COMPETITION POTENTIAL BETWEEN SAUGER AND WALLEYE IN NON-NATIVE SYMPATRY: HISTORICAL TRENDS AND RESOURCE OVERLAP IN THE MIDDLE MISSOURI RIVER, MONTANA

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ABSTRACT

Sauger *Sander canadensis* populations throughout Montana and North America have exhibited declines over the past few decades. Sauger population abundance declined in the middle Missouri and Yellowstone rivers of Montana in the mid-1980s following a period of drought. Higher flows resulted in a rebound of the lower Yellowstone River population; however, the middle Missouri River population has remained at low abundance. Various factors may contribute to the reduced population abundance of sauger in the middle Missouri River, including interspecific competition with walleye *Sander vitreus*. Historical trend data of sauger and walleye were assessed to determine long-term trends of sauger and walleye fitness. To assess competition potential, seasonal migrations, habitat use, and diets of both species were compared in the middle Missouri River. Trophic position of sauger was also compared between the middle Missouri and Yellowstone rivers to evaluate the trophic status of sauger in sympatry and allopatry with walleye. Sauger and walleye were tracked using radio telemetry to establish and compare seasonal migrations. Habitat use was compared at three hierarchical scales, diets were collected on fish sampled using electrofishing, and diet overlap was calculated. Trophic position was calculated using stable isotope analysis. Historical trend data indicated that sauger and walleye are currently at low abundance and sauger had low relative weights, which is likely due to low prey availability. Prior to the presumed spawning period, 96% of the sauger and 57% of the walleye migrated downstream as far as 273 km. After spawning, both species returned to previously-occupied river reaches and demonstrated site fidelity during the non-migratory season. Habitat use and selection by sauger and walleye were similar at all three hierarchical scales. Diet overlap was high during the spring [0.72 (SE=0.003)] and summer [0.95 (SE=0.0008)] and moderate during autumn [0.49 (SE=0.003)]. Sauger trophic position differed statistically between the middle Missouri and Yellowstone rivers; however, the biological consequences of the difference are uncertain. Overall, resource overlap of sauger and walleye in the middle Missouri River, Montana suggests that competition potential between these species is high, which may preclude the recovery of native sauger populations if resources are limiting.

INTRODUCTION

Sauger *Sander canadensis* are a native top predator in large, turbid rivers of the central United States and Canada (Scott and Crossman 1973), but have undergone declines in abundance and distribution throughout their range (Nelson and Walburg 1977; Hesse 1994; Pegg et al. 1997; McMahon and Gardner 2001). Sauger declined in Montana in both the Yellowstone River and middle Missouri River (section between Great Falls and Fort Peck Reservoir) (McMahon and Gardner 2001) and are currently listed as a Montana Species of Special Concern (MNHP 2004). The decline of sauger in both rivers was originally attributed to a drought in the mid-1980s (Penkal 1990). Increased flows in the 1990s corresponded to a rebound of the lower Yellowstone River population (Jaeger 2005); however, the abundance of the middle Missouri River population has remained low (Gardner 2005). The difference in recovery of the two systems suggests that another mechanism may have confounded the effects of drought on sauger and is continuing the suppression of the middle Missouri River population.

Additional factors that may have contributed to the decline and continued low abundance of sauger in the middle Missouri River, Montana include: 1) migratory barriers and habitat loss (e.g., hydropower dams), 2) overexploitation by anglers, 3) hybridization with walleye *Sander vitreus*, and 4) interactions with non-native species (e.g., walleye and smallmouth bass *Micropterus dolomieu*) (McMahon and Gardner 2001). No new dams have been constructed on the middle Missouri River since the late 1950s, thus their impact on the sauger decline in the 1980s was likely negligible. The effect of angler exploitation on the Yellowstone River sauger population was minimal

(Jaeger et al. 2005) and may have similar minimal impacts on the middle Missouri River population. The effects of hybridization may compromise the continued existence of sauger, but were not assessed in this study. Lastly, anecdotal evidence from middle Missouri River biologists suggests that walleye may be competing with sauger for resources since walleye abundance increased following the drought while sauger abundance decreased. Thus, this study was designed to investigate competition potential between sauger and walleye in order to conserve native sauger in the middle Missouri River of Montana.

Walleye are native to large rivers and lakes of central North America, but are not native to Montana (Brown 1971). Walleye grow to larger sizes than sauger and consequently attract the attention of recreational anglers. Thus, social pressure has influenced the continued management and stocking of the species in Montana, despite their potential to alter aquatic ecosystems by depleting prey resources and causing shifts in fish community composition (Colby and Hunter 1989; McMahon 1992; McMahon and Bennett 1996). Walleye were stocked only once (in the late 1970s) in the middle Missouri River, Montana; however, individuals stocked in upstream or tributary reservoirs (e.g., Canyon Ferry and Tiber) and downstream Fort Peck Reservoir since the 1970s are believed to be sources of the population residing in the lotic section. The opportunistic feeding behavior of walleye and their tendency to emigrate from reservoirs where they were stocked increases their potential to impact river fisheries (McMahon 1992).

Sauger and walleye were both present in the middle Missouri River prior to the drought of the 1980s, but walleye comprised less than 0.01 percent of the *Sander* spp. catch (Berg 1981). Following the drought, there was a noticeable decline in the catch per effort of sauger and an increase in the catch per effort of walleye (Penkal 1990). Walleye comprised 30.8 percent of the *Sander* spp. catch in 2003 (Gardner 2005). Although walleye are not believed to be the direct cause of the decline in sauger abundance after the 1980s drought (McMahon and Gardner 2001), it is possible that drought conditions caused changes in river habitat that allowed the expansion of the walleye population.

Resource overlap between sauger and walleye is variable in systems where they are both native and sympatric. In natural lakes, sauger and walleye were found in different habitats while feeding (Swenson 1977), were segregated during summer and fall (Rawson and Scholl 1978), and were separated based on turbidity (Schlick 1978), but had high diet overlap during winter (Priegel 1963) and in June through September (Swenson and Smith 1976). In anthropogenically altered systems (i.e., regulated rivers or man-made reservoirs), sauger and walleye occupied similar habitats during all seasons (Gangl et al. 2000) and during spawning (Rawson and Scholl 1978); however, habitat differences were also found during spawning (Siegwarth 1993). Sauger and walleye also exhibited high diet overlap during winter (Fitz and Holbrook 1978) and May through October (Mero 1992) in altered systems. A low hybridization rate (4.1 %) between sauger and walleye in a system where they both natively occur indicates that spawning habitats are likely spatially or temporally segregated (Billington et al. 1997). Overall, the literature indicates that sauger and walleye are spatially segregated in non-altered systems whereas both species are more likely to exhibit habitat overlap in altered systems. Diet overlap was seen in both altered and non-altered systems, indicating that sauger and walleye may not need to partition food resources to avoid competition.

The close phylogenetic (i.e., congeneric) relationship of sauger and walleye increases their potential for interspecific competition (Ross 1986). Closely-related species have similar morphological and physiological features and as a consequence, may use similar resources. Congeneric, native stream fish assemblages commonly partition food and habitat resources to alleviate competition, which is often believed to be a product of selective forces that have operated during co-evolution (see studies from Ross 1986). Intuitively, assemblages of native and non-native fishes may be more likely to compete because they have not had sufficient time to co-evolve and partition resources.

Three conditions must be met for interspecific competition to occur: 1) two species must use a common resource, 2) the resource must be limiting, and 3) negative effects resulting from competition (e.g., decreased growth rates, population abundance, or another metric correlated with fitness) must be present (Crowder 1990). Ideally, competition is assessed using field or laboratory experiments that demonstrate repeatable changes in the growth or abundance of species when resources or competitors are manipulated (Crowder 1990). However, experimental manipulation of highly migratory species (e.g., sauger and walleye) in a large system (e.g., Missouri River) is not logistically feasible. Laboratory experiments may also be unrealistic because they do not incorporate environmental variability and other biological interactions. Furthermore, basic ecological data on walleye have not been collected in the middle Missouri River and information on resource overlap between sauger and walleye would be a useful first step towards understanding competition potential between these species. Competition potential was defined as high overlap of food and habitat resources because these resources are most commonly partitioned by fish species to avoid competition (Ross 1986).

Evidence for competition can be strengthened by documenting niche shifts of species in sympatry and allopatry (Crowder 1990). Walleye are more abundant than historically and occur sympatrically with sauger in the middle Missouri River (McMahon 1999) whereas walleye are at relatively lower abundance in the lower Yellowstone River and thus, are essentially allopatric with sauger. From 2001 to 2004, relative abundance of sauger in the lower Yellowstone River averaged 23.4 fish per hour whereas walleye averaged 0.4 fish per hour (Jaeger 2005). Comparing sauger in these two systems may yield insight regarding resource use of sauger with and without the influence of walleye. However, evaluating resource use of sauger in both the middle Missouri and Yellowstone Rivers would be a logistically daunting task. Luckily, movement and habitat use data of sauger have been documented recently in the Yellowstone River (Jaeger et al. 2005) and can be compared to sauger in the middle Missouri River. Trophic shifts of species in sympatry and allopatry can be calculated and compared using stable isotope analysis (SIA), which is a relatively new technique available to ecological studies (Peterson and Fry 1987). Long-term diets of predators can also be inferred from SIA and compared to short-term diet information (i.e., from stomach contents analysis) to evaluate trophic interactions (Peterson and Fry 1987). Trophic shifts of native predators resulting from the introduction of non-native predators have resulted in decreased fitness and abundance of the native predator (Olowo and Chapman 1999) as well as deleterious changes in prey-fish diversity and abundance that may affect the fitness of the native predator (Vander Zanden et al. 1999; Vander Zanden et al. 2004).

The goal of this study was to assess competition potential between sauger and walleye and understand the role of competition affecting sauger recovery in the middle Missouri River, Montana. Historical catch data from Montana Fish, Wildlife and Parks were analyzed to assess population trends of sauger and walleye since the late 1970s when sauger were abundant. Seasonal migrations of sauger and walleye were determined and compared using radio telemetry and were related to river discharge and temperature. Habitat use of both species was classified at three hierarchical scales to evaluate habitat overlap during the non-migratory season. Diets of both species were quantified to determine diet overlap. Stable isotope analysis was used to corroborate middle Missouri River diet data and investigate trophic shifts of sauger between the middle Missouri and lower Yellowstone Rivers. Based on the hypothesis that closely-related species in a non-native assemblage are more likely to compete because they have not had sufficient time to co-evolve and partition resources, I predicted that sauger and walleye would exhibit high resource overlap in the middle Missouri River, Montana.

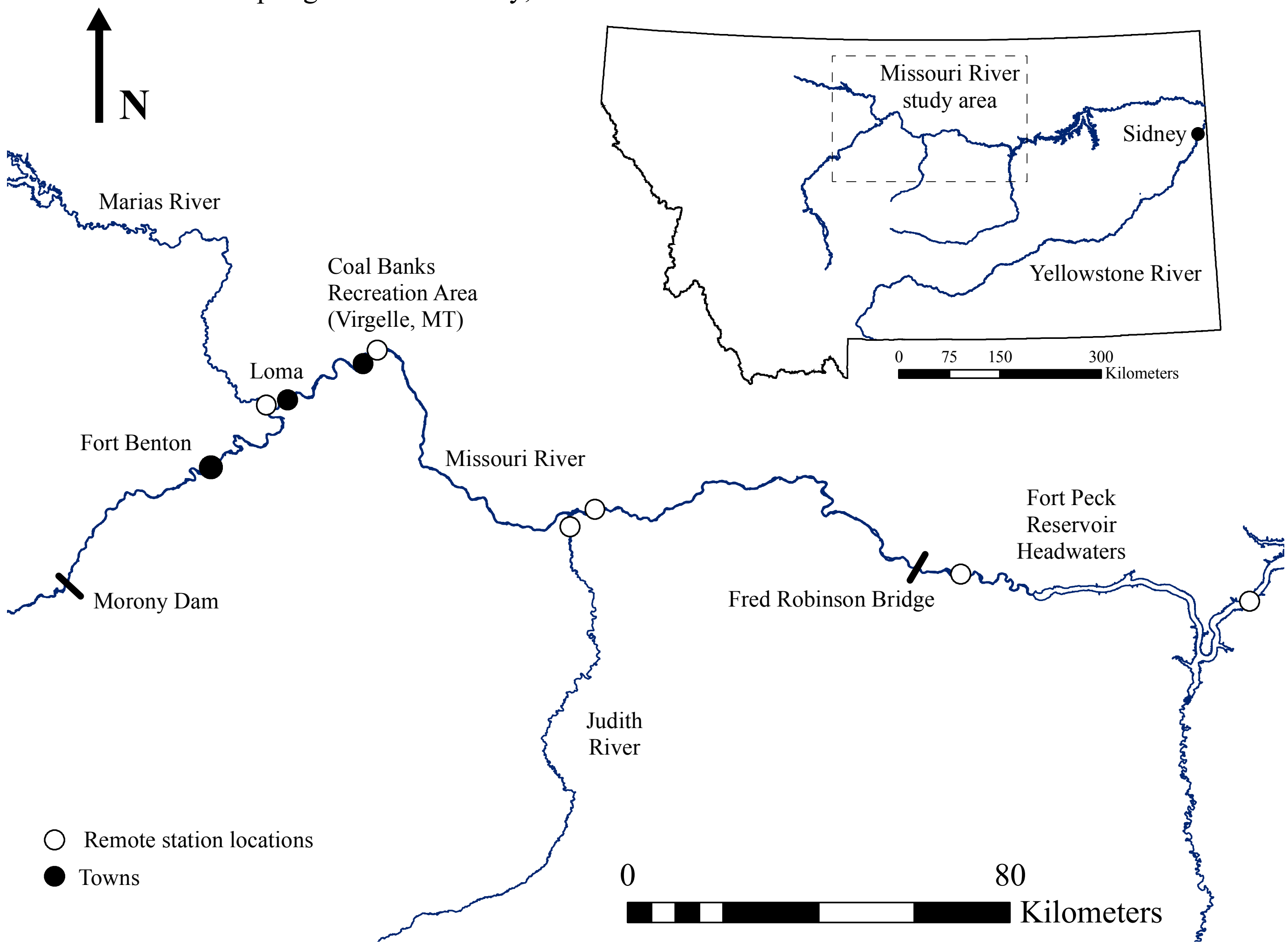
STUDY SITE

The study was conducted in north central Montana and included the middle Missouri River and its tributaries between Morony Dam (river km [rkm] 3388) and the headwaters of Fort Peck Reservoir (about rkm 3000) (Figure 1). The majority of the work was conducted on the section of Missouri River from Fort Benton (rkm 3337) to Coal Banks Recreation Area (rkm 3267) because sauger declined markedly in this area and walleye are relatively abundant (see Historical Catch Data results). Peripheral reaches of the Missouri River and tributaries were used when radio-tagged fish strayed from the primary study site.

The section of Missouri River from Fort Benton to Fred Robinson Bridge, Montana was designated as a Wild and Scenic River in 1976 (USHR 1976). The river channel has remained relatively pristine since it was described by Lewis and Clark in 1805 (Gardner 1999). The Missouri River upstream of Coal Banks Recreation Area is sinuous with relatively wide valleys and land use in the valley is primarily agricultural. The section of river downstream of Coal Banks to Fred Robinson Bridge is contained within the Missouri River National Monument, is less sinuous, and the channel is constricted by limestone cliffs and erosive bluffs. Downstream of the monument to Fort Peck Reservoir, the river channel meanders in a wider valley, which is surrounded by the Charles M. Russell National Wildlife Refuge. The monument and wildlife refuge protect the river corridor from development and natural land cover predominates.

Instream habitat of the middle Missouri River is affected by anthropogenic

Figure 1. Map of middle Missouri River study area, towns, and remote station locations. Map inset includes approximate location of Yellowstone River sampling area near Sidney, Montana.



manipulations (e.g., construction and regulation of eight hydroelectric dams upstream of the study site), despite the pristine surroundings. The 50 km of river downstream of Morony Dam is likely clearer and colder than historical conditions due to hypolimnetic water release from Morony Dam. Additionally, the hydroelectric dams upstream of the study site moderate the peaks and troughs of the historical hydrograph, although timing of discharge is similar to past conditions. Average peak discharge has decreased by 29% and low discharge has increased by 42% since construction of the most recent upstream dam in 1958 (USGS 2006). River discharge since 1958 at Virgelle, Montana has varied from an average high of 741 m^3/s during spring run-off to an average low of 114 m^3/s during winter (USGS 2006). Morony and Fort Peck dams also provide barriers that inhibit migratory species. Water conductivity in the study area currently varies from 300 to 800 μS/cm at 25ºC; however, values above 600 μS/cm are rare (USGS 2006). Substrate in the middle Missouri River consists primarily of gravel, cobble, and boulder in the upper reaches and transitions to primarily sand downstream of Fred Robinson Bridge.

Non-native fish introductions have changed the distribution and composition of the fish assemblage in the study site and habitat modifications have allowed their existence. The tailwater of Morony Dam is cold, clear-water habitat and allows the inhabitance of non-native coldwater species (e.g., rainbow trout *Onchorhynchus mykiss* and brown trout *Salmo trutta*) and decreases the suitability of habitat for native species adapted to warmer, turbid water (e.g., sauger). Non-native coolwater species (e.g., smallmouth bass *Micropterus dolomieu*, and northern pike *Esox lucius*) are also present.

A section of the lower Yellowstone River near Sidney, Montana (rkm 30 to 40 from the confluence with the Missouri River) was used for stable isotope sample collection (Figure 1). This section of the Yellowstone River contains braided and split channels and sand is the primary substrate (Jaeger et al. 2005). Although various low-head dams have altered the historical discharge by diverting water from the river for agricultural use, the historically variable flow regime of the Yellowstone River is relatively intact (Jaeger et al. 2005). Yellowstone River discharge within the last 50 years at Sidney has varied from an average high of 1547 m^3/s during spring run-off to an average low of 82 m^3/s at base flow (USGS 2006).

METHODS

Historical Catch Data

Autumn (August through November) catch data of sauger and walleye from two sampling sites in the middle Missouri River (i.e., Morony Dam and Coal Banks) were obtained from Montana Fish, Wildlife and Parks (MFWP) annual reports or calculated from data provided by MFWP or this study. Catch per effort (i.e., catch per hour) data were plotted to compare changes in sauger and walleye relative abundance over time. Relative weights were compared between species by year at each site using t-tests. Sauger less than 70 mm (total length; TL) and walleye less than 150 mm TL were excluded from relative weight calculations (Anderson and Neumann 1996). Relative weights less than 60 or greater than 140 were considered a product of measurement error and were excluded from analysis. Mean relative weights were only calculated for groups with three or more individuals.

Seasonal Migrations

Adult sauger and walleye were captured using electrofishing and were implanted with radio transmitters in September and October of 2003 and 2004 to record seasonal migrations in 2004 and 2005. Transmitters purchased from Lotek Wireless weighing 10.7 g were programmed to transmit daily from 0800 hours to 2000 hours in 2003. In 2004, transmitters were on 24 h a day so that nocturnal movements could be recorded. Start times of transmitters were delayed until mid-February to preserve battery life so fish could be tracked through the subsequent summer. Sauger and walleye were tagged near Fort Benton (rkm 3337), Loma (rkm 3302), and Coal Banks (rkm 3267), Montana to represent the area where sauger population abundance markedly decreased. Tagging occurred during autumn to reduce the chance of affecting the spawning migration, which occurs in the spring. A minimum fish weight of 385 g was selected to ensure that transmitter weight did not exceed 2% of the body weight (Winter 1996). Anesthetic and surgical techniques generally followed those by Hart and Summerfelt (1975) and Summerfelt and Smith (1990). Sauger and walleye were anesthetized in 25 mg finquel (MS-222)/L prior to surgery and were monitored at least 30 min before being released.

Radio-tagged sauger and walleye were located from February through October in 2004 and February through mid-November in 2005. A fixed-wing airplane with a three element Yagi antenna mounted to the bottom of the aircraft was used to locate fish during the winter and early spring when sauger and walleye were dispersed over a large area (about 300 rkm) and because the river was frozen. More precise boat tracking began after fish returned from the spawning migration and were aggregated within a shorter river reach (about 90 rkm). Sauger and walleye were located monthly by plane during February and March and at least bi-weekly by plane or boat from May through mid-August in 2004 and May through July in 2005. Remote tracking stations were installed at strategic locations to record fish leaving and entering the primary study site, document tributary use, and record fish movements after boat tracking ceased in both years (Figure 1). Radio-tagged fish returned by anglers also contributed to location data.

A five element Yagi antenna was mounted on the boat 3 m above the water surface to initially locate fish during the boat-tracking period. More precise locations were then determined by triangulation or by passing the boat directly over the fish using a hand-held, three element Yagi antenna. Maneuvering the boat over the fish was primarily used because it was more time efficient than triangulation and presumably does not affect fish behavior (Blanchfield et al. 2005). Fish locations were recorded in Universal Transmercator (UTM) coordinates using a boat-mounted global positioning system (GPS) unit. The precision of locating a transmitter by boat was estimated before and after the tracking season and was between two and five meters. To measure precision, one person secretly placed a transmitter in a known location and drove the boat while the other person tracked the transmitter. A buoy was then dropped to mark the fish location and the distance between the buoy and the transmitter was measured.

Migration data were grouped into migratory and non-migratory seasons for analysis based on sauger and walleye life history information (Scott and Crossman 1973) and results from this study. The migratory season was defined as the period from about November through May and included the movements to over-winter areas, migration to spawning grounds, spawning, and post-spawn migration. The non-migratory season included the remainder of the year. Each fish exhibited a temporally unique migration pattern and thus, each fish was categorized into the appropriate season based on its movement. The non-migratory season began after individual fish ceased large-scale movements and ended when the fish migrated back downstream. The length of river used by sauger and walleye during the non-migratory season was compared using a t-test.

Mean daily discharge data were collected from the United States Geological

Survey (USGS) monitoring station at Virgelle (rkm 3270 on the Missouri River) and temperature data were obtained from the USGS station near Fred Robinson Bridge (rkm 3092) to compare with sauger and walleye large-scale migrations. Discharge data were grouped into low, medium, and high categories to compare the effects of varying discharge levels on sauger and walleye location within the channel. Low discharge (<140 m^3/s) corresponded to base flow, which occurred from about July through March. High discharge (>280 m^3/s) coincided with the peak flows of run-off in May and June. Medium discharge (141 to 280 m^3/s) included intermediate flow levels. A repeated measures (with individual fish as the repeated variable) analysis of variance with an experiment-wise error rate of alpha = 0.05 was used to compare the distance of sauger and walleye to the nearest bank during the three discharge levels using individual fish as the experimental unit.

Habitat Use During The Non-Migratory Season

Habitat use was classified and compared between sauger and walleye at three hierarchical scales: channel unit, channel unit quadrant, and point estimates of habitat at fish locations. Habitat use information was collected only sporadically during the migratory season and consequently, sample sizes were too low during the migratory season to evaluate habitat use. Thus, only habitat use during the non-migratory season was evaluated. The non-migratory season used for habitat analyses was defined similarly to the non-migratory season in the movement methods.

Channel units were classified into seven categories: bluff pool, terrace pool, riprap pool, scour pool, channel crossover, perennial secondary channel, and seasonal secondary channel, based on differences in flow, depth, and substrate type (Jaeger et al. 2005). Bluff pools were located at the valley margin and were formed by deflection of the river against exposed bedrock (Rabeni and Jacobson 1993). Terrace pools were created by river scour through glacial-deposited alluvium and colluvium (Jaeger et al. 2005). Channel units intermediate between bluff and terrace pools (i.e., glacial deposits on top of bedrock) were considered bluff pools if bedrock material was exposed to the river. Scour against anthropogenic materials (i.e., riprap and bridge abutments) created riprap pools, which were primarily located at the valley margin and bordered towns or historic railroad easements. Scour pools were created from lateral scour through river-deposited alluvium (Rabeni and Jacobson 1993). Channel crossovers included run and riffle habitats and were located where the thalweg crossed from one side of the river to the other. Perennial secondary channels contained water throughout the year. Seasonal secondary channels were disconnected from the main channel at either the inlet or outlet at some point during the year. Channel units were determined using geologic maps, aerial photos, and from habitat notes taken in the field and were delineated using ArcGIS 9.0 Geographic Information System (GIS) software (ESRI 2004). Availability was quantified as the number of river kilometers of each channel unit from rkm 3242 to 3357, which corresponded to the river section used by fish during the non-migratory season. Fish locations were then overlaid onto availability maps using GIS software to assess use of channel units. One-way chi-square log-likelihood tests and Manly selection ratios (Manly et al. 2002) with 95% simultaneous Bonferroni confidence intervals were calculated for sauger and walleye using FishTel 1.4 software (Rogers and White in press). Individual fish were the experimental unit. Although some expected values used for chi-square analyses were less than the commonly recommended 5, chi-square tests are robust to smaller expected values (Roscoe and Byars 1971; Lawal and Upton 1984).

Channel units most frequently used by sauger and walleye were divided into four equal-sized quadrants to calculate habitat overlap at a finer scale. Channel units were bisected perpendicular to river flow to form two equal-sized regions, which were then bisected parallel to river flow to form four equal-sized quadrants. Delineations were performed using GIS software. Channel units at river bends were labeled as: 1) upstream, inside bend, 2) upstream, outside bend, 3) downstream, inside bend, and 4) downstream, outside bend. Quadrant use and selection by sauger and walleye was analyzed using the same methodology as for whole channel units.

Point estimates of habitat were measured at sauger and walleye locations determined by boat tracking. Turbidity was quantified at each location using a secchi disc mounted to a meter-long dowel. Transects were established to quantify the depth of the fish location in relation to the surrounding depths (i.e., relative depth). One transect was perpendicular to the river flow and bisected the fish location to obtain a cross-sectional depth profile of the entire river width. Another 100-m transect parallel to the river flow was centered over the fish location to assess the longitudinal depth profile. Depth was measured at 5-m intervals along both transects using a depth sounder. A rangefinder was used in conjunction with the depth sounder to delineate 5-m intervals. Five substrate measurements were taken at each fish location: at the fish location, 5 m upstream, 5 m downstream, 5 m to river left, and 5 m to river right. Substrate was classified as fines (0 to 0.6 mm), gravel and cobble (0.6 to 254 mm), or boulder (>254 mm) by "feeling" the substrate with a probe constructed of 0.5-inch electrical conduit. A repeated measures (with individual fish as the repeated variable) analysis of variance with an experiment-wise error rate of alpha = 0.05 was used to compare relative depth between sauger and walleye using individual fish as the experimental unit. Differences in substrate use were assessed with a chi-square test.

Diets

Sauger and walleye were sampled for diets using electrofishing during the non-migratory season in the middle Missouri River between Fort Benton (rkm 3337) and Coal Banks Recreation Area (rkm 3267). The non-migratory season was subdivided into spring (May and June), summer (July and August), and autumn (September to November) periods for diet analysis. Periods were delineated to account for distinct changes in river discharge and changes in prey availability that likely occurred over the diet sampling period. Spring diets were collected during the high discharge of spring run-off. Summer and autumn diets were collected at relatively low discharge. Diets were collected throughout this reach to correspond with the group of fish used for movement and habitat analyses. Stomach contents were removed using a gastric lavage, fixed in 15% formalin, and transferred to 70% ethanol for long-term preservation.

Food items were identified in the laboratory using a dissecting microscope. Identifiable fish were categorized to species and macroinvertebrates were identified at least to order. Prey fish unidentifiable to species were placed in an "unidentifiable fish" category. Empty stomachs and those containing only detritus, sediment, or vegetation were considered empty. Prey fish length (mm) (i.e., total, standard, or backbone length) and wet weight (g) were recorded; macroinvertebrates were counted and wet-weighed by order.

Sauger and walleye diets were compared by season to assess resource overlap. Diet overlap was quantified using Pianka's niche overlap measure:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^{2} \sum_{i}^{n} p_{ij}^{2}}}$$

where O_{jk} = Pianka's measure of overlap, p_{ij} = the proportion that resource i is of the total resources used by species j, p_{ik} = the proportion that resource i is of the total resources used by species k, and n = the total number of resource categories (Pianka 1973). Overlap indices were calculated using prey weight. Values of this index vary from 0 (no overlap) to 1.0 (complete overlap). Overlap estimates were then bootstrapped 5000 times to obtain estimates of variability and to reduce the effect of outliers on the overlap value (Ricklefs and Lau 1980; Smith 1985). Competition potential was considered high when overlap values exceeded 0.6 (Zaret and Rand 1971), low when overlap was less than 0.4 (Ross 1986), and moderate at intermediate values. Frequency of occurrence and percent composition by weight of each prey category were also calculated to supplement overlap value interpretation.

Trophic Position and Diet Corroboration

Stable isotope analysis (SIA) was used to investigate potential trophic shifts of sauger by comparing the trophic levels of sauger in the middle Missouri River to the lower Yellowstone River. Nitrogen stable isotope ratios are enriched from 3-5‰ from prey to consumers and can be used to determine trophic position (Peterson and Fry 1987). A section of the Yellowstone River near Sidney, Montana was chosen for trophic level comparison with the middle Missouri River because walleye are at very low abundance (Jaeger 2005). Thus, sauger may occupy a more "natural" trophic position in this section of the Yellowstone River because of the lesser influence of walleye.

Additionally, SIA was used to corroborate diet data collected in the Missouri River study site by providing a more time-integrated view of diet. Average enrichment of carbon stable isotope ratios in freshwater ecosystems is negligible (0.2‰) (France and Peters 1997) and can be used to trace the diet of consumers (Peterson and Fry 1987). Carbon stable isotope ratios of sauger and walleye were compared to the carbon signatures of potential prey items in both the middle Missouri and lower Yellowstone rivers. Although diets were not sampled at the Yellowstone River study site, stable isotope ratios of predators and prey were used to infer consumption of prey items.

Samples used for stable isotope analysis were collected from June 27 to 30, 2005 in the middle Missouri River (rkm 3267 to 3337) and from July 11 to 14, 2005 in the Yellowstone River near Sidney, Montana (rkm 30 to 40 from the confluence with the Missouri River) using electrofishing and hook-and-line sampling. An attempt was made to capture at least five individuals of each species; however, some species were challenging to sample and less than five individuals were captured for analysis. Dorsal white muscle tissue was non-lethally collected from sauger and walleye using a 5-mm disposable biopsy punch. Each biopsy punch was used about five times to minimize waste; however, the punch was rinsed with de-ionized water between each use to minimize the possibility of sample contamination. Biopsy samples yielded about 10 to 20 mg of tissue after drying, which was sufficient for SIA. Potential prey fish (fish <200 mm total length) of sauger and walleye were also collected. Maximum prey length was set to characterize the largest prey item that adult sauger and walleye could consume, based on prey lengths from diet analysis. Mussels, *Lampsilis siliquoidea* or *Ligumia recta*, were also collected from both sites to establish baseline $\delta^{15}N$ for calculation of sauger and walleye trophic position (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). Mussels were used to calculate baseline $\delta^{15}N$ of primary consumers rather than other primary consumers because mussels are long-lived and contain a $\delta^{15}N$ signature that is temporally less variable than short-lived primary consumers (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). Dorsal muscle biopsy samples, whole prey fish, and mussels used for SIA were placed on ice in the field, frozen at the end of the day in a conventional freezer, and later frozen at -20ºC for long-term preservation.

All samples were thawed and dorsal white muscle tissue was extracted from prey fish in the lab. Tissue was separated from scales and skin and then washed in de-ionized water to provide a pure muscle sample. Dorsal white muscle tissue was used for SIA in order to minimize $\delta^{13}C$ variability, which is greater in tissues with higher lipid content (Pinnegar and Polunin 1999). More accurate comparisons of predator $\delta^{13}C$ and prey $\delta^{13}C$

can be made by minimizing $\delta^{13}C$ variability (Tieszen et al. 1983). Additionally, white muscle tissue has a slower turnover rate than other tissues (e.g., blood and liver) and is ideal for assessing long-term diet (weeks to months) whereas tissues with faster isotope turnover rates are more appropriate when assessing short-term diet (hours to days) (Tieszen et al. 1983). Tissue from the foot of mussels was dissected and used for SIA. All samples were dried at 60ºC for 24 h and then ground to a fine powder with a glass pestle and mortar. A glass pestle and mortar were used rather than ceramic because they created less static electricity, which reduced sample loss when transferring the ground sample to the sample vial. Glass vials were also used for sample storage and shipment in order to minimize the effect of static electricity and subsequent sample loss.

Fish and mussel samples were analyzed at South Dakota State University for stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) using a Europa ANCA-GSL 20-20 IRMS mass spectrometer. Isotope ratios were calculated using the formula:

$$\delta X(‰) = \left(\frac{R_{sample}}{R_{std}} - 1\right) * 1000$$

where X = ^{13}C or ^{15}N, R_{sample} = ^{13}C:^{12}C or ^{15}N:^{14}N of the sample, and R_{std} = ^{13}C:^{12}C or ^{15}N:^{14}N of international standards Pee Dee Belemnite limestone or atmospheric nitrogen, respectively. Trophic position was calculated using the formula:

$$TP_{fish} = \frac{(\delta^{15}N_{fish} - \delta^{15}N_{corrected})}{3.4} + 2$$

where TP_{fish} = fish trophic position, $\delta^{15}N_{fish}$ = $\delta^{15}N$ of fish, $\delta^{15}N_{corrected}$ = $\delta^{15}N$ of mussels, 3.4 = one trophic level increment in $\delta^{15}N$, and 2 = the trophic level of mussels, which are primary consumers (Vander Zanden and Rasmussen 1999; Vander Zanden and

Rasmussen 2001). T-tests were used to compare differences in mean trophic position of sauger and walleye within each site and by species between sites. An alpha value of 0.05 was used for all statistical analyses to indicate significance. The Satterthwaite approximation for degrees of freedom was reported for all tests that did not meet the assumption of equal variances (Satterthwaite 1946).

RESULTS

Historical Catch Data

Historical catch data indicated changes in sauger and walleye relative abundance from 1978 to 2005. Sauger relative abundance at the Morony Dam site varied from 40 fish per hour in 1979 to 0.1 fish per hour in 1994 and did not exceed 4.2 fish per hour between 1995 and 2005 (Figure 2). Walleye catch per hour data were not available for the late 1970s; however, the percent of walleye in the combined sauger and walleye (i.e., *Sander* spp.) catch did not exceed 2.3 percent in the 1970s at the Morony Dam site (Figure 2). The percent of walleye in the *Sander* spp. catch varied from 5.4 to 80 percent and catch rates varied from 0.1 to 3.9 fish per hour between 1988 and 2005 at the Morony Dam site. Catch per hour data of sauger and walleye were only available from 1997 to 2005 at the Coal Banks site and fluctuated similarly, with peaks occurring for both species in 1999 (Figure 2). Similar to the upstream Morony Dam site, the percent of walleye in the *Sander* spp. catch at the Coal Banks site was low (0 to 7 percent) in the late 1970s and was higher (12 to 40 percent) from 1997 to 2005. Although walleye are more abundant than historically at both sites in the middle Missouri River, sauger relative abundance has remained higher than walleye at both sites except 1994 through 1997 at the Morony Dam site.

Mean relative weights of walleye were statistically higher than sauger in six of nine years at the Morony Dam site and in four of seven years at the Coal Banks site (Figure 3). Sauger and walleye relative weights were not statistically different during the

Figure 2. Catch per hour (solid lines) of sauger (black) and walleye (white) and percent of walleye in *Sander* spp. catch (dotted lines) during autumn at the Morony Dam (top panel) and Coal Banks (bottom panel) sites in the middle Missouri River, Montana, 1978 to 2005.

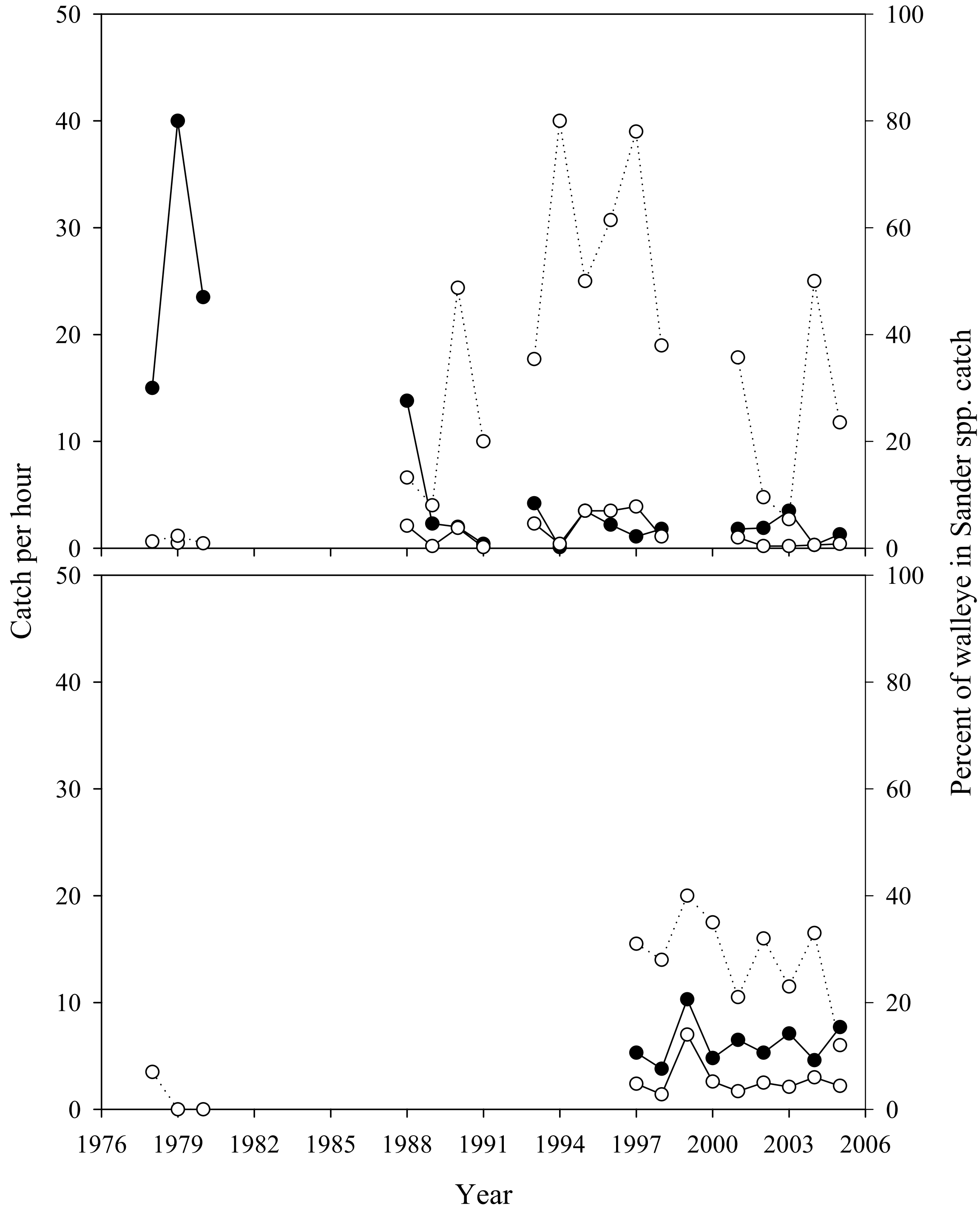
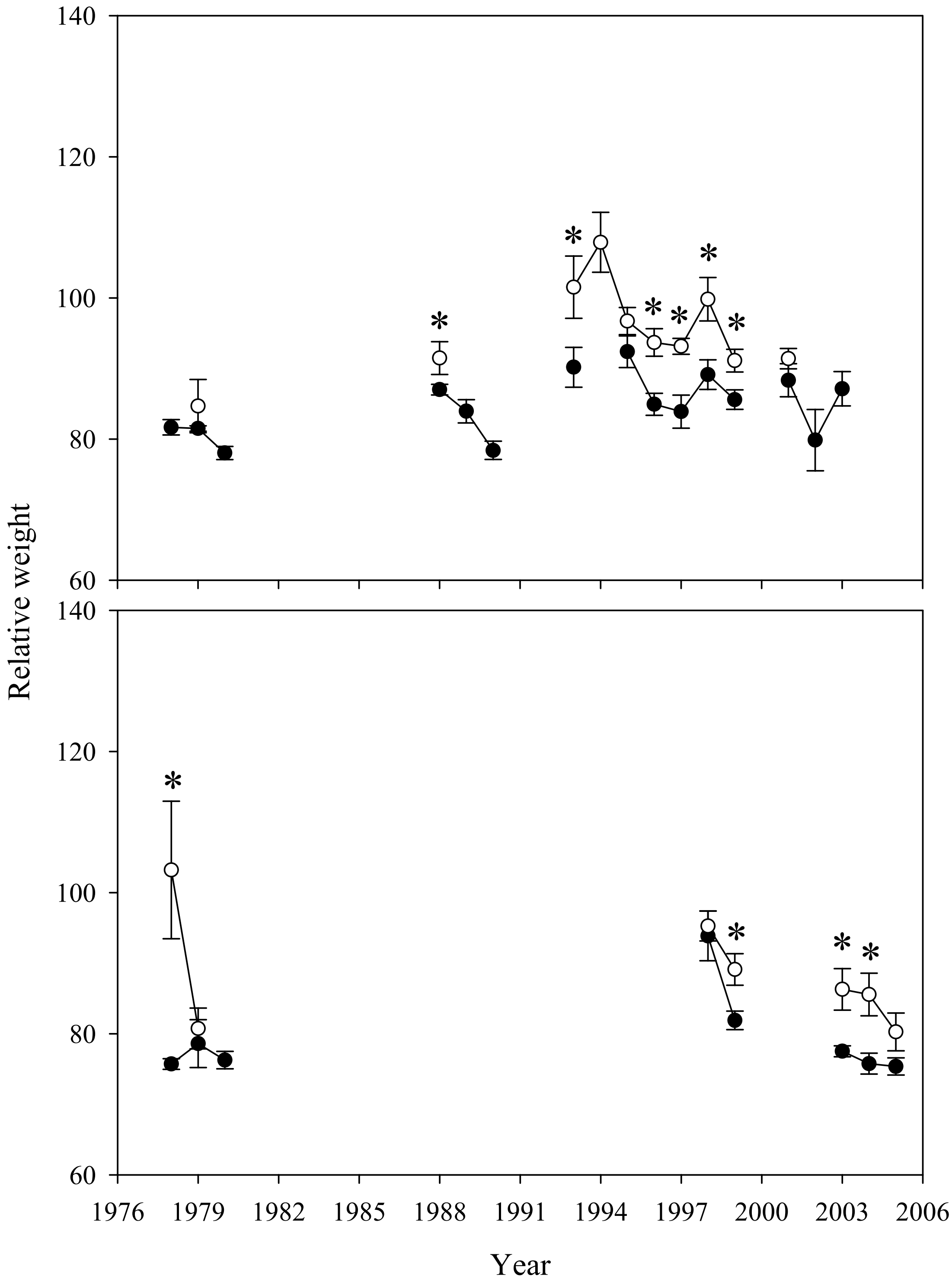


Figure 3. Relative weights of sauger (black) and walleye (white) at the Morony Dam (top panel) and Coal Banks (bottom panel) sites in the middle Missouri River, Montana, 1978 to 2005. Error bars denote one standard error. Asterisks indicate significant differences by year.



remaining years. Mean relative weights of sauger and walleye were positively correlated at the Morony Dam site (r = 0.77; P = <0.0149), indicating that yearly fluctuations of sauger and walleye relative weights were similar. Relative weights of sauger and walleye were not significantly correlated at the Coal Banks site (r = 0.30; P = 0.51).

Seasonal Migrations

Seasonal migration data were provided from 31 sauger and 29 walleye that were captured and radio-tagged in the autumn of 2003 and 2004. Migration data from both years were grouped by species because similar patterns were observed. Two sauger and five walleye were never relocated during the tracking period. Six sauger and six walleye died before any relocations were made. Three additional sauger and six walleye were radio-tagged during the summers of 2004 and 2005 to compensate for the loss of sample size. Two-hundred seventy five relocations were obtained from 26 sauger weighing 350 to 1600 g (Table 1; Figure 4). One-hundred eighty seven relocations were made from 24 walleye weighing 600 to 1750 g (Table 2; Figure 4). About 56 percent of locations were determined by boat, 26 percent by plane, and 18 percent were recorded by remote stations. Twenty-three sauger and 18 walleye were relocated during the migratory season and thus, were used for migratory season analyses. Relocations per fish during the migratory season averaged 7 (SE = 0.7) for sauger and 5 (SE = 0.7) for walleye. Twenty-one sauger and 14 walleye were used for movement and habitat analyses during the non-migratory season; fish with less than three relocations during the non-migratory season were excluded from non-migratory season analyses. Relocations per fish during the non-migratory season averaged 5 (SE = 0.2) for sauger and 5 (SE = 0.5) for walleye.

Table 1. Sauger radio-tagged and used for movement and habitat analyses in the middle Missouri River, Montana, 2003 to 2005.

Code	Radio frequency	Date of capture	Capture location (river km)	Length (mm)	Weight (g)
02	148.380	09/18/2003	2052.0	458	750
06	148.380	09/18/2003	2052.0	457	750
10	148.440	09/18/2003	2052.0	429	650
12	148.440	09/16/2003	2031.0	524	1075
13	148.440	06/15/2004	2031.0	369	350
16	148.500	06/15/2004	2031.0	360	450
17	148.500	09/18/2003	2052.0	492	1000
18	148.500	09/17/2003	2073.0	482	875
20	148.500	09/18/2003	2052.0	442	700
25	148.600	09/17/2003	2073.0	501	1100
27	148.600	09/18/2003	2052.0	449	800
28	148.600	09/17/2003	2073.0	508	1000
34	148.600	09/29/2004	2079.5	560	1600
36	148.600	10/13/2004	2052.5	450	900
39	148.600	09/29/2004	2078.4	437	700
42	148.440	09/30/2004	2073.3	479	1050
43	148.440	10/13/2004	2052.5	466	900
45	148.440	09/09/2004	2031.0	397	600
47	148.440	09/29/2004	2076.0	406	650
50	148.440	09/29/2004	2078.4	437	750
51	148.500	09/16/2004	2054.7	373	450
56	148.500	10/13/2004	2052.5	514	1300
57	148.500	09/29/2004	2079.5	495	1200
58	148.500	09/09/2004	2031.0	421	600
60	148.500	09/09/2004	2031.0	380	550
64	150.280	07/07/2004	2031.0	430	650

Movements of sauger and walleye were generally similar during the migratory season in both years. The majority of sauger (N=22) and walleye (N=14) used for migratory season analyses moved extensive distances downstream between the autumn tagging period and mid-May (Figure 5). Additionally, a majority of both species tagged in 2004 that migrated downstream were downstream of their respective tagging locations

Table 2. Walleye radio-tagged and used for movement and habitat analyses in the middle Missouri River, Montana, 2003 to 2005.

Code	Radio frequency	Date of capture	Capture location (river km)	Length (mm)	Weight (g)
01	148.380	09/17/2003	2073.0	475	1050
05	148.380	09/16/2003	2031.0	565	1750
07	148.380	09/17/2003	2073.0	534	1500
08	148.440	09/18/2003	2052.0	541	1500
09	148.440	09/17/2003	2073.0	476	1100
15	148.440	06/22/2004	2052.0	438	700
22	148.500	09/16/2003	2031.0	473	950
24	148.600	09/18/2003	2052.0	389	650
31	148.600	09/30/2004	2070.7	465	1050
33	148.600	09/09/2004	2031.0	423	900
37	148.600	10/13/2004	2052.5	394	750
40	148.600	09/16/2004	2052.5	393	600
41	148.440	10/13/2004	2052.5	475	1200
44	148.440	09/30/2004	2073.3	432	850
46	148.440	09/09/2004	2031.0	483	950
49	148.440	09/09/2004	2031.0	450	900
52	148.500	10/13/2004	2052.5	406	600
54	148.500	10/13/2004	2052.5	394	700
55	148.500	09/30/2004	2073.3	402	650
59	148.500	05/20/2005	2031.9	413	600
61	150.280	07/05/2004	2073.0	409	600
62	150.280	08/02/2004	2031.0	420	650
63	150.280	07/05/2004	2073.0	383	600
65	150.280	07/19/2004	2073.0	412	600

during the first tracking event in February 2005 (Figure 5). A majority of fish may have also been downstream of their respective tagging locations in February 2004; however, the lower section of river was not tracked until mid-April. Thus, fish locations downstream of their respective tagging locations in February 2004 are only speculative. Downstream sauger migrations varied from 34 to 254 km (mean = 170 km) and walleye migrations varied from 14 to 264 km (mean = 130 km). Both species were located downstream between rkm 3072 and 3242 during the presumed spawning period in April and early May and began returning upstream from late April through May (Figure 5).

Figure 4. Tracking effort in the middle Missouri River, Montana, 2004 (top panel) and 2005 (bottom panel). Points correspond to sauger (white) and walleye (black) locations. Vertical solid lines indicate the reach of river tracked during a given day. Dashed horizontal lines signify dates of operation by remote tracking stations. Points not intersecting lines were fish caught by anglers.

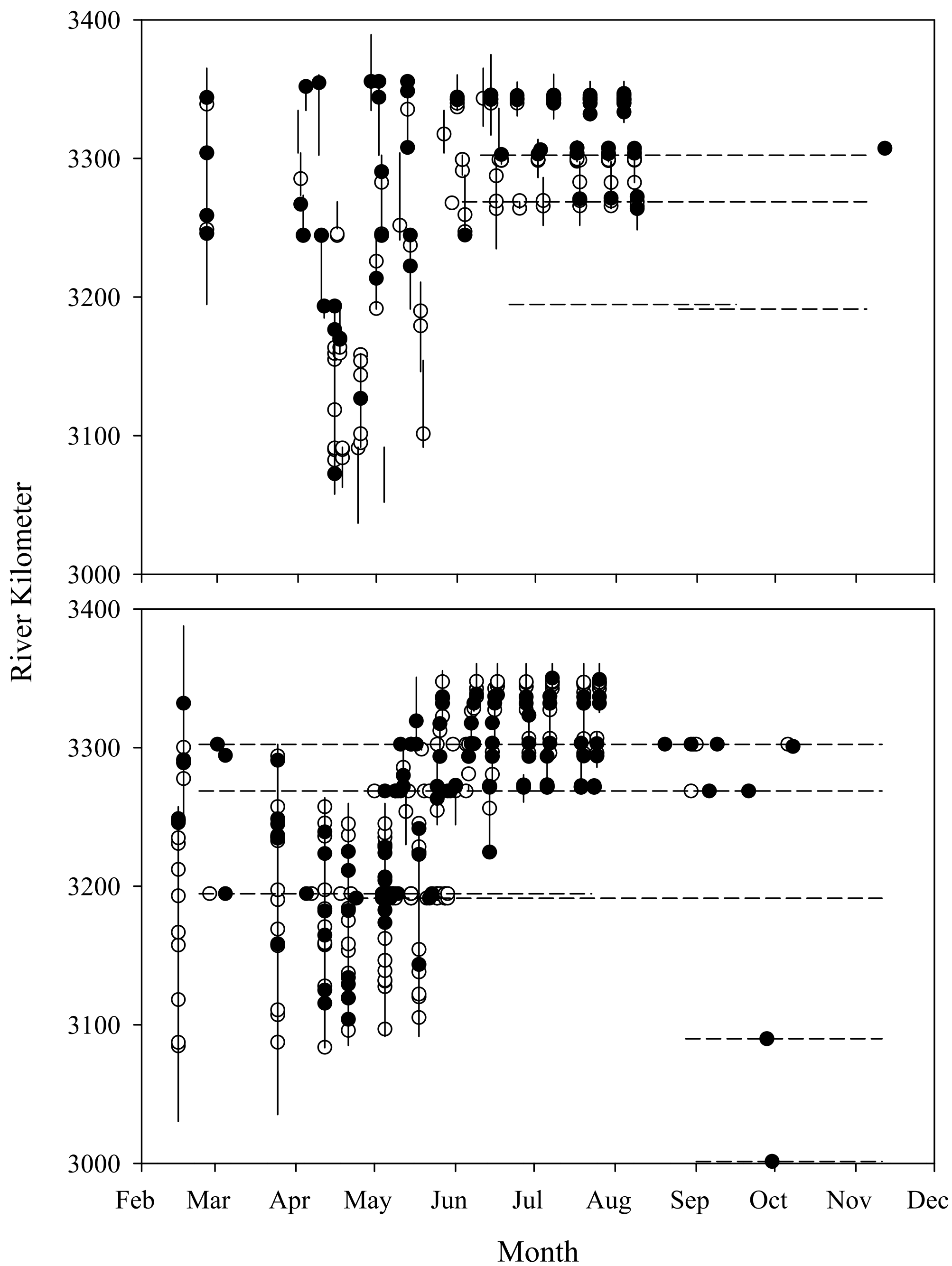
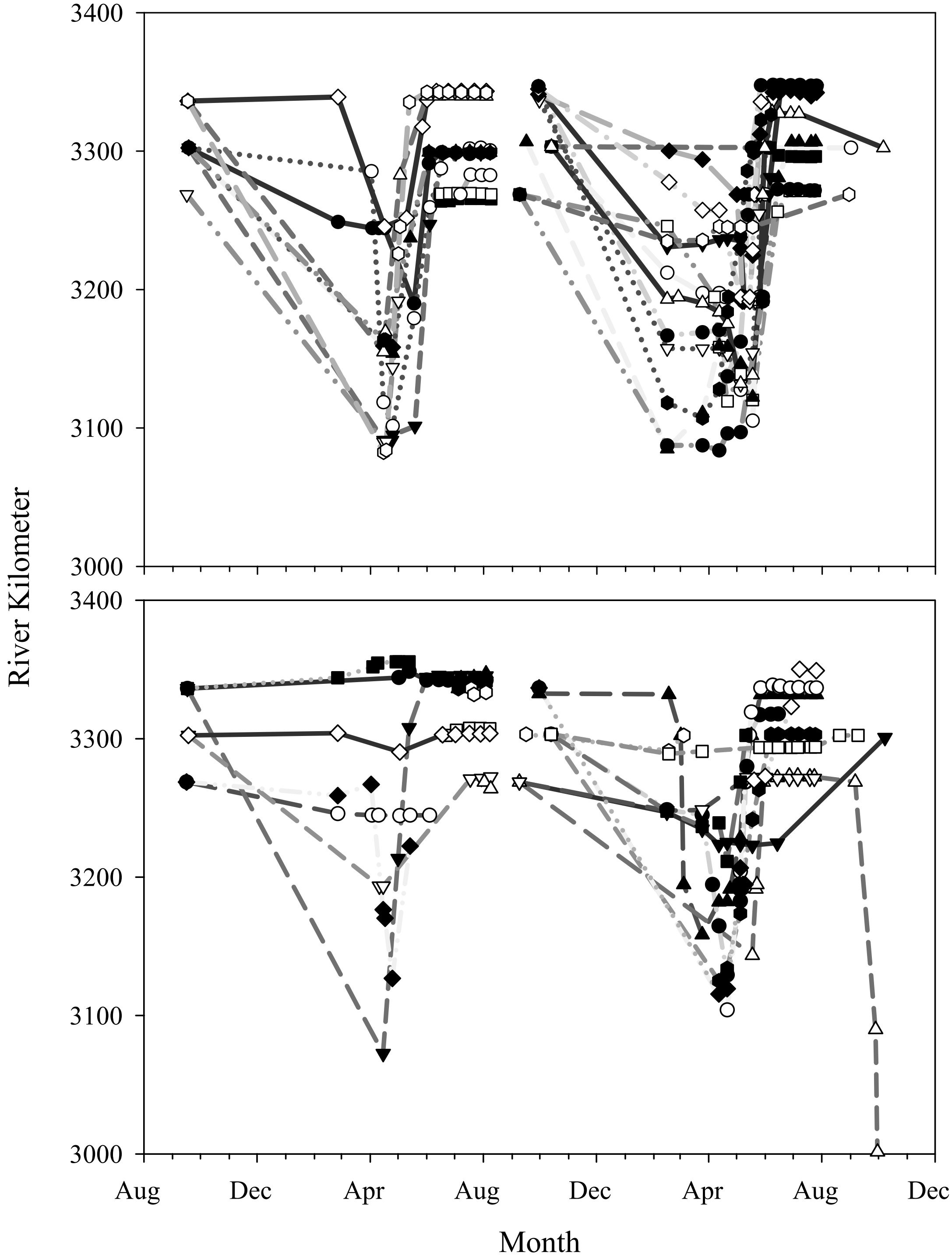


Figure 5. Sauger (top panel) and walleye (bottom panel) movements in the middle Missouri River, Montana, September 2003 to October 2005. Each line indicates the migration of an individual fish. Symbols correspond to individual lines and indicate when a fish was located during tracking. A new cohort of fish was tagged during the gap between August and September 2004.



Locations of sauger and walleye varied with differences in water temperature and discharge in both years (Figure 6). Sauger and walleye were located downstream at water temperatures of 9 to 15ºC and discharge varying from 135 to 167 m^3/s during the presumed spawning period in April 2004. In April 2005, both species were located downstream at water temperatures of 7 to 14ºC and discharge varying from 125 to 172 m^3/s. Thus, both species in both years migrated downstream at some point during the lower water temperatures and discharge between the tagging period and early spring. The locations of both species began to shift upstream as water temperature and discharge increased. A majority of sauger and walleye had returned to their upstream locations by June 2004 at water temperatures of 14 to 22ºC and discharge from 154 to 272 m^3/s. A majority of both species had also returned to their upstream locations by June 2005 at water temperatures of 15 to 23ºC and discharge from 184 to 484 m^3/s.

Lateral movement within the channel was similar between sauger and walleye and varied at the three discharge levels (Figure 7). No differences existed in mean distance to nearest bank between species ($F_{1,41.5} = 1.29$, $P = 0.26$); however, differences among discharge levels existed ($F_{2,44.8} = 8.38$, $P = 0.0008$). Sauger and walleye were nearest to banks during high discharge and closer to mid-channel at low discharge.

Sauger and walleye exhibited site fidelity after the migratory season and both species occupied relatively small areas during the non-migratory season between rkm 3242 and 3357. All sauger (N=23) and 44 percent (N=8) of walleye returned after the migratory season to the same river reach (i.e., Fort Benton, Loma, or Coal Banks) where they were caught and tagged the previous year. Many fish returned to the exact channel

Figure 6. Sauger (top panel) and walleye (bottom panel) locations in relation to discharge (solid line) and water temperature (dotted line) in the middle Missouri River, Montana, August 2003 to October 2005. Location data are grouped by month. Solid lines within boxes represent medians, boundaries of the box indicate the 25th and 75th percentiles, whiskers indicate the 10th and 90th percentiles, and circles represent the 5th and 95th percentiles. All box plots contain at least three locations.

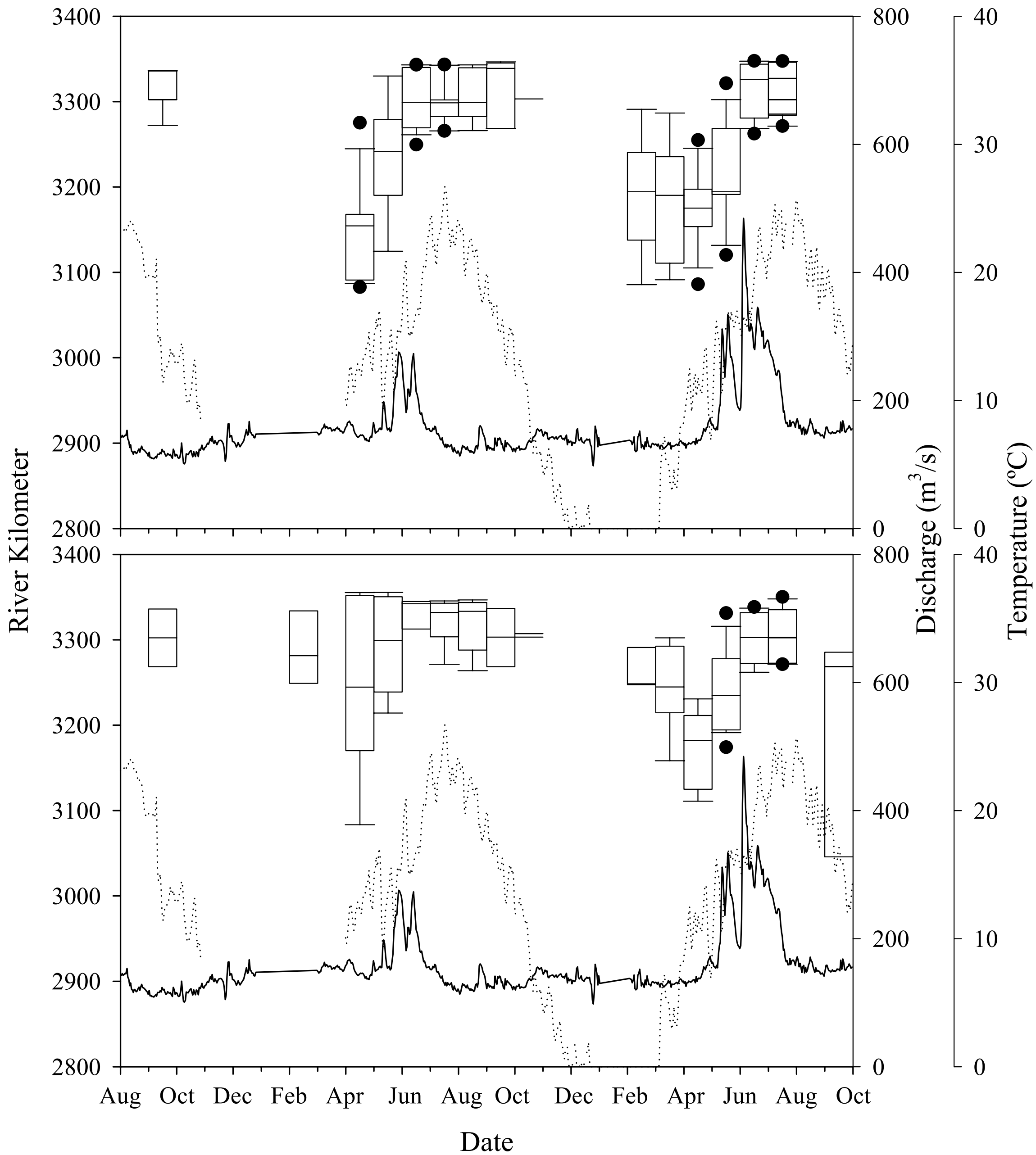
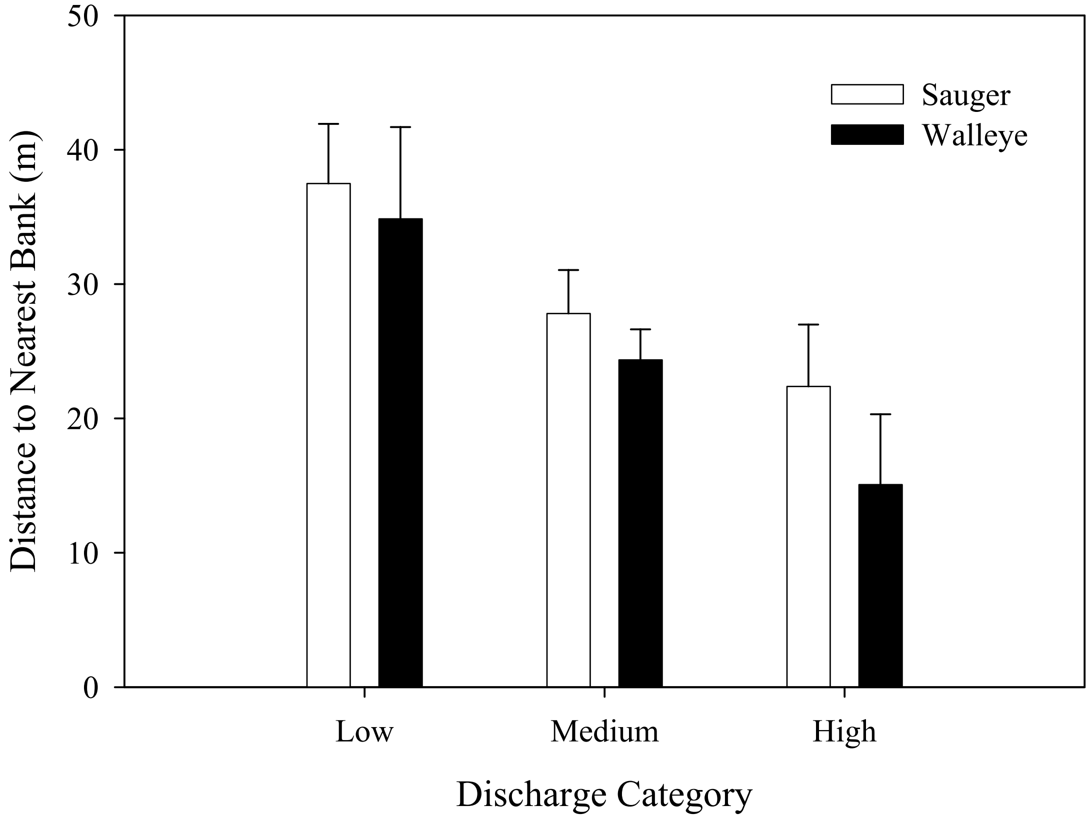


Figure 7. Discharge and distance to nearest bank for sauger and walleye in the middle Missouri River, Montana, 2004 and 2005. Discharge levels are grouped as follows: Low (0 to 140 m^3/s), Medium (141 to 283 m^3/s), High (>284 m^3/s). Error bars denote one standard error.



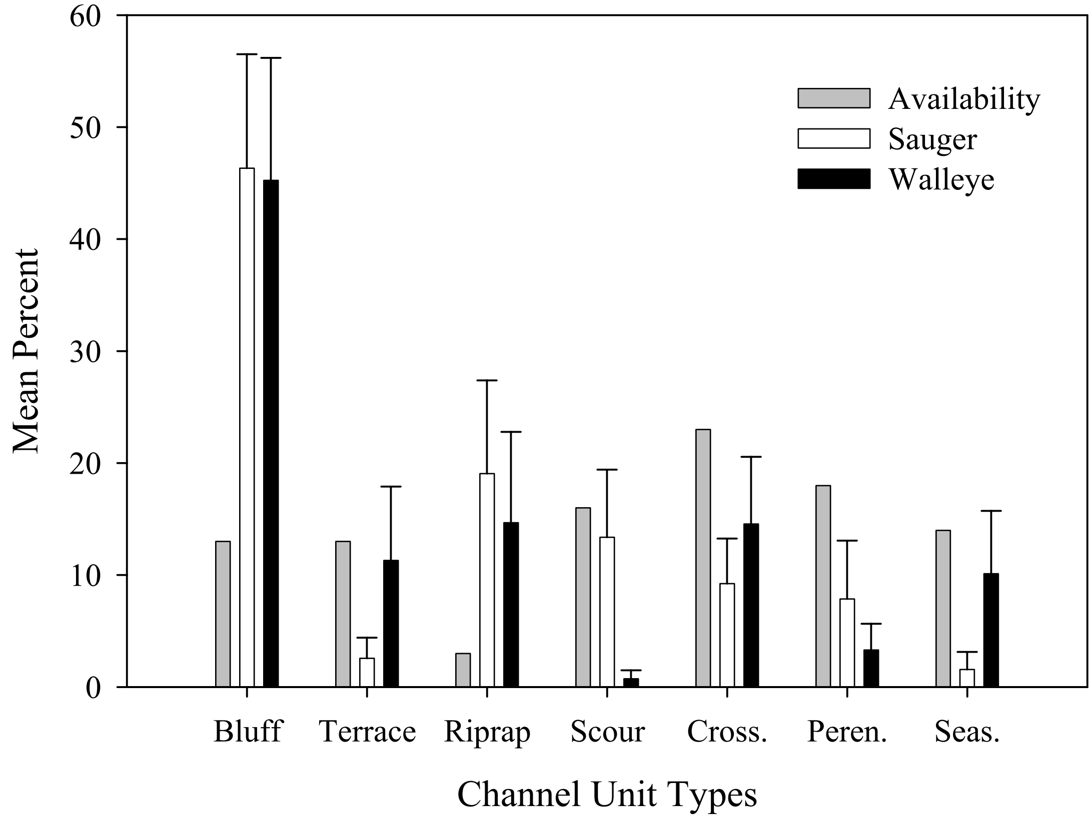
unit where they were tagged. The remaining walleye either did not migrate (N=3), were harvested by an angler (N=1), moved into a tributary after the presumed spawning period (N=2), remained near the presumed downstream spawning area (N=2), returned upstream to a different reach of the river after spawning (N=1), or disappeared (N=1). The amount of river used during the non-migratory season did not differ significantly between sauger (mean = 2.15 km, SE = 1.20) and walleye (mean = 1.05 km, SE = 0.24) ($t_{21.6} = 0.90$; $P = 0.38$). The variability of the sauger mean was highly influenced by a single fish that used 24 km of river during the non-migratory season.

Habitat Use During The Non-Migratory Season

Bluff pools and riprap pools were the most frequently used channel unit types by sauger and walleye (Figure 8). Channel crossovers were the most available channel unit habitat followed by perennial secondary channels, scour pools, seasonal secondary channels, bluff pools, terrace pools, and riprap pools (Figure 8). Sauger and walleye did not select habitats in proportion to availability ($\chi^2_{126} = 405.89$, $P < 0.0001$ for sauger; $\chi^2_{84} = 298$, $P < 0.0001$ for walleye) and selected similar channel units (Figure 9). Sauger selected channel units in proportion to availability except bluff pools, which were positively selected, and terrace pools and seasonal secondary channels, which were negatively selected. Walleye selected bluff pools, riprap pools, channel crossovers, and seasonal secondary channels in proportion to availability. Terrace pools, scour pools, and perennial secondary channels were selected negatively by walleye. Bluff and riprap pools were chosen for quadrant selection analysis because these channel units were used most frequently by sauger and walleye.

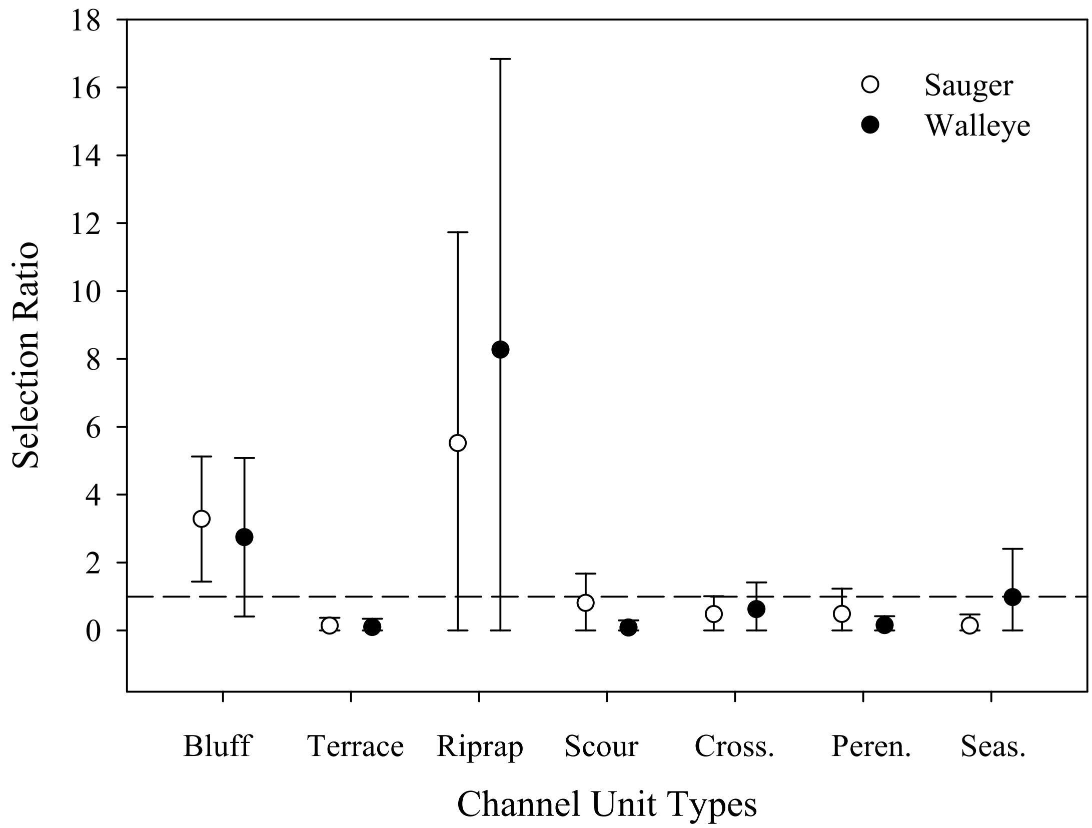
Downstream, outside bends of bluff pools were used most frequently by sauger (46%) and walleye (67%). Sauger and walleye did not select bluff pool quadrants in proportion to availability ($\chi^2_{33} = 86.53$, $P < 0.0001$ for sauger; $\chi^2_{24} = 61.14$, $P < 0.0001$ for walleye) and positively selected similar quadrants (Figure 10). Sauger selected all quadrants in proportion to availability except for upstream, inside bend quadrants, which were negatively selected. Walleye selected the upstream quadrants in proportion to availability whereas downstream, inside bend quadrants were negatively selected and downstream, outside bend quadrants were positively selected.

Figure 8. Mean percent use and availability of channel unit types during the non-migratory season by sauger and walleye in the middle Missouri River, Montana, 2004 and 2005. Channel unit types are: bluff pool (Bluff), terrace pool (Terrace), riprap pool (Riprap), channel crossover (Cross.), perennial secondary channel (Peren.), and seasonal secondary channel (Seas.). Error bars denote one standard error.



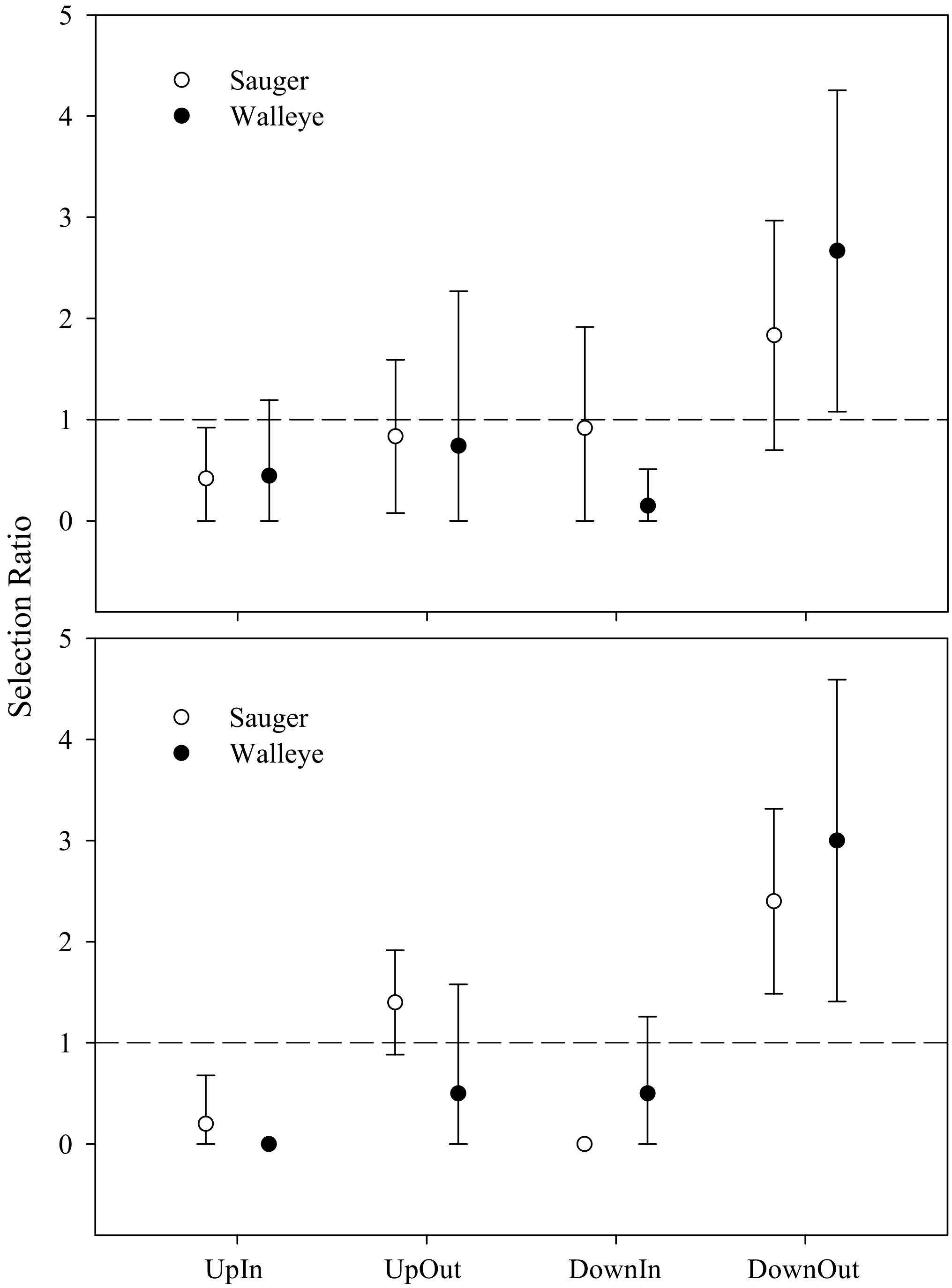
Downstream, outside bends of riprap pools were also primarily used by sauger (60%) and walleye (75%). Sauger and walleye did not select riprap pool quadrants in proportion to availability ($\chi^2_{12} = 27.76$, $P = 0.006$ for sauger; $\chi^2_9 = 28.41$, $P = 0.0008$ for walleye) and positively selected similar quadrants (Figure 10). Sauger selected upstream, outside bend quadrants in proportion to availability, inside bend quadrants were negatively selected, and downstream, outside bend quadrants were positively selected. Walleye selected upstream, outside bend quadrants and downstream, inside bend quadrants in proportion to availability, negatively selected upstream, inside bend quadrants, and positively selected downstream, outside bend quadrants.

Figure 9. Selection ratios and 95% simultaneous Bonferroni confidence intervals of channel unit types during the non-migratory season for sauger and walleye in the middle Missouri River, Montana, 2004 and 2005. Channel units are: bluff pool (Bluff), terrace pool (Terrace), riprap pool (Riprap), scour pool (Scour), channel crossover (Cross.), perennial secondary channel (Peren.), and seasonal secondary channel (Seas.). Values greater than one indicate positive selection, values less than one indicate negative selection, and values equal to one indicate selection in proportion to availability.



Point estimates of habitat at sauger and walleye locations were similar. Mean relative depth of locations did not differ significantly between species within channel unit types ($F_{1,65.4} = 3.35$, $P = 0.0716$); however, relative depth differed between channel unit types ($F_{6,119} = 5.82$, $P = <0.0001$) (Figure 11). Relative depths varied from about 50

Figure 10. Selection ratios and 95% simultaneous Bonferroni confidence intervals of bluff pool quadrants (top panel) and riprap pool quadrants (bottom panel) during the non-migratory season for sauger and walleye in the middle Missouri River, Montana, 2004 and 2005. Quadrants are: upstream, inside bend (UpIn), upstream, outside bend (UpOut), downstream, inside bend (DownIn), and downstream, outside bend (DownOut). Values greater than one indicate positive selection, values less than one indicate negative selection, and values equal to one indicate use in proportion to availability.



percent in bluff pools to 100 percent in seasonal secondary channels. Substrate use was not significantly different between species (χ^2_2 = 0.1068, P = 0.9480) (Figure 12). Gravel and cobble substrates were used most frequently (71 to 76%) whereas fine substrates (i.e., clay, silt, and sand) and boulder substrates were used less frequently (5 to 25%). Mean secchi depth at fish locations did not differ between sauger (mean = 0.46 m, SE = 0.02) and walleye (mean = 0.49, SE = 0.03) (t_{36} = -0.61, P = 0.5444).

Figure 11. Mean relative depth of sauger and walleye locations during the non-migratory season by channel unit type in the middle Missouri River, Montana, 2004 and 2005. Channel units are: bluff pool (Bluff), terrace pool (Terrace), riprap pool (Riprap), scour pool (Scour), channel crossover (Cross.), perennial secondary channel (Peren.), and seasonal secondary channel (Seas.). Error bars denote one standard error.

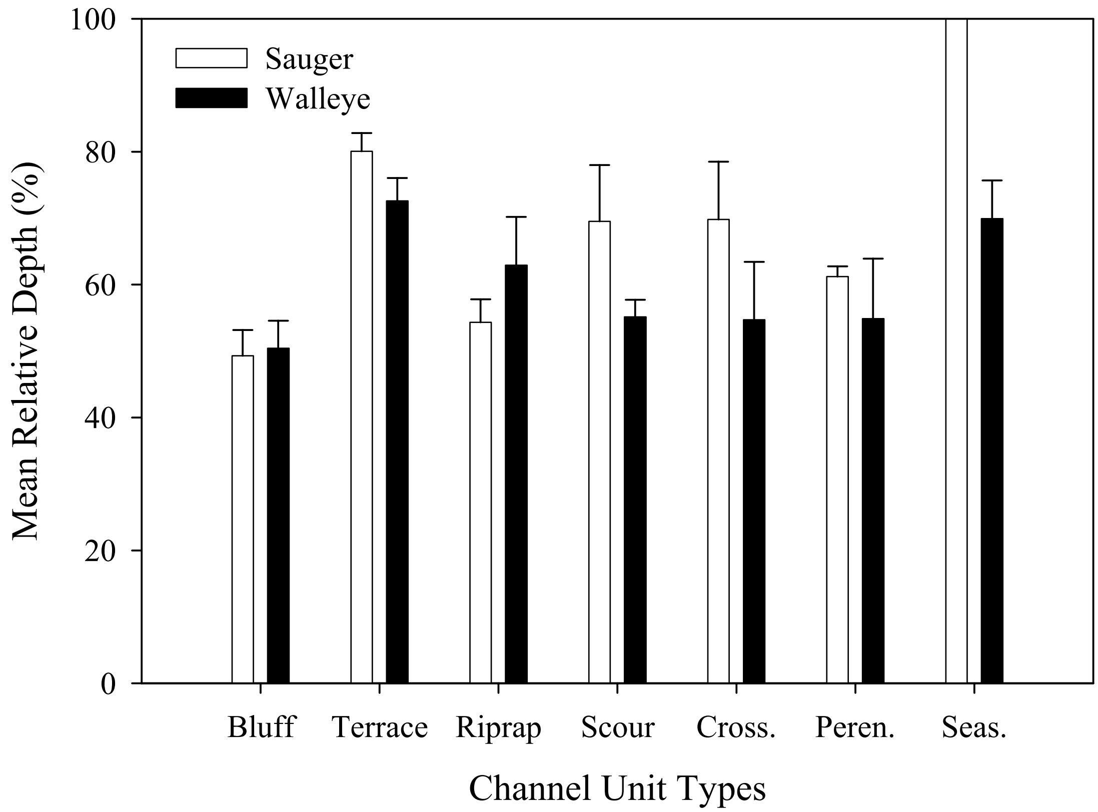
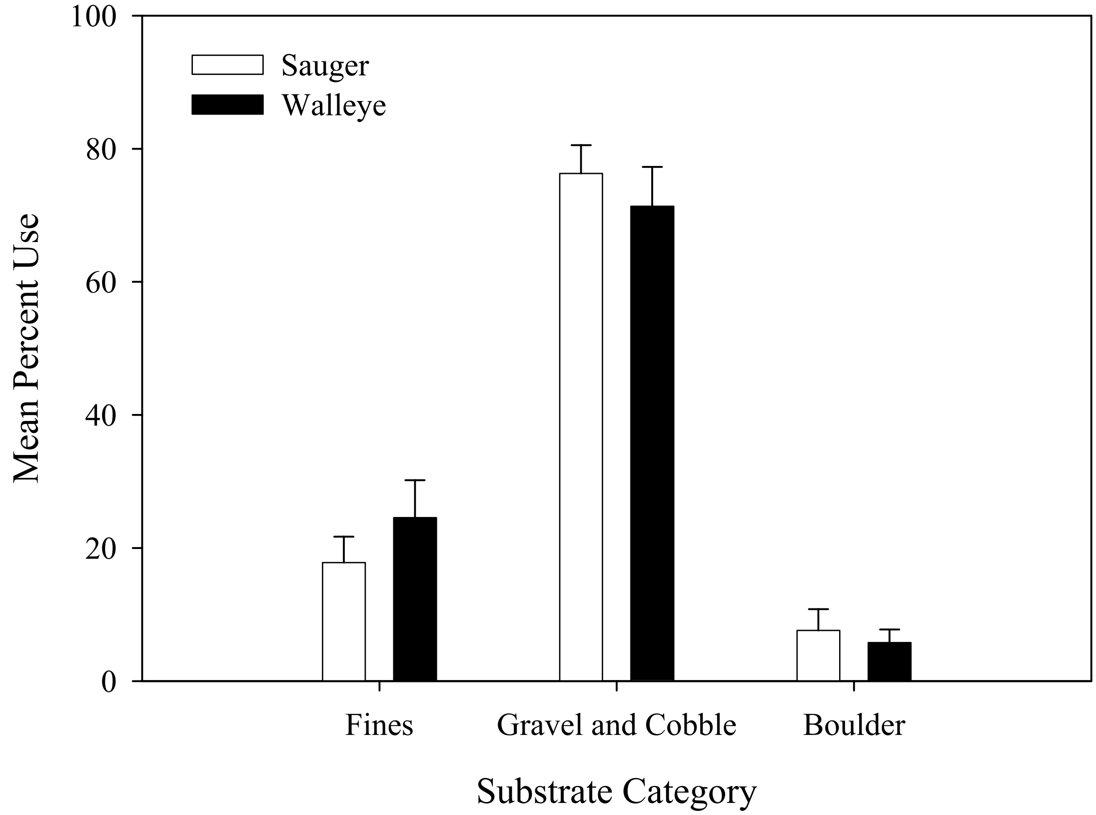


Figure 12. Mean percent substrate use of sauger and walleye at locations during the non-migratory season in the middle Missouri River, Montana, 2004 and 2005. Error bars denote one standard error.



Diets

Ninety-two sauger (mean length = 373 mm, mean weight = 435 g) and 39 walleye (mean length = 394 mm, mean weight = 753 g) were sampled for diet items in the spring of 2004 and 2005 (Figures 13 and 14). Twenty-eight percent of sauger and 33 percent of walleye sampled had empty stomachs (Figures 13 and 14). Unidentified fish were common in diets of both species during all seasons. Spring diet overlap was high (mean Pianka overlap value = 0.72, SE = 0.003) between sauger and walleye and they similarly consumed emerald shiners *Notropis atherinoides* and stonecats *Noturus flavus* (Figures

Figure 13. Percent occurrence of diet items for sauger and walleye during the non-migratory season, grouped into spring (top panel), summer (middle panel), and autumn (bottom panel) periods in the middle Missouri River, Montana, 2004 and 2005. Diet categories are: emerald shiner (ES), macroinvertebrate (MAC), mottled sculpin (MS), stonecat (SC), western silvery minnow (WSM), other (OT), unidentified fish (UF). Percent empty stomachs (Empty) are also included for reference.

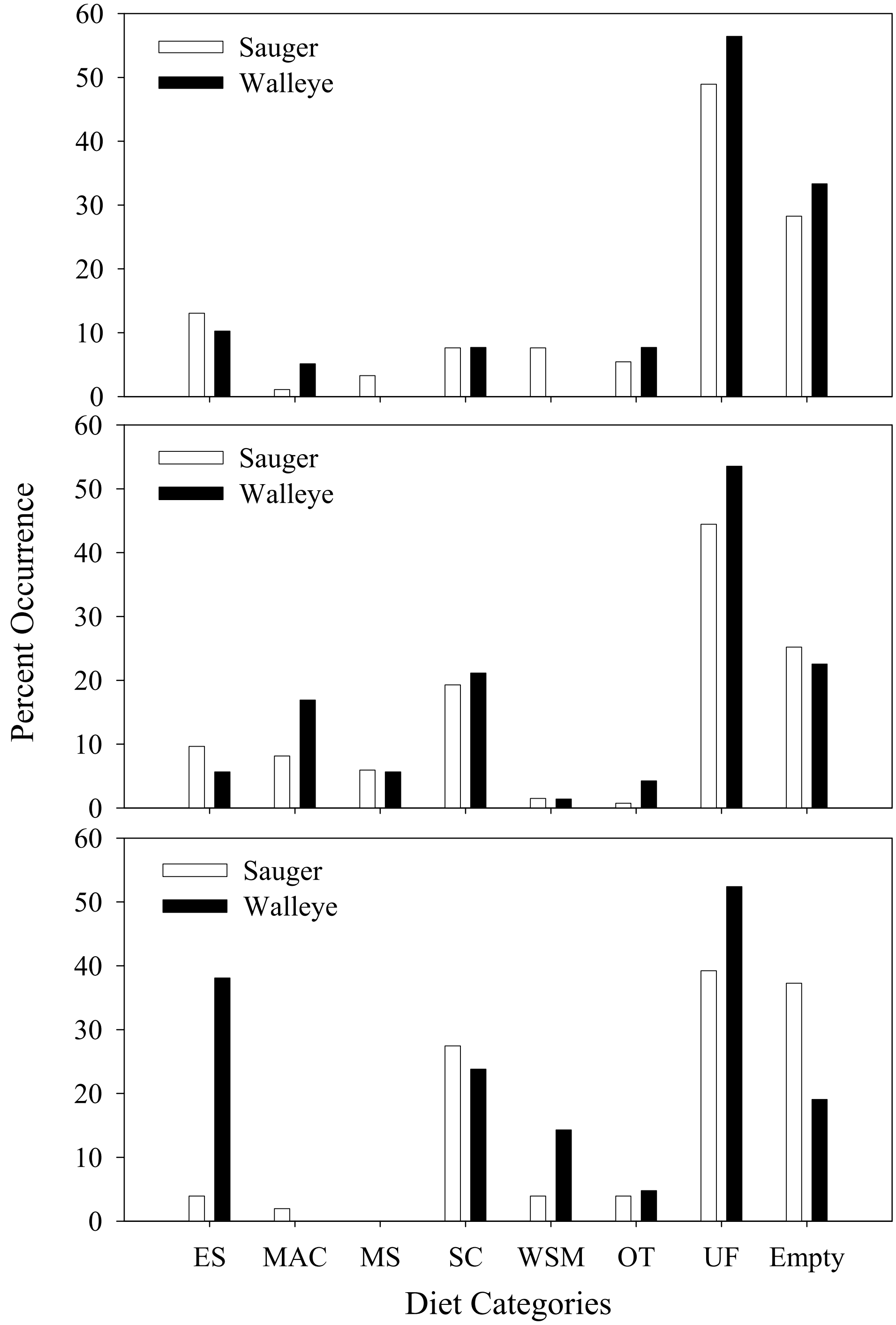
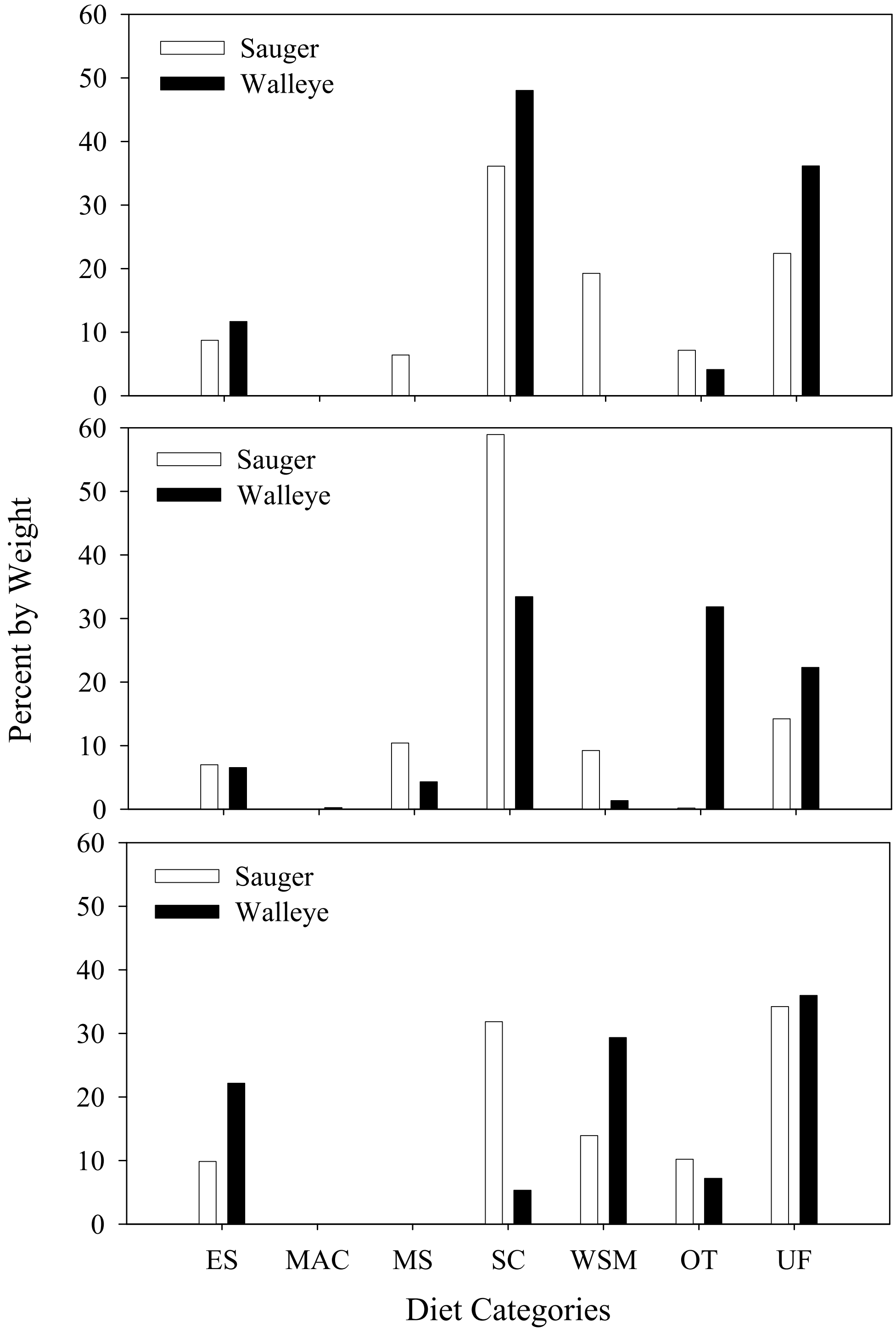


Figure 14. Percent by weight of diet items for sauger and walleye during the non-migratory season, grouped into spring (top panel), summer (middle panel), and autumn (bottom panel) periods in the middle Missouri River, Montana, 2004 and 2005. Diet categories are: emerald shiner (ES), macroinvertebrate (MAC), mottled sculpin (MS), stonecat (SC), western silvery minnow (WSM), other (OT), unidentified fish (UF).



13 and 14). Diet items in the “other” category were brook sticklebacks *Culaea inconstans* and crayfish (family Astacidae) for walleye and longnose sucker *Catostomus catostomus* and flathead chub *Platygobio gracilis* for sauger.

During the summer of 2004 and 2005, 135 sauger (mean length = 377 mm, mean weight = 456 g) and 71 walleye (mean length = 405 mm, mean weight = 685 g) were sampled for diet items (Figures 13 and 14). Twenty-five percent of sauger stomachs and 23 percent of walleye stomachs were empty (Figures 13 and 14). Diet overlap was also high during the summer (mean Pianka overlap value = 0.71, SE = 0.003); however, one large smallmouth bass *Micropterus dolomieu* (total length = 166 mm, weight = 83 g) consumed by a walleye highly influenced the overlap value. The mean Pianka overlap value was 0.95 (SE = 0.0008) when the smallmouth bass was excluded. Sauger and walleye primarily consumed stonecats (Figures 13 and 14). Emerald shiners, macroinvertebrates, and mottled sculpin *Cottus bairdi* were also consumed by both species, but less frequently. The “other” category included longnose sucker for sauger and smallmouth bass, crayfish, and rainbow trout for walleye.

Fifty-one sauger (mean length = 405 mm, mean weight = 555 g) and 21 walleye (mean length = 406, mean weight = 624 g) were sampled for diet items during the autumn of 2005 (Figures 13 and 14). Thirty-seven percent of sauger and 19 percent of walleye stomachs were empty (Figures 13 and 14). Diet overlap was moderate in the autumn between sauger and walleye (mean Pianka overlap value = 0.49, SE = 0.003). Sauger primarily consumed stonecats. Walleye also consumed stonecats, but emerald shiners and western silvery minnows *Hybognathus argyritis* were the primary diet items.

Diet items in the "other" category were smallmouth bass for sauger and longnose sucker for walleye.

Trophic Position and Diet Corroboration

Twelve species (N = 109 samples) from the middle Missouri River and 10 species (N = 57 samples) from the lower Yellowstone River were analyzed for stable carbon and nitrogen isotope ratios (Table 3). Isotope ratios at the Missouri River site varied from -25.90 to -21.05 for $\delta^{13}C$ and from 10.42 to 16.86 for $\delta^{15}N$ (Figure 15). Carbon isotope ratios varied from -26.77 to -22.61 and nitrogen isotope ratios varied from 10.63 to 17.65 at the Yellowstone River site (Figure 15).

Trophic position of sauger and walleye was variable between the two systems. Walleye had the highest trophic position (mean trophic position = 3.85, SE = 0.042) of all species collected from the Missouri River site and walleye trophic position was significantly higher than sauger trophic position (mean trophic position = 3.57, SE = 0.068) ($t_{50.2}$ = -3.40, P = 0.0013) (Figure 15). Walleye trophic position did not differ significantly from sauger in the lower Yellowstone River (walleye mean trophic position = 4.06, SE = 0.30; sauger mean trophic position = 3.84, SE = 0.08) (t_{27} = -0.88, P = 0.3868) (Figure 15). Additionally, sauger trophic position differed significantly between the middle Missouri and lower Yellowstone rivers (t_{58} = -2.53, P = 0.0143) whereas walleye trophic position did not differ between the rivers ($t_{2.08}$ = -0.72, P = 0.5453) (Figure 15).

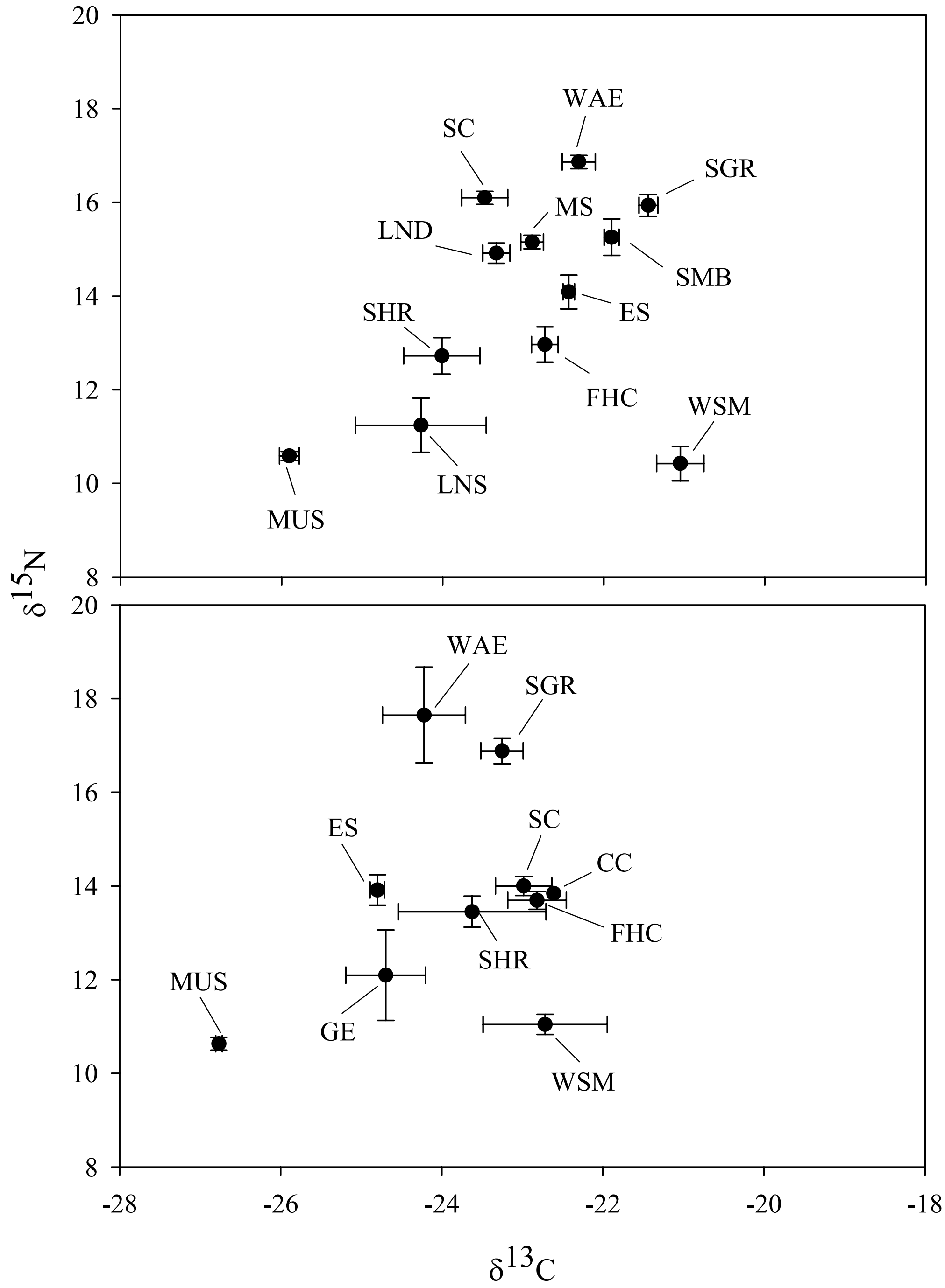
Carbon isotope ratios of sauger and walleye from the Missouri River study site

Table 3. Descriptive statistics of fish and mussel samples used for stable isotope analysis collected from the middle Missouri (river km 3267 to 3337) and Yellowstone (river km 30 to 40) rivers in 2005. One standard error of the length and weight are located in the column to the right of the mean values.

River	Species	N	Mean length (mm)	SE	Mean weight (g)	SE
Missouri	emerald shiner	5	77.8	2.2	4.4	0.4
	flathead chub	5	156.4	10.8	40.2	7.7
	longnose dace	5	88.8	0.9	8.2	1.1
	longnose sucker	5	137.0	10.4	26.4	4.8
	mottled sculpin	5	84.8	3.6	7.6	1.1
	mussel	5			221.2	60.8
	sauger	34	393.0	10.4	493.6	46.5
	shorthead redhorse	6	128.7	23.8	31.3	13.0
	smallmouth bass	5	101.0	9.1	15.6	3.4
	stonecat	4	160.3	11.8	46.8	8.7
	walleye	20	406.3	18.4	717.7	147.3
	western silvery minnow	5	101.0	1.5	10.2	0.7
Yellowstone	channel catfish	1	160.0		31.0	
	emerald shiner	5	85.0	0.7	4.2	0.2
	flathead chub	4	152.0	9.0	30.5	4.3
	goldeye	2	135.0	4.0	18.5	1.5
	mussel	5			54.2	3.4
	sauger	26	369.7	15.4	412.2	51.2
	shorthead redhorse	3	149.0	8.4	31.0	5.6
	stonecat	3	111.3	4.1	13.7	1.2
	walleye	3	441.0	46.8	731.0	266.6
	western silvery minnow	5	83.0	13.1	7.2	2.4

corroborated traditional diet data; however, some differences were evident (Figure 15). The mean carbon ratio of sauger ($\delta^{13}C$ = -21.45, SE = 0.1175) was similar to western silvery minnows ($\delta^{13}C$ = -21.05, SE = 0.2924), emerald shiners ($\delta^{13}C$ = -22.43, SE = 0.0709), and smallmouth bass ($\delta^{13}C$ = -24.01, SE = 0.47). Stable isotope analysis indicated that stonecats ($\delta^{13}C$ = -23.48, SE = 0.29) were not a major food item of sauger, which does not coincide with diet data. The carbon ratio of walleye ($\delta^{13}C$ = -22.31, SE = 0.2064) was similar to emerald shiners, smallmouth bass, flathead chubs ($\delta^{13}C$ = -22.73,

Figure 15. Mean carbon and nitrogen isotope ratios of sauger, walleye, potential prey species, and mussels in the middle Missouri River (top panel) and lower Yellowstone River (bottom panel), Montana, 2005. Species are walleye (WAE), sauger (SGR), mottled sculpin (MS), smallmouth bass (SMB), stonecat (SC), channel catfish (CC), longnose dace (LND), emerald shiner (ES), goldeye (GE), flathead chub (FHC), shorthead redhorse (SHR), longnose sucker (LNS), western silvery minnow (WSM), and mussel (MUS). Error bars denote one standard error.



SE = 0.1648), and mottled sculpin ($\delta^{13}C$ = -22.89, SE = 0.1411). Diet analysis of walleye also indicated stonecats as a major diet item; however, carbon ratios imply walleye consumption of stonecats was limited.

Carbon isotope signatures of Yellowstone River sauger and walleye imply some prey items may be similarly consumed in both the lower Yellowstone and middle Missouri rivers (Figure 15). The mean carbon ratio of sauger ($\delta^{13}C$ = -23.25, SE = 0.26) was similar to stonecats ($\delta^{13}C$ = -22.98, SE = 0.35), channel catfish *Ictalurus punctatus* ($\delta^{13}C$ = -22.61), flathead chubs ($\delta^{13}C$ = -22.82, SE = 0.36), shorthead redhorse *Moxostoma macrolepidotum* ($\delta^{13}C$ = -23.62, SE = 0.92), and western silvery minnows ($\delta^{13}C$ = -22.72, SE = 0.77). The mean carbon ratio of walleye ($\delta^{13}C$ = -24.22, SE = 0.51) was similar to emerald shiners ($\delta^{13}C$ = -24.80, SE = 0.09), shorthead redhorse, and goldeye *Hiodon alosoides* ($\delta^{13}C$ = -24.70, SE = 0.50). Channel catfish, shorthead redhorse, and goldeye were not present in Missouri River sauger and walleye diets and Missouri River SIA did not indicate use of shorthead redhorse, which differed from stable isotope data suggesting their use by sauger and walleye in the lower Yellowstone River.

DISCUSSION

Historical Catch Data

Sauger relative abundance is currently low at the Morony Dam and Coal Banks sites in the middle Missouri River; however, the effect of walleye on sauger may be minimal given that walleye are also at a low abundance. According to competition theory, the competitively dominant species would be expected to increase in abundance while the competitively inferior species would decrease in abundance (Crowder 1990). Thus, if walleye were competitively dominant and sufficiently abundant, sauger abundance would be expected to decline. The low abundance of sauger and walleye within the last decade may suggest that neither species is currently at sufficient abundance to negatively affect the other.

Mean relative weights of walleye were higher than sauger in most years at both sites; however, relative weights of both species were typically lower than the optimal value of 100, which may be due to low prey availability (Anderson and Neumann 1996; Porath and Peters 1997). Interestingly, sauger and walleye relative weights fluctuated similarly between years, which may suggest that both species are affected similarly by prey limitations. Based on similar diets of sauger and walleye found in this study, it seems plausible that body condition of both species would be analogously affected by fluctuations in prey availability. If walleye are competing with sauger for food resources, it might be expected that the relative weight of one species would decline whereas the relative weight of the other would increase or stay the same; however, similar relative weight fluctuations suggest that neither species is presently having negative effects on the other. The relative abundance of sauger and walleye may be too low at present to cause negative effects on the condition of the opposing species; however, high resource overlap between species may indicate that competition is likely in the future, especially if resources become limiting or population abundance increases.

Seasonal Migrations

Seasonal migrations of sauger in the middle Missouri River were similar in length and direction to sauger in the Yellowstone River (Jaeger et al. 2005), but differed from other systems (Siegwarth 1993; Pegg et al. 1997; Gangl et al. 2000). Sauger in pool 16 of the Mississippi River also migrated downstream to spawning sites (Siegwarth 1993), but migrations were shorter (i.e., five to 10 km) than sauger movements in Montana. Conversely, sauger in pool 2 of the Mississippi River migrated upstream and into the Minnesota River during the spawning period (Gangl et al. 2000). Sauger also migrate upstream to spawn in dam tailwaters (Nelson 1968; Pitlo 1989; Pegg et al. 1997). Middle Missouri River and Yellowstone River sauger both exhibited long downstream migrations (up to 245 km in the Missouri and 300 km in the Yellowstone) prior to the presumed spawning period and returned back upstream after spawning (Jaeger et al. 2005). Interestingly, sauger in both rivers also migrated to river reaches with similar geologic features. During the presumed spawning period in the middle Missouri River, sauger used a section of river in the Judith River Geologic Formation, which forms resistant ledges (MBMG 2002). Similarly, sauger in the Yellowstone River selected the

Tullock and Lebo Members of the Fort Union Formation, which form bedrock outcrops (Jaeger et al. 2005). Sauger are known to use rocky substrates and bedrock reefs during the spawning season (Nelson 1968; St. John 1990; Hesse 1994; Jeffrey and Edds 1999), which coincides with their use in the middle Missouri and Yellowstone rivers. A majority of sauger in both rivers began migrating downstream before March. Middle Missouri River and Yellowstone River sauger that did not begin their downstream migration before March migrated quickly downstream during the few weeks prior to the presumed spawning period in April. Only one sauger from the Yellowstone River study (Jaeger et al. 2005) and one sauger from the present study used a tributary during the spawning period (i.e., the Marias River), despite the historical use of tributaries as sauger spawning areas in Montana (Berg 1981; Penkal 1992). Sauger in both systems also exhibited site fidelity after spawning by returning upstream to areas occupied the previous year (Jaeger et al. 2005). The similarity of sauger movement in the middle Missouri and Yellowstone rivers suggests that anthropogenic moderation of middle Missouri River discharge has not greatly affected sauger migratory behavior; however, historical migratory patterns of middle Missouri River sauger are not completely known.

Walleye movements during the migratory season were unique in the middle Missouri River and overlapped the sauger migration. The extensive downstream migrations of walleye (>200 km) prior to the spawning season and the return migration upstream are not known to occur in any other system. However, upstream migrations of walleye from lakes into rivers and wholly within rivers have been documented (Bodaly 1980; Paragamian 1989; Pitlo 1989; DiStefano and Hiebert 2000) with some migrations exceeding 150 km (Priegel 1967). Short downstream migrations (five to 10 km) by walleye to spawning sites have also been reported (Siegwarth 1993), but are much less extensive than the distances recorded in this study. The overlap of walleye and sauger seasonal migrations in the middle Missouri River suggests that both species occupy similar river reaches at similar times during the year.

Walleye seasonal movements in the middle Missouri River were more variable than sauger. A majority of walleye moved downstream prior to the spawning season; however, a few walleye did not exhibit any migratory behavior. After the presumed spawning period, some walleye did not return upstream and exhibited weaker site fidelity than sauger. Walleye that returned upstream were less likely to return to the area where they were tagged the previous year and a few occupied a different section of river. One walleye was recorded moving into the headwaters of Fort Peck Reservoir in September 2005 and may have also moved to Fort Peck the previous year, but the spring 2005 tracking effort was concentrated on river sections farther upstream. Several other walleye may have also resided in Fort Peck reservoir during the winter because their first location dates were not until late spring and were in the downstream reaches of the tracking area.

Walleye migrations may be more variable than sauger in the middle Missouri River due to their recent introduction and stocking ancestry in connecting reservoirs. The site fidelity of walleye to spawning and feeding areas is increased with repeated trips and is likely learned from older individuals in the population (Olson et al. 1978). Assuming that sauger have similar site fidelity characteristics as walleye, sauger migrations may be more established because they are native to the middle Missouri River and migrations have been strengthened by repeated trips over thousands of years. Additionally, the differences in walleye migration patterns may be related to their stocking location. For example, walleye residing in the middle Missouri River that were stocked in Fort Peck may be more inclined to return to the reservoir whereas walleye that have flushed from an upstream reservoir may have an affinity for the upstream section of river.

Habitat Use

Use of substrate and depth was related to the geomorphologic features of channel units used and selected similarly by sauger and walleye. Sauger primarily used and positively selected bluff pools that recruit rocky substrates (e.g., gravel, cobble and boulders) to the river channel. Bluff pools were also primarily used by walleye, but were selected in proportion to availability. Various other studies have recorded sauger and walleye use of rocky substrates during all seasons (Nelson 1968; Paragamian 1989; Pitlo 1989; Jeffrey and Edds 1999; Jaeger et al. 2005). Riprap pools also recruit rocky substrates to the channel and were secondarily used by sauger and walleye, although both species selected riprap pools in proportion to availability. Selection in proportion to availability of bluff pools by walleye and riprap pools by both species is due to large confidence intervals. Large confidence intervals are often a product of low expected values in chi-square tests; however, confidence intervals calculated with low expected values are most likely conservative (Roscoe and Byars 1971). Thus, a higher number of locations per fish (i.e., increased expected values) would likely result in smaller confidence intervals and may indicate positive selection of bluff and riprap pools by sauger and walleye. Bluff and riprap pools also contain slow water areas that provide velocity refuge and greater depths than other channel unit types, which are important to sauger and walleye during high light conditions. Sauger and walleye have an ocular adaptation that allows them to see and predate during low light conditions (Ali and Anctil 1968). Consequently, the decreased water turbidity and increased light intensity of summer may negatively affect the predation ability of both species if a light refuge is not available. The depth variation available in bluff and riprap pool habitats may allow sauger and walleye to adjust their depth as light intensity changes.

The primary use of downstream, outside bend quadrants of bluff and riprap pools by both species and positive selection of this quadrant by walleye in bluff pools and both species in riprap pools may be related to the microhabitat characteristics of those quadrants. Bluff pools are formed by impingement of the channel against resistant bedrock material, which scours and deepens the channel on the outside of the bend (Rabeni and Jacobson 1993). This scouring also erodes rocky substrates (e.g., gravel, cobble, and boulders) into the channel, particularly on the outside bend where the bank scour is occurring. Riprap pools are essentially man-made bluff pools and scour similarly by deepening the channel on the outside bend and recruiting rocky substrates to the river channel. The reason sauger and walleye selected the downstream half of the outside bend may be due to flow. Secondary currents and bed shear stress are lowest near the downstream ends of river bend pools (Bridge and Jarvis 1982) and may act as a velocity refuge for sauger and walleye. Spiral currents adjacent to the outside bank are also present at the downstream end of pools as the thalweg crosses over (Bridge and Jarvis 1982) and may also provide velocity refuge. The lower velocities of downstream, outside bends combined with deep water and rocky substrates may contribute to the similar use and selection of these areas by sauger and walleye.

Similar use and selection of habitats suggests sauger and walleye have the potential to compete in the middle Missouri River, although habitat use was only assessed during the non-migratory season. Understanding the seasonal variability of habitat use between species would yield a more complete picture of competition potential. Nevertheless, competition potential may be high during the non-migratory season and may influence the interactions between sauger and walleye more strongly than during other seasons. Low discharge during the non-migratory season directly affects the available habitat by limiting the amount of water. Thus, the potential for competition may increase as water levels drop and confine sauger and walleye to a smaller area. Increased water temperature during the non-migratory season may also contribute to competition potential. Higher water temperatures increase the metabolic rate (Cai and Summerfelt 1992) of walleye and may exacerbate competition between the species, assuming that sauger respond similarly to higher water temperatures. Higher metabolic rates increase the demand for food, which combined with the concentration of sauger and walleye at low discharge during the non-migratory season, may create higher competition potential during the non-migratory season than any other period of the year.

Diets and Diet Corroboration

Prey items consumed by sauger and walleye were relatively diverse and reflected their habitat use in the middle Missouri River. The relationship between prey consumption and habitat use has also been demonstrated with trout in Idaho (Hilderbrand and Kershner 2004). Stonecats are benthic-oriented species that are found in pool and riffle habitats with rocky substrates (Scott and Crossman 1973). Consumption of stonecats coincides with the bluff and riprap pool channel units and pool quadrants primarily used by both species. Sauger and walleye may also move into riffle habitats (e.g., channel crossovers) to feed on stonecats; however, these habitats were not positively selected by either species in this study. Riffle habitats may have been used by sauger and walleye during crepuscular or nocturnal feeding periods, but fish were not tracked during these times. Pelagic minnows (e.g., emerald shiners and western silvery minnows) are found in association with slower water areas near the river bank (Scott and Crossman 1973) and were also consumed, indicating sauger and walleye use of near shore habitats.

Diet overlap was high during the spring and summer and indicates competition potential for food resources. Diets of sauger and walleye were also similar in other systems where they are sympatric (Priegel 1963; Swenson and Smith 1976; Fitz and Holbrook 1978; Mero 1992), although diet differences have also been observed (Rawson and Scholl 1978). Sauger and walleye were assumed to be competing for food resources during June and July in Lake of the Woods, Minnesota based on resource overlap and low prey availability (Swenson and Smith 1976). Competition then decreased in August and September as prey abundance increased and sauger and walleye were spatially separated (Swenson and Smith 1976). Diet overlap was high in this study during the spring (May and June) and summer (July and August) and habitats were similarly used by sauger and walleye, which indicates high competition potential. Diet overlap during the autumn (September and October) was moderate indicating decreased competition potential for food. Diet overlap results were temporally similar to those found in Lake of the Woods, Minnesota; however, information on prey availability by season in the middle Missouri River is needed to more thoroughly assess competition.

Using only traditional diet data to evaluate fish diets may be misleading since diet data from individual fish are only assessed at a single point in time. Stable isotope analysis provides a more time-integrated view of diet and can be used to corroborate stomach content data (e.g., Beaudoin et al. 1999). Stonecats were a major diet item of sauger and walleye based on traditional diet data, but carbon and nitrogen stable isotope signatures suggest cyprinids were primarily consumed. Thus, it is possible that stonecats were not a major diet item of sauger and walleye, but are only consumed during the spring, summer, and autumn in small quantities. Stonecats are easily identifiable even at advanced levels of digestion because of decay-resistant hard parts (i.e., pectoral and dorsal spines), which may have overestimated their abundance in diets of sauger and walleye. Conversely, cyprinids may have been underestimated because they are quickly digested and have few identifiable hard parts. The high percent by weight and occurrence of unidentified fish in sauger and walleye stomachs were likely cyprinids that were difficult to identify. Sauger and stonecats from the middle Missouri River also occupied a similar trophic level according to nitrogen isotope analysis, suggesting that stonecats are not a major diet item of sauger. Likewise, smallmouth bass had a similar carbon ratio as sauger and walleye, but consumption of smallmouth bass was probably limited since the trophic position of all three top predators was similar. This more likely indicates that smallmouth bass consume prey with similar carbon ratios as sauger and walleye. The conclusions provided from stable isotope and traditional diet data denote that each method provides valuable insight; however, a more complete picture of diet is available when the two are used in conjunction.

Trophic Position

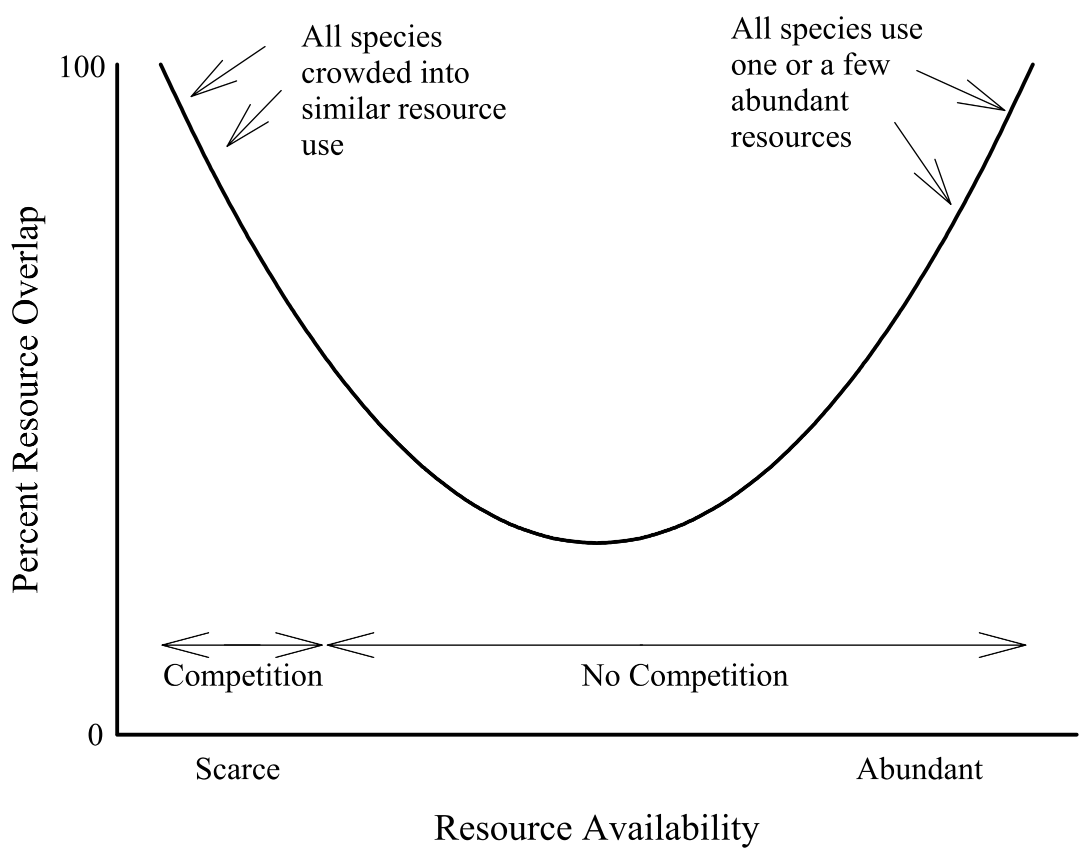
The difference in trophic position of middle Missouri River and lower Yellowstone River sauger was statistically significant, but may not be biologically significant. Trophic shifts by native predators resulting from competition with non-native predators are sometimes drastic, causing the natives to switch to prey at a lower trophic level (Olowo and Chapman 1999; Vander Zanden et al. 1999). The decreased energetic value of prey may then have consequences on individual and population fitness and survival, leading to population declines of the native species; however, trophic shifts may also permit coexistence of the competing species (Olowo and Chapman 1999). A trophic shift of native lake trout in the presence of non-native smallmouth bass resulted in a 0.6 trophic level shift (i.e., to a lower trophic level), calculated using SIA (Vander Zanden et al. 1999). Although the direct effect of a 0.6 trophic shift was not assessed, the changes in food web structure may have future effects on the native ecosystem (Vander Zanden et al. 1999; Vander Zanden et al. 2004). Sauger trophic position differed by 0.2 between the middle Missouri and lower Yellowstone rivers, but diet and isotope data imply that sauger still occupy the top trophic level in the middle Missouri River (i.e., sauger did not shift to an entirely lower trophic level in the presence of walleye). However, diets from the remainder of the year (December through April) in the middle Missouri River were not collected in this study and might elucidate that sauger feed at a lower trophic level during that period, resulting in the 0.2 trophic level shift. The consequences of a 0.2 trophic shift were not assessed in this study, but would be useful in understanding the potential impacts of a walleye-induced trophic shift on sauger.

Resource Overlap and Competition Potential

Overall, use of habitat and food resources was similar between sauger and walleye in the middle Missouri River and indicates competition potential. However, understanding resource availability is a crucial component to actually deducing competition. Although not quantified in this study, resource availability fluctuates in some systems (Wiens 1977) and may be especially pronounced in lotic systems where abiotic factors are an influential determinant of community structure (Townsend 1989). Accordingly, competition for resources among ecologically similar, sympatric species also fluctuates (Wiens 1977; Matthews 1998). Species with similar resource use are not likely to compete when resources are abundant whereas competition will occur when resources are scarce (Wiens 1977; Figure 16 from Matthews 1998). Resource availability is also related to the population abundance of the competing species. Population abundances lower than the amount required to fully utilize a scarce resource will result in no competition. Nevertheless, fluctuations in the availability of similarly used habitat and food resources may result in periods where resources are limiting and competition is likely to occur between sauger and walleye.

Habitat and food resources similarly used by sauger and walleye undoubtedly fluctuate temporally and spatially in the middle Missouri River. The amount of available habitat fluctuates in response to changing discharge. Fish populations are also known to

Figure 16. Hypothetical relationship between resource availability, resource overlap, and competition potential (modified from Matthews 1998).



fluctuate both within and among years in response to varying discharge (Welcomme and Hagborg 1977). High discharge events within years correspond to a greater density and biomass of fish whereas low discharge periods regulate the amount of fish surviving to the following year (Welcomme and Hagborg 1977). Thus, intensity of spring flooding in the middle Missouri River and the amount of water during the base flow period may be related to prey fish population abundance and biomass. Discharge variability would directly affect the amount of prey available to sauger and walleye within and among years and may cause limitations of prey, particularly during drought years.

Ecologically similar species will be influenced by the same resource limitations and one species may be phenotypically favored (Wiens 1977). Hence, walleye may have morphological, behavioral, and physiological traits that make them more competitive than sauger in the current middle Missouri River. Walleye grow to larger average sizes than sauger (Scott and Crossman 1973) and subsequently, have a larger average gape size. Thus, walleye have the ability to switch to larger prey items during periods of low prey fish recruitment whereas sauger are restricted to smaller prey. Walleye are also efficient predators and have drastically depleted prey fish populations in systems where they were introduced, leading to shifts in fish community composition and competition for food resources with other piscivores (McMahon 1992; McMahon and Bennett 1996). Naturalized walleye populations also affect prey fish populations and alter community structure (e.g., Lyons and Magnuson 1987). Similarly, the efficient predation skills of walleye may lead to food supply depletion in the middle Missouri River, especially during years of low prey abundance, causing high competition potential between sauger and walleye. Lastly, anthropogenic alterations to the middle Missouri River (i.e., dams) have affected the river by decreasing water turbidity below dams and moderating the peaks and troughs in the hydrograph. Consequently, aquatic habitats of the middle Missouri River may be less suitable for sauger than historically, and more suitable for walleye. Walleye are better adapted and can feed more effectively than sauger at higher light conditions caused by decreased turbidity (Ali and Anctil 1968). Additionally, walleye are primarily adapted to lentic habitats (Scott and Crossman 1973) and may gain a competitive edge over sauger in rivers with an anthropogenically moderated flow regime. Sauger are primarily adapted to large rivers (Scott and Crossman 1973) with variable flow regimes and populations do not thrive in some lentic systems. Sauger population abundance often declines following the construction of dams on large rivers (Nelson and Walburg 1977; St. John 1990; Hesse 1994).

Non-native predators other than walleye may also potentially compete with sauger in the middle Missouri River; however, these interactions were not assessed in this study. Smallmouth bass are non-native to the middle Missouri River and were first recorded in sampling surveys in 1993. Relative abundance of smallmouth bass at the Morony Dam site increased to 19.2 fish per hour in 2003 (Gardner 2005) and may contribute to further competition for resources with sauger. Additionally, northern pike, rainbow trout, and brown trout are also present in the middle Missouri River at low abundances (Gardner 2005) and may compete with sauger for resources. The impacts of these non-native predators should also be considered when understanding the potential interactions with native sauger.

Research and Management Implications

Establishing resource overlap between two species is an essential first step in evaluating interspecific competition (Ross 1986; Crowder 1990). Sauger and walleye exhibited high overlap of seasonal migrations, habitat use during the non-migratory season, and diets during spring and summer in the middle Missouri River, which will lead to competition if resources are limiting. The evidence from this study suggests that walleye abundance is presently not increasing nor is sauger abundance decreasing (i.e., walleye are not competitively excluding sauger) and the abundances of both species are relatively low. Assuming that walleye are occupying historical sauger niche-space, it might be expected that the combined sauger and walleye abundance would equal the abundance of sauger in the late 1970s. However, the low abundance of both species suggests that environmental conditions may have changed the carrying capacity of *Sander* species in the middle Missouri River. Nevertheless, similar resource use between these species in the middle Missouri River suggests that if resources become limiting, competitive interactions may increase and walleye may be more competitive than sauger. Thus, the abundance and other metrics correlated with sauger and walleye fitness (e.g., relative weight, growth rates) should continually be monitored so that negative effects on the sauger population can be observed and resolved.

Although the definitive effects of walleye on sauger cannot be determined based on the results from this study, certain management actions may help promote the sustainability of sauger and control walleye populations in the middle Missouri River. Anthropogenic alterations have created changes in river habitat that may be more suitable to walleye than sauger. Restoring the natural flow regime and increasing river turbidity may have negative effects on the walleye population whereas the sauger population would be favored because of their adaptability to historic conditions. Morony Dam could be regulated to restore the historic amplitude of peaks and troughs in the hydrograph. Tailwater turbidity could be increased by transporting sediment around the dam; however, this management action would likely be very costly.

The best way to minimize the potential impacts of walleye on sauger in the middle Missouri River is to decrease the size of the walleye population. Potential management actions to reduce the walleye population include:

(1) Changing current harvest regulation to an unlimited creel limit of walleye and zero creel limit for sauger,
(2) Requiring anglers to harvest all walleye caught,
(3) Promoting the removal of walleye using angling tournaments,
(4) Removing walleye by agency personnel,
(5) Removing and relocating walleye to reservoirs,
(6) Removing and donating walleye to food banks, and
(7) Cease or decrease the stocking of walleye in connecting reservoirs.

However, removing walleye from the middle Missouri River or discontinuing stocking of reservoirs would likely be a contentious issue among anglers and other stakeholders. Thus, public meetings with pertinent stakeholders may be required to calculate the feasibility of walleye removal or changes in the stocking regime. Additionally, public meetings and other forms of public involvement could be used to educate the public about the effects of non-native species and the importance of native species to ecosystem function.

Despite the potential benefits of walleye removal to sauger in the middle Missouri River, walleye from connecting reservoirs may emigrate from reservoirs into the river. Although our study does not provide direct evidence that walleye are transient between the middle Missouri River and connecting reservoirs, walleye likely move between lotic and lentic habitats (McMahon 1999). Thus, the management actions proposed above could be used to decrease walleye populations in connecting reservoirs. However, removing walleye from reservoirs would also be a contentious issue and would require stakeholder involvement before decisions could be made. Alternatively, reservoir walleye populations may be prohibited from the river through restrictive devices, such as:

(1) Weirs that prohibit walleye movement into the river and

(2) Dam turbines that kill walleye flushing from reservoirs.

In addition to competition potential, current hybridization between sauger and walleye in the middle Missouri River (about 20 %) (Billington et al. 2005) may further the need to reduce the abundance of walleye. The relatively high hybridization rates corroborate the results from this study showing that sauger and walleye use similar areas at similar times for spawning. Hybridization between sauger and walleye may pose serious threats to sauger conservation by diluting sauger genetic purity and masking advantageous traits that allow sauger to adapt to their native environment. Reducing the abundance of pure walleye and hybrids would help to slow the dilution of sauger genetics; however, morphological identification of hybrids is difficult (Van Zee et al.

1996). Identification of F1 hybrids (first generation hybrids of sauger and walleye) is possible because of intermediate morphological characteristics between the parent species, but F2 hybrids (backcrosses of F1 hybrids with pure strains) are more difficult to identify (Van Zee et al. 1996). Consequently, the removal of unidentifiable F2 hybrids may not be logistically feasible. Nevertheless, the removal of F1 hybrids and pure-strain walleye may decrease the rate of hybridization and aid in the conservation and preservation of native sauger in the middle Missouri River of Montana.

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APPENDIX A

RELOCATION DATA

Table 4. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, February 26 to April 25, 2004. Text within a cell indicates a tributary fish location (Jud=Judith River); rivermile location within the tributary is in parentheses.

		Date												
Species	Code	Feb 26	Apr 2	Apr 3	Apr 4	Apr 9	Apr 10	Apr 11	Apr 15	Apr 16	Apr 17	Apr 18	Apr 24	Apr 25
Sauger	02	2018.7		2015.9			2015.9			2015.9				
	06		2041.4						1937.8					1927.1
	10								1920.7			1920.7	1920.7	1923
	12								1919.9			1920		1953.4
	13													
	16													
	17								1963.1		1963.2			1962.5
	18	2074.8								2016.6				
	20													1959.7
	25								1960.4		1969.4			
	27								1965.7		1965.8			
	28								1915.3			1916.3		
	64													
Walleye	01													
	05	2016.8		2016.1			2016.1							
	07								1909.2					
	08							1984.3	Jud (4)					
	09	2077.8			2082.7	2084.4								
	15													
	22	2024.9	2030						1973.7		1969.9			1942.9
	24	2053												
	61													
	62													
	63													
	65													

Table 5. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, April 29 to June 3, 2004.

		Date												
Species	Code	Apr 29	May 1	May 2	May 3	May 10	May 13	May 14	May 18	May 19	May 27	May 30	Jun 1	Jun 3
Sauger	02								1982.1					2045
	06								1975.4					
	10									1927.1				
	12		1983.2									2030.5		
	13													
	16													
	17													
	18					2020.5					2061.4		2073.5	
	20							2011.5						2050
	25				2039.8								2075.2	
	27													2050
	28		2004.4		2016.6		2072.5						2077	
	64													
Walleye	01			2077.9			2080.7						2076.8	
	05				2015.9			2016.1						
	07		1996.7				2055.4						2078	
	08													
	09	2085		2085			2085							
	15													
	22							2002.3						
	24				2044.5									
	61													
	62													
	63													
	65													

Table 6. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, June 4 to July 8, 2004.

		Date											
Species	Code	Jun 4	Jun 11	Jun 14	Jun 16	Jun 17	Jun 18	Jun 24	Jun 25	Jul 2	Jul 3	Jul 4	Jul 8
Sauger	02					2050				2049.7			
	06	2025.3			2042.7								
	10	2017.7					2050			2049.6			
	12												
	13				2028				2028.1			2029.1	
	16				2031.3				2031.5			2031.6	
	17												
	18		2077.4					2077.4					2077.5
	20						2049.7			2050.1			
	25			2075.2				2075.3					2075.2
	27						2049.6			2049.7			
	28			2077				2077.1					2077
	64												
Walleye	01			2076.9				2076.8					2076.8
	05	2016.1											
	07			2078.9				2078.6					2078.8
	08												
	09												
	15										2054.3		
	22												
	24						2052.3			2052.4			
	61												2077.5
	62												
	63												2075.3
	65												

Table 7. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, July 17 to November 12, 2004.

		Date								
Species	Code	Jul 17	Jul 18	Jul 22	Jul 29	Jul 30	Aug 4	Aug 8	Aug 9	Nov 12
Sauger	02	2049.2			2049.8			2049.8		
	06	2051.6			2052			2050.8		
	10	2050.1			2049.5			2050		
	12									
	13		2029.2			2029.2			2029	
	16		2031.6			2031.4			2031	
	17									
	18			2077.5			2077.4			
	20	2050.2			2049.9			2049.9		
	25			2075.2			2075.1			
	27	2049.7	2049.7		2049.7			2049.7		
	28			2076.9			2076.8			
	64		2039.9			2039.7		2039.7		
Walleye	01			2076.7			2076.7			
	05									
	07			2078.8			2078.6			
	08		2032.4			2032.7			2033.3	
	09									
	15	2055.2			2055.1			2055		2055
	22									
	24	2052.8			2052.6			2052.8		
	61			2077.9			2079.6			
	62								2028	
	63			2075.3			2075.4			
	65			2070.4			2071.3			

Table 8. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, February 15 to April 22, 2005.

		Date											
Species	Code	Feb 15	Feb 17	Feb 27	Mar 2	Mar 5	Mar 25	Apr 5	Apr 7	Apr 12	Apr 18	Apr 21	Apr 22
Sauger	34	1967.7					1969.1			1970.2		1949.4	
	36	1995.9					1986.7			1986.7	1985		
	39	2007.5					2008.7			2010.8		2011.2	
	42	1961.9					1961.7			1962		1959.5	
	43												
	45	2016.8							1985	1962.5		1938.2	
	47		2050.6				2046.7						
	50		2036.6				2024			2024			
	51	1916.8					1932.9			1963		1962.4	
	56	1984		1985			1982.3			1978.3		1973	
	57	1937.5					1930.7			1943.6		1978.4	1985
	58	2010					2010.5			2016.6		2016.3	
	60	1918.3					1918.4			1916.1		1923.7	
Walleye	31		2070.4		2052	1985	1962.5			1977.2		1977.4	
	33												
	37									1941.8		1947.4	
	40		2045			2047							
	41	2018.6					2016.2	1985		1966.4		1944.4	
	44											1928.7	
	46	2017.5					2009.9			2003		2003.9	
	49	2018.1					2018.5						
	52	2017.9					2011.1			2012.7		1995.4	
	54		2043.7				2044.8						
	55									1935.9		1938.3	
	59												

Table 9. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, April 24 to May 13, 2005.

		Date											
Species	Code	Apr 24	May 1	May 4	May 5	May 6	May 7	May 8	May 9	May 10	May 11	May 12	May 13
Sauger	34				1964.9			1983					2021.8
	36				1943.3								
	39				2010.2				1983				
	42				1945.8								
	43												
	45				1950.4								
	47		2031		2006.9		1983						
	50				1984.7								
	51				1955.1								
	56				1946.2								
	57				2012.2				2031			2041.6	
	58				2016.4								
	60				1924.3								
Walleye	31	1983			2005.8				2031				
	33												
	37				1972		1983						
	40												
	41				1977.6	1983					2031	2038	
	44			1985	1990.9					2031			
	46				2003.3								
	49											2033	
	52				2031						2052		
	54												
	55			1983	1992.5			1985		1985			
	59												

Table 10. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, May 14 to May 27, 2005.

		Date											
Species	Code	May 14	May 15	May 17	May 18	May 19	May 20	May 21	May 22	May 23	May 25	May 26	May 27
Sauger	34	2031		2052									2080
	36				1929.5						1985		
	39												
	42				1960			1983			1985	2031	
	43												
	45				1938.8								
	47		1985		2003.7				2031		2052	2058.1	
	50		1985		2006		2031						2072.6
	51				1940								
	56				1949.9						1983	1985	
	57					2049.8							2064.5
	58				2016.5								
	60												
Walleye	31			2052									2070.3
	33				2014.2				1983	1985			
	37										2027.7		2031
	40												
	41		2052									2061.2	
	44		2052	2062.4									2073.3
	46				2002.6								
	49										2033.1		
	52												
	54											2046.5	
	55												
	59												

Table 11. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, May 28 to June 15, 2005. Text within a cell indicates a tributary fish location (Mar=Marias River); rivermile location within the tributary is in parentheses.

		Date											
Species	Code	May 28	May 29	May 30	May 31	Jun 1	Jun 5	Jun 6	Jun 7	Jun 8	Jun 9	Jun 14	Jun 15
Sauger	34										2080.2		
	36					2031	2052		Mar (0.4)	2052.2			Mar (0.5)
	39	1985					2031	2038.7					
	42										2073.3		
	43							2052					2048.6
	45											2023.3	
	47										2076.9		
	50												
	51	1985											2038.5
	56		2031		2052					2068.1			
	57								2066.8				
	58												
	60		1983									2033.4	
Walleye	31									2070.4			
	33			2031		2033.4						2033	
	37								2052.4	2052.2			2052.5
	40												
	41								2061.4				2061.6
	44										2074.5		
	46											2003.6	
	49					2033.1						2032.7	
	52									Mar (10)			
	54							2046.5					2046.5
	55												
	59			2033.6									

Table 12. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, June 16 to July 25, 2005. Text within a cell indicates a tributary fish location (Mar=Marias River); rivermile location within the tributary is in parentheses.

		Date											
Species	Code	Jun 16	Jun 17	Jun 27	Jun 28	Jun 29	Jul 6	Jul 7	Jul 8	Jul 19	Jul 20	Jul 24	Jul 25
Sauger	34		2080.1		2080				2080.1		2079.8		
	36					Mar (0.6)		Mar (0.9)		Mar (0.5)			Mar (0.8)
	39		2078		2077.9				2078.6		2078.7		
	42												
	43					2048.1		2048			2047.9		2048.1
	45			2032.7			2032.7			2032.7		2032.7	
	47	2077			2077.7				2076.9		2075.2		
	50												
	51					2054.6		2054.6			2054.5		2054.7
	56	2067.4			2067.4			2067.4		Mar. (0)			Mar. (0)
	57		2079.6		2079.6				2079.7		2079.7		
	58												
	60			2033.4			2033.3			2032.8		2032.8	
Walleye	31	2070.4			2070.3			2070.3			2070.3		
	33			2033.7			2033.8			2033.4		2033.4	
	37					2052.5		2052.5		2052.5			2052.3
	40												
	41												
	44	2073.4	2074.1		2073.2			2073.4			2073.2		
	46												
	49			2032.7			2032.7			2032.7		2032.7	
	52												
	54					2046.5	2046.6				2046.7		2046.7
	55												
	59			2065			2081.7					2081	

Table 13. Rivermile locations of sauger and walleye in the middle Missouri River, Montana, July 26 to October 8, 2005.

		Date											
Species	Code	Jul 26	Aug 20	Aug 30	Aug 31	Sep 1	Sep 6	Sep 9	Sep 21	Sep 28	Sep 30	Oct 6	Oct 8
Sauger	34	2079.8				2052							
	36												
	39	2078.6											
	42												
	43												
	45												
	47	2076.8			2052								
	50												
	51												
	56											2052	
	57	2079.7											
	58			2031									
	60												
Walleye	31	2070.3											
	33						2031			1920	1865		
	37			2052									
	40												
	41												
	44	2073.3							2031				
	46												2031
	49												
	52												
	54		2052					2052					
	55												
	59												