often altered by river regulation. The effects of spring discharge and water temperature variation on the spawning of shovelnose sturgeon *Scaphirhynchus platyrynchus* and other fishes in the upper Missouri River have not been well documented. In 2006, 2007, and 2008, I had the unique opportunity to study the effects of experimental discharge levels on ichthyoplankton density in the lower Marias River, a regulated tributary to the upper Missouri River. The objective of this study was to evaluate the effects of contrasting discharge treatments and water temperature variation on spatial and temporal variation in spawning of shovelnose sturgeon (and other species sampled as bycatch) as measured by embryonic and larval fish density in the lower Marias River. Ichthyoplankton was sampled about every four days in June and July of 2006, 2007, and 2008. Overall larval fish density was greater in 2006 than in 2007, and increased density was associated with increased discharge in 2006. In 2006, shovelnose sturgeon spawning occurred in the Marias River in conjunction with the ascending, peak (134 m$^3$/s), and descending portions of the spring hydrograph and water temperatures from 16°C to 19°C. No evidence of sturgeon spawning was documented in the lower Marias River in 2007 when peak discharge remained low (9 m$^3$/s to 14 m$^3$/s) despite the occurrence of water temperatures suitable for shovelnose sturgeon embryo development. In 2008, shovelnose sturgeon spawning occurred in conjunction with the peak (118 m$^3$/s) and descending portions of the spring hydrograph, and during a prolonged period of increased discharge (28 m$^3$/s to 39 m$^3$/s), coupled with water temperatures from 11°C to 23°C in the lower Marias River. These data suggest that discharge must reach a threshold level (28 m$^3$/s), and should be coupled with water temperatures suitable (12°C to 24°C) or optimal (16°C to 20°C) for shovelnose sturgeon embryo development, to provide a spawning cue to shovelnose sturgeon in the lower Marias River.
INTRODUCTION

Most rivers in the world have been altered for anthropogenic needs, such as power generation, flood control, water supply, and transportation (Benke 1990; Revenga et al. 2000). A common method of altering rivers is by regulating them through the use of dams. Dams enable water managers to modify natural patterns of variation in discharge to provide for anthropogenic needs (Richter et al. 2006). However, river regulation can alter natural river conditions and negatively impact native aquatic biota (Galat et al. 1996; Stanford et al. 1996). For example, river regulation can transform and fragment habitat, modify sediment transport, disconnect the floodplain from the channel, alter water temperature, and decouple natural fluctuations in discharge and water temperature (Junk et al. 1989; Sparks et al. 1990; Stanford et al. 1996; Poff et al. 1997). Aquatic biota in regulated rivers can adapt to these human-induced environmental changes, emigrate to find suitable conditions, or be extirpated (Stanford et al. 1996).

The aquatic biota affected by river regulation includes lotic fishes, which are adapted to natural variation in discharge and water temperature (Fausch and Bestgen 1997; Poff et al. 1997). For example, discharge variation coupled with suitable water temperature can act as a cue for initiation of life-history events in lotic fishes such as seasonal migrations (Chapman and Carr 1995; Swanberg 1997) and spawning (Nesler et al. 1988; Tyus 1990; Chapman and Carr 1995; Keiffer and Kynard 1996; Schrank et al. 2001; Paragamian and Wakkinen 2002). Decoupling of natural variation in discharge and water temperature through river regulation can result in removal of cues or an

Sturgeon (family Acipenseridae) can be influenced by river regulation because they rely on natural variation in discharge and water temperature for part or all of their life-cycle requirements (e.g., Rochard et al. 1990; Dryer and Sandvol 1993; Chapman and Carr 1995; Kieffer and Kynard 1996; Beamsderfer and Farr 1997; Keenlyne 1997; Duke et al. 1999). Thus, given the global propensity to regulate rivers, natural river environments are disappearing and most extant sturgeon populations are in a state of decline or endangered (Birstein 1993; Birstein et al. 1997; Secor et al. 2002). However, the mechanisms by which river regulation causes declines in sturgeon are poorly understood (Secor et al. 2002). Shovelnose sturgeon *Scaphirhynchus platostomus* and pallid sturgeon *S. albus* are two North American species that have experienced declines throughout their range (Dryer and Sandvol 1993; Keenlyne 1997). Intensive regulation of the Missouri River and many of its tributaries has been implicated in the declines of shovelnose sturgeon and pallid sturgeon (Dryer and Sandvol 1993; Keenlyne 1997). Regulation of the Missouri River and its tributaries has resulted in river fragmentation, reduced sediment transport, alteration of physical habitat, disconnection of the floodplain from the channel, altered water temperatures, and a decoupling of the natural variation in discharge and water temperature (Hesse and Sheets 1993; Galat et al. 1996). These altered conditions may influence spawning success of shovelnose sturgeon and pallid sturgeon (DeLonay et al. 2007).

The sequence of events from migration to egg deposition has not been observed for shovelnose sturgeon or pallid sturgeon; therefore, specific locations and habitat types
used for spawning by these species are unknown (DeLonay et al. 2007; Wildhaber et al. 2007). Based on capture of ripe and spent females, shovelnose sturgeon and pallid sturgeon spawning in the Missouri River is believed to occur in late spring and early summer when discharge is naturally high (Dryer and Sandvol 1993; Keenlyne 1997; Jacobson and Galat 2008). Thus, it is possible that this seasonal increase in discharge provides a cue for shovelnose sturgeon and pallid sturgeon spawning in the Missouri River. During spawning, shovelnose sturgeon and pallid sturgeon deposit demersal, adhesive eggs that typically attach to substrate until hatching (Jacobson and Galat 2008). Upon hatching, shovelnose sturgeon and pallid sturgeon larvae are dispersed downstream by river currents (Kynard et al. 2002; Braaten et al. 2008). Rates of survival to hatch and development in shovelnose sturgeon and pallid sturgeon embryos are dependent on water temperature (K. M. Kappenman and M. A. H. Webb, U. S. Fish and Wildlife Service, personal communication). Thus, it is likely that water temperature also influences the timing of spawning in these species.

I used shovelnose sturgeon as a cornerstone species to study the relationship between spawning and discharge-water temperature coupling, given the global and regional importance of understanding the effects of river regulation on sturgeon. The specific environmental conditions (e.g., discharge and water temperature) required by shovelnose sturgeon for spawning are currently unknown (DeLonay et al. 2007; Jacobson and Galat 2008). Therefore, understanding of the effects of discharge and water temperature on shovelnose sturgeon spawning is needed to guide water management in rivers containing shovelnose sturgeon populations (Jacobson and Galat 2008). For example, if shovelnose sturgeon spawning is cued by pre-dam levels of spring discharge
coupled with suitable spawning temperatures, then alterations of spring discharge from river regulation may negatively influence shovelnose sturgeon spawning migrations, gonadal maturation, and release of gametes. Changes in dam operations to study the effects of varying discharge and water temperature on sturgeon are often difficult to implement because of economic and social constraints (Beamesderfer and Farr 1997). However, large-scale manipulative studies are critical to improvement of environmental management decisions because these studies can match the scale of management and provide results directly applicable to management problems (Carpenter 1998). I had the rare opportunity to conduct a large-scale, manipulative experiment in the lower Marias River, Montana, to test the impacts of varying discharge and water temperature on larval shovelnose sturgeon density (an index to spawning success).

The U.S. Bureau of Reclamation (USBR) regulates discharge in the lower Marias River through Tiber Dam, and in the upper Missouri River through Canyon Ferry Dam. In the spring of 2006, 2007, and 2008 discharge in the lower Marias River was manipulated, creating experimental hydrograph treatments to test the effects of varying discharge and water temperature on shovelnose sturgeon spawning. Discharge in the adjacent reach of the Missouri River was also manipulated to test the synergistic effects of discharge in this basin on shovelnose sturgeon spawning. Knowledge of the timing, location, and success of shovelnose sturgeon spawning in relation to variation in discharge and water temperature can provide insight to water managers and fishery managers about the ecological role of these fluctuations and about how dams should be operated to optimize water use for environmental (e.g., native fish) and human needs (e.g., flood control). The objective of this study was to evaluate the effects of contrasting
discharge treatments and water temperature variation on spatial and temporal variation in embryonic and larval fish density (primarily shovelnose sturgeon, but also other species sampled as bycatch) in the lower Marias River, upper Missouri River, and lower Teton River.
STUDY AREA

The study was conducted in the Marias River, Teton River, and the Missouri River immediately upstream and downstream of the confluence with the Marias River (Figure 1). The Marias River originates at the confluence of Two Medicine River and Cut Bank Creek about 80 km east of Glacier National Park, Montana, and flows 275 km southeast through north-central Montana where it enters the Missouri River at rkm 3,302. The Marias River basin drains 18,485 km²; the western portion of the basin consists of rugged mountains along the Continental Divide and the central and eastern portions of the basin are composed of broad, rolling plains used primarily as rangeland for livestock (Garvin and Botz 1975; USGS 2009). Construction of Tiber Dam (rmk 129) on the Marias River was completed in 1957, forming Lake Elwell (USBR 2009). This reservoir has a storage capacity of 1.920 km³ and was constructed for flood control, irrigation, recreational use, and municipal water supply (Gardner and Berg 1983). Prior to impoundment of the Marias River, discharge peaked in the spring as a result of mountain snowmelt and minimum discharge occurred in late fall and winter (Scott et al. 1997). Currently, discharge in the lower Marias River is almost entirely controlled by the operation of Tiber Dam and water temperatures downstream from Tiber Dam are reduced from historical levels as a result of hypolimnetic releases (Gardner and Berg 1983). Peak annual discharge in the lower Marias River has been reduced in nearly every year on record since Tiber Dam was constructed (Figure 2) (USGS 2009). This reduction in peak discharge that occurred in May or June allows for augmented discharge during late summer and fall (Rood and Mahoney 1995).
Figure 1.—Map of the upper Missouri River, lower Marias River, lower Teton River, and the study area (denoted by the red line).
Figure 2.—Comparison of peak annual discharge (m$^3$/s) in the Marias River upstream (USGS gauging station at Shelby, Montana) and downstream (USGS gauging station at Chester, Montana) of Tiber Dam from 1956 to 2005.

The Missouri River originates at the confluence of the Jefferson, Madison, and Gallatin rivers near Three Forks, Montana. At Fort Benton, Montana (rkm 3,337) the Missouri River drains an area of 64,100 km$^2$. Terrain in this basin varies from large mountain ranges of the Continental Divide to broad, rolling plains and agricultural valleys, and livestock grazing is the primary land use (Kaiser and Botz 1975; Braico and Botz 1976). Discharge in the upper Missouri River is mainly regulated by Canyon Ferry Dam (rkm 3,611). Canyon Ferry Dam was completed in 1954 and Canyon Ferry Reservoir has the largest storage capacity (2.530 km$^3$) of the reservoirs upstream of Fort
Peck Reservoir. Water released from dams in the upper Missouri River is colder and less turbid than pre-dam conditions (Dryer and Sandvol 1993). In addition, the average of peak annual discharge has decreased by 27% from pre-dam (1891 to 1953) to post-dam (1954 to 2005) levels at Fort Benton, Montana (USGS 2009).

The Teton River originates at the confluence of the North Fork Teton and South Fork Teton rivers east of the Continental Divide and flows 296 km in a path roughly parallel to the Marias River through north-central Montana. The Teton River drains 5,206 km² of rolling plains before entering the lower Marias River (rkm 1.6) (Garvin and Botz 1975; USGS 2009) (Figure 1). The Teton River remains undammed and has historically produced large flood pulses (e.g., 1,546 m³/s in 1964) (Bovee and Scott 2002; USGS 2009).

The lower Marias, upper Missouri, and Teton rivers support a diverse fish assemblage including 46 species (32 native fishes and 14 non-native fishes) (Table 1) (Berg 1981; Gardner 1997). The majority of these species are adapted to warm and cool water (Hesse et al. 1989). However, alteration of habitat (e.g., reduced water temperatures below dams) has allowed the presence of non-native, coldwater species (e.g., rainbow trout *Oncorhynchus mykiss*) in tailwater reaches and has altered the distribution of native fishes adapted to warmer, more turbid water (Hesse et al. 1989; Gardner 1997).
Table 1.—Fish species of the lower Marias and upper Missouri rivers (Berg 1981; Gardner 1997) with present status in Montana (MTFWP 2009). Non-native species are denoted by an asterisk.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Montana Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scaphirhynchus albus</td>
<td>pallid sturgeon</td>
<td>endangered</td>
</tr>
<tr>
<td>Scaphirhynchus platorynchus</td>
<td>shovelnose sturgeon</td>
<td>uncommon</td>
</tr>
<tr>
<td>Polyodon spathula</td>
<td>paddlefish</td>
<td>species of special concern</td>
</tr>
<tr>
<td>Hiodon alosoides</td>
<td>goldeye</td>
<td>common</td>
</tr>
<tr>
<td>Carassius auratus</td>
<td>goldfish*</td>
<td>none</td>
</tr>
<tr>
<td>Couesius plumbeus</td>
<td>lake chub</td>
<td>common</td>
</tr>
<tr>
<td>Cyprinus carpio</td>
<td>common carp*</td>
<td>none</td>
</tr>
<tr>
<td>Hybognathus argyritis</td>
<td>western silvery minnow</td>
<td>uncommon</td>
</tr>
<tr>
<td>Hybognathus hankinsoni</td>
<td>brassy minnow</td>
<td>uncertain</td>
</tr>
<tr>
<td>Hybognathus plactitus</td>
<td>plains minnow</td>
<td>uncertain</td>
</tr>
<tr>
<td>Macrhybopsis gelida</td>
<td>sturgeon chub</td>
<td>species of special concern</td>
</tr>
<tr>
<td>Macrhybopsis meeki</td>
<td>sicklefin chub</td>
<td>species of special concern</td>
</tr>
<tr>
<td>Notropis atherinoideis</td>
<td>emerald shiner</td>
<td>common</td>
</tr>
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<td>Notropis hudsonius</td>
<td>spottail shiner*</td>
<td>none</td>
</tr>
<tr>
<td>Notropis stramineus</td>
<td>sand shiner</td>
<td>uncommon</td>
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METHODS

Hydrograph treatments

The planned Marias River hydrograph treatment in 2006 represented an increase in the magnitude and duration of elevated discharge relative to normal Tiber Dam operations. The hydrograph in 2006 (“experimental hydrograph”) was modeled after the 1982 hydrograph upstream of Tiber Reservoir (Figure 3). This hydrograph was selected because it best represented the average of several years of hydrograph data. One limitation to the 2006 hydrograph was discharge had to remain below 150 m$^3$/s to minimize nuisance flooding and property damage. Given this limitation, I surmised that the 1982 hydrograph was the best approximation of conditions that would occur below Tiber Dam if it was not present. The 2007 planned hydrograph treatment (“normal hydrograph”) represented the normal operation of Tiber Dam during a low-water year (Figure 3). In 2008, a fortuitous increase in late-spring precipitation allowed for planning an additional experimental hydrograph treatment similar to 2006, but with a decreased magnitude of peak discharge and a protracted duration of increased discharge following the peak (Figure 3).

The Missouri River planned hydrograph treatments for 2006, 2007, and 2008 were based on historical-hydrograph data from the Missouri River at Virgelle, Montana (rkm 3,261), prior to completion of Canyon Ferry Dam (pre-1954). The 1943 hydrograph was selected as a representative hydrograph for the Missouri River in terms of timing and duration of increased discharge; however, the planned magnitude of peak discharge was reduced to 1,000 m$^3$/s to minimize nuisance flooding and property damage (Figure 4).
Figure 3.—Mean daily discharge in the Marias River at Shelby, Montana, from 1 May to 24 July in 1982, and the planned hydrograph treatments for the Marias River in 2006, 2007, and 2008.

Figure 4.—Mean daily discharge in the Missouri River at Virgelle, Montana, from 1 May to 24 July in 1943, and the planned hydrograph treatment for Missouri River discharge in 2006, 2007, and 2008.
The Teton River is used for irrigation but is unregulated. Thus, hydrograph treatments could not be implemented. Discharge variation in the Teton River was caused by annual variation in snowpack, precipitation, and irrigation withdrawals.

Site Selection

In 2006 and 2007, embryonic and larval fish were sampled at five fixed sites in the lower 11 rkm of the Marias River (Figure 5). Sampling locations were selected subjectively to evaluate spatial variation in embryonic and larval fish density relative to suspected shovelnose sturgeon spawning locations (i.e., large riffles). Sampling sites were located at river bends immediately upstream and downstream of two large-riffles representing potential shovelnose sturgeon spawning locations (Figure 5). In addition, sampling was conducted upstream and downstream of the Teton River confluence to estimate spatial and temporal variation in ichthyoplankton density in the Marias River relative to input from the Teton River (Figure 5). In 2008, sampling was conducted at Marias River sites one and two only, because of logistical constraints (Figure 5). Two subsamples were conducted per sampling occasion at each fixed site in the Marias River; one in the outside bend and one mid-channel.

In 2006 and 2007, embryonic and larval fish were sampled at two fixed sites in the Missouri River located at the first river bend upstream and downstream of the Marias River confluence (Figure 5). These locations were selected to estimate spatial and temporal variation in embryonic and larval fish density in the Missouri River relative to the contribution from the Marias River. Three subsamples were collected per sampling
Figure 5.—Map of study area with sampling locations (denoted by black bars) in the Marias, Missouri, and Teton rivers, and locations of hypothesized shovelnose sturgeon spawning habitat (i.e., large riffles).
occasion at each fixed site in the Missouri River; one in the outside bend and two mid-channel. No sampling was conducted in the Missouri River in 2008 because of logistical constraints.

In 2006, 2007, and 2008, embryonic and larval fish were sampled at one fixed site located at the first bend in the Teton River (rkm 0.2) to evaluate spatial and temporal variation in embryonic and larval fish density between the Marias and Teton rivers (Figure 5). However, in 2006 and 2007, water velocities in the Teton River were too low to acquire accurate measures of embryonic and larval fish density. Thus, only taxonomic composition data were obtained from Teton River samples in 2006 and 2007.

Estimates of daily discharge (m$^3$/s) in the Marias and Teton rivers were provided by the United States Geological Survey (USGS) gauging stations at Loma, Montana. Estimates of daily discharge (m$^3$/s) in the Missouri River were provided by the USGS gauging station at Fort Benton, Montana. Water temperature (°C) was measured hourly from April to August in 2006, 2007, and 2008 using continuous-reading temperature loggers placed in the Marias River (rkm 2) and in the Missouri River (rkm 3,303). Estimates of mean daily water temperature (°C) in the Teton River in 2006, 2007, and 2008 were provided by the USGS gauging station at Loma, Montana.

**Embryonic and Larval Fish Collection and Identification**

Shovelnose sturgeon spawning in the upper Missouri River basin occurs from late May to mid-July (Berg 1981). Thus, in 2006 and 2007, embryonic and larval fish samples were collected every three to four days (depending on logistics) at fixed sampling locations from late May to mid-July in the Marias, Missouri, and Teton rivers.
The three to four day intervals between sampling occasions were selected because typical hatch times for shovelnose sturgeon are from four to eight days at water temperatures from 16°C to 20°C (K. M. Kappenman and M. A. H. Webb, U. S. Fish and Wildlife Service, unpublished data; Colombo et al. 2007). Thus, if shovelnose sturgeon spawning occurred, then it was likely that either embryos or larvae would be present during the following sampling event. In 2008, samples were collected every three to six days from early June to mid-July due to logistical constraints.

Samples were collected from either a jet boat or a raft depending on accessibility to sampling locations. Sampling gear consisted of two plankton nets; one conical plankton net (0.20-m² opening) and one rectangular plankton net (0.20-m² opening), each with 1.5 m of 750-µm mesh with an attached 750-mL collection cup and weighted with a 4.5-kg lead weight. Two net types were used to estimate differences in embryonic and larval shovelnose sturgeon capture success between net types. Embryonic and larval shovelnose sturgeon capture rates were similar between net types and density data from paired samples using different net types were pooled for all data analyses. Nets were lowered from both sides of the bow until they reached the riverbed and boat position was maintained nearly stationary relative to the shoreline during sampling. The benthic position of larval drift nets was selected to increase efficiency of sampling for larval shovelnose sturgeon and pallid sturgeon because their density is greatest in the lower 0.5 m of the water column (Braaten et al. 2004; Braaten et al. 2008). The pooled sample (two nets combined) was considered a subsample for each fixed site sample. Sampling lasted from 2 to 20 minutes depending on water velocity and the rate of debris accumulation. Each net was fitted with a General Oceanics flow meter (model 2030R) to
estimate water velocity; I estimated the volume (m$^3$) of water filtered by multiplying water velocity by net opening dimensions. Subsamples were placed in Whirl-Pak® bags and preserved in 10% formalin and dyed with Phloxine-B dye.

Larval fish and embryos were removed from the debris and placed in vials containing 70% ethanol. Larval fishes were identified to family, genus, or species using keys from Auer (1982), Kay et al. (1994), and Wallus et al. (1990). In 2008, only sturgeon larvae and embryos were identified due to personnel and logistic constraints. Larval fish counts were converted to density at a fixed site using volume estimates from the flow meters and the net dimensions. Of the eggs and embryos collected, only chondrostean eggs and embryos were identified. Chondrostean eggs and embryos were distinguished from other eggs and embryos by their opaque coloration, relative size, and holoblastic form of development (Dettlaff et al. 1993; Colombo et al. 2007).

**Estimation of Shovelnose Sturgeon Spawning Dates**

Chondrostean embryos and larvae collected during sampling were used to estimate shovelnose sturgeon spawning dates. The chondrostean fishes present in the Missouri River basin include shovelnose sturgeon, pallid sturgeon, and paddlefish; embryos of these chondrostean fishes cannot be distinguished by morphology. I am confident that all chondrostean embryos collected in the current study are *Scaphirhynchus* spp. embryos (i.e., shovelnose sturgeon or pallid sturgeon) because previous studies have found no evidence of paddlefish spawning in the study reach (Berg 1981; Gardner 1997) and all larval chondrostean collected in the current study were identified as *Scaphirhynchus* spp. Further, it is unlikely that embryonic and larval...
Scaphirhynchus spp. are pallid sturgeon as evidence of natural recruitment to the pallid sturgeon population in this river section has not been documented for over 30 years and abundance has been estimated at 50 adults (Gardner 1997). In addition, no radio-tagged adult pallid sturgeon came within 100 km of the Marias River during a concurrent pallid sturgeon telemetry study (Gardner and Jensen 2007; Gardner and Jensen 2008; Jensen and Gardner 2009). In contrast, shovelnose sturgeon continue to successfully recruit in this river section, as verified by annual collection of juveniles (W. M. Gardner, Montana Fish, Wildlife and Parks, personal communication). Further, radio-tagged adult shovelnose sturgeon were located in the Marias River during all years of this study (Gardner and Jensen 2007; Gardner and Jensen 2008; Jensen and Gardner 2009). Thus, it is highly likely that all embryonic and larval Scaphirhynchus spp. collected in this study are shovelnose sturgeon, and these will be hereafter referred to as such.

Chorions were removed from sampled shovelnose sturgeon embryos to enhance clarity of important morphological features because the chorion can become cloudy as a result of preservation, which can interfere with identification of developmental stage. Stage of embryonic development was determined using descriptions of developmental stages from Dettlaff et al. (1993) and Colombo et al. (2007). An interval of time required to reach the observed stage of development was estimated based on rates of embryonic shovelnose sturgeon development from K. M. Kappenman and M. A. H. Webb (U. S. Fish and Wildlife Service, personal communication), and Colombo et al. (2007). Spawning dates were estimated by subtracting the time required to reach the observed stage of development at a given temperature from the time of collection. Sample photographs of embryos used in spawning date estimation are in Appendix A.
Data Analysis

In laboratory studies designed to determine threshold and optimal temperatures for shovelnose sturgeon embryo survival, temperatures from 12°C to 24°C showed similar survival, with 100% mortality at 8°C and 28°C (K. M. Kappenman and M. A. H. Webb, U. S. Fish and Wildlife Service, unpublished data). These studies suggest that water temperatures from 12°C to 24°C are suitable for successful shovelnose sturgeon spawning and embryo survival in natural conditions. In addition, metabolic efficiency (conversion of yolk sac to tissue) in shovelnose sturgeon embryos was greatest from 16°C to 20°C suggesting that these water temperatures are optimal for shovelnose sturgeon spawning and embryo development (K. M. Kappenman and M. A. H. Webb, U.S. Fish and Wildlife Service, unpublished data). These suitable and optimal water temperature thresholds were used to estimate the availability of suitable and optimal water temperatures for shovelnose sturgeon spawning during hydrograph treatments.

Larval fish density was compared between the Marias and Missouri rivers, and between 2006 and 2007, and the experimental unit was sampling date (N = 46; rivers and years pooled). Welch’s two-sample t-test was used to compare mean bycatch density between rivers and years. Data were transformed \( \sqrt[3]{x} \) to approximate a normal distribution. Statistical calculations were conducted using R (R Development Core Team 2009). An \( \alpha = 0.10 \) was established a priori and used to determine statistical differences.

Larval fish density was compared among sampling dates in the Marias, Missouri, and Teton rivers, and the experimental unit was fixed site by sampling date (N = 209; rivers and years pooled). Analysis of daily variation in density was restricted to
shovelnose sturgeon, catostomids, and cyprinids because of small sample sizes for remaining taxa. Density data were unavailable for Teton River samples in 2006 and 2007 because of low water velocity; thus, these samples were not included. No statistical tests were conducted in comparisons among sampling dates.
RESULTS

Hydrograph Treatments

The realized hydrograph treatments varied from planned hydrograph treatments in the Marias River in 2006, 2007, and 2008 (Figures 3 and 6); however, distinct hydrograph treatments were created. In the 2006 experimental hydrograph treatment (“pulse treatment”), spring discharge reached the greatest magnitude of the three years, but the duration of increased magnitude was short (17 days). On 29 May 2006, discharge was 19 m$^3$/s, began rising on 10 June, peaked on 16 June (134 m$^3$/s), descended to a minimum (18 m$^3$/s) on 27 June, and remained at this minimum level into mid-July (Figure 6). In the 2007 hydrograph treatment (“normal treatment”), discharge remained at minimum levels; discharge peaked (14 m$^3$/s) on 30 May and descended to minimum discharge (9 m$^3$/s) on 15 July (Figure 6). In the 2008 experimental hydrograph treatment (sustained-pulse treatment), spring discharge reached a peak magnitude less than the peak in 2006; however, the duration of increased discharge in 2008 was greater than in 2006 (Figure 6). On 29 May 2008, discharge was 8 m$^3$/s, began rising on 31 May, peaked on 9 June (118 m$^3$/s), descended to a post-peak minimum (28 m$^3$/s) on 30 June, ascended to 39 m$^3$/s on 10 July, and descended to 38 m$^3$/s by 17 July (Figure 6). Peak discharge was 184 percent (2006), 19 percent (2007), and 162 percent (2008) of the average of peak annual discharge for the Marias River from 1958 to 2005 (i.e., post Tiber Dam) (USGS 2009). Mean discharge from 1 June to 31 July was 78 percent (2006), 31 percent (2007), and 98 percent (2008) of the average discharge from 1 June to 31 July in the Marias River from 1958 to 2005 (USGS 2009).
Figure 6.—Mean daily discharge (top) and water temperature (bottom) in the Marias River at Loma, Montana (rkm 2), from 29 May to 17 July in 2006, 2007, and 2008. Optimal and suitable shovelnose sturgeon spawning temperature ranges are denoted by the dotted lines (optimal) and dashed lines (suitable).

Water temperature during the Marias River hydrograph treatments varied among 2006 (mean = 20°C; minimum = 13°C; maximum = 24°C), 2007 (mean = 22°C; minimum = 14°C; maximum = 27°C), and 2008 (mean = 19°C; minimum = 11°C;
maximum = 23°C). The 2006 hydrograph peak occurred at a later date (16 June) than the 2008 hydrograph peak (9 June) and mean water temperature in conjunction with peak discharge was greater in 2006 (16°C) than in 2008 (14°C) (Figure 6). In addition, water temperature decreased in conjunction with both peaks in discharge (Figure 6). From 29 May to 17 July, suitable shovelnose sturgeon spawning temperatures (12°C to 24°C) occurred on 50 days in 2006, 38 days in 2007, and 49 days in 2008 (Figure 6). Optimal shovelnose sturgeon spawning temperatures (16°C to 20°C) occurred on 21 days in 2006, 17 days in 2007, and 15 days in 2008 (Figure 6).

Realized hydrographs varied from planned hydrographs in the Missouri River in magnitude and duration of increased discharge (Figures 4 and 7). In 2006, discharge was 317 m³/s on 22 May, descended to 228 m³/s on 9 June, peaked on 12 June (532 m³/s), and descended to a minimum (137 m³/s) on 17 July (Figure 7). In 2007, discharge was 229 m³/s on 22 May, increased to 345 m³/s on 31 May, descended to 267 m³/s on 6 June, peaked on 8 June (371 m³/s), and descended to a minimum (138 m³/s) on 15 July (Figure 7). In 2008, discharge was 243 m³/s on 22 May, peaked on 27 May (850 m³/s), remained greater than 600 m³/s until 20 June, and descended to a minimum (217 m³/s) on 17 July (Figure 7). In 2006 and 2007, peak discharge was less than the average of peak annual discharge from 1955 to 2005 (675 m³/s), whereas peak spring discharge was greater than average in 2008 (USGS 2009). Mean discharge from 1 June to 31 July was 65 percent (2006), 59 percent (2007), and 142 percent (2008) of the average discharge from 1 June to 31 July in the Missouri River from 1955 to 2005 (324 m³/s) (USGS 2009).
Figure 7.—Mean daily discharge (top; Fort Benton, Montana; rkm 3,337) and water temperature (bottom; rkm 3,303) in the Missouri River from 22 May to 17 July in 2006, 2007, and 2008. Optimal and suitable shovelnose sturgeon spawning temperature ranges are denoted by the dotted lines (optimal) and dashed lines (suitable).

Water temperature during Missouri River hydrographs varied among 2006 (mean = 20°C; minimum = 13°C; maximum = 24°C), 2007 (mean = 20°C; minimum = 13°C; maximum = 25°C), and 2008 (mean = 16°C; minimum = 10°C; maximum = 21°C) (Figure 7). Temporal variation in water temperature was similar between 2006 and 2007,
whereas water temperature in 2008 was colder than the previous years on nearly every date (Figure 7). The 2006 and 2007 hydrograph peaks (12 June and 8 June, respectively) occurred later than the 2008 hydrograph peak (27 May) and water temperature was greater in conjunction with peak discharge in 2006 (16°C) and 2007 (16°C) than in 2008 (10°C) (Figure 7). In addition, water temperature decreased in conjunction with peaks in discharge (Figure 7). From 22 May to 17 July, suitable shovelnose sturgeon spawning temperatures occurred on 57 days (2006), 52 days (2007), and 48 days (2008) in the Missouri River, and optimal shovelnose sturgeon spawning temperatures occurred on 30 days (2006), 21 days (2007), and 28 days (2008).

Contrasting patterns of discharge occurred in the Teton River in 2006, 2007, and 2008 (Figure 8). In 2006, discharge in the Teton River was zero on 22 May, began rising on 28 May, increased sharply on 12 June, peaked on 13 June (10 m$^3$/s), and descended to zero on 5 July (Figure 8). In 2007, discharge in the Teton River remained low; peak spring discharge occurred on 1 June (1 m$^3$/s) and descended to zero by 21 June (Figure 8). In 2008, discharge remained greater than zero throughout the sampling period; discharge started at 1 m$^3$/s (22 May), peaked early on 29 May (24 m$^3$/s), descended to 7 m$^3$/s on 10 June, spiked to 13 m$^3$/s on 15 June, and descended to a minimum (3 m$^3$/s) on 10 July (Figure 8). Historical discharge data for this location are unavailable.

Water temperature in the Teton River when discharge was greater than zero varied among 2006 (mean = 21°C; minimum = 14°C; maximum = 26°C), 2007 (mean = 19°C; minimum = 12°C; maximum = 25°C), and 2008 (mean = 19°C; minimum = 11°C; maximum = 26°C) (Figure 8). The hydrograph peak in 2006 (13 June) occurred at a later
Figure 8.—Mean daily discharge (top) and water temperature (bottom) in the Teton River at Loma, Montana (rkm 0.7), from 22 May to 17 July in 2006, 2007, and 2008. Optimal and suitable shovelnose sturgeon spawning temperature ranges are denoted by the dotted lines (optimal) and dashed lines (suitable).

date than the 2008 hydrograph peak (29 May) and water temperature was greater in conjunction with the 2006 peak (21°C) than with the 2008 peak (16°C) (Figure 8).

During the secondary discharge spike in 2008 (15 June), mean daily water temperature
was 18°C (Figure 8). In the unregulated Teton River, decreases in water temperature did not coincide with hydrograph peaks (Figure 8). From 22 May to the day when discharge reached zero, suitable shovelnose sturgeon spawning temperatures occurred on 37 days (2006), 29 days (2007), and 49 days (2008) and optimal shovelnose sturgeon spawning temperatures occurred on 18 days (2006), 12 days (2007), and 16 days (2008).

**Ichthyoplankton Assemblage**

The ichthyoplankton assemblage sampled in this study was composed of shovelnose sturgeon (the cornerstone species) and bycatch. In 2006 and 2007 in the Marias, Missouri, and Teton rivers, 2,490 larval fish (all data pooled) were sampled representing six families. Larval catostomids were numerically dominant composing 92.0% (N = 2,157) of all larval fish sampled. Larval cyprinids (6.0%; N = 141) and acipenserids (shovelnose sturgeon) (1.4%; N = 32) composed smaller percentages of sampled larvae. Larval cottids, hiodontids, and ictalurids each composed less than 0.5% of all larval fish sampled. Photographs of larval fishes representative of the families collected in this study are in Appendix B.

In the Marias River in 2006 and 2007, larval catostomids (92.7%; N = 1,703), cyprinids (5.7%; N = 104), acipenserids (shovelnose sturgeon) (1.3%; N = 23), hiodontids (0.3%, N = 5), cottids (0.1%; N = 2), and ictalurids (0.1%, N = 1) were sampled. In the Missouri River in 2006 and 2007, larval catostomids (92.3%; N = 405), cyprinids (4.6%; N = 20), acipenserids (shovelnose sturgeon) (1.8%, N = 8), and hiodontids (1.4%; N = 6) were sampled. In the Teton River in 2006 and 2007, larval
catostomids (73.1%; N=50), cyprinids (25.4%; N=20), and acipenserids (shovelnose sturgeon) (1.5%; N=1) were sampled.

**Effects of Hydrograph Treatments on Shovelnose Sturgeon**

**Larval Density**

During the Marias River pulse treatment, larval shovelnose sturgeon were sampled on two of 12 sampling occasions (22 June and 26 June) (Figure 9). Mean larval shovelnose sturgeon density was greatest on 22 June, six days after peak discharge (Figure 9) when mean daily water temperature was 19°C (Figure 6). No variation in the timing of peak larval shovelnose sturgeon density was observed among sampling locations in the Marias River in 2006 (Figure 9). Suitable shovelnose sturgeon spawning temperatures (12°C to 24°C) occurred on all 50 days. Optimal shovelnose sturgeon spawning temperatures (16°C to 20°C) occurred on 21 of 50 days and occurred in conjunction with the experimental discharge pulse (5 days before and 7 days after peak discharge) (Figure 6). Thus, the occurrence of shovelnose sturgeon larvae during the pulse treatment was associated with the experimental discharge pulse coupled with optimal shovelnose sturgeon spawning temperatures.

In contrast to the 2006 hydrograph treatment, no shovelnose sturgeon larvae were sampled in the Marias River during the 2007 normal hydrograph treatment (Figures 6 and 9). Shovelnose sturgeon larvae were absent from samples despite the occurrence of water temperatures suitable for shovelnose sturgeon spawning on 38 of 50 days and the occurrence of optimal shovelnose sturgeon spawning temperatures on 17 of 50 days.
Figure 9.—Density of larval shovelnose sturgeon by sampling date and location in the Marias River in 2006 (top), 2007 (middle), and 2008 (bottom). Black squares represent overall mean density (Marias River sites combined) of larval shovelnose sturgeon by date.
(Figure 6). Thus, the absence of shovelnose sturgeon larvae in Marias River samples during the normal treatment was associated with the low levels of peak discharge and mean June-July discharge.

During the 2008 Marias River sustained-pulse treatment, larval shovelnose sturgeon occurred in samples on 6 of 12 sampling occasions (Figure 9). An early spike in larval shovelnose sturgeon density occurred on 20 June (Figure 9), 11 days after peak discharge when mean daily water temperature was 20°C (Figure 6). Water temperature during peak discharge (14°C) was below optimal shovelnose sturgeon spawning temperatures (Figure 6). The peak in mean larval shovelnose sturgeon density occurred later (7 July) in the Marias River (Figure 9) when mean daily water temperature was 22°C and mean daily discharge was 29 m³/s, 28 days after the occurrence of peak discharge (Figure 6). A third spike in mean larval shovelnose sturgeon density occurred on the last sampling occasion (16 July) when mean daily water temperature was 19°C following a late-season increase in discharge (from 29 m³/s on 7 July to 39 m³/s on 10 July) (Figures 6 and 9). The peak in mean larval shovelnose sturgeon density in the Marias River in 2008 occurred in July at both sampling sites during the sustained period of increased discharge (Figures 6 and 9). In the Marias River in 2008, water temperatures suitable for shovelnose sturgeon spawning (49 of 50 days) and optimal for shovelnose sturgeon spawning (15 of 50 days) occurred on fewer days than in 2006. Nevertheless, the increased proportion of sampling occasions at which shovelnose sturgeon larvae occurred in the Marias River in 2008 (relative to 2006 and 2007) was associated with the experimental period of increased discharge coupled with water temperatures suitable for shovelnose sturgeon spawning.
In 2006, no larval shovelnose sturgeon occurred in Missouri River samples (Figure 10) despite water temperatures suitable for shovelnose sturgeon spawning on all 57 days and optimal shovelnose sturgeon spawning temperatures on 26 of 57 days. In addition, optimal shovelnose sturgeon spawning temperatures occurred in conjunction with increased discharge (including 3 days before and 3 days after peak discharge).

![Figure 10](image)

Figure 10.—Density of larval shovelnose sturgeon by sampling date and location in the Missouri River in 2006 (top) and 2007 (bottom). Black squares represent overall mean density (Missouri River sites combined) of larval shovelnose sturgeon by date.
In 2007, larval shovelnose sturgeon occurred in samples on two sampling occasions in the Missouri River (17 June and 20 June) (Figure 10). Mean larval shovelnose sturgeon density in the Missouri River peaked on 17 June (Figure 10) when mean daily water temperature was 18°C, nine days after the occurrence of peak discharge (Figure 7). No longitudinal variation in the timing of peak larval shovelnose sturgeon density occurred in the Missouri River in 2007 as density at both sites peaked on 17 June (Figure 10). Shovelnose sturgeon larvae occurred in more samples in 2007 than in 2006 despite a decrease in the occurrence of water temperatures suitable for shovelnose sturgeon spawning (52 of 57 days) and optimal for shovelnose sturgeon spawning (17 of 57 days).

In 2006, one larval shovelnose sturgeon occurred in a Teton River sample collected on 23 June, 10 days after the occurrence of peak discharge at a mean daily water temperature of 22°C (Figure 8). In 2007, no larval shovelnose sturgeon were sampled in the Teton River; however, sampling only occurred on 4 days because of low discharge. In 2008, larval shovelnose sturgeon occurred in samples on 4 of 11 sampling occasions (Figure 11). An initial increase in larval shovelnose sturgeon density occurred on 9 June (Figure 11), 11 days after peak discharge when mean daily water temperature was 16°C (Figure 8). However, peak larval shovelnose sturgeon density occurred on 20 June (Figure 11) when mean daily water temperature was 22°C, five days after a secondary spike in spring discharge (Figure 8).
Figure 11.—Density of larval shovelnose sturgeon by sampling date in the Teton River in 2008.

**Timing of Spawning**

Thirteen shovelnose sturgeon eggs and embryos were collected in the Marias River in 2006, and all were sampled from 14 June to 18 June. Only five of the 13 had been fertilized and could be staged (Table 2). In addition, 23 shovelnose sturgeon larvae were captured in the Marias River in 2006 (Table 2). All shovelnose sturgeon larvae captured in the Marias River in 2006 were in the protolarval stage of development (0 to 24 hours post-hatch) and were captured four to eight days after the last shovelnose sturgeon embryo was collected (Table 2). Shovelnose sturgeon spawning was estimated to have occurred in conjunction with the ascending, peak, and descending portions of the pulse treatment (11 June to 22 June) coupled with water temperatures optimal for shovelnose sturgeon spawning (16°C to 19°C) in the Marias River in 2006 (Table 2; Figure 12).
Table 2.—Estimates of fertilization timing for shovelnose sturgeon embryos and larvae collected in the Marias River, Missouri River, and Teton River, Montana, in 2006, 2007, and 2008. Developmental stages of embryos and larvae were estimated using descriptions of development from Dettlaff et al. (1993) and Colombo et al. (2007). Number of hours post-fertilization for each embryo and larva was estimated using development rates from K. M. Kappenman and M. A. H. Webb (USFWS, personal communication) and Colombo et al. (2007).

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Day</th>
<th>Mean Temp. (°C)</th>
<th>Embryos</th>
<th>Developmental Stage</th>
<th>Larvae</th>
<th>Developmental Stage</th>
<th>Hours Post-Fertilization</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Marias</strong></td>
<td>2006</td>
<td>6/14</td>
<td>17.6</td>
<td>2</td>
<td>11 to 14</td>
<td>0</td>
<td></td>
<td>9 to 50</td>
</tr>
<tr>
<td>River</td>
<td></td>
<td>6/15</td>
<td>17.1</td>
<td>1</td>
<td>17</td>
<td>0</td>
<td></td>
<td>27 to 50</td>
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<td></td>
<td></td>
<td>6/18</td>
<td>16.4</td>
<td>2</td>
<td>26 to 29</td>
<td>0</td>
<td></td>
<td>52 to 95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6/22</td>
<td>16.8</td>
<td>0</td>
<td>18</td>
<td>0</td>
<td>0 to 24 hrs post-hatch</td>
<td>87 to 264</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6/23</td>
<td>17.0</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0 to 24 hrs post-hatch</td>
<td>87 to 264</td>
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<tr>
<td></td>
<td></td>
<td>6/26</td>
<td>18.9</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0 to 24 hrs post-hatch</td>
<td>87 to 225</td>
</tr>
<tr>
<td>2008</td>
<td>6/20</td>
<td>17.7</td>
<td>0</td>
<td>2</td>
<td>0 to 24 hrs post-hatch</td>
<td>87 to 225</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Missouri</td>
<td>2006</td>
<td>6/18</td>
<td>16.6</td>
<td>2</td>
<td>14 to 32</td>
<td>2</td>
<td>0 to 24 hrs post-hatch</td>
<td>17 to 174</td>
</tr>
<tr>
<td>River</td>
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<td>6/13</td>
<td>16.6</td>
<td>7</td>
<td>11 to 25</td>
<td>0</td>
<td></td>
<td>9 to 95</td>
</tr>
<tr>
<td>Teton</td>
<td>2006</td>
<td>6/23</td>
<td>19.3</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0 to 24 hrs post-hatch</td>
<td>87 to 225</td>
</tr>
<tr>
<td>River</td>
<td>2008</td>
<td>6/9</td>
<td>16.7</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0 to 24 hrs post-hatch</td>
<td>87 to 264</td>
</tr>
<tr>
<td></td>
<td>6/16</td>
<td>15.5</td>
<td>0</td>
<td>1</td>
<td>0 to 24 hrs post-hatch</td>
<td>153 to 351</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 12.—Mean daily discharge and water temperature in the Marias River at Loma, Montana (rkm 2), in 2006. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae.

In 2008, eight shovelnose sturgeon eggs and embryos were collected in the Marias River from 3 July to 16 July, but only four had been fertilized and were staged (Table 2). In addition, 78 shovelnose sturgeon protolarvae (0 to 24 hours post-hatch) were collected from 20 June to 16 July (Table 2). Estimated fertilization dates indicate that shovelnose sturgeon spawning in the Marias River in 2008 (9 June to 20 June; 26 June to 16 July) occurred during periods of increased discharge in the sustained-pulse treatment coupled with mean daily water temperatures from 11°C to 23°C (Table 2; Figure 13).
Figure 13.— Mean daily discharge and water temperature in the Marias River at Loma, Montana (rkm 2) from 29 May to 17 July in 2008. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae.

Nine shovelnose sturgeon eggs and embryos were sampled in the Missouri River in 2006, from 14 June to 18 June. However, only two eggs had been fertilized (Table 2). Estimated fertilization dates indicate that shovelnose sturgeon spawning in the Missouri River in 2006 (14 June to 17 June) occurred in conjunction with the descending limb of the spring hydrograph coupled with optimal shovelnose sturgeon spawning temperatures (16°C to 18°C) (Table 2; Figure 14).
In 2007, sixteen shovelnose sturgeon eggs and embryos were sampled in the Missouri River from 13 June to 24 June, but only nine had been fertilized and were staged (Table 2). In addition, eight shovelnose sturgeon protolarvae (0 to 24 hours post-hatch) were collected from 17 June to 20 June (Table 2). Estimated fertilization dates indicate that shovelnose sturgeon spawning in the Missouri River in 2007 (9 June to 23 June) occurred in conjunction with the descending limb of the spring pulse hydrograph.
Figure 15.— Mean daily discharge and water temperature for the Missouri River (rmk 3,337 for discharge and rkm 3,303 for water temperature) from 29 May to 17 July in 2007. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon embryos and larvae.

coupled with water temperatures suitable for shovelnose sturgeon spawning 15°C to 21°C (Table 2; Figure 15).

One shovelnose sturgeon protolarva (0 to 24 hours post-hatch) was sampled in the Teton River on 23 June 2006 (Table 2). The estimated fertilization date for this larva (14 June to 19 June) indicates that shovelnose sturgeon spawning occurred in conjunction
Figure 16.— Mean daily discharge and water temperature in the Teton River (rkm 0.7) from 29 May to 10 July in 2006. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon larvae.

with the descending limb of the spring hydrograph coupled with water temperatures suitable for shovelnose sturgeon spawning (17°C to 21°C) (Table 2; Figure 16).

In the Teton River in 2008, 14 shovelnose sturgeon protolarvae (0 to 24 hours post-hatch) were collected from 9 June to 23 June (Table 2). Estimated fertilization dates indicate that shovelnose sturgeon spawning in the Teton River in 2008 (30 May to 20 June) occurred in conjunction with the descending limb of the spring hydrograph coupled
Spawning Conditions

In the Marias River in 2006 and 2008, mean water temperatures during development of all larval shovelnose sturgeon sampled varied from 16°C to 22°C (Table 2). Based on development rates at temperatures from 16°C to 22°C, shovelnose sturgeon

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**Figure 17.**—Mean daily discharge and water temperature in the Teton River (rkm 0.7) from 22 May to 10 July in 2008. The crosshatched area delineates the spawning period for shovelnose sturgeon estimated from analysis of developmental stages of shovelnose sturgeon larvae.

with water temperatures suitable for shovelnose sturgeon spawning (12°C to 22°C) (Table 2; Figure 17).
spawning events that produced these larvae likely occurred three to nine days prior to collection (K. M. Kappenman and M. A. H. Webb, U. S. Fish and Wildlife Service, personal communication; Colombo et al. 2007). Thus, daily density of larval shovelnose sturgeon was compared to mean discharge and water temperature three to nine days prior to estimate the effects of varying discharge and water temperature on larval shovelnose sturgeon density (an index to shovelnose sturgeon spawning).

Shovelnose sturgeon larvae were absent from 20 of 20 samples when mean discharge in the Marias River (three to nine days prior) was from 9 m$^3$/s to 27 m$^3$/s despite the occurrence of suitable and optimal shovelnose sturgeon spawning temperatures in conjunction with these discharge levels (Figure 18). However, when suitable and optimal spawning temperatures occurred in conjunction with mean discharge from 28 m$^3$/s to 112 m$^3$/s in the Marias River, larval shovelnose sturgeon were sampled on 8 of 15 sampling occasions (Figure 18). The greatest mean density of larval shovelnose sturgeon occurred after the period of greatest mean discharge coupled with optimal shovelnose sturgeon spawning temperatures (Figure 18).

**Spawning Locations**

Larval shovelnose sturgeon were sampled at all sites in the Marias River in 2006 (Figure 19), but were only sampled on two sampling occasions. Density of larval shovelnose sturgeon was similar among sites in the Marias River in 2006 (Figure 19). No larval sturgeon were sampled in the Marias River in 2007 (Figure 19). In contrast to the Marias River, no larval shovelnose sturgeon were sampled in the Missouri River in 2006
Figure 18.— Mean daily larval shovelnose sturgeon density in the Marias River (all years) as a function of mean discharge and water temperature. Means of discharge and water temperature are from the period 3 to 9 days prior to each sampling day.

(Figure 19). In 2007, shovelnose sturgeon larvae were sampled at both sites in the Missouri River (Figure 19); however, larval shovelnose sturgeon were only sampled on 2 sampling days. Mean density of larval shovelnose sturgeon was similar between sites in the Missouri River (Figure 19).
Overall Bycatch Density

Mean larval bycatch density was significantly greater in the Marias River than in the Missouri River for all years pooled ($t = 3.32, P = 0.0019, df = 40.23$). Mean larval bycatch density in the Marias River was significantly greater in 2006 than in 2007 ($t = $
1.73, P = 0.0500, df = 19.64; Table 3). Conversely, mean larval bycatch density in the Missouri River was not significantly different between 2006 and 2007 (t = 0.71, P = 0.2441, df = 15.96; Table 3).

Mean densities of larval catostomids and larval cyprinids were greater in the Marias River than in the Missouri River in 2006 and in 2007 (Table 3). In 2006, mean density of larval hiodontids was greater in the Marias River than in the Missouri River (Table 3). In contrast, mean density of larval hiodontids was greater in the Missouri River in 2007 (Table 3). Larval cottids and ictalurids were only sampled in the Marias River and only in 2007 (Table 3).

Larval Catostomid Density

In the Marias River, larval catostomids were present on all sampling occasions in 2006 and 2007 (Figure 20). In addition, timing of peak mean density of larval catostomids was similar between years (early to mid-June) (Figure 20). In the Marias River in 2006, mean larval catostomid density peaked on 7 June (Figure 20) at a water temperature of 20°C and discharge of 19 m³/s (Figure 6)—four days prior to the occurrence of peak discharge. Mean larval catostomid density decreased at all Marias River sites during the period of peak discharge in 2006 (15 June to 19 June) and another increase in density occurred on 26 June (Figure 20). Larval catostomid density at sites one through four peaked in early June whereas density at site five peaked on 26 June suggesting some longitudinal variation in the timing of peak density (Figure 20). In 2007, mean larval catostomid density in the Marias River peaked on 6 June (0.1922 larvae/m³) at a water temperature of 20°C and discharge of 14 m³/s (Figures 6 and 20).
Table 3.—Mean bycatch density (larvae/m$^3$, with minimum and maximum densities in parentheses) by family of larval fish sampled in the Marias and Missouri rivers in 2006 and 2007. Density data are not available for the Teton River in 2006 and 2007 because of low water velocity.

<table>
<thead>
<tr>
<th>Family</th>
<th>Marias River</th>
<th>Missouri River</th>
<th>Marias River</th>
<th>Missouri River</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2006</td>
<td>2007</td>
<td>2006</td>
<td>2007</td>
</tr>
<tr>
<td>Catostomidae</td>
<td>0.1862 (0.0163, 0.7397)</td>
<td>0.0759 (0.0035, 0.1922)</td>
<td>0.0605 (0, 0.1998)</td>
<td>0.0293 (0.0069, 0.0635)</td>
</tr>
<tr>
<td>Cottidae</td>
<td>0.0000 (0, 0)</td>
<td>0.0002 (0, 0.0012)</td>
<td>0.0000 (0, 0)</td>
<td>0.0000 (0, 0)</td>
</tr>
<tr>
<td>Cyprinidae</td>
<td>0.0101 (0, 0.0229)</td>
<td>0.0046 (0, 0.0147)</td>
<td>0.0026 (0, 0.0109)</td>
<td>0.0013 (0, 0.053)</td>
</tr>
<tr>
<td>Hiodontidae</td>
<td>0.0002 (0, 0.0022)</td>
<td>0.0002 (0, 0.0013)</td>
<td>0.0000 (0, 0)</td>
<td>0.0013 (0, 0.0123)</td>
</tr>
<tr>
<td>Ictaluridae</td>
<td>0.0000 (0, 0)</td>
<td>0.0001 (0, 0.0013)</td>
<td>0.0000 (0, 0)</td>
<td>0.0000 (0, 0)</td>
</tr>
<tr>
<td>Unknown</td>
<td>0.0094 (0, 0.0359)</td>
<td>0.0093 (0, 0.0678)</td>
<td>0.0005 (0, 0.0039)</td>
<td>0.0023 (0, 0.0075)</td>
</tr>
<tr>
<td>Total Larvae</td>
<td>0.2060 (0.186, 0.7815)</td>
<td>0.0903 (0.0035, 0.8838)</td>
<td>0.0636 (0, 0.1998)</td>
<td>0.0343 (0.0069, 0.0833)</td>
</tr>
<tr>
<td>Volume (m$^3$)</td>
<td>5250.3</td>
<td>10866.5</td>
<td>4497.1</td>
<td>4822.3</td>
</tr>
<tr>
<td>N</td>
<td>12</td>
<td>11</td>
<td>12</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure 20.—Density of larval catostomids by sampling date and location in the Marias River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Marias River sites combined) of larval catostomids by date.
Density at each sampling location in the Marias River peaked prior to 22 June in 2007 (Figure 20).

In the Missouri River, larval catostomids occurred in samples on 11 of 12 sampling occasions in 2006 and on 11 of 11 sampling occasions in 2007. Mean density of larval catostomids peaked in June in both years. In 2006, mean larval catostomid density peaked on 10 June (Figure 21) at a mean temperature of 18°C and mean discharge of 289 m³/s (Figure 7). Larval catostomid density at each site in the Missouri River peaked prior to 19 June 2006 (Figure 21). In 2007, mean larval catostomid density peaked on 5 June (Figure 21) at a mean temperature of 20°C and mean discharge of 286 m³/s (Figure 7). However, peak larval catostomid density at Missouri River site one peaked on 29 June whereas site two peaked on 5 June suggesting some longitudinal variation in peak larval catostomid density (Figure 21).

**Larval Cyprinid Density**

In the Marias River, larval cyprinids occurred in samples on 10 of 12 sampling occasions in 2006 and 9 of 11 sampling occasions in 2007. The timing of peak mean density of larval cyprinids varied from early June to early July in the Marias River. In the Marias River in 2006, mean density of larval cyprinids peaked on 5 July (Figure 22) at a mean temperature of 23°C and mean discharge of 18 m³/s (Figure 6). However, a smaller increase in larval cyprinid density occurred in early June and larval cyprinids were present at both the start and end of the sampling period (Figure 22). In 2007, the peak of mean larval cyprinid density in the Marias River occurred on 6 June (Figure 22) at a
mean temperature of 20°C and mean discharge of 14 m³/s (Figure 6). However, a smaller spike in larval cyprinid density occurred in early July (Figure 22). The timing of peak density in Marias River sites one and two (furthest downstream) occurred in early to mid-
Figure 22.—Density of larval cyprinids by sampling date and location in the Marias River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Marias River sites combined) of larval cyprinids by date.
June in both years whereas peak density in sites four and five (furthest upstream) occurred in late June to early July (Figure 22).

In the Missouri River, larval cyprinids occurred in samples on 7 of 12 sampling occasions in 2006. In the Missouri River in 2006, peak mean density of larval cyprinids occurred on 8 July (Figure 23) at a mean daily temperature of 23°C and mean daily discharge of 157 m³/s (Figure 7). However, a smaller spike occurred in early June (Figure 23). Collection of larval cyprinids occurred on more sampling occasions at site one (downstream of the Marias River) than at site two, and no larval cyprinids were captured in the Missouri River during the period of peak discharge (10 June to 22 June) (Figures 7 and 23). Larval cyprinids were only sampled on 4 of the 11 sampling days in 2007 (three times at site one and once at site two) (Figure 23). Mean larval cyprinid density peaked on 29 June 2007 (Figure 23) at a mean daily temperature of 22°C and mean daily discharge of 165 m³/s (Figure 7).
Figure 23.—Density of larval cyprinids by sampling date and location in the Missouri River in 2006 (top) and 2007 (bottom). Black squares represent mean density (Missouri River sites combined) of larval cyprinids by date.
DISCUSSION

Effects of Hydrograph Treatments on Shovelnose Sturgeon

Shovelnose sturgeon spawning in the Marias River was initiated in conjunction with peak spring discharge during the pulse and sustained-pulse treatments, suggesting that peak discharge provided a spawning cue. Shovelnose sturgeon spawning in the Missouri and Teton rivers also occurred immediately after peak discharge suggesting that peak discharge provided a cue for shovelnose sturgeon spawning. The lack of shovelnose sturgeon spawning during the normal hydrograph treatment provides further evidence that discharge influences spawning. The timing of peak shovelnose sturgeon spawning relative to peak discharge varied between treatments in the Marias River and was likely related to water temperature. During the pulse treatment (2006), peak larval shovelnose sturgeon density occurred six days after peak discharge. In contrast, peak larval shovelnose sturgeon density occurred later during the sustained-pulse treatment (2008) (i.e., 33 days after peak discharge) when water temperature had stabilized and elevated discharge was maintained. Colder water temperatures during peak discharge and immediately after peak discharge during the sustained-pulse treatment may have contributed to the later peak in shovelnose sturgeon spawning. In addition, the prolonged period of increased discharge in the Missouri River may have influenced the later peak in shovelnose sturgeon spawning during the Marias River sustained-pulse treatment.

Interestingly, water temperature in the Marias River was suitable for shovelnose sturgeon spawning for the majority of the normal treatment (2007), but was not coupled with an increase in discharge. This decoupling is likely the mechanism for the lack of shovelnose
spawning in the Marias River during the normal treatment. Previous studies have indirectly linked shovelnose sturgeon spawning with increased spring discharge (Elser et al. 1977; Berg 1981; Mayden and Kuhajda 1997) and water temperature (Christenson 1975; Elser et al. 1977; Moos 1978; Berg 1981); however, a direct link between shovelnose sturgeon spawning and the coupling of increased discharge with suitable water temperature has not been previously documented (DeLonay et al. 2007; Wildhaber et al. 2007; Jacobson and Galat 2008).

The cause of the temporal gaps between estimated spawning periods reported in this study (e.g., 2 gaps during the sustained-pulse treatment) are unknown. During the sustained-pulse treatment in the Marias River, the early spike in larval shovelnose sturgeon density may have been influenced by spawning in the Teton River as density of larval shovelnose sturgeon was greater downstream of the Teton River than upstream. In addition, peak density of larval shovelnose sturgeon in the Teton River occurred on the same day as the early spike in larval shovelnose sturgeon density in the Marias River. The late peak in larval shovelnose sturgeon density (mid-July) in conjunction with water temperatures at the upper end of the optimal spawning temperature range during the sustained-pulse treatment may have been related to the rapid increase in water temperature that occurred in conjunction with the descent from peak discharge. For example, lake sturgeon spawning is often delayed until the upper end of their optimal spawning temperature range in years with a rapid increase in water temperature (Bruch and Binkowski 2002). In addition, the temporal gaps in shovelnose sturgeon spawning periods observed in this study may be related to variation in optimal spawning temperatures among individuals. For example, some female lake sturgeon are
predisposed to spawn at the lower end of the optimal spawning temperature range, while others are predisposed to spawn at the middle or upper end of this range (Bruch and Binkowski 2002). Such temporal variation in spawning may be related to variation in endogenous reproductive rhythm among individual females (e.g., Webb et al. 2001).

The lack of embryonic and larval shovelnose sturgeon in the Marias River during the normal hydrograph treatment suggests that there is a discharge threshold that cues shovelnose sturgeon spawning in the Marias River. Shovelnose sturgeon spawning occurred in the Marias River when discharge ≥ 28 m³/s was coupled with suitable and optimal spawning temperatures. The occurrence of suitable and optimal spawning temperatures during the normal hydrograph treatment and the corresponding absence of larval shovelnose sturgeon suggest that water temperature alone does not provide a cue for shovelnose sturgeon spawning. Rather, these results suggest that suitable or optimal shovelnose sturgeon spawning temperatures must be coupled with a threshold level of discharge (e.g., 28 m³/s) to provide a spawning cue. The Marias River may not be suitable for shovelnose sturgeon spawning use when discharge is less than 28 m³/s because low discharge may render spawning adults and hatching larvae more vulnerable to predation and stranding. However, two radio-tagged adult shovelnose sturgeon were located in the Marias River in 2007 (Gardner and Jensen 2008) indicating that shovelnose sturgeon still used the Marias River during low discharge but were not cued to spawn.

The increased use of the Marias River for spawning by shovelnose sturgeon during the pulse and sustained-pulse treatments in this study is corroborated by the results of a concurrent radio telemetry study of adult shovelnose sturgeon. In this concurrent study, a greater proportion of radio-tagged adult shovelnose sturgeon moved into the
Marias River during the pulse treatment (9 of 34; 26%) and the sustained-pulse treatment (11 of 88; 13%), than during the normal treatment (2 of 55; 4%) (Gardner and Jensen 2007; Gardner and Jensen 2008; Jensen and Gardner 2009).

In the Missouri River, larval shovelnose sturgeon density was greater in 2007 than in 2006 despite similar patterns of variation in discharge and water temperature between years. Decoupling of increased discharge with suitable spawning temperature in the Marias River in 2007 may have caused an increase in the use of the Missouri River for spawning by shovelnose sturgeon. Thus, the use of tributaries in the upper Missouri River basin for spawning by shovelnose sturgeon may be dependent on coupling of increased discharge with suitable spawning temperatures. Use of tributaries for spawning by shovelnose sturgeon has been reported elsewhere (e.g., Cross 1967; Elser et al. 1977; Berg 1981; Bramblett and White 2001; Engel et al. 2006). However, the effects of discharge and water temperature coupling on use of tributaries for spawning by shovelnose sturgeon have not been previously documented (Jacobson and Galat 2008).

These results suggest that water management in regulated rivers should couple an increase in discharge with suitable spawning temperatures for shovelnose sturgeon, if maintaining shovelnose sturgeon spawning is a management goal. River regulation that reduces spring discharge can decrease the amount of available spawning habitat for shovelnose sturgeon and may negatively impact the spawning success of shovelnose sturgeon. The occurrence of shovelnose sturgeon spawning when mean discharge was from 28 m$^3$/s to 112 m$^3$/s, coupled with a variety of suitable shovelnose sturgeon spawning temperatures, suggests discharge must reach a threshold level in the Marias River to provide a cue for shovelnose sturgeon spawning. Maintaining spring discharge
above this threshold in the Marias River may increase the duration of shovelnose sturgeon spawning activity. For example, spring discharge in the Marias River remained \( \geq 28 \text{ m}^3/\text{s} \) for only 12 days in 2006 and the duration of the estimated shovelnose sturgeon spawning period was short (11 days). In comparison, Marias River discharge remained \( \geq 28 \text{ m}^3/\text{s} \) from June 3 to the end of the sampling period (July 16) in 2008 and the duration of the estimated shovelnose spawning period was longer than in 2006 (33 days). Further, the shovelnose sturgeon spawning period in the Marias River may have continued beyond July 16 in 2008 (i.e., after cessation of sampling) as discharge remained \( \geq 28 \text{ m}^3/\text{s} \) until August 28 and water temperature remained between 12\(^\circ\)C and 24\(^\circ\)C into September.

The importance of discharge and water temperature coupling for sturgeon spawning in regulated rivers has been documented in other North American sturgeons. Conditions for white sturgeon spawning in the regulated Kootenai River are optimal when increased spring discharge (630 \text{ m}^3/\text{s} to 1,200 \text{ m}^3/\text{s}) is coupled with water temperatures from 9\(^\circ\)C to 12.5\(^\circ\)C (Paragamian and Wakkinen 2002). Reproductive readiness of lake sturgeon *Acipenser fulvescens* in the regulated Sturgeon River, Michigan, is cued by optimum spawning temperatures (10\(^\circ\)C to 15\(^\circ\)C) coupled with natural patterns of spring discharge (Auer 1996). Migrations and spawning of Gulf of Mexico sturgeon *Acipenser oxyrinchus de sotoi* were correlated with increased discharge coupled with water temperatures from 15\(^\circ\)C to 20\(^\circ\)C (Chapman and Carr 1995). Shortnose sturgeon *Acipenser brevirostrum* spawning was linked with decreasing discharge and water temperatures from 10\(^\circ\)C to 14\(^\circ\)C (Kieffer and Kynard 1996).

Estimated shovelnose sturgeon spawning dates in this study were derived from developmental rates in hatchery conditions with little or no diel variation in water
temperature. The shovelnose sturgeon embryos and larvae collected in this study developed in natural conditions (i.e., with diel variation in water temperature). The effects of these variable conditions on embryonic and larval shovelnose sturgeon development rates are undocumented. This potentially increases the variability in embryonic and larval sturgeon development rates; however, estimates of shovelnose sturgeon spawning dates used in this study were conservative, encompassing developmental rates from water temperatures greater than and less than the mean observed temperature. Thus, it is likely that the true spawning times are within the estimates reported.

Several species of North American sturgeons spawn over gravel, cobble, boulder, and bedrock substrates including gulf sturgeon (Fox et al. 2000), lake sturgeon (Bruch and Binkowski 2002), and white sturgeon (Parsley et al. 2002). Spawning substrates used by shovelnose sturgeon are unknown (Keenlyne 1997; DeLonay et al. 2007; Wildhaber et al. 2007), but spawning is assumed to occur over coarse substrates in tributaries (Christenson 1975; June 1977; Elser et al. 1977) and on the borders of main river channels (Moos 1978). Specific locations of shovelnose sturgeon spawning were not identified in this study because larval shovelnose sturgeon density was similar among sites in the Marias River. However, shovelnose sturgeon spawning occurred upstream of rkm 11 (the most upstream sampling location) in the Marias River, and in the Missouri River upstream of the confluence with the Marias River. The collection of embryonic and larval shovelnose sturgeon upstream of rkm 11 in the Marias River and in the Missouri River upstream of the Marias River confluence represents the first documentation of successful shovelnose sturgeon spawning in these locations.
Previously, larval shovelnose sturgeon have only been collected in the lower 2 rkm of the Marias River and in the Missouri River downstream of the Marias River confluence (Berg 1981; Gardner 1997).

Effects of Hydrograph Treatments on Ichthyoplankton Bycatch

The assemblage of larval fish in the Marias, Missouri, and Teton rivers was similar to previous larval fish studies in these rivers. For example, larval catostomids and cyprinids were the most abundant families collected in the Marias, Missouri, and Teton rivers in 1978, 1996, and 1997, and larval cottids, hiodontids, and ictalurids were found at relatively lower densities (Berg 1981; Gardner 1997). However, differences in density among larval fish taxa may not accurately represent the relative taxonomic density of all larval fishes in the Marias and Missouri rivers. The benthic position (i.e., lower 0.5 m), channel locations (i.e., in or adjacent to the thalweg), and timing (e.g., diurnal) of drift net samples in this study were designed to maximize capture of shovelnose sturgeon larvae (Braaten et al. 2004; Braaten et al. 2008). Location and timing of larval fish drift varies among taxa (e.g., Gale and Mohr 1978; Gallagher and Conner 1983; Muth and Schmulbach 1984; Scheidegger and Bain 1995; Gadomski and Barfoot 1998; Reeves 2006) and likely influenced collection of ichthyoplankton bycatch in this study. For example, no larval percids were captured in this study whereas larval percids were collected at low densities in previous studies (Berg 1981; Gardner 1997). Peak densities of larval percids in the Missouri River occurred in mid-May to early-June and spawning was estimated to have occurred between late-April and mid-May (Berg 1981; Gardner 1997). Sampling for this study was initiated on 29 May in 2006 and on 2 June in 2007;
therefore, the absence of larval percids is likely related to temporal differences in sampling and not sampling methods because the methods were similar among studies. Similarly, absence of other families of larval fish in samples (i.e., Polyodontidae, Esocidae, Salmonidae, Gadidae, Gasterosteidae, Centrarchidae, and Sciaenidae) may reflect sampling bias and does not necessarily represent a lack of spawning of these fishes in the study area.

Overall ichthyoplankton bycatch density was greater in 2006 than 2007 in the Marias River, and was likely a function of greater peak and mean discharge in 2006 given both years had similar temperature profiles. Variation in larval fish density in association with discharge variation has been observed in other rivers. In the Illinois River, Illinois, densities of several larval fish species were greater during years with discharge patterns emulating pre-regulation conditions (Koel and Sparks 2002). In addition, total larval fish density was three to four times greater in the unregulated Cahaba River than in the regulated Tallapoosa River, Alabama (Scheidegger and Bain 1995). In the lower Milk River, Montana, variation in larval fish density was associated with the timing of peak spring discharge; greatest larval density occurred when discharge peaked in June and minimum density occurred when discharge peaked in May (Bednarski et al. 2008). Although discharge and water temperature are important cues for spawning, other factors such as photoperiod, mate availability, and habitat availability can influence spawning (Lam 1983; Bye 1984). Concluding that an increase in larval density is a result of increased discharge and water temperature alone is likely too simplistic an explanation for a highly complex process. However, the results of this study suggest that increased spring discharge results in increased density of larval fish.
Ichthyoplankton bycatch density was greater in the Marias River than in the adjacent reach of the Missouri River in 2006 and 2007. Similarly, greater larval fish density was documented in the Marias River compared to the adjacent reach of the Missouri River by Berg (1981) and Gardner (1997). The importance of tributary habitat for native larval fish production has been documented in other tributaries to the Missouri River (e.g., Muth and Schmulbach 1984; Brown and Coon 1994; Bednarski et al. 2008). In the James River, South Dakota, freshwater drum were the most abundant species sampled in 1978, and 10 million larvae recruited to the Missouri River in one month (Muth and Schmulbach 1984). In the Milk River, Montana, native larval catostomids were the most abundant taxon sampled during three years of sampling (Bednarski et al. 2008). In addition, overall density of larval fish in tributaries was greater than in the adjacent reaches of the main river channel in the Missouri River, Missouri (Brown and Coon 1994).

Peak larval catostomid density occurred in early June in the Marias and Missouri rivers in 2006 and 2007. In addition, larval catostomids were collected on all June sampling dates in both years, and most July sampling dates, suggesting that catostomids spawn over a wide range of discharge levels and water temperatures. Catostomid spawning occurs from April through July in the Missouri River in Montana and all catostomids present in the Marias and Missouri rivers can spawn in either May or June (Brown 1971; Berg 1981). Similarly, in the Milk River, native catostomids spawned successfully over a wider range of dates than other fishes (Bednarski et al. 2008). The occurrence of peak larval catostomid density prior to peak discharge in both years suggests that the peak in discharge during the Marias River pulse treatment was not an
important spawning cue for catostomids. Rather, increased larval catostomid density in 2006 compared to 2007 was likely a result of greater minimum discharge.

The Marias River pulse treatment was associated with increased larval cyprinid density suggesting that larval cyprinid density may be influenced by discharge. Temperature has the predominant effect on spawning in many cyprinid species (Bye 1984). However, other factors (e.g., spawning substrate) have been shown to influence cyprinid spawning behavior and success. For example, exposure to aquatic vegetation induces ovulation in goldfish *Carassius auratus* (Stacey et al. 1979) and spawning of bighead carp *Hypophthalmichthys nobilis* has been associated with an increase in discharge after temperatures stabilize above 22°C (Schrank et al. 2001). Common carp larvae comprised a greater proportion of all larval fish sampled in the Milk River when increased discharge occurred in June (Bednarski et al. 2008). Thus, an increase in Marias River discharge similar to the 2006 hydrograph treatment may improve spawning conditions for some cyprinid species.

**Management Implications**

Efforts to improve spawning conditions for shovelnose sturgeon in the Marias River should couple an increase in spring discharge with optimal shovelnose sturgeon spawning temperatures (i.e., 16°C to 20°C). If optimal temperatures are unavailable, then increased discharge should be coupled with suitable shovelnose sturgeon spawning temperatures (i.e., 12°C to 24°C). The magnitude of increased spring discharge in the Marias River should be ≥ 28 m³/s and ≤ 134 m³/s to cue shovelnose sturgeon spawning. The effects of discharge levels > 134 m³/s on shovelnose sturgeon spawning in the
Marias River are unknown; however, discharge $> 134$ m$^3$/s could be beneficial as the greatest density of sturgeon larvae followed the period of greatest discharge in this study. Finally, the duration of the period of increased spring discharge should be extended for as long as optimal or suitable spawning temperatures occur because this may increase the duration of shovelnose sturgeon spawning in the Marias River.

This study is the first field experiment to demonstrate the effects of discharge and water temperature on shovelnose sturgeon spawning. The results of this study provide water managers and biologists with needed evidence of a causal relationship between increased spring discharge and shovelnose sturgeon spawning (Jacobson and Galat 2008). Large-scale experiments such as this one are valuable because they can apply directly to management decisions (Carpenter 1998). However, this study has a small sample size (N=1 for each treatment) and inter-annual variation in the response of shovelnose sturgeon to variation in discharge and water temperature is likely to exist. Hydrograph treatments conducted in the current study should be replicated to assess inter-annual variation, and alternative hydrographs should be tested to evaluate the effects of discharge and water temperature combinations untested in this study (e.g., high discharge coupled with high water temperature). In addition, this study should be replicated in other tributaries and other sections of the Missouri River to begin to establish generalities in shovelnose sturgeon spawning behavior.

The Marias River was an ideal system for study of shovelnose sturgeon spawning because manipulation of discharge was possible and adult shovelnose sturgeon are common in the study area (W. M. Gardner, Montana Department of Fish, Wildlife and Parks, personal communication). Because the nearest relocation of a radio-tagged adult
pallid sturgeon was about 100 rkm downstream of the Marias River during this study (Gardner and Jensen 2007; Gardner and Jensen 2008; and Jensen and Gardner 2009), it is unlikely that pallid sturgeon used the Marias River. Thus, the effects of variation in discharge and water temperature on pallid sturgeon spawning were not documented. Further research is recommended to evaluate differences between shovelnose sturgeon and pallid sturgeon spawning in response to discharge and water temperature variation.

Finally, this study only assessed the effects of river regulation on spawning success, not recruitment to the population. While increased spring discharge in the Marias, Missouri, and Teton rivers may cue shovelnose sturgeon spawning, the effects of increased discharge on larval survival and juvenile recruitment remain unknown. Additional research on the effects of river regulation (i.e., the timing, magnitude, and duration of increased spring discharge in relation to water temperature variation) on recruitment of shovelnose sturgeon and other fishes is needed.
LITERATURE CITED


Christenson, L. M. 1975. The shovelnose sturgeon, Scaphirhynchus platorynchus (Rafinesque) in the Red Cedar-Chippewa River system. Wisconsin Department of Natural Resources, Madison, Wisconsin.


APPENDIX A

PHOTOGRAPHS OF SHOVELNOSE STURGEON EMBRYOS WITH NOTES ON DEVELOPMENTAL STAGE
Figure 24.—Shovelnose sturgeon embryo collected on 14 June 2006 in the lower Marias River (site three) estimated to be at developmental stage 11 or 12 (early to late blastula) (Dettlaff et al. 1993; Colombo et al. 2007).

Figure 25.—Shovelnose sturgeon embryo collected on 14 June 2006 in the upper Missouri River (site one) estimated to be at developmental stage 12 (late blastula) (Dettlaff et al. 1993; Colombo et al. 2007).
Figure 26.—Shovelnose sturgeon embryo collected on 14 June 2006 in the lower Marias River (site three) estimated to be at developmental stage 14 (formation of dorsal blastopore lip) (Dettlaff et al. 1993; Colombo et al. 2007).

Figure 27.—Shovelnose sturgeon embryo collected on 15 June 2006 in the lower Marias River (site five) estimated to be at developmental stage 17 (small yolk plug visible) (Dettlaff et al. 1993; Colombo et al. 2007).
Figure 28.—Shovelnose sturgeon embryo collected on 18 June 2006 in the lower Marias River (site five) estimated to be at a stage of development from 27 to 29 (heart rudiment is present and is slightly s-shaped) (Dettlaff et al. 1993; Colombo et al. 2007).

Figure 29.—Shovelnose sturgeon embryo collected on 3 July 2008 in the lower Marias River (site two) estimated to be at a stage of development from 32 to 35 (tail extends past head) (Dettlaff et al. 1993; Colombo et al. 2007).
APPENDIX B

PHOTOGRAPHS REPRESENTING THE FAMILIES OF LARVAL FISH SAMPLED
Figure 30.—Shovelnose sturgeon protolarvae: protolarval shovelnose sturgeon (0 to 24 hours post hatch) obtained from the hatchery for reference (top) and a protolarval shovelnose sturgeon sampled in the lower Marias River on 23 June 2006 (bottom).

Figure 31.—Larval representative of the family Catostomidae sampled in the lower Marias River.
Figure 32.—Larval representative of the family Cottidae sampled in the lower Marias River.

Figure 33.—Larval representative of the family Cyprinidae sampled in the lower Marias River.
Figure 34.—Common carp larva (family Cyprinidae) sampled in the lower Marias River.

Figure 35.—Goldeye larva (family Hiodontidae) sampled in the lower Marias River.
Figure 36.—Larval representative of the family Ictaluridae sampled in the lower Marias River.