



Habitat selection of adult walleye (*Stizostedion vitreum*) in Holter Reservoir, Missouri River
by Keith Michael Binkley

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University
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Abstract:

Twenty five adult walleye, *Stizostedion vitreum*, were implanted with ultrasonic transmitters and tracked in Holter Reservoir during 1991 and 1992. The objectives of this research were to collect information on fish behavior and habitat use relevant to the management of walleye in this Missouri River impoundment. Fish with transmitters were located 848 times during the study. Walleye exhibited a distinct preference towards habitats found in the lower, northern portion of the reservoir where the range and diversity of depths were greatest and percent of littoral habitat was high. This preference was evident during all seasons of the year and appeared related to the presence of spawning habitat and areas where foraging opportunities are maximized. Home range size averaged about 6.5 km during the study and was consistent between years. Movement rates were greatest during spring and least during summer.

Habitat surveys indicate that the areas frequented by walleye were characterized by unique morphometric and substrate features favorable to feeding and spawning. Spawning habitat was spatially abundant within the reservoir, however utilization of specific spawning areas was noted and may be related to a combination of proximity to feeding areas, traditional use, or homing behavior. Substrate and shoreline characteristics were instrumental in establishing walleye feeding areas. Habitat use appeared to be strongly influenced by the presence of actively eroding shoreline habitats in the lower reservoir. Eroding shoreline areas of high clay content enhanced water turbidity, often resulting in the creation of optimal daytime foraging conditions for the light sensitive walleye. The depths utilized by walleye were highly variable both on a seasonal and diel basis. This variability is likely associated with a high degree of utilization of highly turbid, shallow areas of the reservoir. Habitat use in Holter Reservoir does not appear to be influenced by current reservoir operations.

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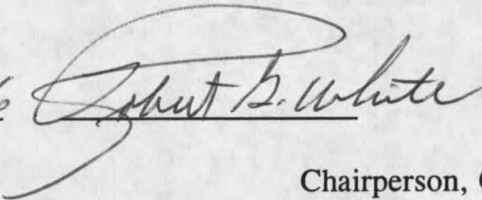
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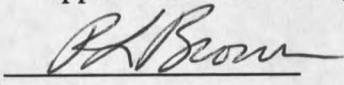
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ABSTRACT

Twenty five adult walleye, *Stizostedion vitreum*, were implanted with ultrasonic transmitters and tracked in Holter Reservoir during 1991 and 1992. The objectives of this research were to collect information on fish behavior and habitat use relevant to the management of walleye in this Missouri River impoundment. Fish with transmitters were located 848 times during the study. Walleye exhibited a distinct preference towards habitats found in the lower, northern portion of the reservoir where the range and diversity of depths were greatest and percent of littoral habitat was high. This preference was evident during all seasons of the year and appeared related to the presence of spawning habitat and areas where foraging opportunities are maximized. Home range size averaged about 6.5 km during the study and was consistent between years. Movement rates were greatest during spring and least during summer. Habitat surveys indicate that the areas frequented by walleye were characterized by unique morphometric and substrate features favorable to feeding and spawning. Spawning habitat was spatially abundant within the reservoir, however utilization of specific spawning areas was noted and may be related to a combination of proximity to feeding areas, traditional use, or homing behavior. Substrate and shoreline characteristics were instrumental in establishing walleye feeding areas. Habitat use appeared to be strongly influenced by the presence of actively eroding shoreline habitats in the lower reservoir. Eroding shoreline areas of high clay content enhanced water turbidity, often resulting in the creation of optimal daytime foraging conditions for the light sensitive walleye. The depths utilized by walleye were highly variable both on a seasonal and diel basis. This variability is likely associated with a high degree of utilization of highly turbid, shallow areas of the reservoir. Habitat use in Holter Reservoir does not appear to be influenced by current reservoir operations.

INTRODUCTION

The walleye (Stizostedion vitreum) is rapidly gaining increased popularity among anglers throughout North America and most recently in the northwestern United States (Conover 1986). The challenge inherent in walleye angling, the excellent eating quality, and the abundance of new opportunities and locations for catching walleye are responsible for this increase in popularity. With this upsurge in popularity, increased pressure has been placed upon resource agencies to provide opportunities for walleye anglers while still maintaining opportunities for the traditional angling interests. In many western states that have historically harbored prized salmonid fisheries, the management of walleye fisheries presents a unique challenge to biologists as the introduction of such an efficient top predator has been shown to significantly alter the composition of existing fish communities (Colby and Hunter 1989).

Walleye fishing in Montana has paralleled the trend in many western states as their establishment in many lakes and reservoirs has provided a new opportunity for anglers. The widespread stocking of walleye in Montana has been well received by many anglers and has simultaneously created concern among others. Walleye became established in Holter Reservoir as a result of an inadvertent introduction stemming from the intentional draining of an upstream impoundment, Lake Helena, during the early 1960's. Since the time of their introduction, the walleye population of Holter Reservoir has remained relatively stable at low density (MDFWP 1992).

Holter Dam is owned and operated by the Montana Power Company (MPC) as one

of a series of seven impoundments along the Missouri River in Montana. The current Federal Energy Regulatory Commission (FERC) license for these hydroelectric operations expired on November 30, 1994. As a requirement of the relicensing application, the MPC, in cooperation with the Montana Department of Fish, Wildlife, and Parks (MDFWP) initiated several studies to assess the status of the existing fisheries and to address environmental concerns related to project operations.

The MPC has historically operated Holter dam as run-of-the-river facility resulting in relatively constant and stable reservoir water levels. However, there have been occasional fluctuations in reservoir levels due to equipment maintenance requirements, short term load control, power peaking requirements, and upstream dam operations. My study focused on gaining increased knowledge of the life history requirements, habitat preferences, and general behavior of adult walleye in Holter Reservoir and to identify potential concerns related to the MPC's project operations.

The specific objectives of my study were:

1. Determine seasonal and diel patterns of habitat use by adult walleye.
2. Describe physical characteristics of habitat used by adult walleye.
3. Describe habitat preferences exhibited by adult walleye.
4. Describe the distribution and availability of preferred habitats within Holter Reservoir.

STUDY AREA

The Jefferson, Madison, and Gallatin rivers join near the town of Three Forks, Montana to form the Missouri River. The Missouri River remains essentially free-flowing to the town of Toston, where a small dam operated by the State of Montana exists. The Missouri River from Toston to Great Falls contains three major reservoirs; Canyon Ferry, Hauser, and Holter. Canyon Ferry Reservoir, the uppermost of the three, is the largest with a storage capacity of more than 2.4 billion m³ of water. The Bureau of Reclamation operates Canyon Ferry as a storage reservoir and regulates seasonal downstream flow releases for irrigation and flood control. My study was conducted in Holter Reservoir, the lowermost of the three major impoundments found along the upper Missouri River.

Holter Reservoir is located on the Missouri River in central Montana, near the town of Wolf Creek. Holter Dam was constructed in 1904 and presently impounds approximately 300,000,000 m³ of water at full pool (USGS 1992), with a surface area at full pool of approximately 1943 ha. Water depth averages about 15.2 m, with an approximate maximum depth of 38.1 m. Holter Reservoir is roughly 45.1 km in length and varies in width from 0.16 to 1.93 km. The shoreline development index value (a comparative figure relating shoreline length to the circumference of a circle with the same area as the body of water) for Holter Reservoir is relatively high at 2.9, attributable to the elongate shape of the reservoir.

The variability in widths and depths found along the length of Holter Reservoir

results in areas that substantially differ as physical habitat for fish species. The canyon portion of the reservoir, found within the Gates of the Mountain Recreation Area, does not vary substantially from pre-impoundment width, however water depth has increased significantly. In contrast to the canyon section, the lower portion of Holter Reservoir, immediately upstream of Holter Dam, exhibits morphometric features that are more characteristic of a typical lentic basin. These features include broad width, moderately sloping shoreline topography, high diversity in depths, and the presence of well developed littoral areas.

The topography of the Holter Reservoir shoreline is comprised predominantly of steep slopes (52%), followed by moderate (31%) and low (17%) gradient slopes (EA 1992). Substrate types found along the shoreline vary widely and include bedrock cliffs, talus slopes, grassy meadows, and areas of exposed soil. Shoreline substrate appears to influence walleye habitat selection within Holter Reservoir. Previous studies (EA 1992) have documented the use of rocky shoal / shoreline areas for spawning by walleye in Holter Reservoir. Exposed shoreline areas of highly erodible soils comprised of silts, sands, and clay within Holter Reservoir were quantified during a soil resource investigation (Stensatter et al. 1991) conducted for the MPC. Turbid conditions are frequently observed in the waters associated with and immediately proximate to these shoreline areas. Wind speed and direction, wave action, bank topography and soil composition are important in determining the vertical and horizontal extent of these turbid areas.

Flow patterns within Holter Reservoir are influenced by the upstream operations of

Hauser Reservoir, and to a greater extent, Canyon Ferry Reservoir. Mean annual discharge at the United States Geological Survey (USGS) gauge (#06066500) below Holter Dam for the period of record is 4.9 billion m³ per year (USGS 1991). The retention (residence) time of the water within Holter Reservoir is relatively short, averaging 21.8 d for the period of record (USGS 1991). During my study, retention times averaged 32.3 and 27.6 d for USGS Water Years 1990 and 1991, respectively. This short retention time strongly influences the thermal regime and overall productivity of Holter Reservoir.

The thermal characteristics of Holter Reservoir are typical of an impoundment with relatively rapid flow through (short retention time). The reservoir typically becomes free of ice during the month of March (February to late March) and consistently warms to a summer maximum temperature that rarely exceeds 22 °C (MDFWP, unpublished data). Furthermore, Holter Reservoir thermally stratifies for a relatively short period, contrasted to other lentic systems, which is again attributable to short retention times.

My study area encompassed the 37.1 km impounded portion of Holter Reservoir extending between 8.0 to 45.1 km downstream of the Hauser Dam. For my study, Holter Reservoir was divided into six zones characterizing the broad availability of physical habitat types present within the reservoir (Figure 1). These included:

- Zone A: Upper Holter (extending between 8.0 and 11.3 km downstream of Hauser Dam)
- Zone B: Gates of the Mountain (extending between 11.3 and 19.3 km downstream of Hauser Dam)

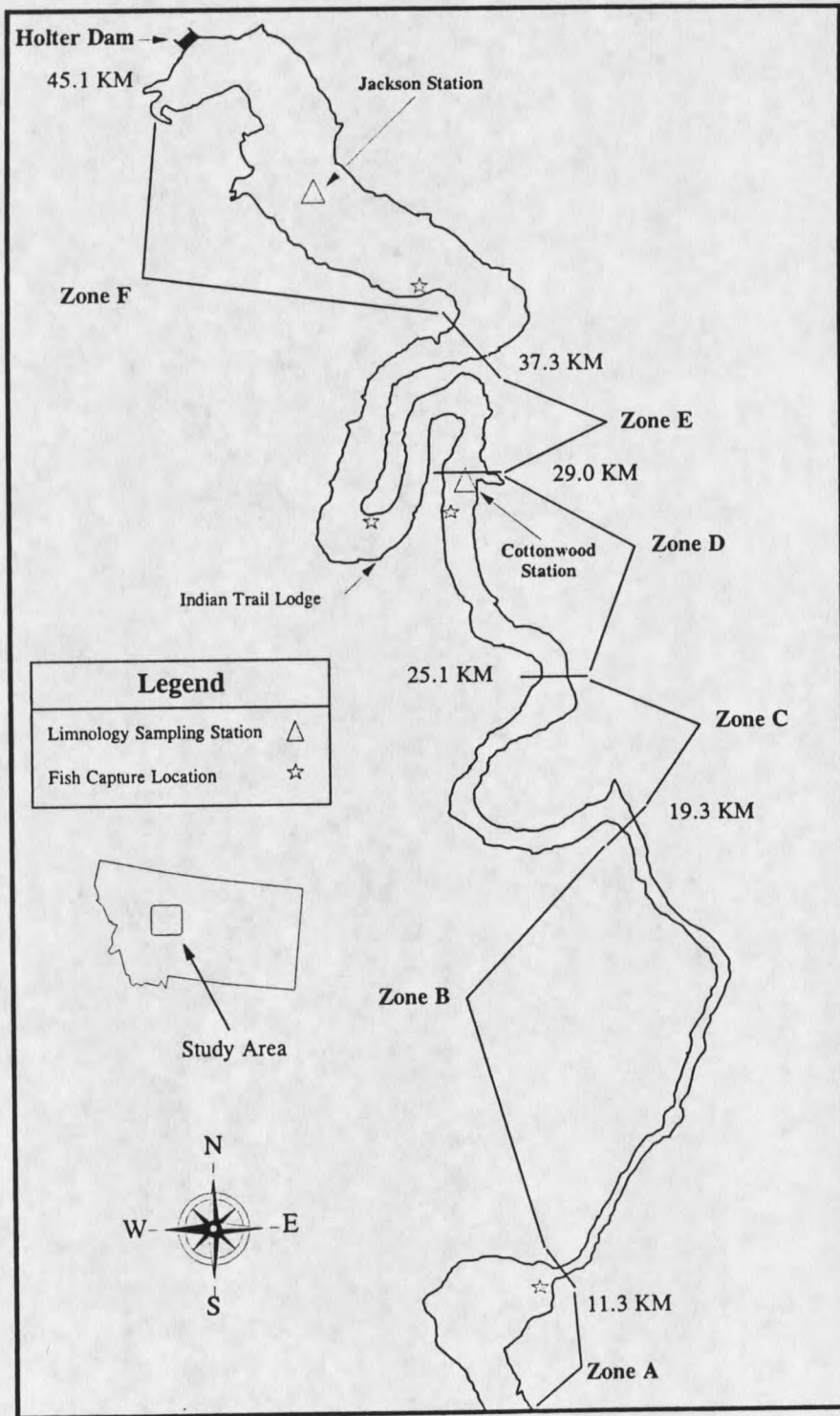


Figure 1. Study area, zones, capture locations, and limnological sampling stations within Holter Reservoir (distances are kilometers below Hauser Dam).

- Zone C: Ming Bar (extending between 19.3 and 25.1 km downstream of Hauser Dam)
- Zone D: Hack Rock to Cottonwood Creek (extending between 25.1 and 29.0 km downstream of Hauser Dam)
- Zone E: Oxbow Bend (extending between 29.0 and 37.3 km downstream of Hauser Dam)
- Zone F: Lower Holter (extending between 37.3 and 45.1 km downstream of Hauser Dam)

The reservoir was further subdivided into 0.25 ha plots for microhabitat quantification. Universal Traverse Mercator (UTM) coordinates were used to establish a grid dividing the reservoir into approximately 7700 individual plots. This grid pattern facilitated both habitat quantification and the analysis of fish movement and habitat utilization.

METHODS AND MATERIALS

Physical Habitat Quantification

The quantification of the physical habitat within Holter Reservoir consisted of three components: 1) the characterization of depth and general reservoir bathymetry, 2) the quantification of substrate characteristics, and 3) the classification of shoreline soil types.

Depth data were systematically collected throughout the reservoir in summer 1991. A total of 317 transects were established at 200 m intervals along the length of the reservoir to collect depth data. Depth data were collected at full reservoir pool (1090 m above mean sea level) at approximately 20 m spacing intervals along each transect line. A global positioning system (GPS) receiver was used to track boat position with respect to UTM coordinates. Depth measurements were collected with an electronic echo-sounding depth meter. Depth data and the corresponding UTM coordinates were integrated into a Lotus spreadsheet for bathymetric analysis. Depth and position information were compiled at 6,847 individual points within the reservoir study area. The composition of depths measured along transects was used to compute the amount of depth-dependent habitats (i.e. littoral, sub-littoral, and profundal habitat) present in each zone. Littoral habitat was defined as that less than 4 m in depth. Sub-littoral habitat was defined as that in the range from 4 to 14 m in depth and profundal habitat was greater than 14 m in depth. Diversity of depths was determined for each zone by calculating the portion of measurements in a each specific depth increment,

multiplying the portion by the log of the portion, summing the products for all portions in each zone, and multiplying by -1. Between-zone comparisons of the amount of habitat at specific depths and diversity in depths were made.

Substrate quantification was conducted using both surface and subsurface ocular methods. Surface visual methods included the classification of dominant substrates present along the reservoir periphery. Substrate type and size data were visually estimated during clear water conditions from a boat traveling along the shoreline of the reservoir periphery. Substrate type was classified as firm (consolidated or unconsolidated) or soft. Unconsolidated firm substrates were categorized in four size gradations including: coarse gravel (2.5 to 7.5 cm), cobble (7.5 to 12.5 cm), rubble (12.5 to 20.0 cm), and boulder (> 20.0 cm). Substrate quantification using this procedure was generally limited to water depths of less than 3.0 m. Additional data regarding shoreline substrate type were collected by MPC personnel on September 16, 1993 during a 1 m reservoir drawdown.

Subsurface quantification was conducted at representative locations within the study area where large concentrations of walleye were observed. Subsurface quantification was conducted with the assistance of MPC personnel using self contained underwater breathing apparatus (SCUBA). A total of 24 h (12 h, 2 divers) were expended on this task resulting in an estimated 15,000 m² of substrate being quantified. Substrate type and size were classified following the procedure utilized in the surface visual estimation.

Soil types were classified at locations along the reservoir shoreline as part of a

shoreline bank erosion assessment for Holter Reservoir prepared for the MPC by the consulting firm of Stensatter, Druyvestein and Associates (Stensatter et al. 1991). Soil type, soil characteristics, bank slope, and an assessment of the susceptibility of banks to future erosion were compiled as part of this effort (Appendix A).

Quantification of Temporal Habitat Changes

Water quality and general climatic data were gathered to describe temporal changes and patterns in habitat quality. Data were collected between the months of March and November at representative shoreline and open water locations throughout the reservoir.

Open water subsurface temperature profiles were collected on a monthly basis by MDFWP personnel at the two limnological sampling stations within the reservoir during the study period (Figure 1). Shoreline water temperatures were collected on a hourly basis during the ice-free months of the year using Ryan Tempmentor thermographs positioned at two locations within the lower reservoir in proximity to the established limnological stations. Hourly temperature readings were averaged for both stations for each day to produce mean daily temperatures values. Open water and shoreline temperature data were collected within the same general reservoir location (within 1 km).

Light transmission data were collected via Secchi disk and photometer. Data were gathered at limnological stations to assess temporal changes in light transmission and at other locations to coarsely quantify spatial variability in light transmission within the reservoir. General climatic data were recorded in conjunction with each sonic tracking

episode. In addition, local meteorological data were obtained from the town of Cascade, MT, located 38 km north of Holter Dam.

Determination of Habitat Selection and Behavioral Patterns

Information on habitat selection and patterns in habitat use were obtained by monitoring the movements and locations of 25 adult walleye over a 2-year period using ultrasonic telemetry equipment (Sonotronics Inc. of Tucson, Arizona).

Transmitter tags were cylindrical in shape with a diameter of 18 mm and length of 100 mm. Each tag weighed approximately 13 g, ranging from 0.6 to 1.3% of fish body weight, and had a life expectancy of approximately 2 years. The transmitters operated on one of four radio frequencies; 69 KHz, 74 KHz, 76 KHz, and 78 KHz to allow differentiation between signals. Each transmitter emitted a unique aural pulse code (i.e. 2 beeps, rest, 2 beeps, rest, 4 beeps, rest, 8 beeps, rest, repeat) which refined signal separation and permitted the identification of individual fish. Tagged fish were detected using a handheld Sonotronics DH-2 directional hydrophone mounted on a 2 m section PVC pipe. A Sonotronics USR-4B receiver was used to translate the signal into an audible sound.

Fish Collection / Tagging Procedure

Adult walleye were captured at four locations within the reservoir (Figure 1) by electrofishing, gill netting and angling during the spring of 1991. Capture locations were selected to represent potential spatial variation in the behavioral characteristics of the walleye population. Most sonic tagged fish were between 457 and 610 mm total length, since angling regulations prohibited the harvest of fish in this size range.

Upon capture, each fish was transported to a nearby processing location where transmitters were implanted. Each fish was initially sexed based upon external features (body girth, presence of milt). Spawning condition was noted on each fish prior to surgery. Fish that were in advanced spawning condition were not used due to concerns about increased physiological stress. Total length and weight were measured and a dorsal spine was collected from each fish (Table 1).

Each fish was anesthetized with MS-222 and placed in a surgical trough with the ventral side oriented upwards. Prior to surgery, scales were removed from the incision area. A 5 cm incision was made into the ventral body cavity immediately lateral and parallel to the midline of the body. Each transmitter was cleaned with alcohol, and dried prior to the insertion into the body cavity. After insertion, the incision was stitched with nylon sutures and swabbed with Betadine antiseptic. Care was taken to assure that the gills of the fish remained irrigated with water throughout the surgical process to minimize stress. The surgical operation took approximately 8 minutes to complete. Finally, an external Carlin dangler tag was attached posterior to the dorsal fin of each fish identifying its importance as a research subject. Once the fish regained total equilibrium and normal movement, it was released at the capture location.

Data Collection

During the spring of 1991, weekly tracking episodes were conducted by selecting random 7 h time blocks (0700-1400, 1400-2100, and 2100-0400). Bi-weekly tracking was attempted during ice-free months for the remainder of the 2-year study period. In conjunction with the random sampling effort, seven 24 h observation periods were

Table 1. Ultrasonic tag information and biological characteristics of adult walleye studied within Holter Reservoir during 1991 and 1992 (Zone A - Upper Holter, Zone B - Gates of the Mountain to Willow Creek, Zone C - Willow Creek to Hacking Box Rock, Zone D - Hacking Box Rock to Cottonwood Creek, Zone E - Cottonwood Creek to Split Rock, Zone F - Split Rock to Holter Dam).

Zone	Fish number	Radio frequency	Pulse code	Age (years)	Sex	Total length (mm)	Weight (gms)	Date implanted
A	1	69 KHZ	258		Female	585	2180	3/9/91
A	2	69 KHZ	249		Female	618	2770	3/9/91
A	3	76 KHZ	465	5	Male	551	1840	3/17/91
A	4	76 KHZ	88	5	Female	589	2220	3/19/91
A	5	74 KHZ	384	5	Female	606	2410	3/1/92
A	6	78 KHZ	2246	9	Male	585	1775	3/1/92
D	1	78 KHZ	2327		Male	552	1730	5/2/91
D	2	78 KHZ	2264	9	Male	610	2160	5/8/91
D	3	69 KHZ	276	6	Male	592	2130	5/8/91
D	4	78 KHZ	2237	8	Male	630	2470	5/8/91
E	1	74 KHZ	375	5	Female	562	2120	3/22/91
E	2	76 KHZ	555	5	Male	531	1600	3/22/91
E	3	69 KHZ	285	6	Female	603	2620	3/22/91
E	4	76 KHZ	456	5	Female	561	2050	3/23/91
E	5	74 KHZ	348	6	Female	600	2450	3/30/91
E	6	69 KHZ	294	16	Female	793	5613	3/30/91
E	7	76 KHZ	97	7	Male	623	2340	5/1/91
F	1	74 KHZ	447	6	Female	590	2350	3/30/91
F	2	69 KHZ	267	6	Male	526	1510	3/30/91
F	3	74 KHZ	339	5	Female	563	2150	3/30/91
F	4	74 KHZ	357	7	Female	603	2420	3/30/91
F	5	78 KHZ	2255	7	Male	580	2220	4/13/91
F	6	74 KHZ	366	7	Female	651	3289	4/23/91
F	7	76 KHZ	2228	7	Male	600	2060	4/23/91
F	8	78 KHZ	2273	6	Male	590	2180	5/9/91

integrated into the sampling program to assess short term movement patterns. When possible, the entire reservoir was traversed during each tracking period.

The presence or absence of a tagged fish was initially determined following a systematic procedure where signals were received at fixed "listening" stations spaced 0.8 km apart from the upper end of Zone A to the lower end of Zone F. When a signal was first received, the approximate location was determined by following the strongest signal. The exact location of the fish was defined via repeated triangulation to the audible signals. Once a tagged walleye was located, the location was plotted on an enlarged United States Geological Survey map of the reservoir with a scale of 1:24,000. Date, time, and distance to shore were also recorded. Water depth was recorded during a subsequent tracking period since boat activity in the immediate vicinity of the tagged fish appeared to influence fish behavior. Adjustment of water depths was not necessary as reservoir elevations remained consistent throughout the study period.

Statistical Analysis

Descriptive statistics were calculated for each habitat variable where tagged adult walleye were located within Holter Reservoir. Descriptive statistics for habitat variables included the mean, minimum, maximum, standard deviation, and upper and lower confidence intervals. Results of Kolmogorov-Smirnov tests for normality on habitat data (including reservoir location, and depth) indicated that distributions were not normal. Consequently, I employed the nonparametric Mann-Whitney Rank Sum Test and the Kruskal-Wallis One Way Analysis of Variance on Ranks to determine if

median values of habitat variables were significantly different between observation time (day vs. night), seasons, years, and sexes.

RESULTS

Physical Habitat Quantification

The creation of a bathymetric map of Holter Reservoir was not possible from the data collected during the survey due to the poor accuracy (± 100 m) of the GPS receiver. However, 6,847 depth measurements were systematically collected throughout the reservoir. Depths ranging to 36 m were recorded during the survey. Marked differences in depth composition were found between zones due to the dominant geomorphic features of the reservoir basin. Zone A, upper Holter Reservoir, was comprised mostly of relatively shallow waters (< 6 m) and had a depth diversity of 0.50, the lowest of all zones (Table 2). The diversity of depths in Zone B was 0.71 with depths generally less than 8 m, ranging to 12 m. Zones C and D were similar in composition and diversity of depths (Table 2). Zone E exhibited a high diversity of 1.16 with depths to 32 m (Table 2). Zone F (lower Holter Reservoir) also exhibited a high depth diversity of 1.21, with depths ranging up to 36 m (Table 2). A distinct longitudinal, down-reservoir trend of increased depths and increased diversity in depths was evident (Table 2).

Littoral habitats (< 4 m) were more abundant in Zone A than in other zones (Table 3). The abundance of littoral habitat in Zone F was second to Zone A (Table 3). Zones B and E were similar in amount of littoral and sub-littoral habitat, however Zone E had substantially more profundal habitat (> 14 m)(Table 3). Zones C and D were similar in amount, composition, and diversity of depths (Table 3).

Table 2. Cumulative percentage of habitat found at 2 m water depth intervals within study zones of Holter Reservoir (Zone A - Upper Holter, Zone B - Gates of the Mountain to Willow Creek, Zone C - Willow Creek to Hacking Box Rock, Zone D - Hacking Box Rock to Cottonwood Creek, Zone E - Cottonwood Creek to Split Rock, Zone F - Split Rock to Holter Dam).

Depth (m)		Zone A	Zone B	Zone C	Zone D	Zone E	Zone F	All Zones
0	Littoral	10.9	9.0	20.2	20.6	5.1	8.1	11.0
2	Littoral	68.3	26.5	33.8	34.3	13.1	18.7	23.5
4	Littoral	86.1	37.0	40.7	39.8	19.3	23.8	29.8
6	Sub-Littoral	100.0	72.0	49.0	46.3	27.5	31.3	37.7
8	Sub-Littoral		94.7	54.5	50.2	34.0	36.7	43.0
10	Sub-Littoral		99.5	60.3	55.1	40.4	41.7	48.4
12	Sub-Littoral		100.0	69.8	60.4	48.2	48.9	55.6
14	Profundal			83.7	64.9	54.1	54.4	62.2
16	Profundal			93.3	73.5	59.6	57.6	68.0
18	Profundal			96.2	83.8	64.4	63.0	73.4
20	Profundal			99.2	91.4	74.3	66.3	79.3
22	Profundal			100.0	99.9	82.0	69.0	84.1
24	Profundal				100.0	93.4	75.9	90.0
26	Profundal					96.6	82.1	93.1
28	Profundal					98.8	89.7	96.4
30	Profundal					99.6	96.5	98.8
32	Profundal					100.0	99.2	99.7
34	Profundal						99.9	100.0
36	Profundal						100.0	100.0
Depth Diversity		0.50	0.71	0.99	1.03	1.16	1.21	1.19

Table 3. Total surface area (ha) of habitat found at or above specific water depths (2 m intervals) within study zones of Holter Reservoir, 1991-1992 (Zone A - Upper Holter, Zone B - Gates of the Mountain to Willow Creek, Zone C - Willow Creek to Hacking Box Rock, Zone D - Hacking Box Rock to Cottonwood Creek, Zone E - Cottonwood Creek to Split Rock, Zone F - Split Rock to Holter Dam).

Depth (m)		Zone A	Zone B	Zone C	Zone D	Zone E	Zone F	All Zones
0	Littoral	30	11	38	37	18	67	214
2	Littoral	188	32	63	61	46	155	457
4	Littoral	238	45	76	71	67	197	578
6	Sub-Littoral	276	88	92	83	96	260	732
8	Sub-Littoral		116	102	90	118	305	835
10	Sub-Littoral		121	113	99	140	346	939
12	Sub-Littoral		122	130	108	168	406	1081
14	Profundal			157	116	188	452	1209
16	Profundal			174	132	207	478	1322
18	Profundal			180	150	224	523	1427
20	Profundal			185	164	258	551	1541
22	Profundal			187	179	285	573	1633
24	Profundal				179	325	630	1748
26	Profundal					336	681	1808
28	Profundal					344	744	1873
30	Profundal					347	801	1920
32	Profundal						823	1938
34	Profundal						829	1942
36	Profundal						830	1943
38	Profundal							
40	Profundal							

Shoreline Substrate

The shoreline of Holter Reservoir is comprised of a mixture of soft (fine grained) and firm (coarse grained / rock) substrates. The reservoir shoreline is dominated by firm substrates (85.2%) including bedrock, boulder, and fractured materials (Table 4). Large (boulder) and consolidated (bedrock) substrates were commonly present along the reservoir periphery, accounting for 78.2% of the total shoreline length (Table 4). Unconsolidated (fractured talus, rubbles, cobbles) substrate types were present intermittently along the reservoir shoreline, accounting for 7.0% of the total shoreline length (Table 4). Soft substrates (sands, silts, and clays) were present intermittently along the reservoir, comprising 14.8% of the total reservoir shoreline (Table 4).

Distinct between-zone differences in shoreline substrate composition were evident. The percent of zone shoreline comprised of unconsolidated firm substrates ranged from 1.9% in Zone A to 9.8% in Zone E (Table 4). Unconsolidated substrates were substantially more abundant in the lower reservoir (Zones D, E, and F) than in the upper reservoir (Zone A, B, and C). The percent of zone shoreline comprised of soft substrates (silt, clay, sand) ranged from 0% in Zone B to 37.6% in Zone F (Table 4). Soft substrates were most abundant in Zones D and F accounting for 23.4 and 37.6% of the zone shoreline, respectively (Table 4). Soft substrates were least abundant in Zones B and C comprising less than 1.6% of the shoreline (Table 4).

Table 4. Quantification of shoreline substrate in Holter Reservoir.

	Zone A	Zone B	Zone C	Zone D	Zone E	Zone F	All
Shoreline length (m)	6,562	18,956	12,029	9,113	18,591	20,049	85,300
Firm - consolidated (m)	5,453	18,256	11,232	6,152	15,044	10,584	66,721
Firm - consolidated (%)	83.1	96.3	93.4	67.5	80.9	52.8	78.2
Firm - uncons. (m)	125	700	600	825	1,825	1,925	6,000
Firm - uncons. (%)	1.9	3.7	5.0	9.1	9.8	9.6	7.0
Soft - silt, clay, sand (m)	984	0	197	2,136	1,722	7,540	12,579
Soft - silt, clay, sand (%)	15.0	0	1.6	23.4	9.3	37.6	14.7

Shoreline substrate quantification provided an efficient means of assessing the overall composition and distribution of specific substrate types. While this visual quantification technique was depth limited, it was assumed that shoreline substrate composition was representative of the general composition to depths of 12 m. SCUBA diving confirmed that substrate found along the shoreline were representative of the general substrate composition at greater depths. Diving confirmed that fractured talus slopes that angled into the water at about 45° extended to depths of at least 18 m.

Quantification of Potential Spawning Areas

Potential spawning areas were identified and mapped during the quantification of shoreline substrates. Shoreline areas that met specific depth (< 3 m) and substrate (firm, unconsolidated) criteria (Colby et al. 1979) were classified as suitable walleye spawning areas. Sixty-one potential walleye spawning areas were identified (Table 5).

Table 5. Location and physical characteristics of potential spawning sites within Holter Reservoir.

Zone designation	Site location		Site length (m)	Mean particle size (cm)
	UTM Coordinates			
A		5,186,350 427,150	25	9
A		5,185,350 427,350	25	6
A		5,186,100 428,600	25	9
A		5,186,600 428,500	25	9
A	+	5,186,750 428,000	25	6
B		5,192,500 430,000	50	10
B		5,191,850 430,400	100	9
B	+	5,192,400 430,200	50	10
B		5,193,000 430,000	150	9
B		5,187,300 429,500	200	9
B		5,188,700 430,500	25	9
B		5,189,250 430,850	25	10
B		5,189,700 430,800	25	8
B		5,191,350 431,000	25	8
B		5,189,700 430,650	25	9
B		5,189,250 430,600	25	9
B		5,186,550 428,800	25	6
C		5,194,750 428,333	150	9
C		5,192,850 429,300	50	10
C		5,192,900 428,250	200	9
C		5,193,250 427,650	200	8
C		5,194,000 428,000	25	9
D	+	5,198,350 427,350	400	11
D		5,197,600 427,250	150	5
D		5,196,450 427,450	100	9
D		5,195,300 428,700	100	9
D		5,195,850 428,400	100	9
D	+	5,196,200 428,000	25	6

* denotes areas of isolated or intermittent patches of spawning gravel
+ denotes prime area for spawning or documented spawning area

Table 5. Continued.

Zone designation		Site location UTM Coordinates		Site length (m)	Mean particle size (cm)
E		5,200,100	427,100	50	8
E	+	5,197,650	425,600	250	6
E		5,196,850	425,800	150	8
E	+	5,197,000	426,500	300	5
E		5,197,600	426,850	25	6
E	+	5,197,750	426,900	75	9
E	+	5,198,000	427,000	200	9
E		5,198,600	427,450	150	9
E		5,198,500	427,450	50	9
E		5,198,950	427,900	150	9
E		5,199,450	427,300	100	10
E		5,199,200	426,800	25	9
E	+	5,198,250	426,700	100	6
E		5,198,000	426,250	300	9
E		5,198,500	426,450	25	9
F		5,201,000	428,000	50	13
F		5,201,000	428,000	100	13
F		5,201,250	427,750	75	9
F		5,201,666	427,333	150	9
F	+	5,201,800	427,000	75	6
F	+	5,201,800	427,000	50	6
F	+	5,202,000	426,700	50	5
F		5,202,500	425,800	25	9
F		5,203,200	425,600	100	9
F	+	5,204,500	424,150	200	8
F		5,204,333	423,500	100	13
F	+	5,203,500	424,500	300	9
F		5,203,200	424,500	75	8
F		5,201,900	424,750	75	15
F	+	5,201,500	425,200	200	8
F	+	5,201,250	425,600	200	8
F		5,200,800	426,350	75	9
F		5,200,100	427,200	100	9
Total Length of Potential Spawning Areas				6300	
* denotes areas of isolated or intermittent patches of spawning gravel					
+ denotes prime area for spawning or documented spawning area					

Sixteen (26.1%) of the areas were classified as patchy (isolated or intermittent patches of spawning gravel) and thus considered to have marginal potential as spawning habitat. Of the remaining 45 areas with good potential for spawning use, 29 (64%) were greater than 100 m in length and 16 (36%) were less than 100 m in length. The areas greater than 100 m in length collectively comprised 5000 m of spawning habitat accounting for 84.7% of the total potential spawning habitat identified.

Potential spawning habitat was present throughout the study area but variable between zones. Areas in Zone A that exhibited characteristics suitable for spawning were present along 125 m of shoreline accounting for 2.1% of the total reservoir spawning habitat. In Zone B, 700 m of shoreline exhibited characteristics suitable for spawning accounting for 11.7% of the total reservoir spawning habitat. Zone C had 600 m of potential spawning habitat accounting for 10.0% of the total reservoir spawning habitat. Approximately 825 m of spawning habitat were identified in Zone D accounting for 13.8% of the total reservoir spawning habitat. Zone E accounted for 1,825 m (30.4%) of the reservoir spawning habitat. The amount of potential spawning habitat in Zone F was 1,925 m accounting for 32.1% of the reservoir total. Zones D, E, and F combined contained 4575 m (76.3%) of the potential spawning habitat present in Holter Reservoir. Twenty-six of the 29 (89.7%) areas > 100 m were uniformly scattered in the lower 25.4 km portion of the study area (Zones C, D, E, and F).

Classification of Shoreline Soil Types

In 1991, a soil resource investigation was conducted (Stensatter et al. 1991) to document, quantify, and describe the properties and condition of the soils found along

the shoreline of Holter Reservoir. Stensatter et al. (1991) reported minor, moderate, and active shore erosion occurring in certain areas of the reservoir. Of the 60 erosion sites evaluated by field investigation (Stensatter et al. 1991), 14 were considered to be in an active erosion condition (Figure 2). The remaining sites were either in a minor or moderate activity condition classification. The 13 active erosion sites identified in the 1991 survey plus 1 additional site, not previously identified (Figure 2) collectively comprise 12.6 km (14.8%) of shoreline within the study area (Appendix A). These sites vary in length from 30 to 3,465 m (Appendix A). Eleven of these sites, comprising 11.3 of the 12.6 (89.7%) km of eroding shoreline, are found in the lower portion of the reservoir near or down reservoir of RKM 29.0 (Appendix A).

Quantification of Temporal Habitat Changes

Temperature, light intensity and climatic factors work in concert with physical characteristics (depth, substrate) to determine the quantity and quality of walleye habitat in Holter Reservoir. During my study, the ice cover thawed during March in 1991 and February in 1992. Seasonal temperature patterns were generally similar for 1991 and 1992.

During the spring surface water temperature rapidly warmed after disappearance of ice cover. Mean daily water temperatures in spring 1992 were 2 to 3 °C warmer than those measured at similar times during 1991 (Figure 3). Mild winter conditions and warm weather during February of 1992 resulted in the early thawing of reservoir ice-cover. The temperature differential between years decreased to about 1.5°C as summer approached. Mean daily surface water temperatures were approximately

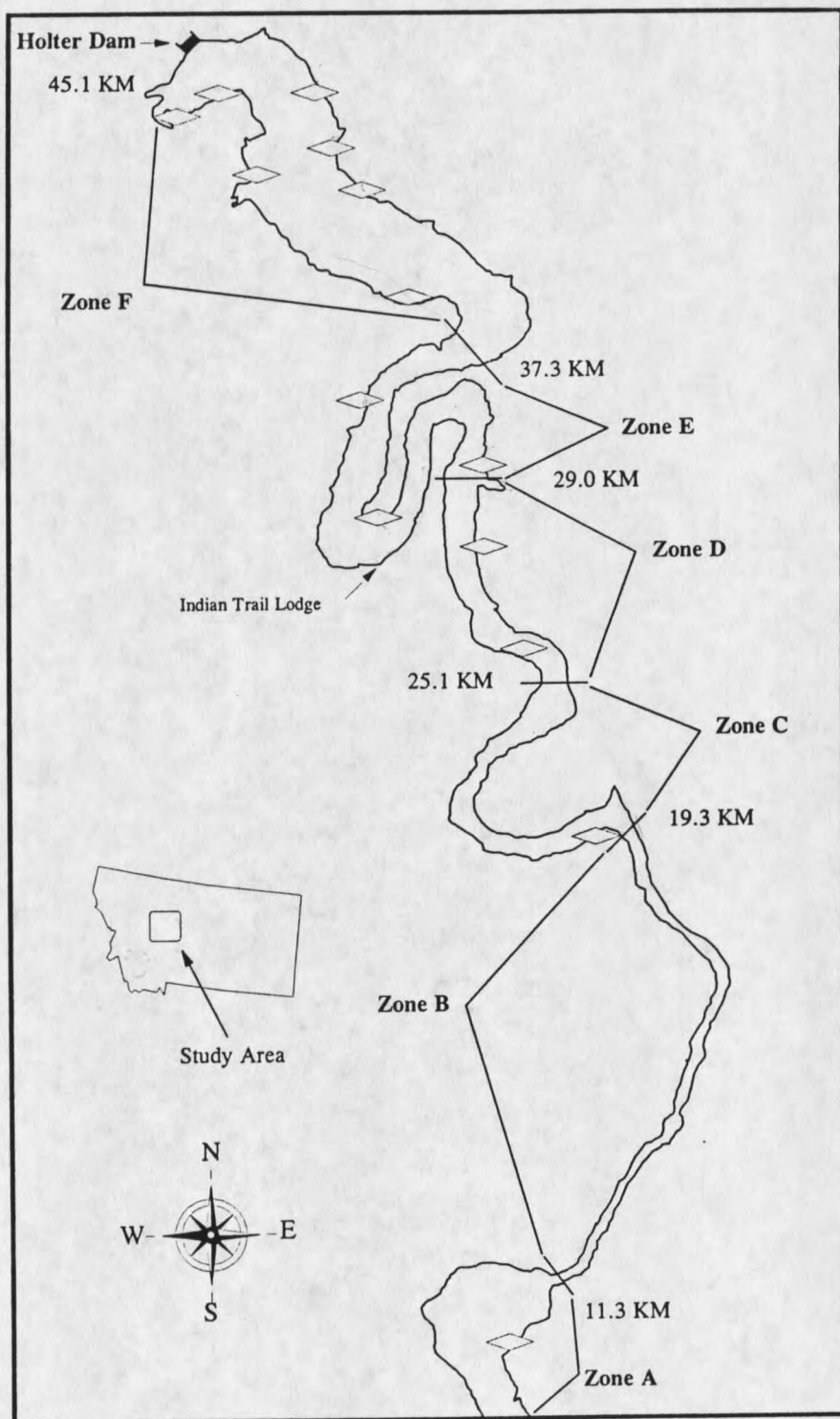


Figure 2. Location of Active Erosion Condition sites identified along the shoreline of Holter Reservoir (see Appendix A).

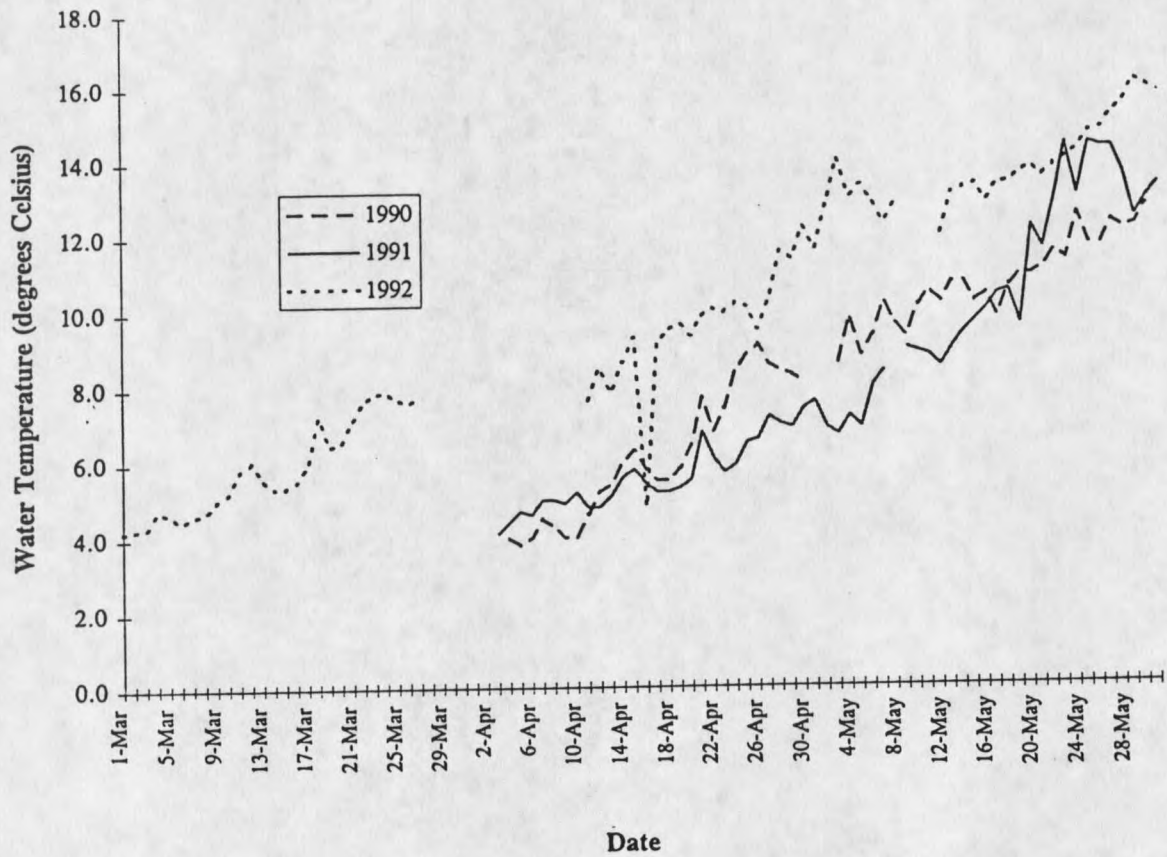


Figure 3. Mean daily water temperatures of Holter Reservoir during spring 1990, 1991, and 1992.

20°C by late June and remained fairly consistent at that level through mid to late August (Figure 4). Mean daily water temperatures during the fall appeared to drop at a consistent rate during both years of the study (Figure 5).

Monthly temperature profiles collected at the Montana Department of Fish, Wildlife, and Parks limnology sampling stations (Figure 1) were used to assess the vertical variation in water temperatures. Stratification was most pronounced during the months of July and August at both the Jackson and Cottonwood stations (Appendix B). Temperature profiles at the Cottonwood station exhibited weak signs of stratification with a surface to bottom differential not greater than 5.2 °C and bottom temperatures of 14.2 to 16.1° C (Appendix B). In contrast, temperature profiles collected at the Jackson station displayed evidence of pronounced thermal stratification during the summer months with a surface to bottom differential as great as 14.2°C and bottom temperatures of 7.5 to 7.8° C (Appendix B). A thermocline developed at the Jackson station at approximately 18.3 m of depth. These differences in thermal profile are probably related to marked differences in localized retention times and associated current velocities between the two sampling locations, as a result of differences in general basin morphometry.

Light Availability/Intensity

Secchi disk (S.D.) and photometer readings indicated a high degree of temporal and spatial variability in the extent of light penetration (water transparency) within the reservoir attributable to seasonal changes in reservoir productivity, retention time, and shoreline erosion. Secchi readings taken monthly at MDFWP Limnology Sampling

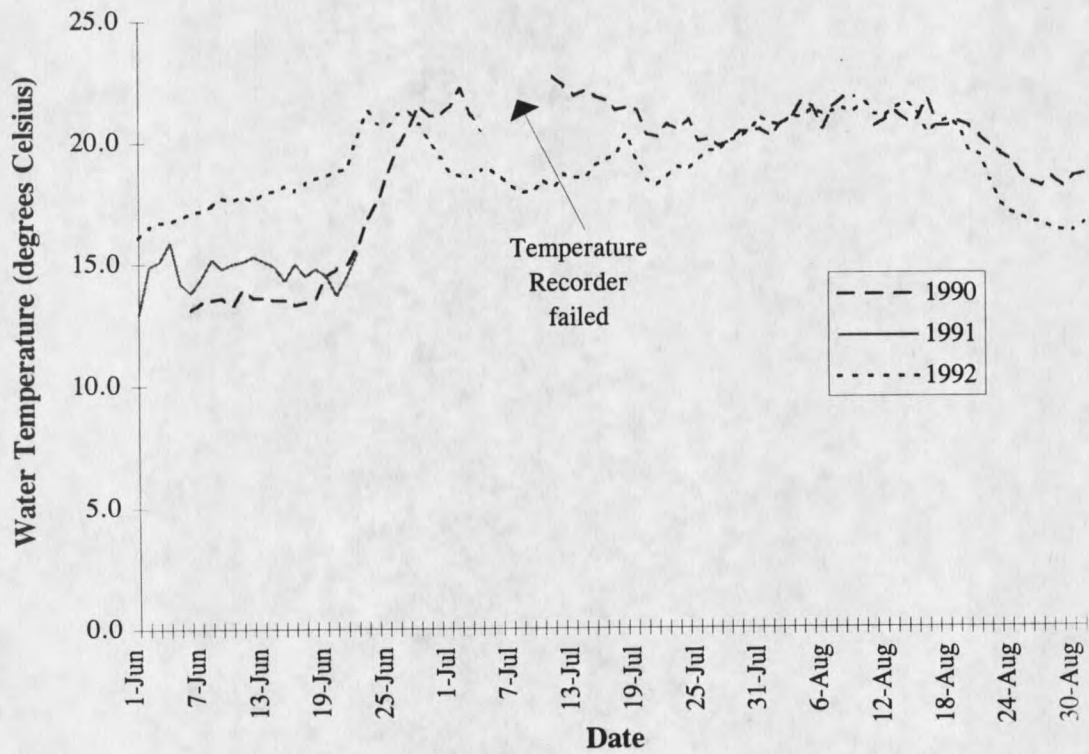


Figure 4. Mean daily water temperatures of Holter Reservoir during summer 1990, 1991, and 1992.

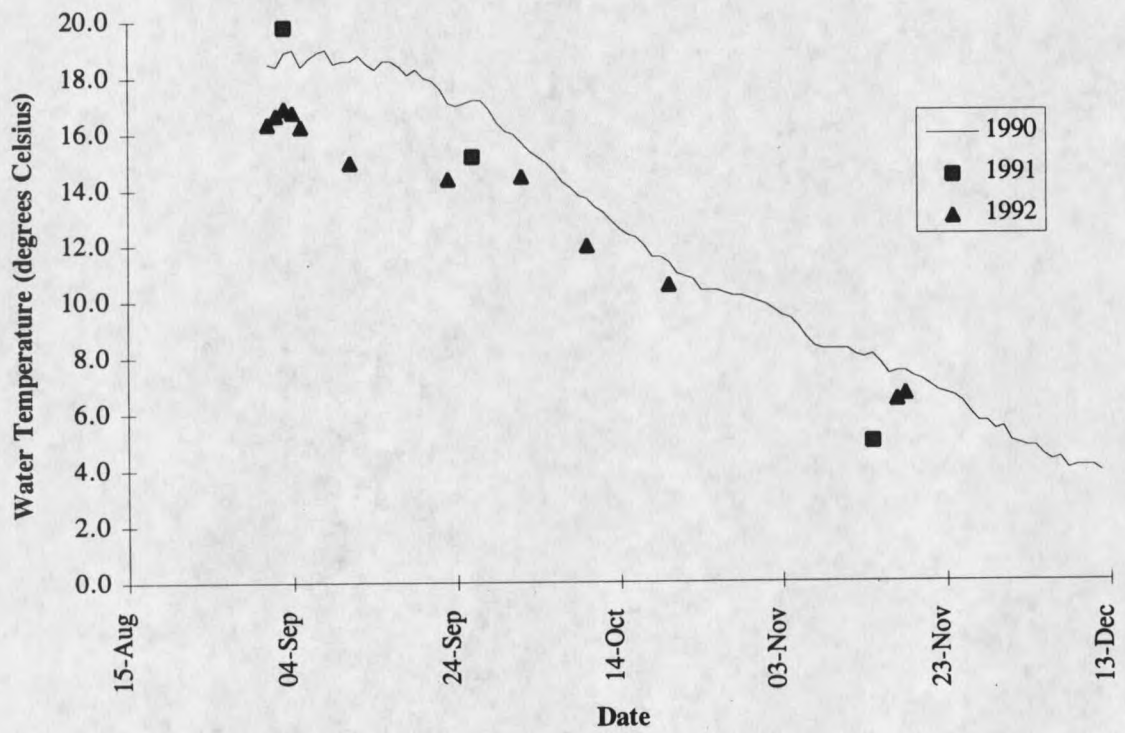


Figure 5. Mean daily water temperatures of Holter Reservoir during fall 1990, 1991, and 1992.

Stations (Figure 1) indicated that light penetration was typically highest during the month of July, after spring run-off and between seasonal peaks in plankton abundance (MDFWP 1992). Monthly S.D. transparency ranged from 1.4 (5/91) to 4.4 m (7/92) at the Cottonwood Station (Figure 6) and from 1.7 (5/91) to 6.9 m (7/92) at the Jackson Station (Figure 7).

Monthly water transparency at the Cottonwood Station averaged 2.6, 2.8, and 3.1 m for 1990, 1991, and 1992, respectively. Maximum recorded S.D. transparencies were 3.6, 3.8, and 4.4 m for years 1990, 1991, and 1992, respectively (Figure 6). Minimum S.D. transparencies were 2.1, 1.4, and 2.6 m for 1990, 1991, and 1992, respectively (Figure 6).

S.D. transparency at the Jackson Station was typically greater than at the Cottonwood Station. Monthly S.D. transparency at the Jackson Station averaged 3.6, 3.5, and 4.4 m with a maximum of 5.5, 5.5, and 6.9 m for 1990, 1991, and 1992, respectively (Figure 7). Minimum S.D. transparencies were 2.1, 1.7 and 2.6 m for 1990, 1991, and 1992, respectively (Figure 7).

On a more localized level, S.D. transparency was measured in areas of elevated turbidity associated with eroding shoreline areas. Secchi disc readings ranged from 0.4 to 1.2 m in the highly turbid portions of the reservoir with variation associated with wind direction and intensity. Approximately 51% of the winds originate from the west in the study area (Figure 8). Wind speed was greatest for winds from the southwest (24 km/h) followed by winds from the west (19 km/h) (Figure 9).

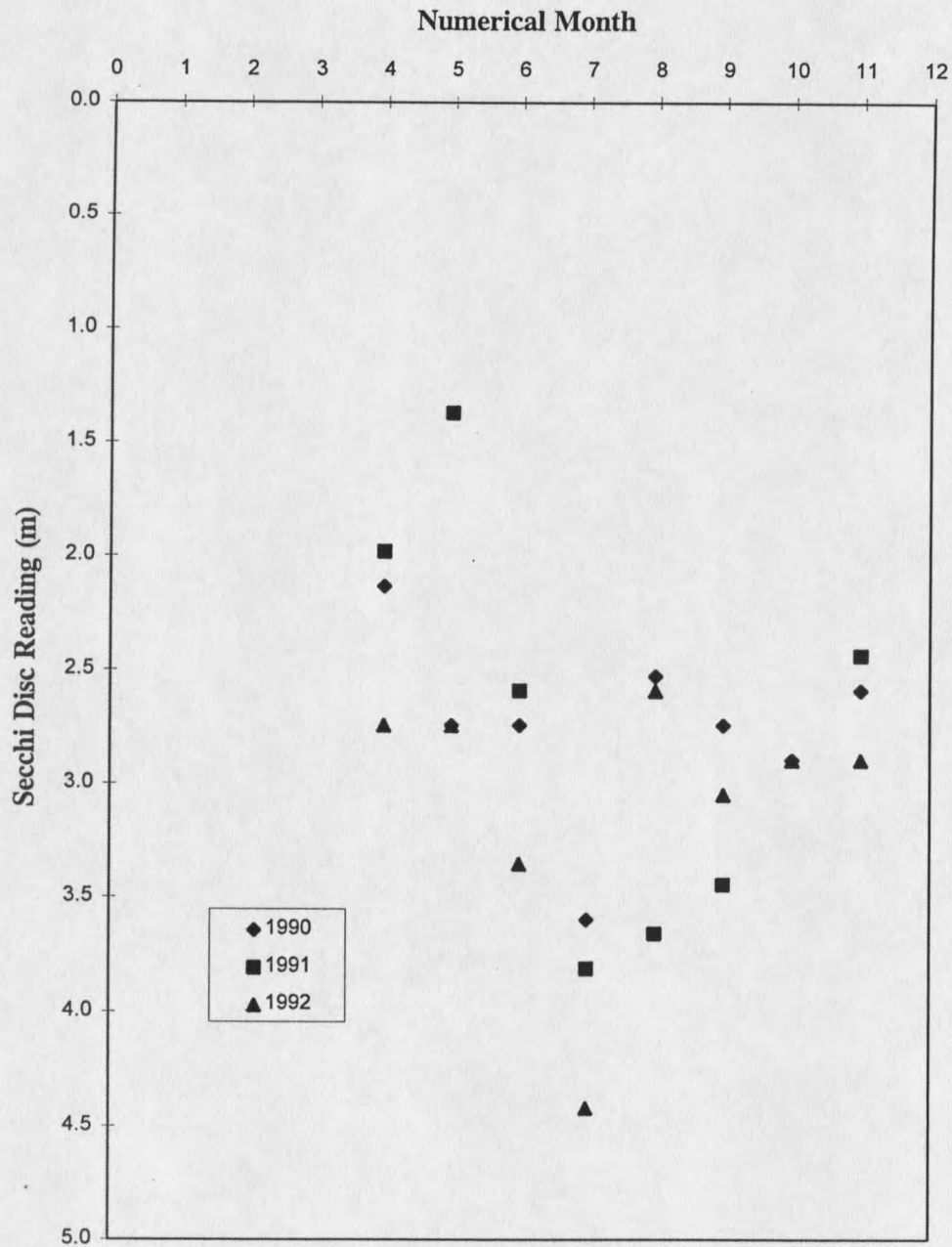


Figure 6. Monthly Secchi disk / water transparency readings collected at the Cottonwood limnological sampling station, Holter Reservoir, 1990-1992.

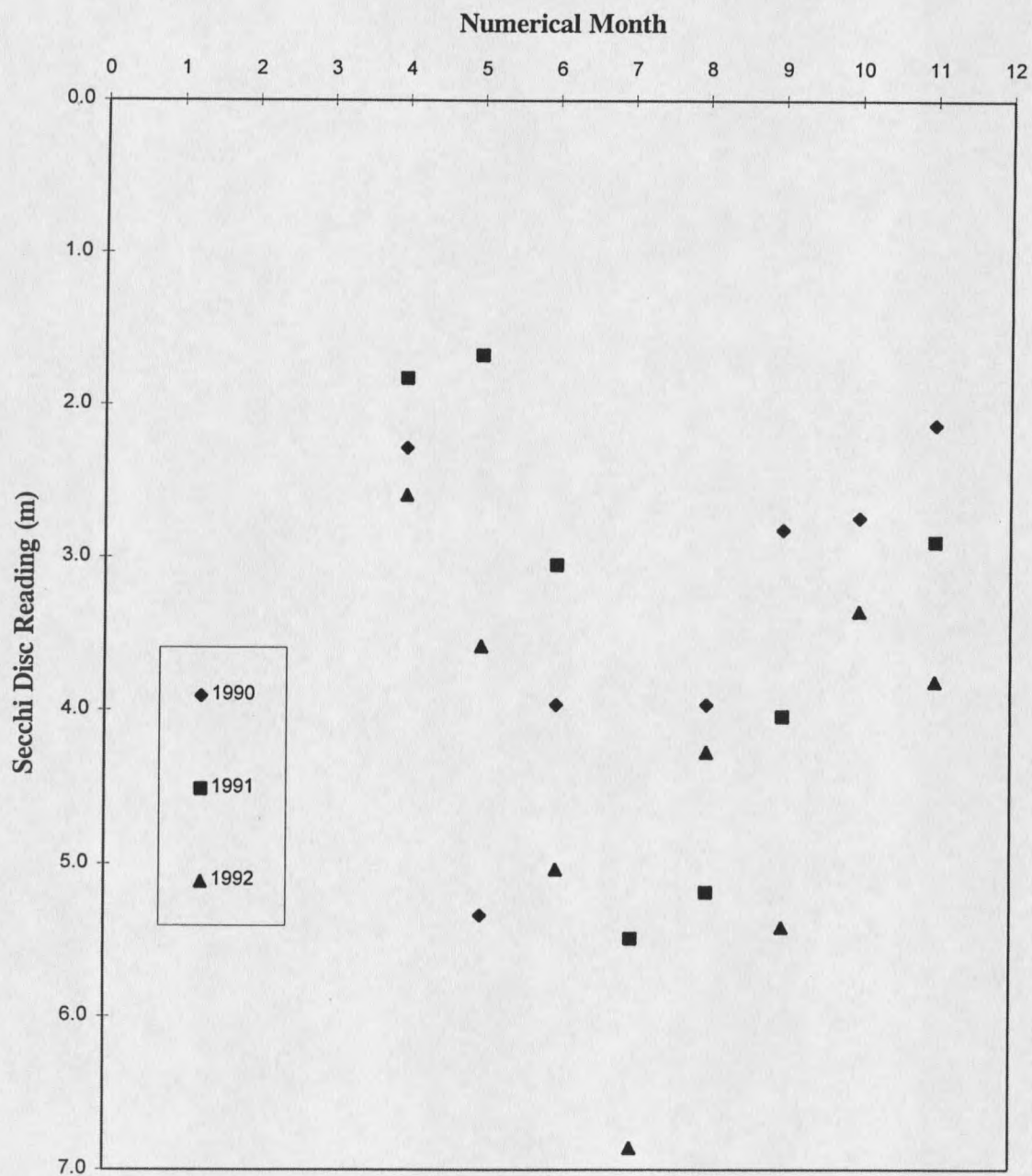


Figure 7. Monthly Secchi disk / water transparency readings collected at the Jackson limnological sampling station, Holter Reservoir, 1990-1992.

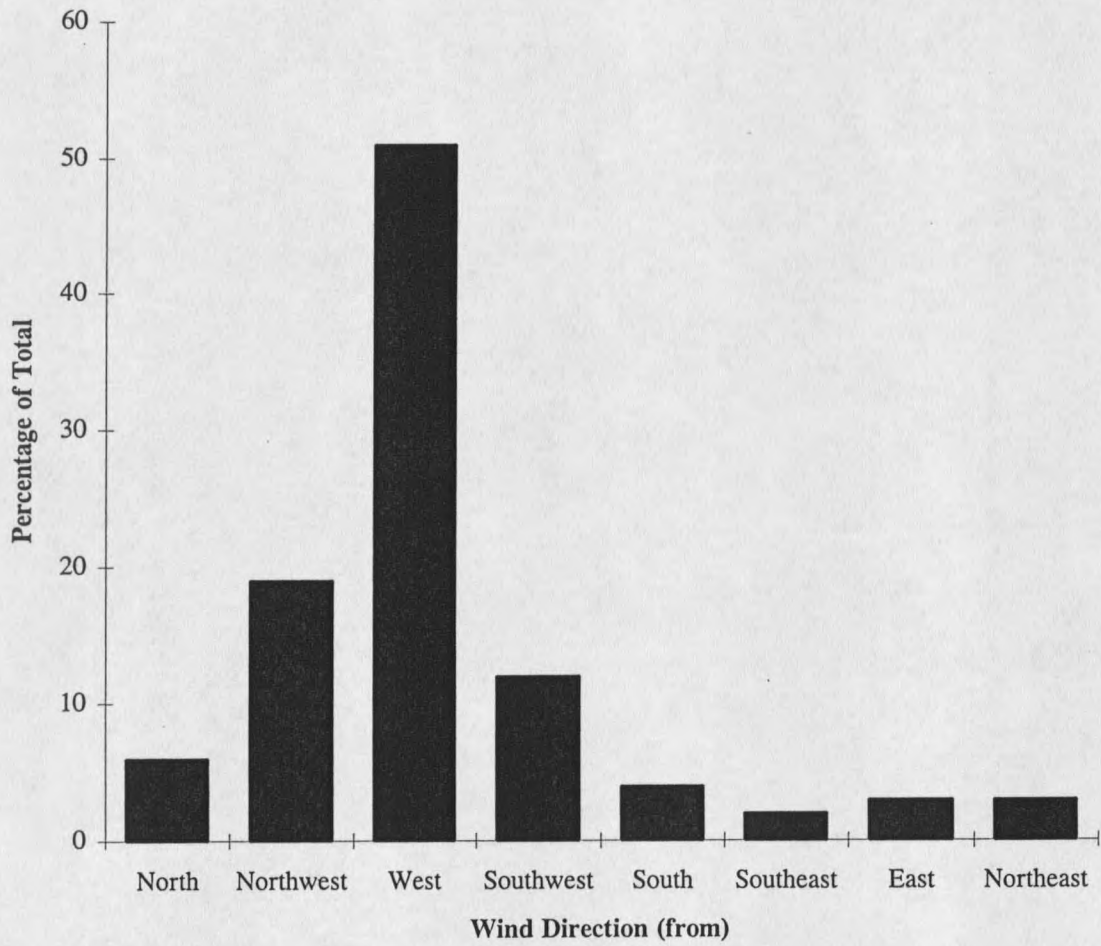


Figure 8. Percentage of total measurable wind from specific bearings near Cascade, MT (Montana Wind Energy Atlas).

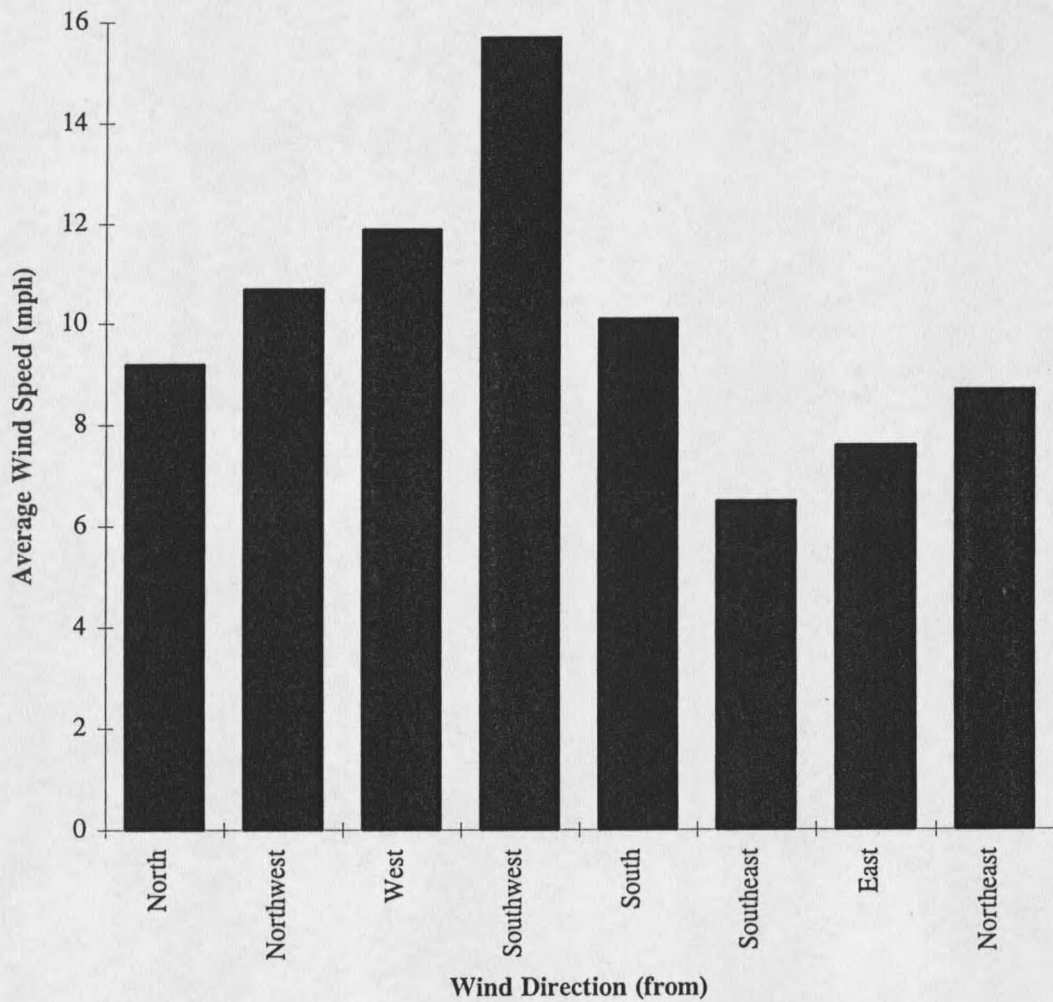


Figure 9. Average wind speed for specific bearings as measured near Cascade, MT (Montana Wind Energy Atlas).

Habitat Selection

Tagged walleye were located during 67 tracking episodes over the 2 year study period. Spring tracking (39 episodes) accounted for 58.2% of the effort. The focus of spring tracking was to determine spawning-related behavior and identify habitats selected for spawning. Twenty-two tracking episodes, accounting for 32.8% of the total effort, were conducted during summer. Tracking during fall was difficult due to high winds and water turbulence, resulting in hydrophone static interference, and therefore constituted a small percentage (12.0%) of the total sampling effort. Sonic tagged walleye were relocated 848 times during my study. Spring, summer, and fall observations, respectively, accounted for 53.8%, 36.1%, and 10.0% of the relocations. I made 514 relocations during 1991; 299 (58.2%) were female fish and 215 (41.8%) were males (Table 6). Observations included 251 (48.8%) during spring, 224 (43.6%) during summer and 39 (7.6%) during fall 1991 (Table 6). During 1992, 334 observations were made; 206 (61.7%) were female walleye and 128 (38.3%) were males (Table 7). Spring, summer, and fall observations accounted for 206 (61.7%), 82 (24.6%) and 46 (13.8%) relocations, respectively (Table 7).

Distribution of sonic-tagged fish located by telemetry

Adult walleye located with ultrasonic telemetry equipment were distributed throughout the study area, but were most commonly located in the lower zones, E and F. Less than 5% of the observations were made in Zones A and B (RKM 8.0 to 19.3, Figure 10). Locations within Zones C and D (RKM 19.3 to 29.0) accounted for 13.8% of the observations recorded (Figure 10). Most (81.3%) fish observed were

Table 6. Total, seasonal, and diel number of walleye observations made within Holter Reservoir during 1991 (grouped by individual and sex).

Record of walleye observations - Holter Reservoir, 1991											
Fish I.D. No.	Sex	Total observations	Seasonal observations			Day observations			Night observations		
			Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall
555	Male	19	10	9	0	7	6	0	3	3	0
276	Male	21	7	13	1	5	9	1	2	4	0
465	Male	28	14	12	2	10	7	1	4	5	1
97	Male	24	12	11	1	8	9	1	4	2	0
2228	Male	23	11	9	3	6	5	2	5	4	1
267	Male	27	14	10	3	9	8	2	5	2	1
2327	Male	16	7	8	1	5	5	0	2	3	1
2273	Male	14	4	7	3	3	3	2	1	4	1
2264	Male	10	3	7	0	2	7	0	1	0	0
2237	Male	13	5	6	2	4	5	1	1	1	1
2255	Male	20	9	10	1	5	8	0	4	2	1
Males observed		215	96	102	17	64	72	10	32	30	7
249	Female	32	19	10	3	13	6	2	6	4	1
258	Female	30	15	14	1	10	9	1	5	5	0
285	Female	27	16	10	1	11	7	0	5	3	1
294	Female	27	13	11	3	8	7	2	5	4	1
339	Female	27	11	13	3	8	8	2	3	5	1
348	Female	24	11	12	1	8	9	1	3	3	0
357	Female	26	14	10	2	9	7	1	5	3	1
366	Female	24	10	11	3	6	7	2	4	4	1
375	Female	25	14	11	0	8	6	0	6	5	0
447	Female	22	12	6	4	9	3	3	3	3	1
88	Female	22	10	11	1	7	8	1	3	3	0
456	Female	13	10	3	0	7	3	0	3	0	0
Females observed		299	155	122	22	104	80	15	51	42	7
Total observed		514	251	224	39	168	152	25	83	72	14

Table 7. Total, seasonal, and diel number of walleye observations made within Holter Reservoir during 1992 (grouped by individual and sex).

Record of walleye observations - Holter Reservoir, 1992											
Fish I.D. No.	Sex	Total observations	Seasonal observations			Day observations			Night observations		
			Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall
555	Male	0									
276	Male	0									
465	Male	21	13	4	4	9	4	4	4	0	0
97	Male	0									
2228	Male	24	16	7	1	14	6	1	2	1	0
267	Male	18	12	6	0	9	4	0	3	2	0
2327	Male	20	11	5	4	7	4	4	4	1	0
2273	Male	23	14	5	4	13	5	4	1	0	0
2246	Male	7	7	0	0	3	0	0	4	0	0
2264	Male	0									
2237	Male	15	8	4	3	6	4	3	2	0	0
2255	Male	0									
Males observed		128	81	31	16	61	27	16	20	4	0
249	Female	23	12	6	5	10	4	5	2	2	0
258	Female	0									
285	Female	23	14	4	5	11	4	4	3	0	1
294	Female	12	12	0	0	9	0	0	3	0	0
339	Female	24	13	5	6	10	4	6	3	1	0
348	Female	14	8	6	0	7	4	0	1	2	0
357	Female	18	12	6	0	10	6	0	2	0	0
366	Female	24	13	7	4	13	5	3	0	2	1
375	Female	15	11	4	0	10	2	0	1	2	0
384	Female	15	7	3	5	7	3	4	0	0	1
447	Female	20	12	4	4	8	4	4	4	0	0
88	Female	18	11	6	1	6	4	1	5	2	0
456	Female	0									
Females observed		206	125	51	30	101	40	27	24	11	3
Total observed		334	206	82	46	162	67	43	44	15	3

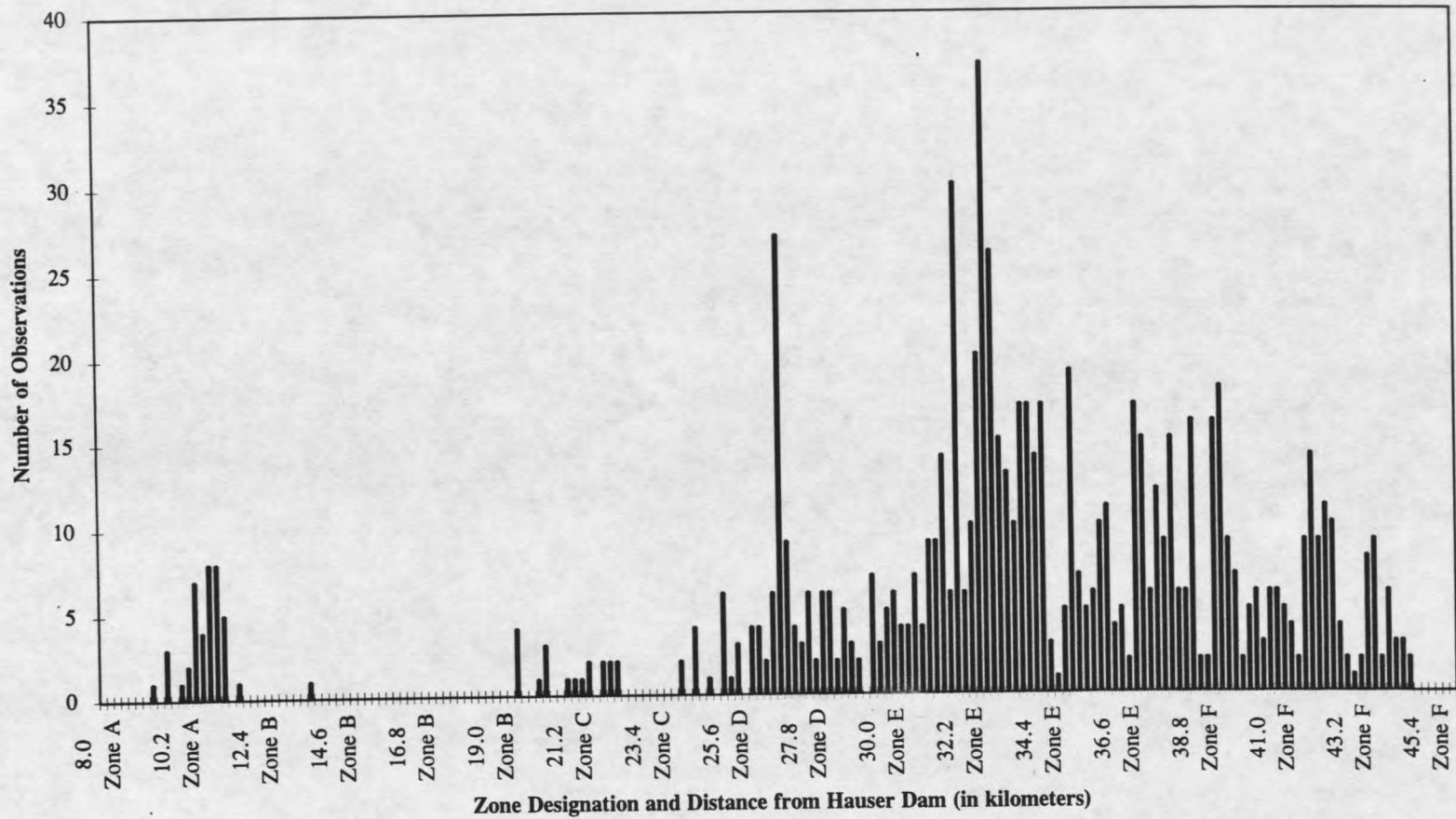


Figure 10. Locations of sonic-tagged walleye within Holter Reservoir during 1991 and 1992, referenced by reservoir km (distance from Hauser Dam).

located in Zones E and F (RKM 29.0 to 45.1, Figure 10) within the northern portion of the reservoir. The mode of all locations recorded was at RKM 32.8, near Indian Trail Lodge within the Oxbow Bend portion (Zone E) of the reservoir. The distribution of fish relocations was similar during 1991 and 1992 (Figures 11 and 12).

Seasonal patterns of habitat use within the reservoir were evident. During 1991, several fish were initially located within Zone A (RKM 10.0) in March, before the ice cover melted (Figures 13 and 14). As spring advanced, fish were located in the lower 25 km of the reservoir (Zones D, E, and F) with the greatest frequency of observations recorded at RKM 33.0 near the Indian Trail Lodge in Zone E (RKM 29.0 to 37.3). During the summer of 1991, fish locations were concentrated in the lower 16.1 km of the reservoir within Zones E and F (RKM 29.0 to 45.1)(Figures 13 and 15). The mode of the summer observations was near RKM 33.8, with similar frequency of utilization observed near RKM 38.0. By fall, fish were less concentrated and occupied locations throughout the reservoir (Figure 13 and 16) with a mode near RKM 31.6. Median values of spring and summer observations and spring and fall observations were significantly ($p < 0.05$) different (Kruskal-Wallis ANOVA on Ranks) while those between summer and fall 1991 were not.

The trend in the temporal distribution of walleye during 1992 was similar to that observed during 1991 (Figure 17). Spring observations were distributed throughout the reservoir (Figure 18) with the greatest frequency of observations at RKM 27.0 (Zone D) and RKM 32.8 (Zone E). During summer 1992, fish locations were distributed throughout the lower 19.5 km (RKM 24.5 to 44.0) of the reservoir in

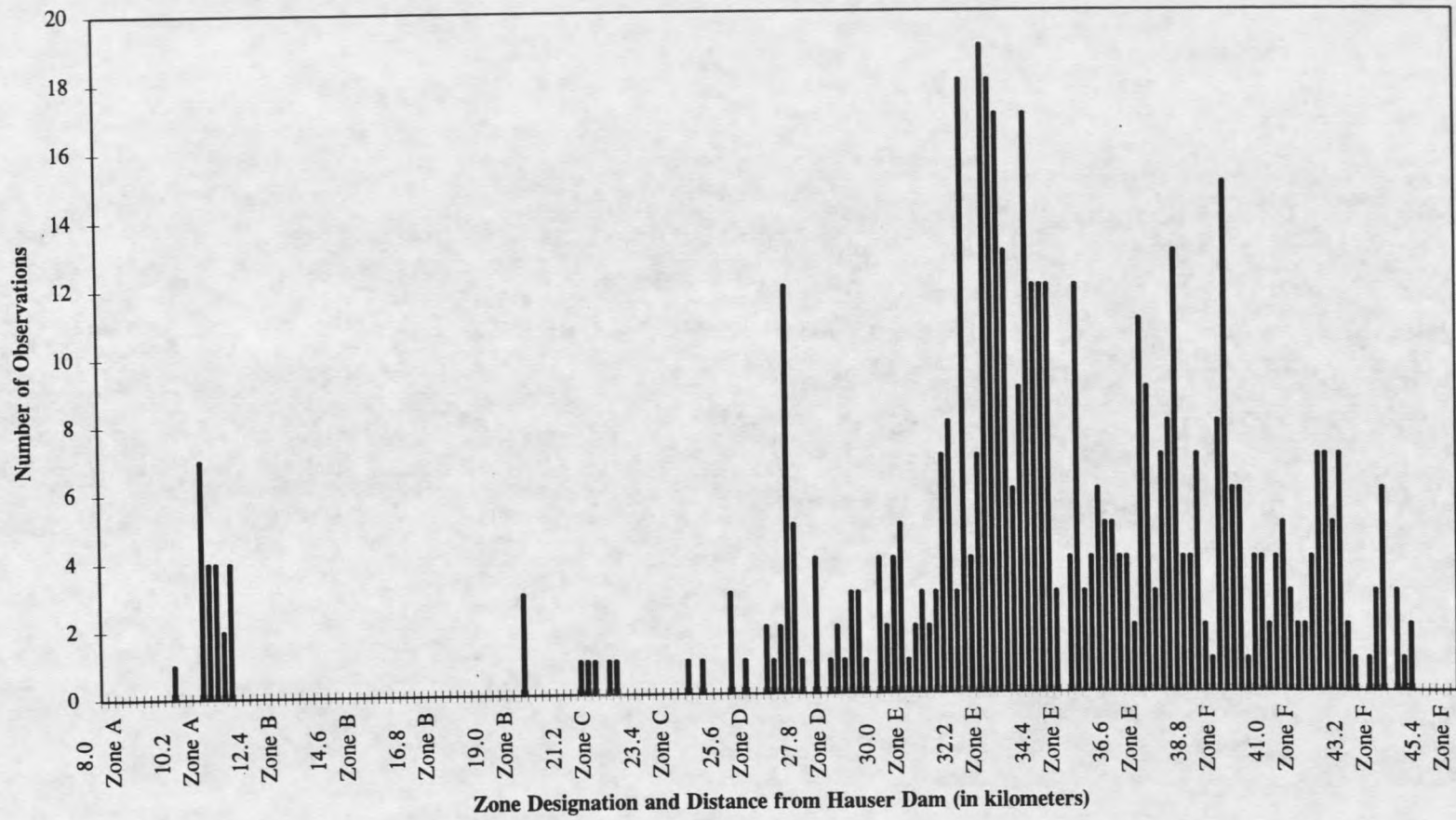


Figure 11. Locations of sonic-tagged walleye within Holter Reservoir during 1991, referenced by reservoir km (distance from Hauser Dam).

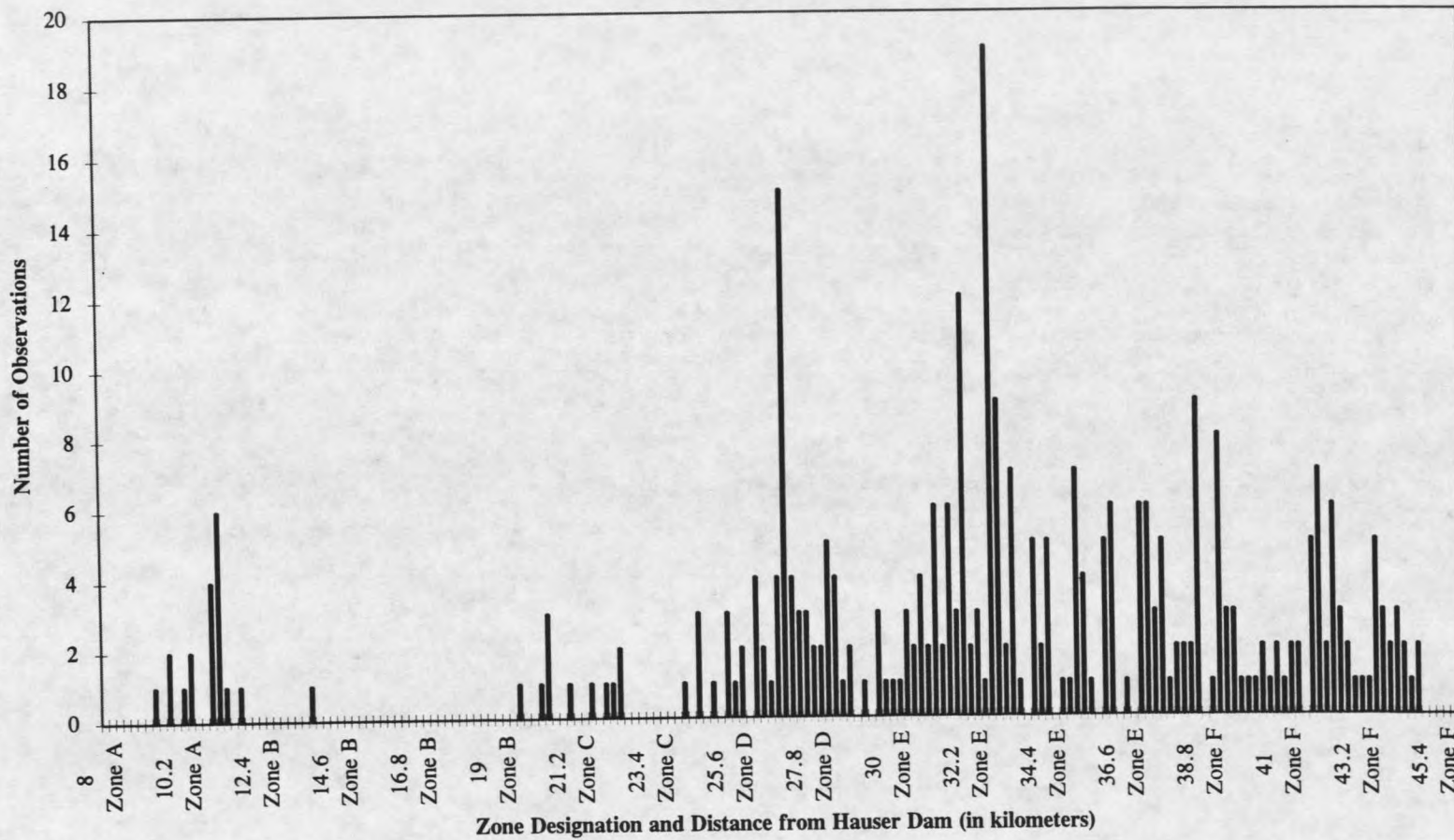


Figure 12. Locations of sonic-tagged walleye within Holter Reservoir during 1992, referenced by reservoir km (distance from Hauser Dam).

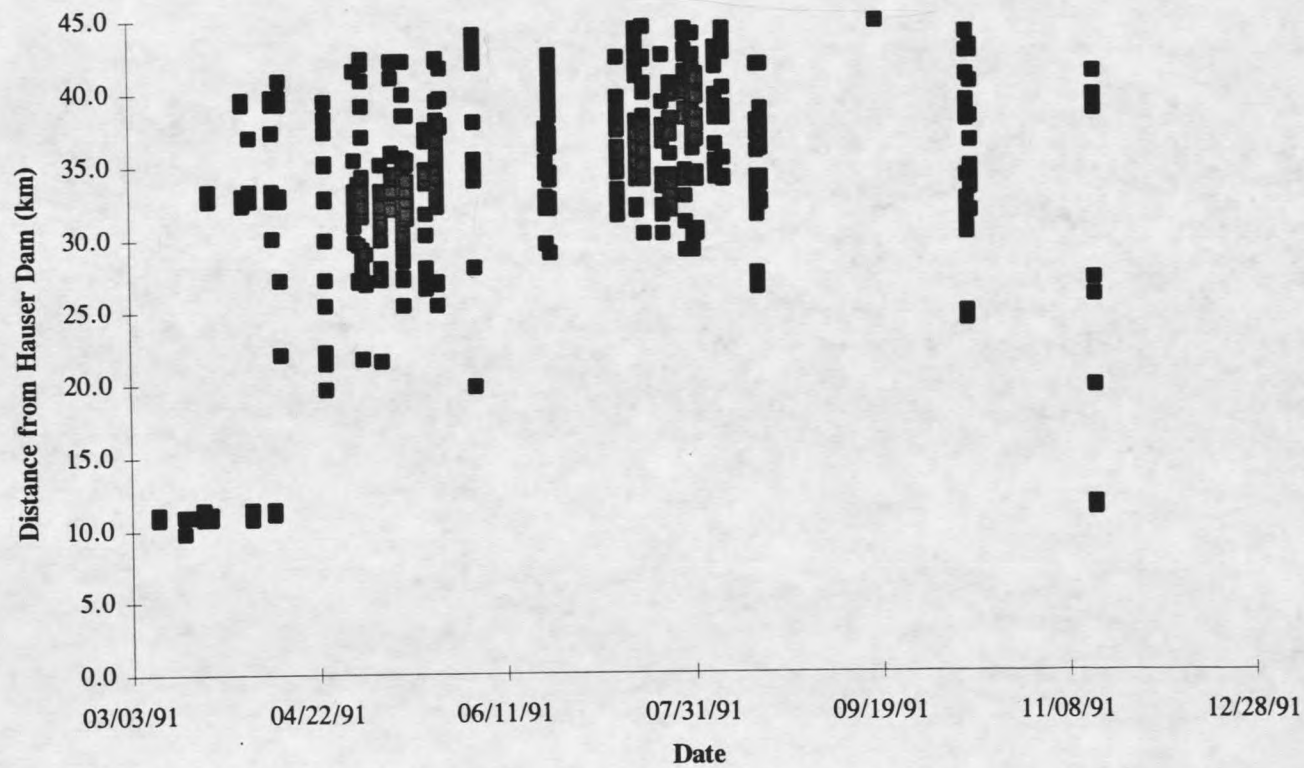


Figure 13. Walleye locations in Holter Reservoir on different dates in 1991.

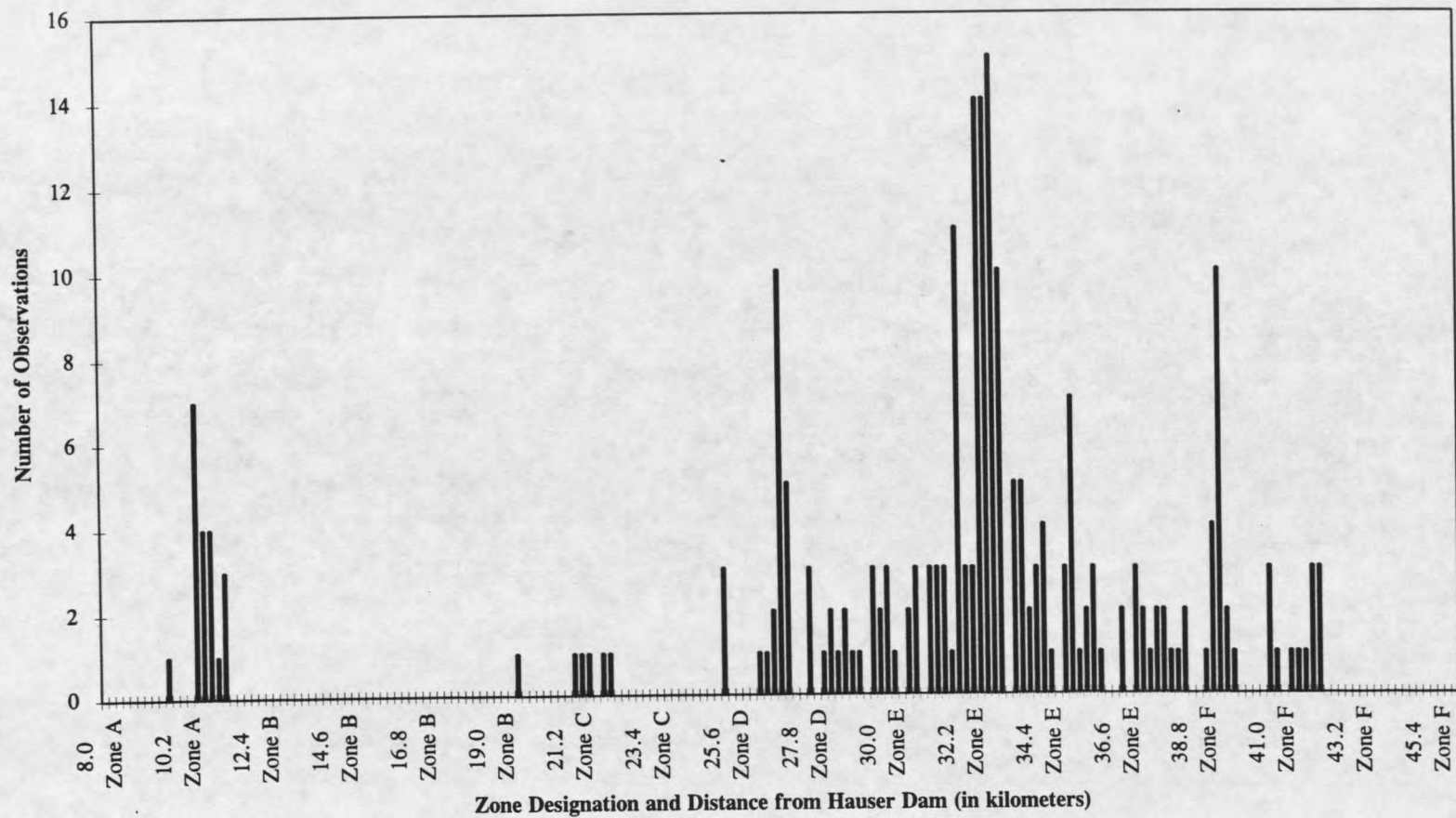


Figure 14. Locations of sonic-tagged walleye within Holter Reservoir during spring 1991, referenced by reservoir km (distance from Hauser Dam).

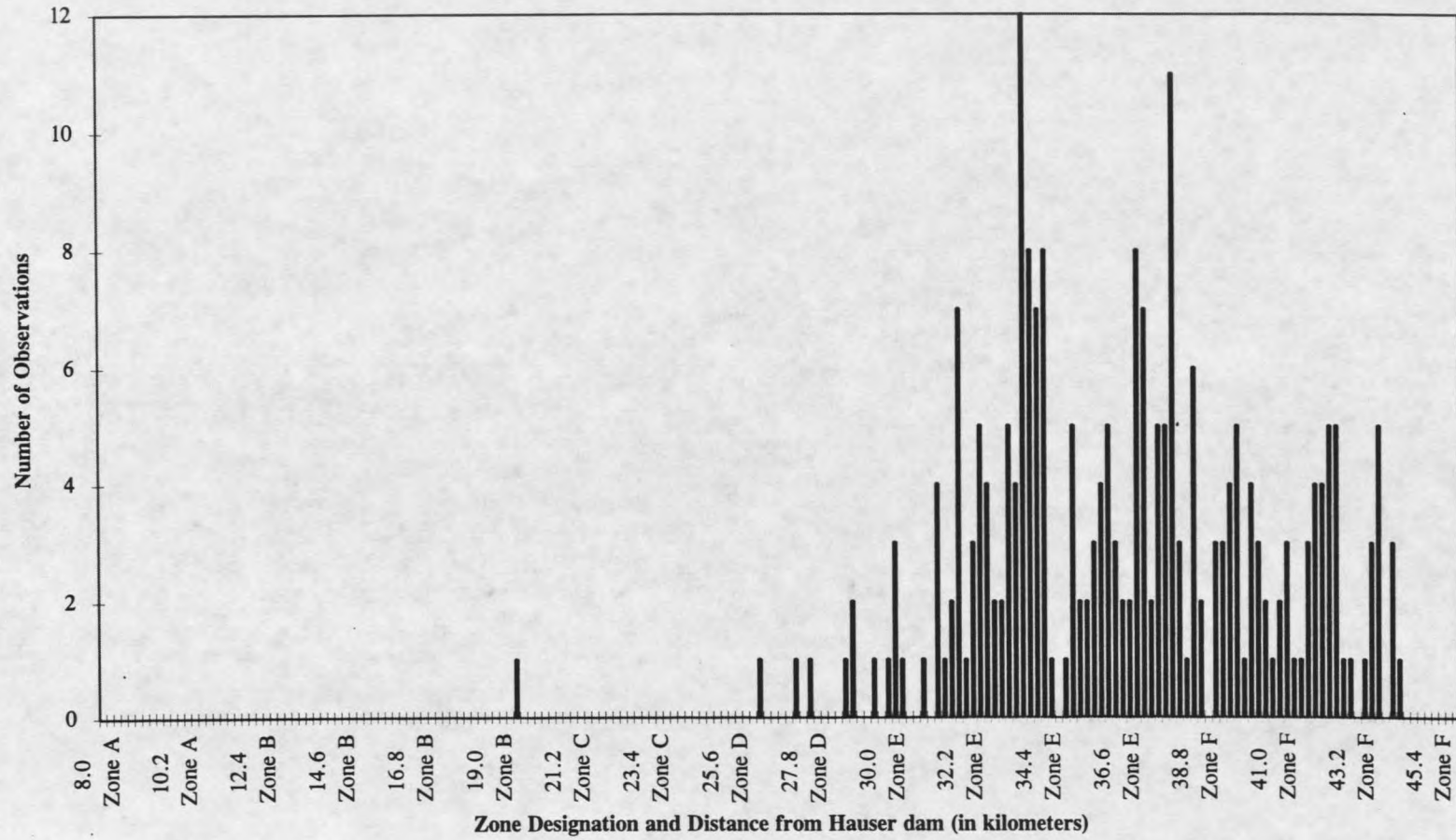


Figure 15. Locations of sonic-tagged walleye within Holter Reservoir during summer 1991, referenced by reservoir km (distance from Hauser Dam).

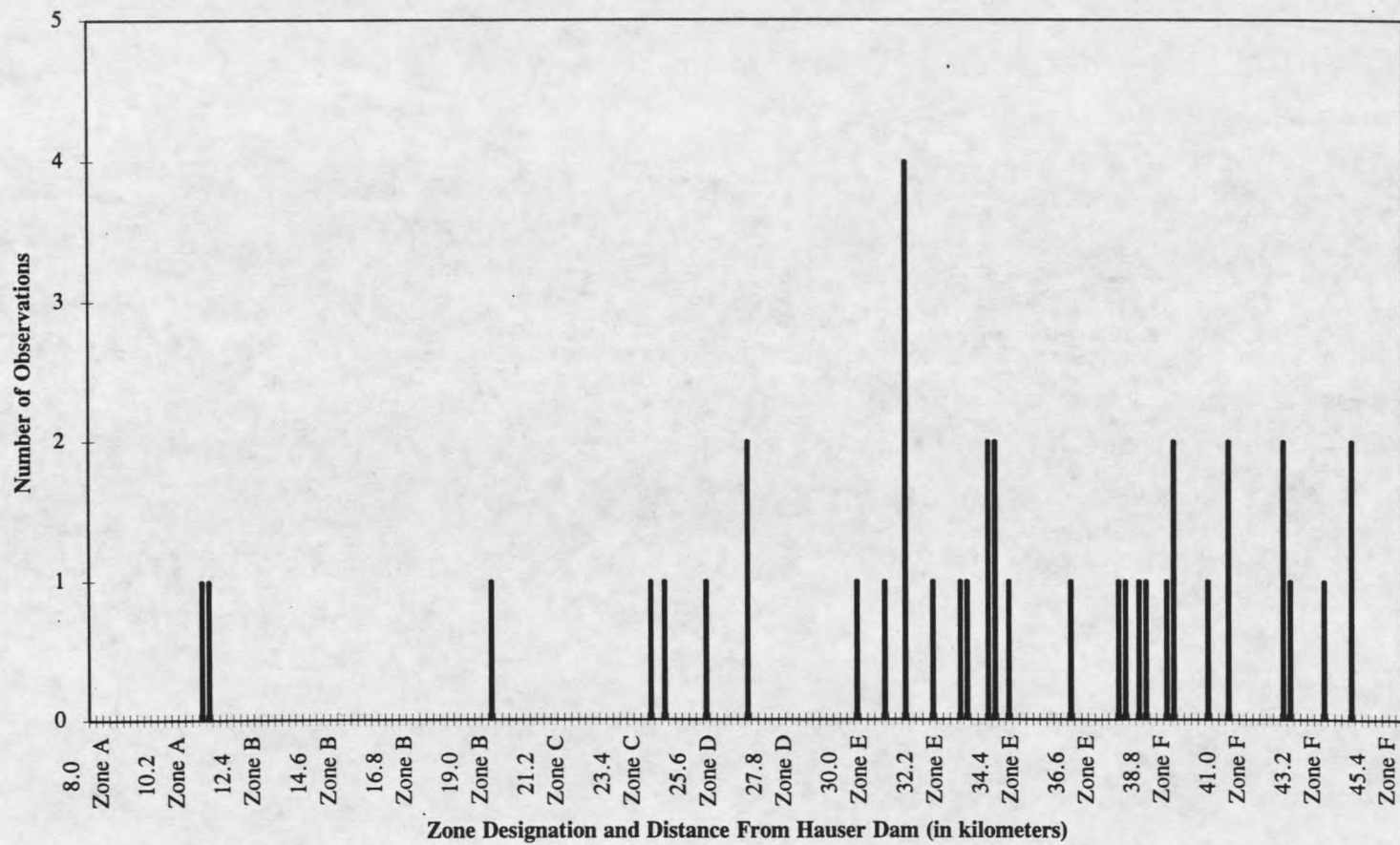


Figure 16. Locations of sonic-tagged walleye within Holter Reservoir during fall 1991, referenced by reservoir km (distance from Hauser Dam).

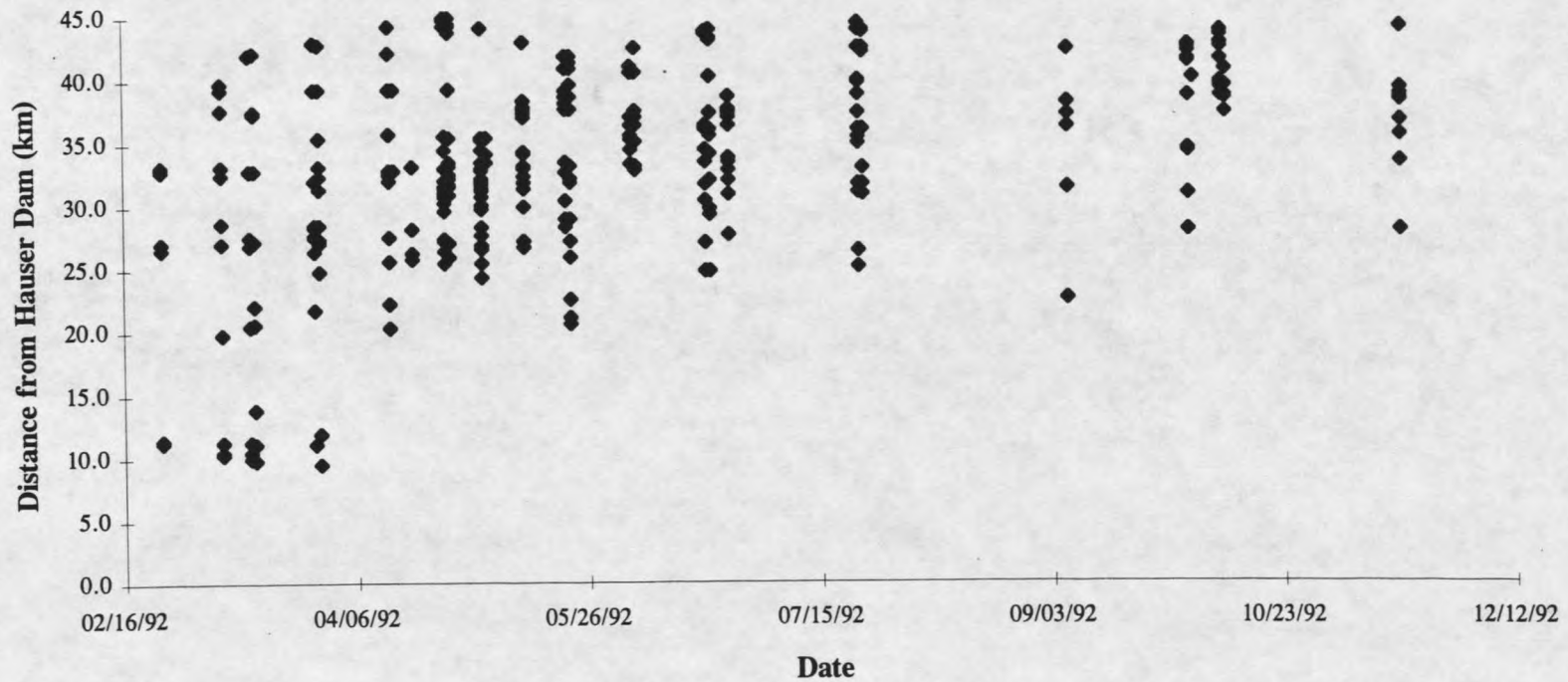


Figure 17. Walleye locations in Holter Reservoir on different dates in 1992.

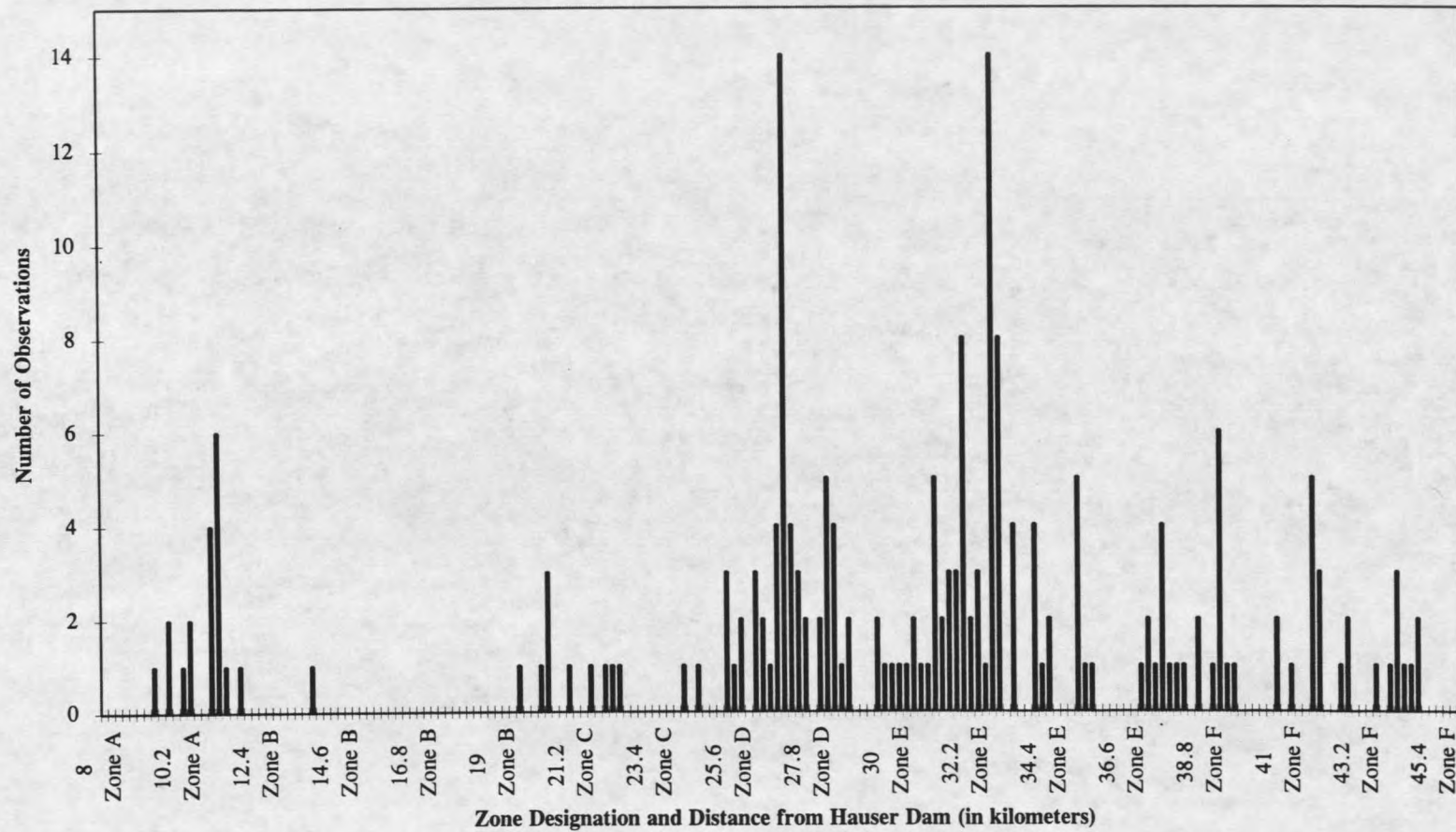


Figure 18. Locations of sonic-tagged walleye within Holter Reservoir during spring 1992, referenced by reservoir km (distance from Hauser Dam).

Zones E and F (Figures 17 and 19) but were less concentrated than in 1991. Within Zone E (RKM 29.0 to 37.3), utilization was greatest at RKM 32.8, 36.0, and 36.2 (Figure 19). During the fall of 1992, fish were located within the lower 25 km (RKM 20.1 to 45.1) of the reservoir with the greatest number observed near RKM 38.6 (Figure 20). Median values were significantly different (Kruskal-Wallis ANOVA on Ranks, $p < 0.05$) between spring and summer observations and between spring and fall observations but not between summer and fall locations for 1992. Tagged walleye frequented zones where the range and diversity of depths were highest.

Depth Utilization

Sonic tagged walleye were located in waters with depths ranging from 1.2 to 29.9 m, during the study (Figure 21). The mean and standard deviation of the depths at sites occupied by walleye were 6.9 and 3.7 m, respectively. The modal depth at sites where sonic-tagged walleye were found was approximately 5.5 m during monitoring periods. Most (82.4%) depths utilized were normally distributed about the mean with a range from 3.7 to 11.0 m (Figure 21). Waters with depths in this range accounted for 422 ha (21.7%) of the total reservoir surface area (Table 3). Approximately 50% of the observations were at locations with depths ranging between 4.9 and 8.2 m.

Walleye exhibited both seasonal and diel depth use patterns which were highly variable, with utilization often dictated by short-term and localized conditions. During the spring, adult walleye were monitored during the day at sites with depths ranging from 2.1 to 20.7 m; mean depth was 6.3 m (Figure 22). Mean daytime depths during the spring season for 1991 and 1992 were 6.2 and 6.5 m, respectively. Median depths

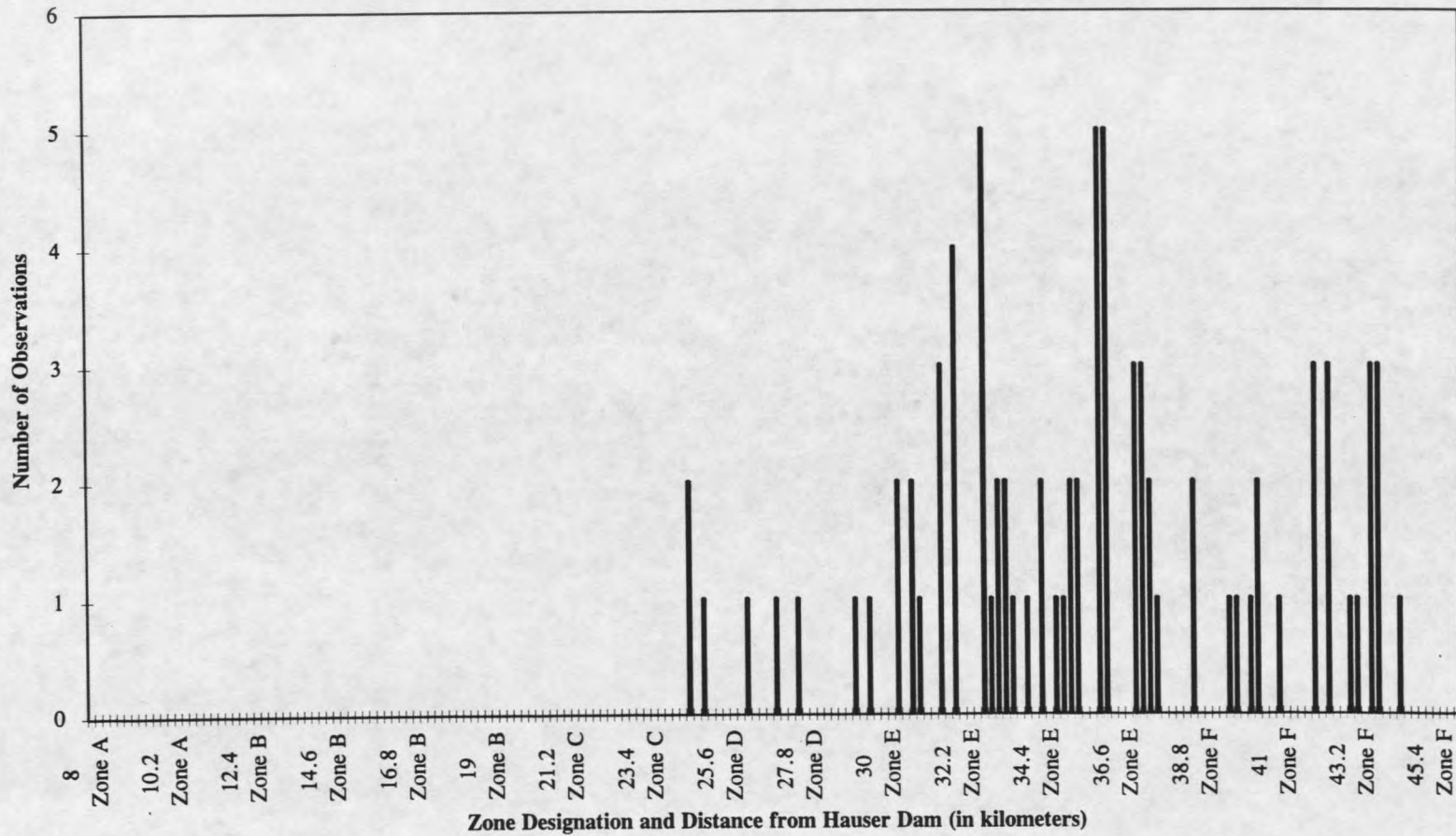


Figure 19. Locations of sonic-tagged walleye within Holter Reservoir during summer 1992, referenced by reservoir km (distance from Hauser Dam).

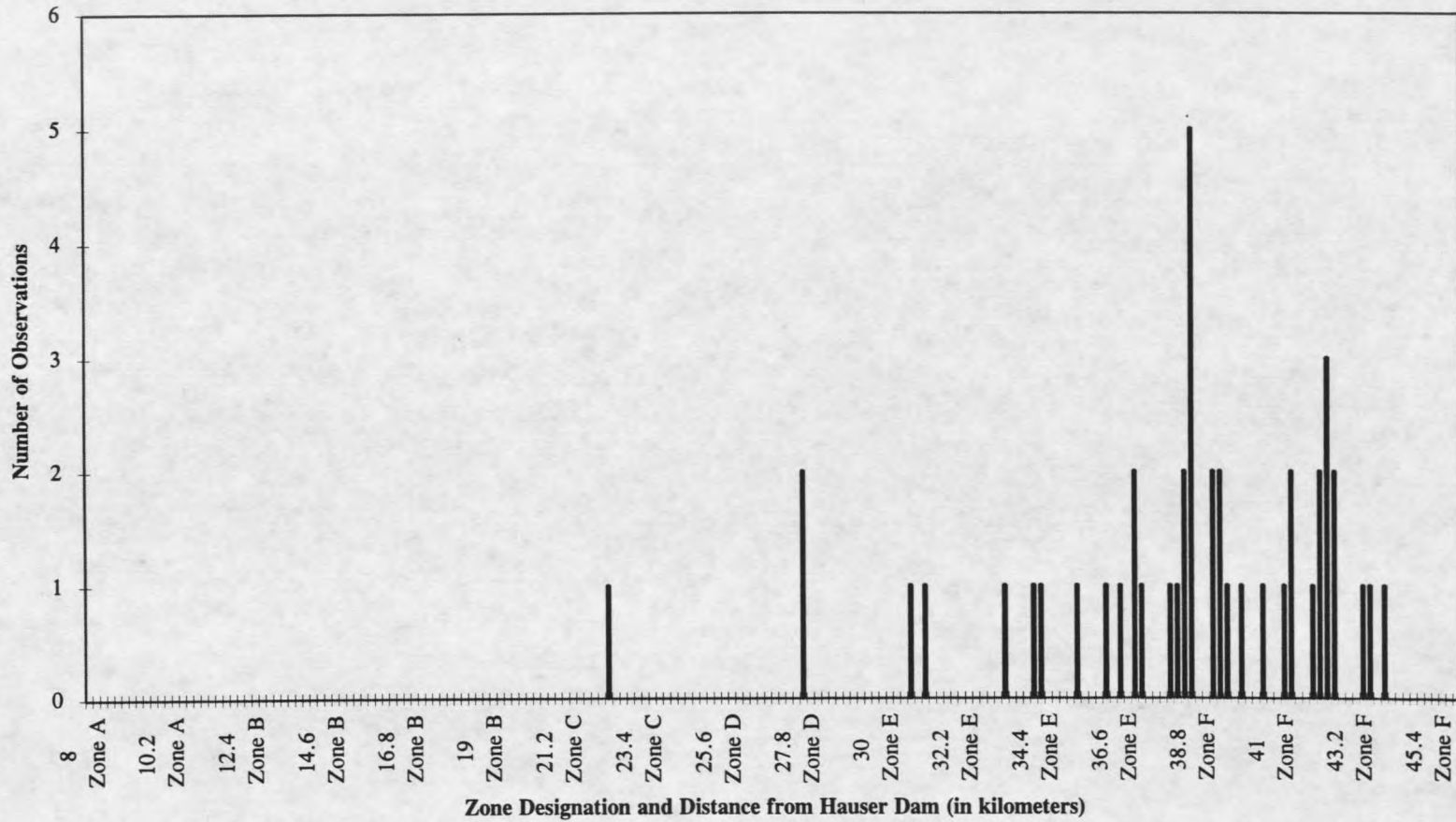


Figure 20. Locations of sonic-tagged walleye within Holter Reservoir during fall 1992, referenced by reservoir km (distance from Hauser Dam).

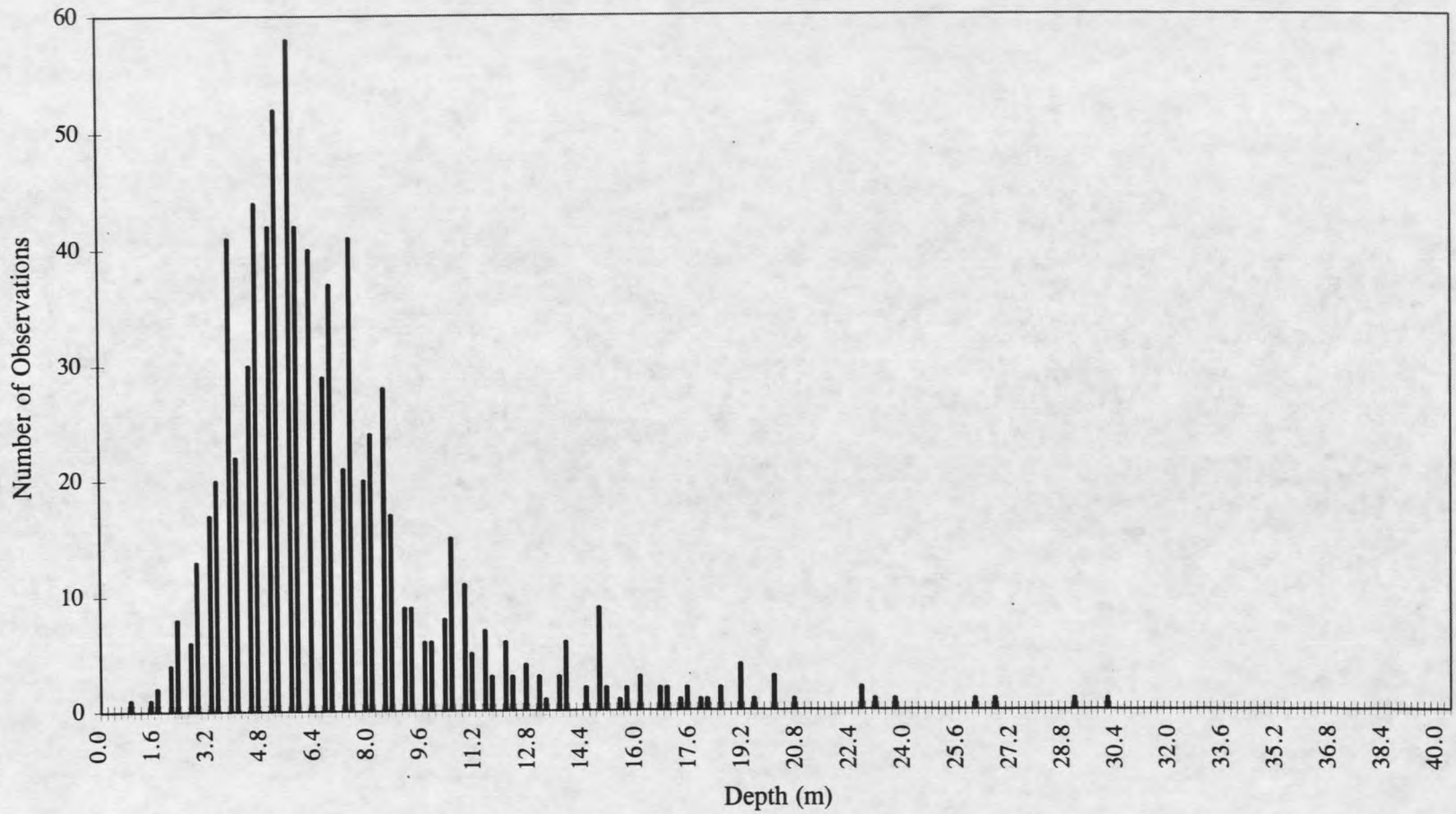


Figure 21. Depths at walleye relocation sites within Holter Reservoir during 1991 and 1992.

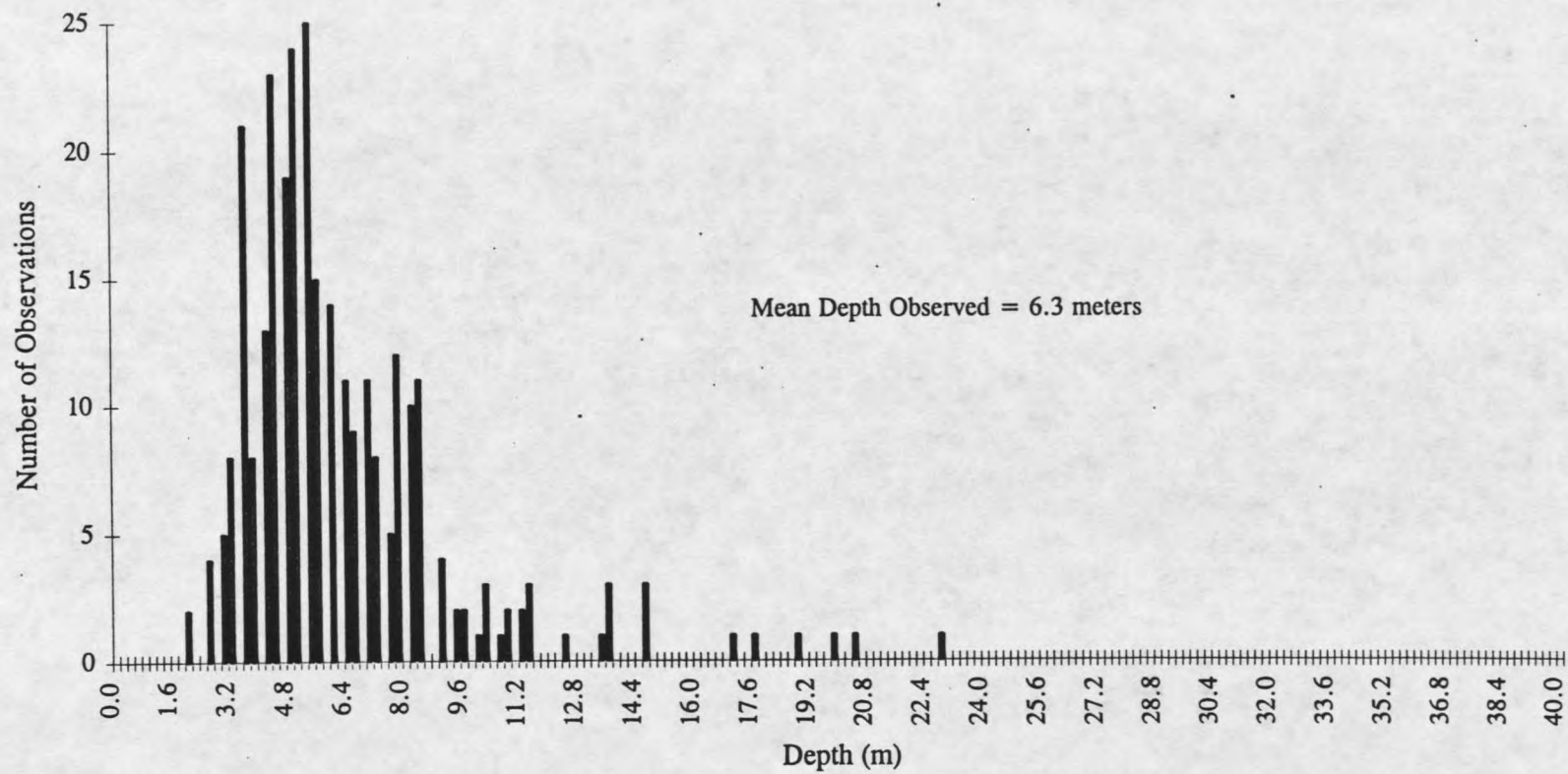


Figure 22. Depths at daytime sites where walleye were located within Holter Reservoir, spring 1991 and 1992.

at sites where walleye were located were significantly different between years ($P < 0.01$) (Mann Whitney Rank Sum Test).

During the spring, walleye were located at night at sites with depths ranging from 1.2 to 22.6 m (Figure 23) with a mean of 5.4 m (Figure 23). Mean nighttime depths used during spring 1991 and 1992 were 5.4 and 5.6 m, respectively. Median values for depths where walleye were located were significantly different between years (Mann Whitney Rank Sum Test, $P < 0.01$). Significant differences (Mann Whitney Rank Sum Test) were also observed between median values for day versus night observations during spring 1991 ($P < 0.01$) and 1992 ($P < 0.01$).

Walleye were located during summer days at water depths ranging from 2.1 to 25.9 m, with a mean of 8.4 m (Figure 24). The mean daytime depths identified during summer 1991 and 1992 were 9.1 and 7.3 m, which were significantly different (Mann Whitney Rank Sum Test, $P < 0.01$).

Walleye were located during summer nights in waters ranging from 1.8 to 29.9 m in depth, with a mean of 8.4 m (Figure 25). The mean nighttime depths observed during the summer season for 1991 and 1992 were 8.7 and 5.5 m, respectively and were not significantly different between years (Mann Whitney Rank Sum Test, $P = 0.258$). The median depths observed were not significantly different between summer day versus night observations during 1991 ($P = 0.618$) and 1992 ($P = 0.305$).

In fall, walleye were observed during the day at sites with depths ranging from 2.4 to 18.9 m (Figure 26). The mean depth utilized by walleye during the day was 6.8 m during the fall season (Figure 26). The mean daytime depths observed during fall 1991

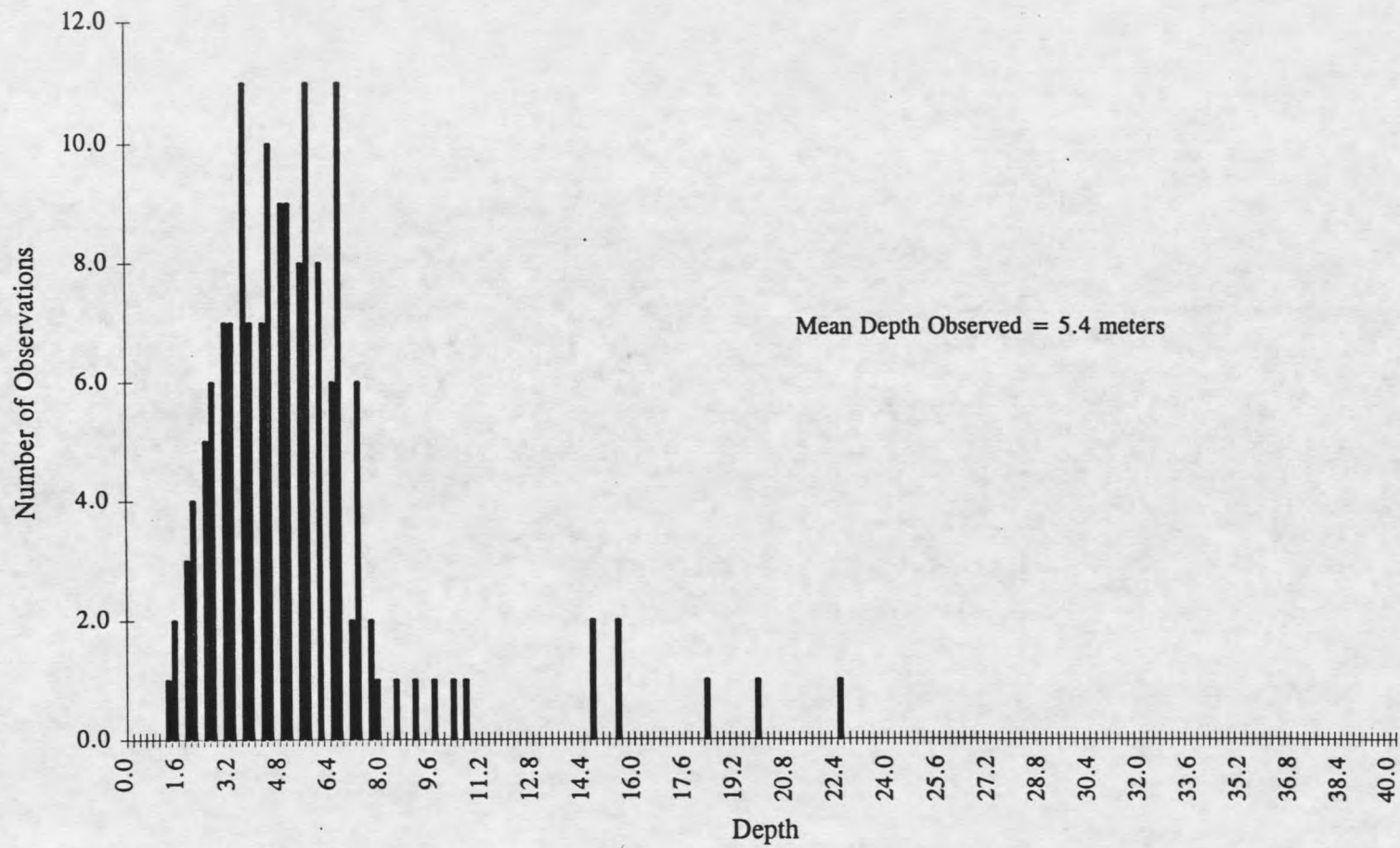


Figure 23. Depths at nighttime sites where walleye were located within Holter Reservoir, spring 1991 and 1992.

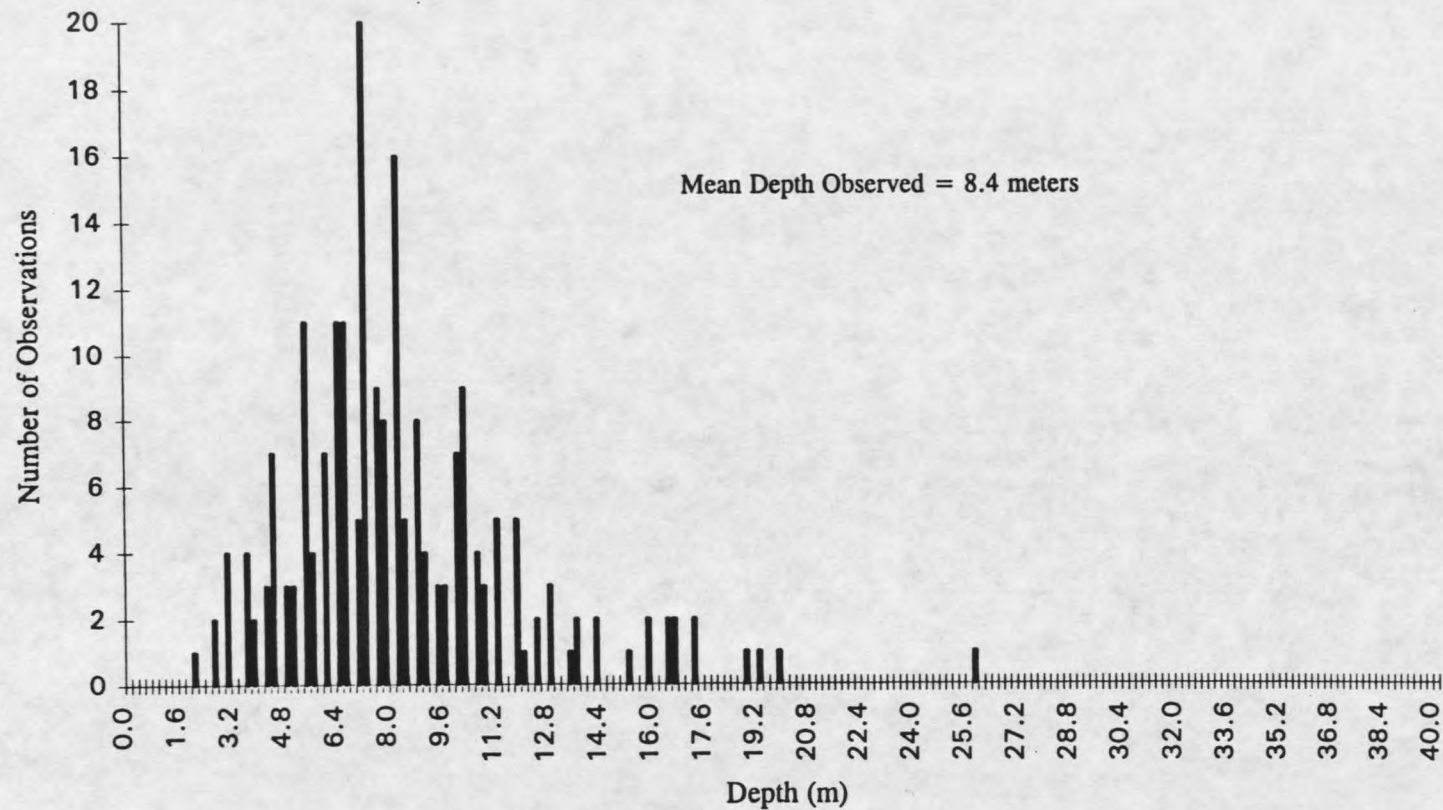


Figure 24. Depths at daytime sites where walleye were located within Holter Reservoir, summer 1991-1992.

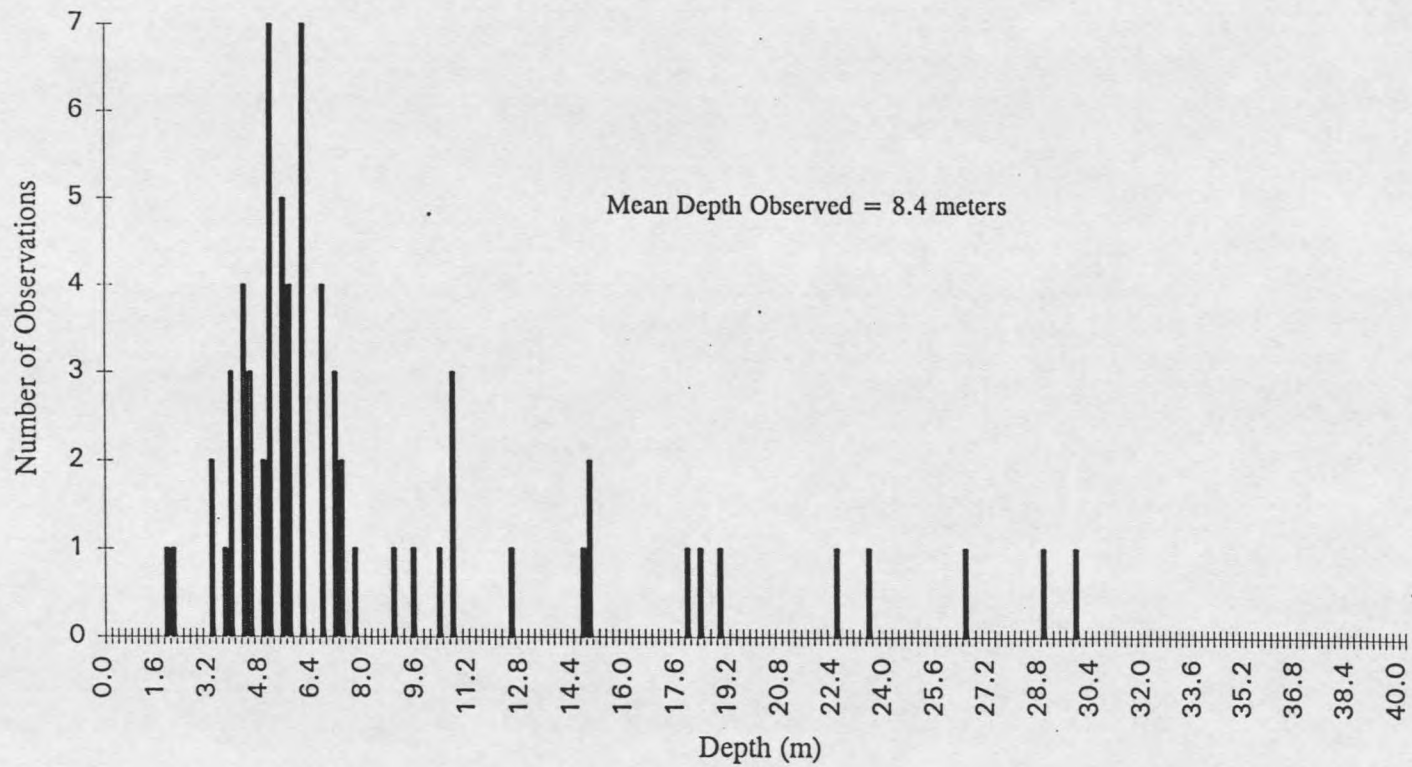
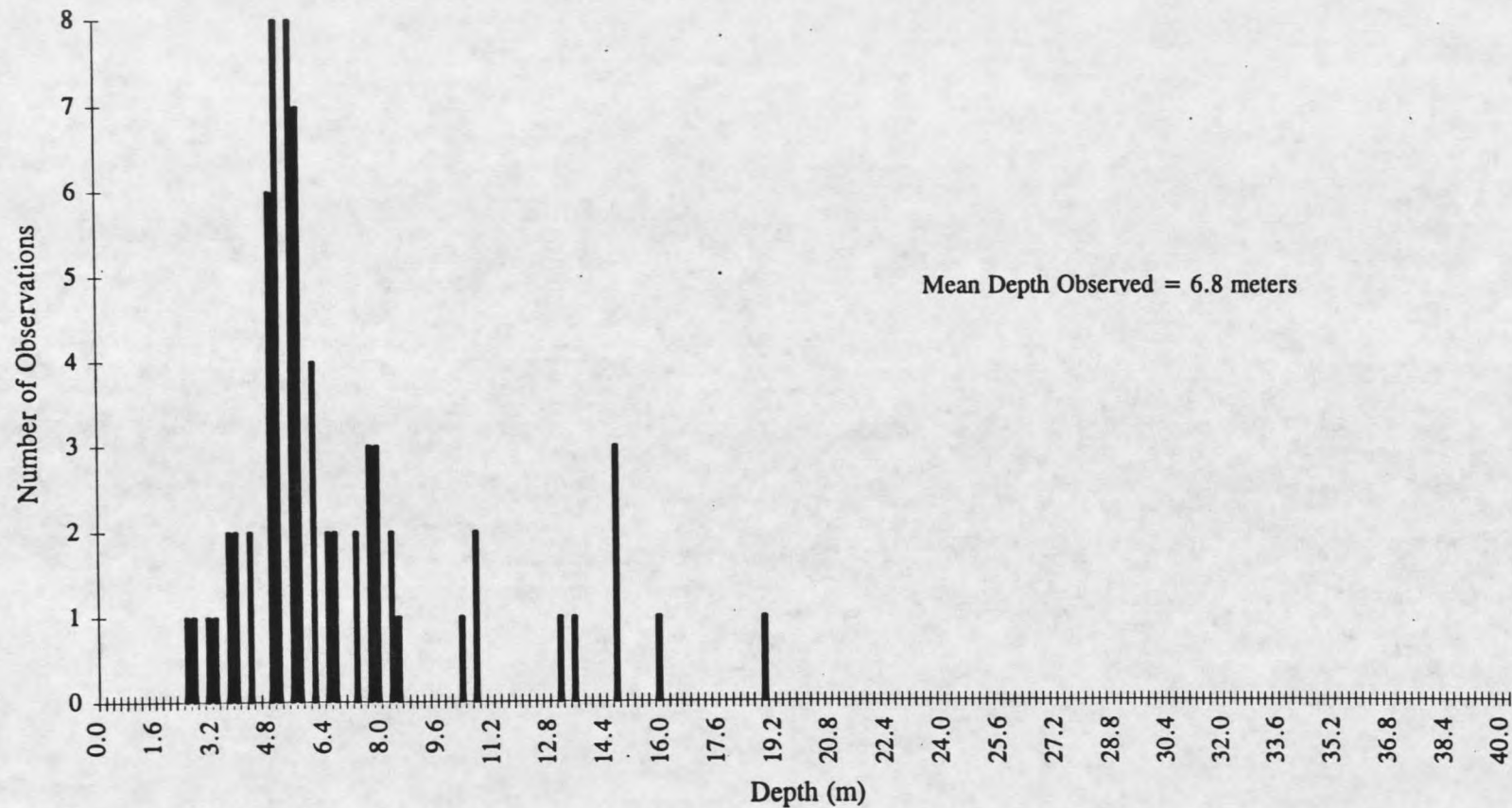


Figure 25. Depths at nighttime sites where walleye were located within Holter Reservoir, summer 1991-1992.



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Figure 26. Depths at daytime sites where walleye were located within Holter Reservoir, fall 1991-1992.

and 1992 were 7.2 and 6.6 m, respectively, which were not significantly different between years (Mann Whitney Rank Sum Test, $P = 0.912$). Walleye were located during fall nights at sites with depths averaging 6.6 m and ranging from 3.1 to 13.7 m (Figure 27). The mean nighttime depths observed during fall 1991 and 1992 were 5.8 and 8.2 m, respectively. Depths observed during fall nighttime were not significantly different between years (Mann Whitney Rank Sum Test, $P = 0.687$). Median values were not significantly different (Mann Whitney Rank Sum Test) between day versus night observations during fall 1991 ($P = 0.658$) and 1992 ($P = 0.209$).

Variations in depth utilization between seasons were statistically evident during 1991 but not 1992. Daytime depth utilization during spring versus summer, and summer versus fall 1991 were statistically different (Kruskal Wallis ANOVA on Ranks, $P < 0.05$) but not between spring versus fall. Significant differences ($P < 0.05$) in nocturnal depth utilization were evident between spring versus summer but not between summer versus fall or spring versus fall. No significant differences were detected between seasons for either day ($P = 0.113$) or night ($P = 0.0874$) observations during 1992. Tagged walleye tended to be present in littoral and sublittoral habitat types, however utilization was concentrated in the lower reservoir despite the fact that these habitat types were present throughout the reservoir. While tagged walleye frequented zones where profundal habitat was present they generally were not found in these deeper habitats.

Substrate Utilization

Adult walleye were located more frequently in areas with firm substrates (65.6%)

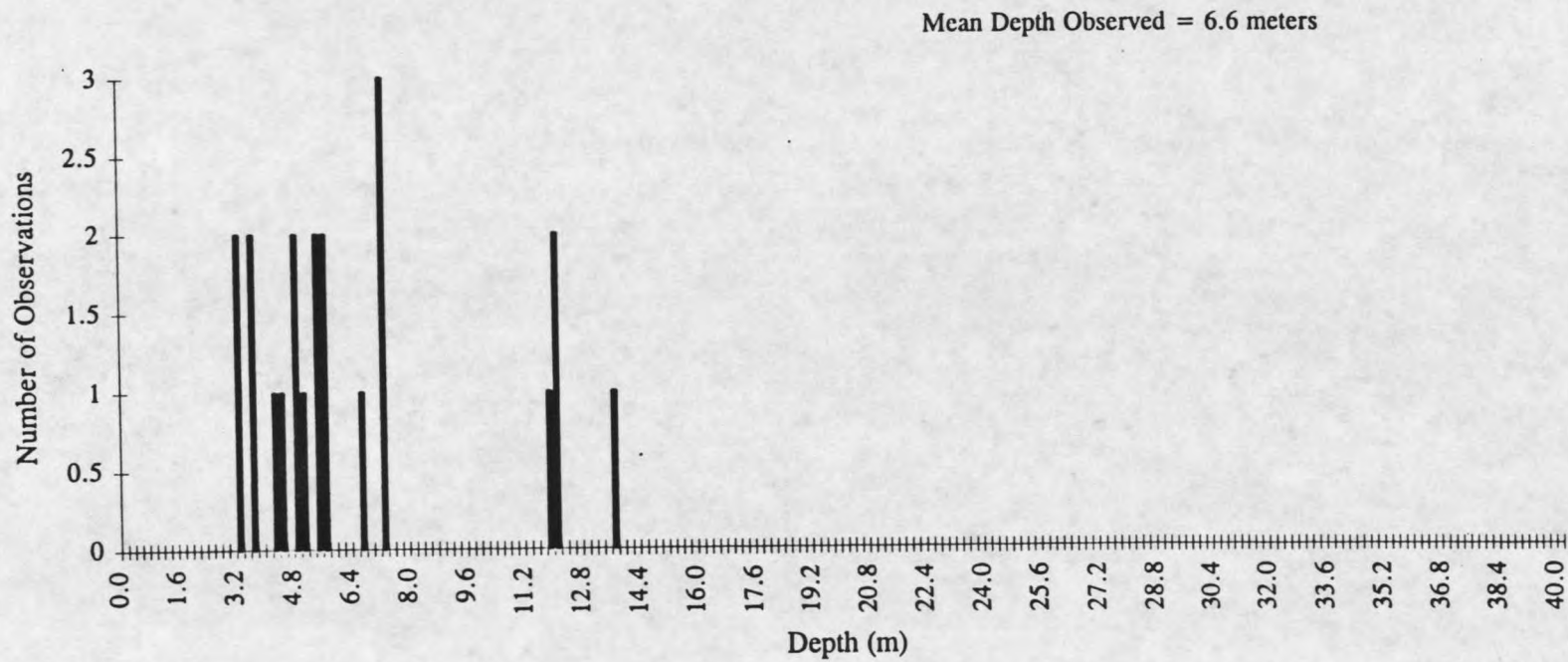


Figure 27. Depths at nighttime sites where walleye were located within Holter Reservoir, fall 1991-1992.

than with soft substrates (34.3%). Of the daytime observations, 61% were recorded over firm substrates and 39% over soft substrates (Figure 28). During spring, the percentages of daytime observations recorded over firm and soft substrates were similar at 50.9% and 49.1%, respectively (Figure 28). During the summer, 84.4% of daytime locations were recorded over firm substrates (Figure 28). During the fall, more observations were recorded over soft substrates (56.7 %).

At night, 76.1% of walleye relocations were over firm substrates and 23.9% over soft substrates (Figure 28). During the spring and summer, nighttime relocations were most frequently over firm substrates accounting for 77.1 and 77.6%, respectively (Figure 28). During the fall, 60% of the nocturnal observations were over firm substrates and 40% over soft substrates (Figure 28). A consistently greater percentage of the observations were made over soft substrates during the day compared to the night for all seasons except summer.

Adult walleye relocations over soft substrates were generally at shallower water depths than those over firm substrates. The depth recorded at fish locations over soft substrates averaged 5.1 m (s.d. = 2.09) compared to an average of 8.0 m (s.d. = 4.01) over firm substrates.

The distribution of tagged fish appeared to be tied to the percent of soft and unconsolidated firm substrates present. With the exception of Zone A, walleye frequented zones (Zones D, E, and F) where the percent of soft substrate along shoreline areas exceeded 9% (Table 4). Walleye also frequented zones (Zones D, E, and F) where the percent of unconsolidated firm substrate along shoreline areas

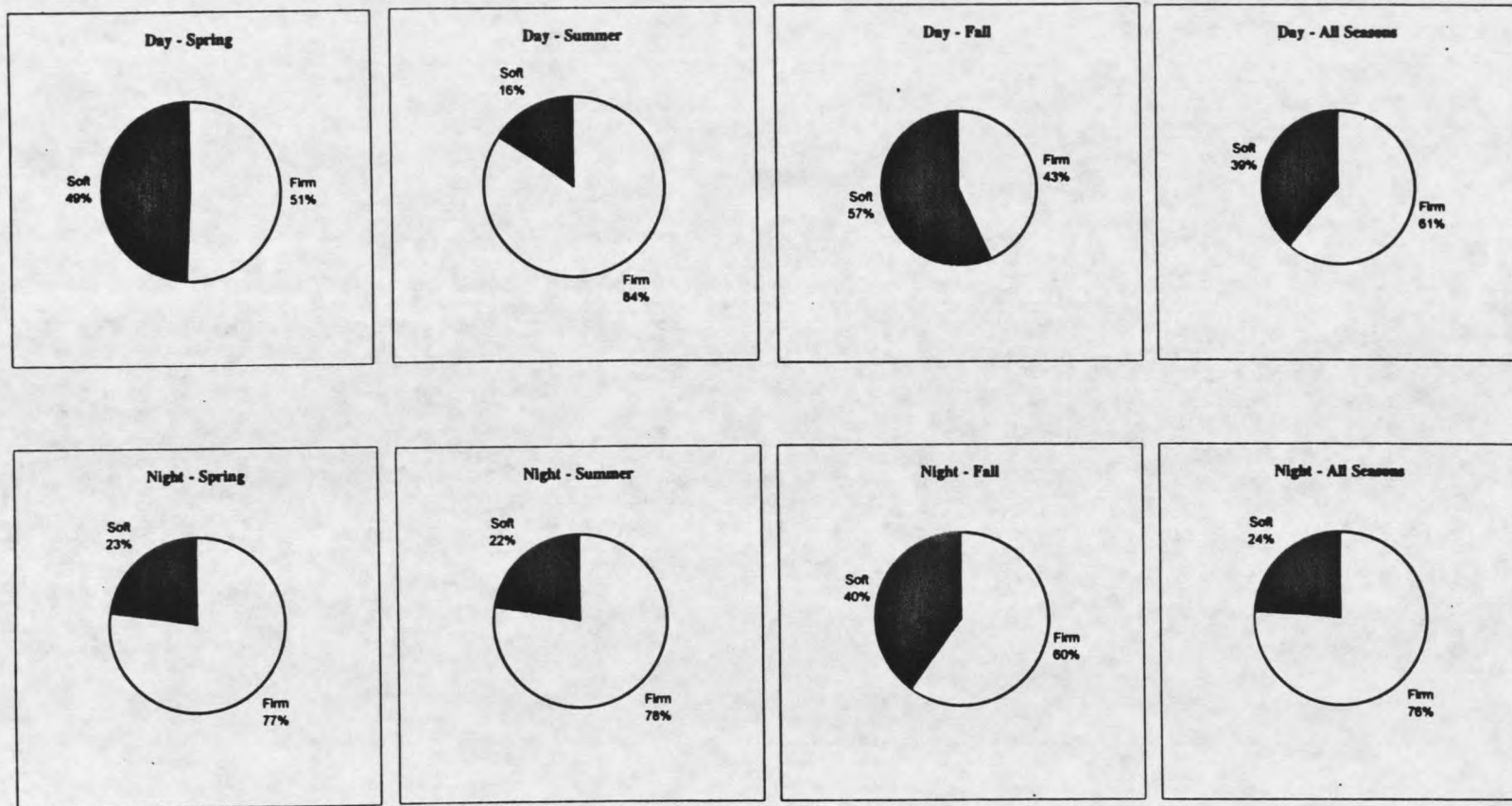


Figure 28. Percentage of day (top graphs) and night (bottom graphs) walleye observations associated with firm and soft substrate types during spring, summer, and fall within Holter Reservoir, 1991-1992.

exceeded 9% (Table 4). Walleye use was concentrated in zones where soft and unconsolidated firm substrates accounted for greater than 19% of the reservoir shoreline. Walleye were concentrated in areas where soft and unconsolidated firm substrates were most abundant.

Annual Variation in Utilization of Different Reservoir Zones

I made 514 relocations of adult walleye during 1991, and 334 relocations in 1992. The median reservoir locations for both years was within Zone E, at RKM 34.1 in 1991 and RKM 33.1 in 1992 (Figure 1). Median reservoir locations in 1991 and 1992 were significantly different between the spring seasons ($P = 0.0429$, Mann-Whitney Rank Sum Test) but not during the summer ($P = 0.0752$) or fall ($P = 0.406$) seasons.

Annual and Seasonal Variation in Reservoir Utilization by Sex

Of the 848 total relocations for both years, 505 (59.6%) were of female walleye and 343 (40.4%) were of male walleye. Median locations of the males versus females within the reservoir were not significantly different in 1991 ($P = 0.649$, Mann-Whitney Rank Sum Test; 299 females, 215 males), but were significantly different in 1992 ($P = 0.0301$, Mann-Whitney Rank Sum Test; 206 females, 128 males).

Male walleye used the reservoir in a similar pattern in 1991 and 1992 and median locations within the reservoir were not significantly different ($P = 0.345$, Mann-Whitney Rank Sum Test) between years. Median reservoir locations were not significantly different (Mann-Whitney Rank Sum Test) for male walleye between 1991 and 1992 for the spring ($P = 0.669$), summer ($P = 0.444$), or fall ($P = 0.597$) seasons.

Female walleye utilized the reservoir differently between 1991 and 1992 with significant differences ($P < 0.01$, Mann-Whitney Rank Sum Test) between median locations used in 1991 versus 1992. Significant differences (Mann-Whitney Rank Sum Test) in median reservoir location were detectable for female walleye between 1991 versus 1992 for the spring ($P < 0.01$) and fall ($P < 0.01$) seasons but were not detectable for the summer season ($P = 0.123$).

During 1991 and 1992, male walleye resided primarily in the lower reservoir. In 1991, median reservoir locations were RKM 33.0 during spring, 37.2 during summer, and 36.5 during fall. Significant differences (Kruskal Wallis ANOVA on Ranks) in reservoir utilization by males were detected between spring versus summer, and spring versus fall locations, but not between summer versus fall. During 1992, median reservoir locations of male walleye were RKM 32.8 during spring, RKM 36.0 during summer, and 38.6 during fall. Significantly different (Kruskal Wallis ANOVA on Ranks) patterns of reservoir utilization were detected between spring versus fall locations but not between spring versus summer, and summer versus fall locations.

During 1991 and 1992, female walleye resided primarily in the lower reservoir. In 1991, median reservoir locations were RKM 32.8 during spring, 36.5 during summer, 33.9 during fall. Significantly different (Kruskal Wallis ANOVA on Ranks) utilization was evident between spring versus summer, and summer versus fall locations but not between spring versus fall. During 1992, median reservoir locations of female walleye were RKM 28.6 during spring, 36.0 during summer, and 39.3 during fall (Figure 1). A significantly different (Kruskal Wallis ANOVA on Ranks) pattern of utilization was

detected between spring versus summer, and spring versus fall locations but not between summer versus fall locations.

Home Range Size and Location

Analysis of sizes and locations of home ranges required relocations to be expressed in UTM Coordinates, rather than reservoir kilometer. The Geographical Activity Center (GAC) for individual fish was determined by averaging the north and east UTM coordinates for relocations within a given time period (season, year). GAC statistics used to generate information on home range size and location for individual fish are presented in Appendix C.

Walleye home ranges averaged 6,337 m in diameter during my study. During 1991, the mean home range diameter was 5,835 m, ranging from 1,081 m to 13,009 m (Figure 29). During 1992, the mean home range diameter was 6,924 m and ranged from 2,051 m to 19,138 m.

Sixteen fish were tracked through the entire study. The coefficient of variation (CV) in home range size (diameter) between years was slight ($CV < 0.22$) for 11 of these fish. Five fish (31.3%) exhibited a substantial change in home range size between years; two (#348 and #375) had a greater home range size during 1992 and three (#2237, #249, and #357) had a greater home range size during 1991.

GAC positions of sonic-tagged walleye indicate that they tended to occupy the lower parts of the reservoir, Zones D, E, and F during spring, summer, and fall of both years. GAC positions during spring 1991 (Figure 30) suggest a strong affinity to areas near the Holter Reservoir oxbow (Zone E). GAC positions during spring 1992

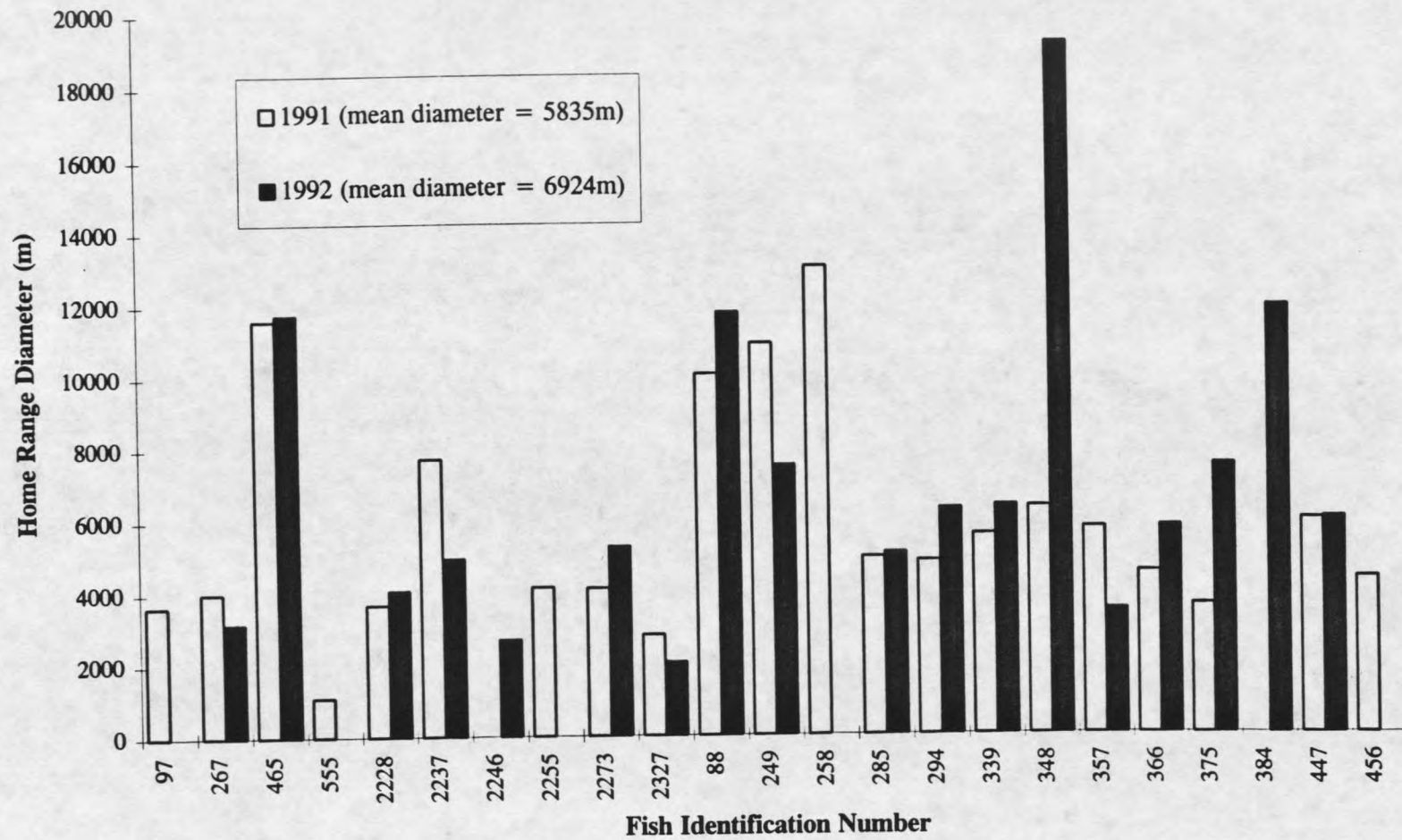


Figure 29. Home range size of adult walleye in Holter Reservoir, 1991-1992.

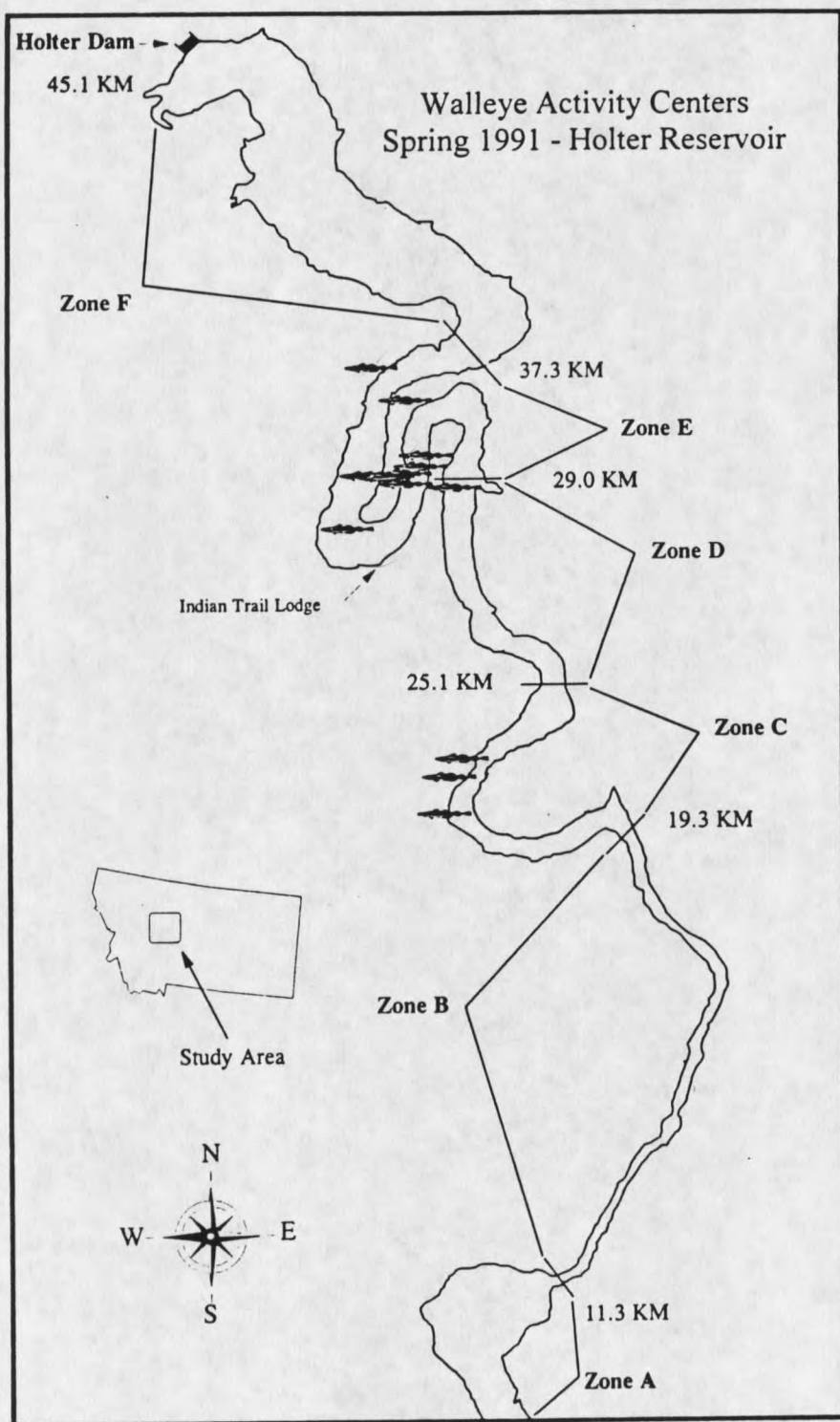


Figure 30. Geographical Activity Centers for individual walleye tracked during the spring of 1991 within Holter Reservoir.

indicated fish used the same general areas, and in addition, Zone D (Figure 31). During the summer months, walleye were generally concentrated within Zones E and F. GAC positions showed a fairly distinct concentration of fish near the boundary between Zones E and F during the summer of 1991 (Figure 32) and dispersal of fish over the lower portion of the reservoir including Zones D, E, and F during summer 1992 (Figure 33). During the fall of 1991, GAC statistics indicated that walleye were widely scattered throughout the lower reservoir in Zones C, D, E, and F (Figure 34). In contrast, tagged walleye were located only in Zones E and F during the fall 1992 (Figure 35).

The GAC values for all 1991 (Figure 36) and all 1992 (Figure 37) walleye relocations indicate a strong preference for residency within the lower portion of the reservoir. Walleye observed during 1991 utilized portions of Zones D, E, and F with the highest utilization in Zone E (Figure 36). This pattern was similar during 1992 as indicated by GAC values for that time period (Figure 37). As expected, utilization over the entire study period (as measured by GAC position) reaffirms the apparent strong preference for lower reservoir habitats (Figure 38).

Movement Rates

Movement rates, computed for walleye with multiple observations within a 24 h period, were highly variable with evidence of distinct seasonal patterns. Movement rates (km/24 h) were greatest during March (Figure 39), averaging 8.2 km/24 h. Mean movement rates during the months of April, May, and June were 3.7, 3.2, and 4.8 km/24 h, respectively (Figure 39). Movement rates during summer were low

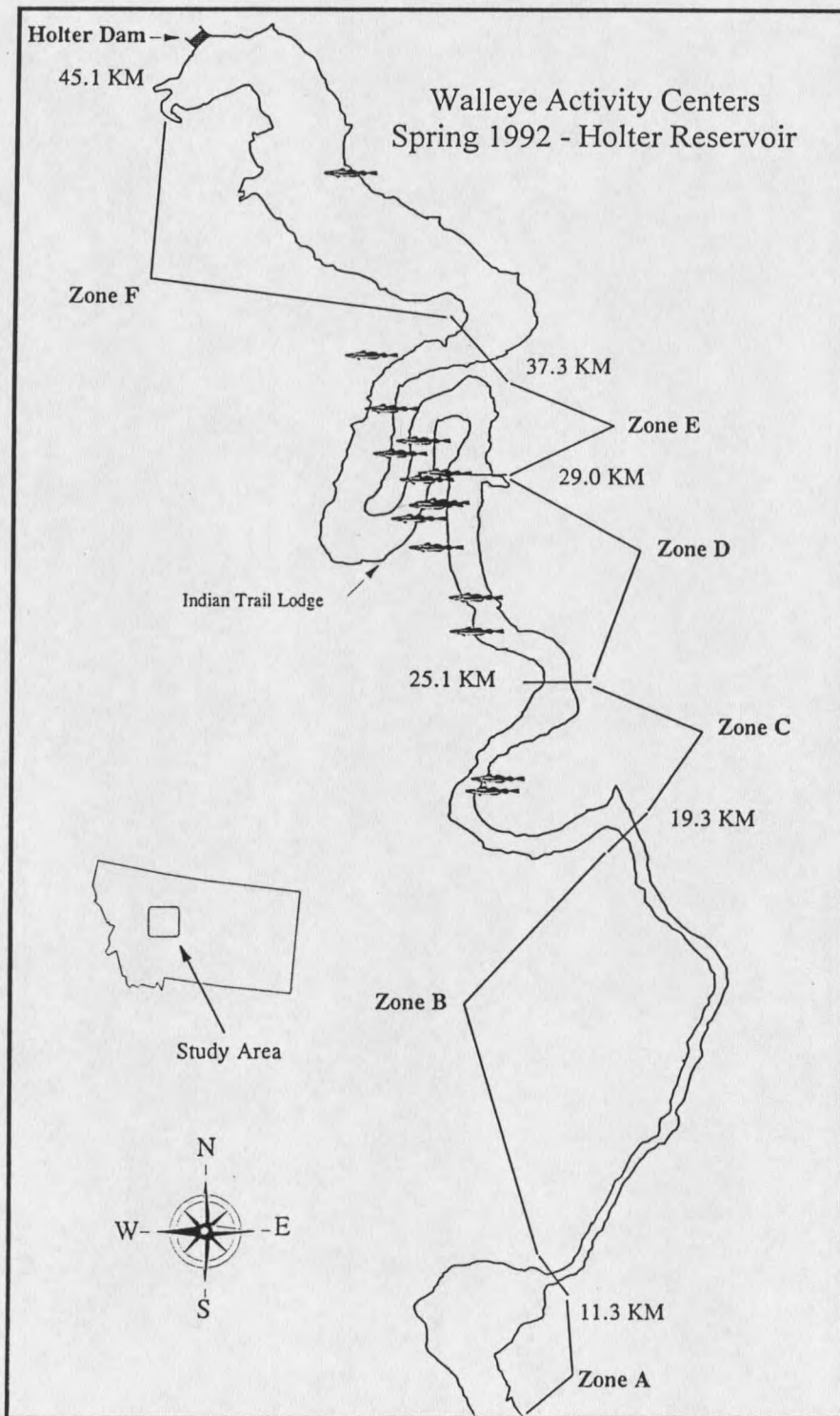


Figure 31. Geographical Activity Centers for individual walleye tracked during the spring of 1992 within Holter Reservoir.

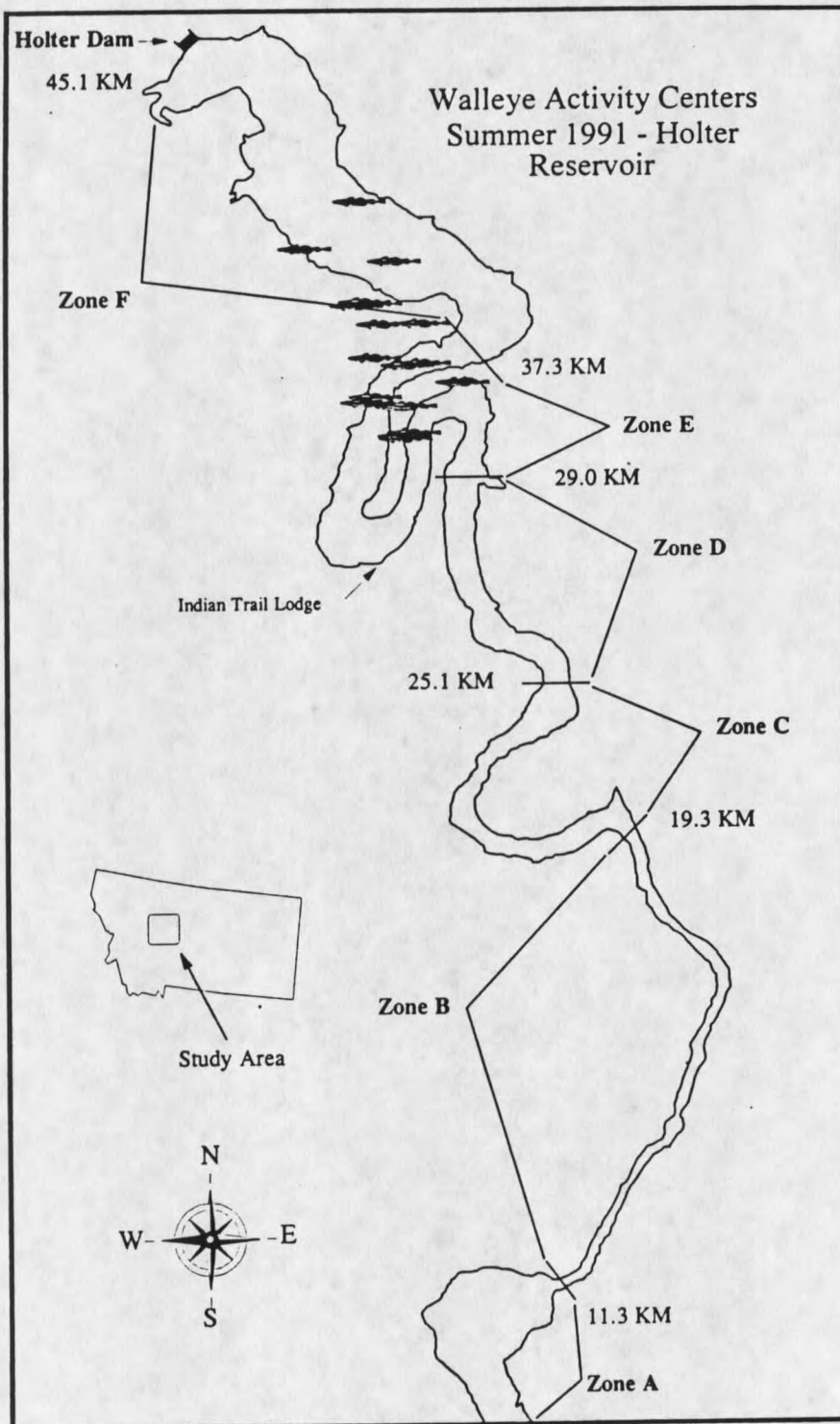


Figure 32. Geographical Activity Centers for individual walleye tracked during the summer of 1991 within Holter Reservoir.

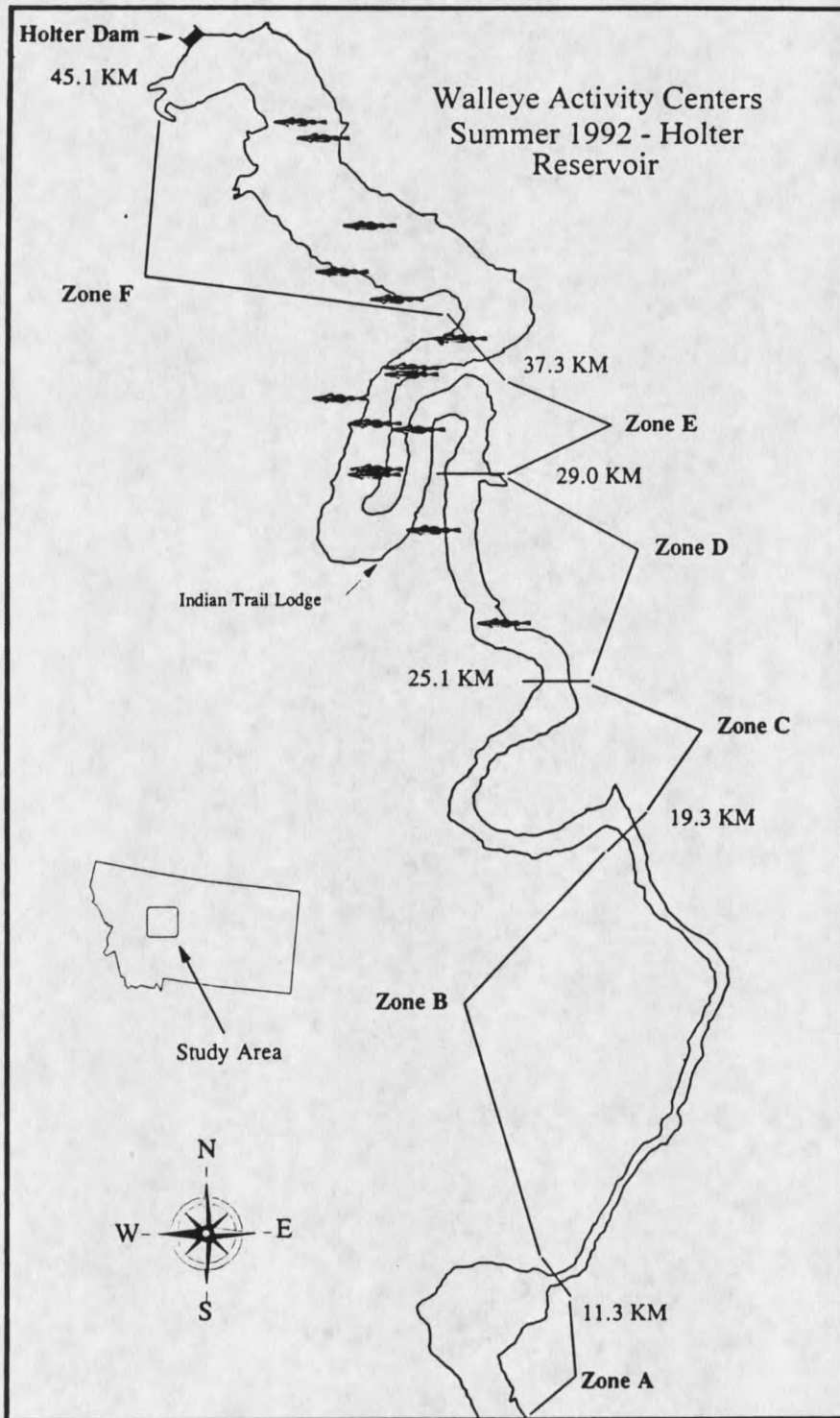


Figure 33. Geographical Activity Centers for individual walleye tracked during the summer of 1992 within Holter Reservoir.

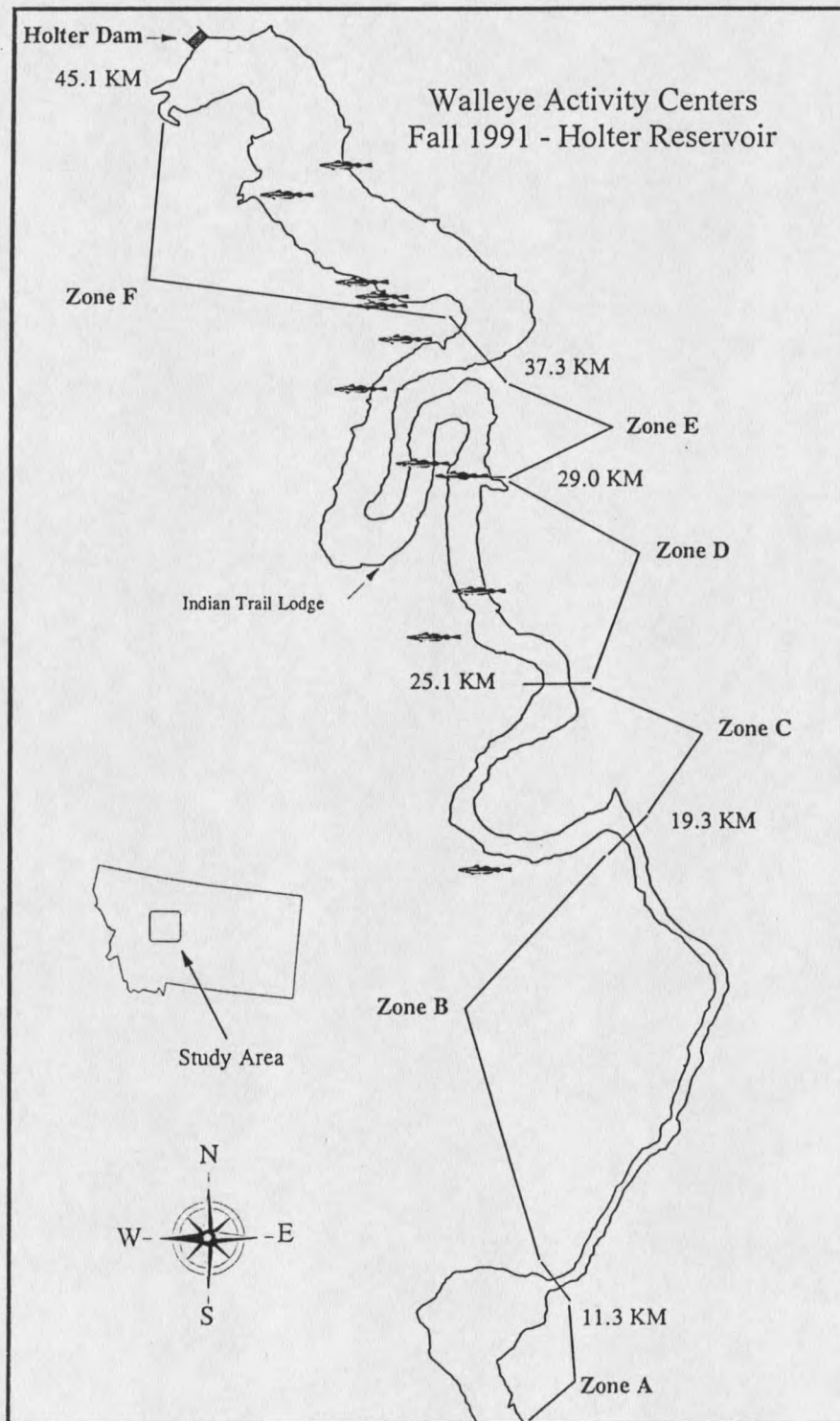


Figure 34. Geographical Activity Centers for individual walleye tracked during the fall of 1991 within Holter Reservoir.

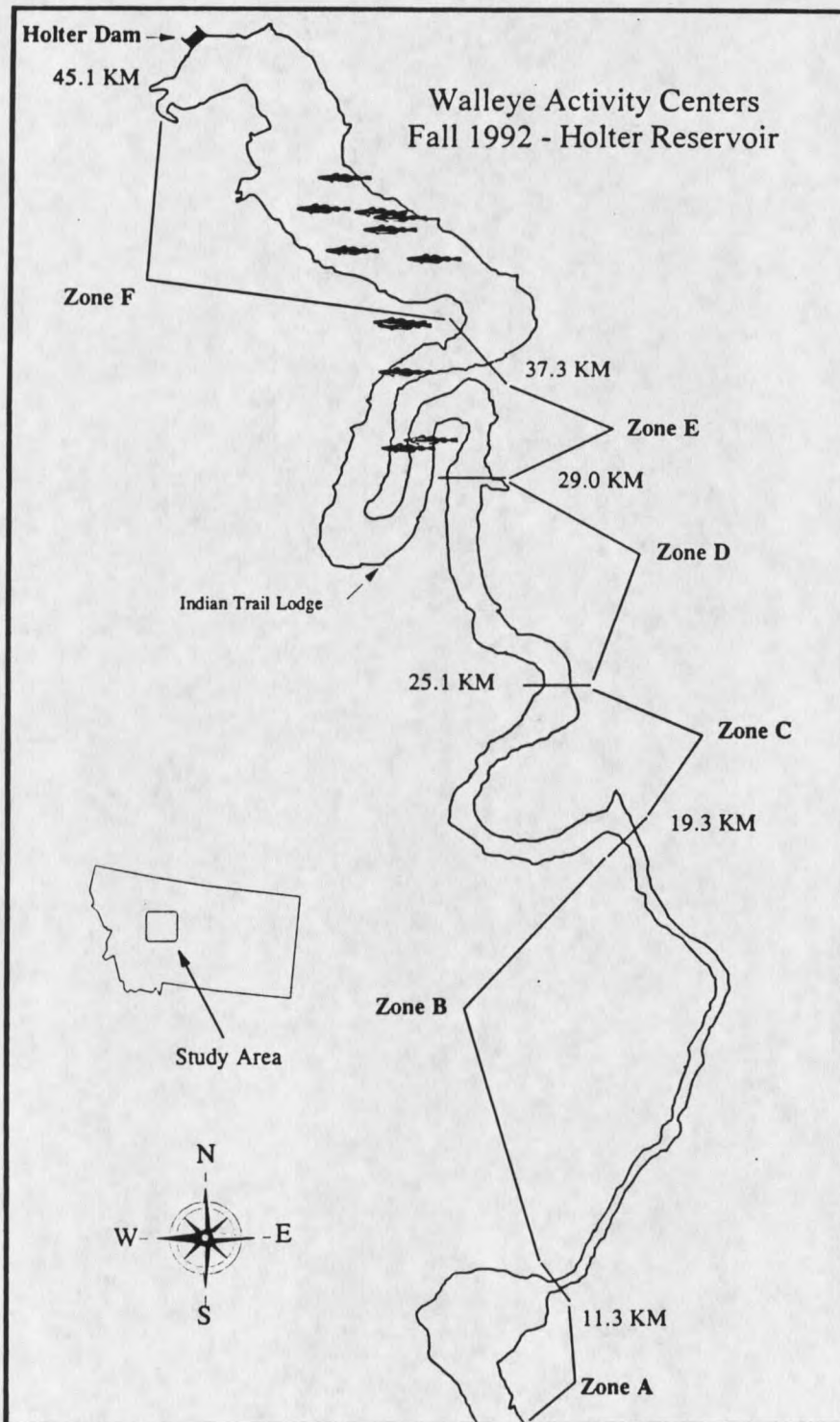


Figure 35. Geographical Activity Centers for individual walleye tracked during the fall of 1992 within Holter Reservoir.

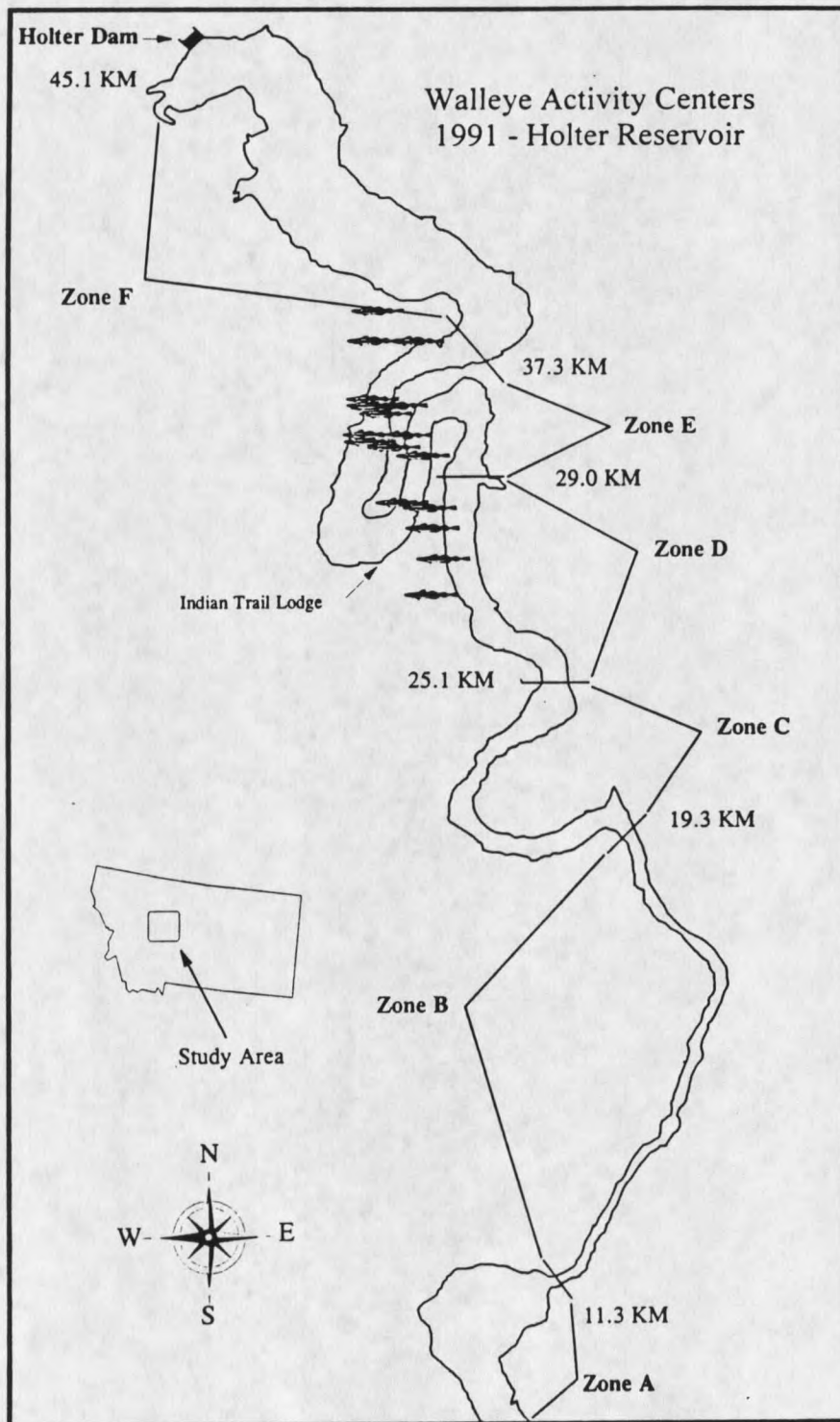


Figure 36. Geographical Activity Centers for individual walleye tracked during 1991 within Holter Reservoir.

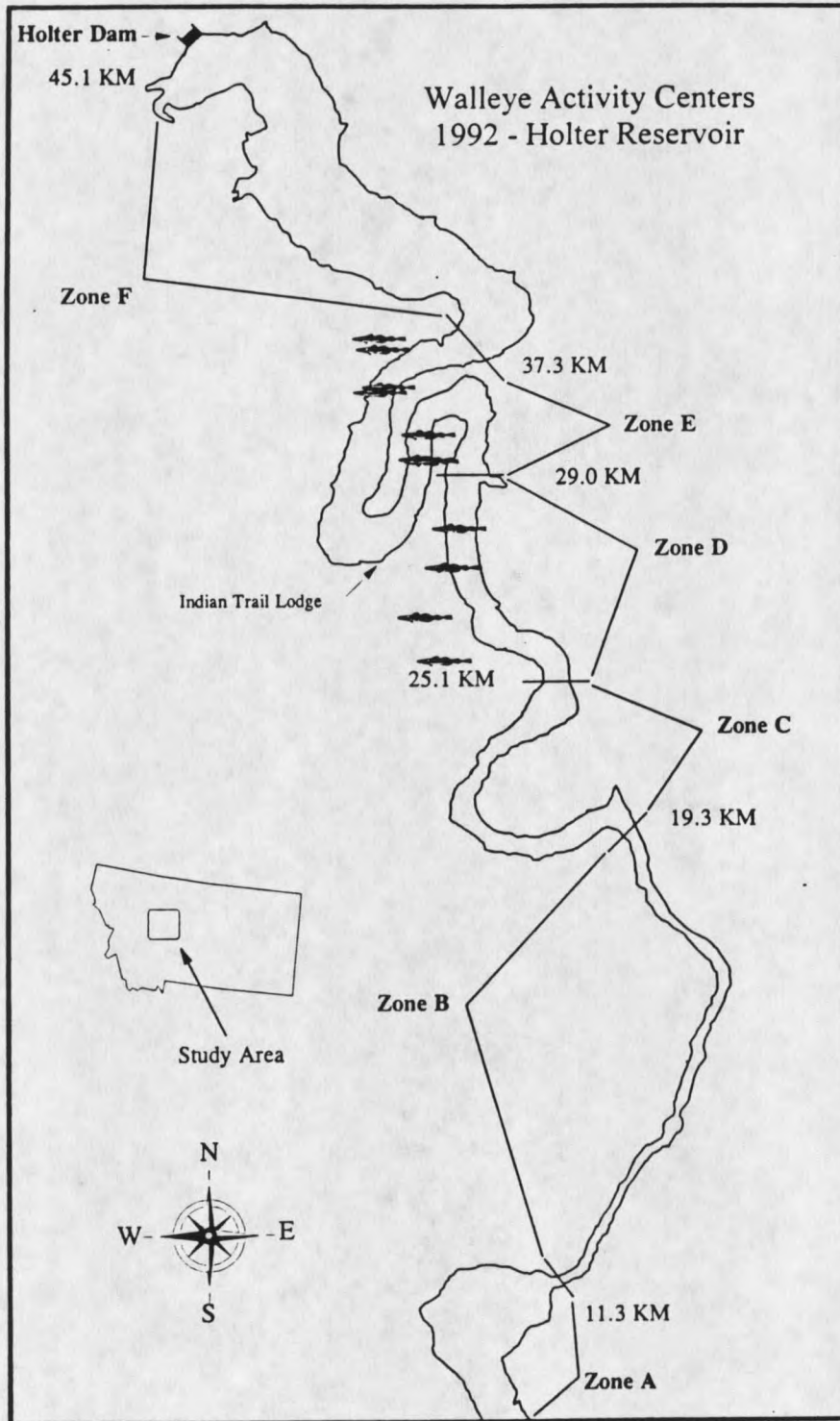


Figure 37. Geographical Activity Centers for individual walleye tracked during 1992 within Holter Reservoir.

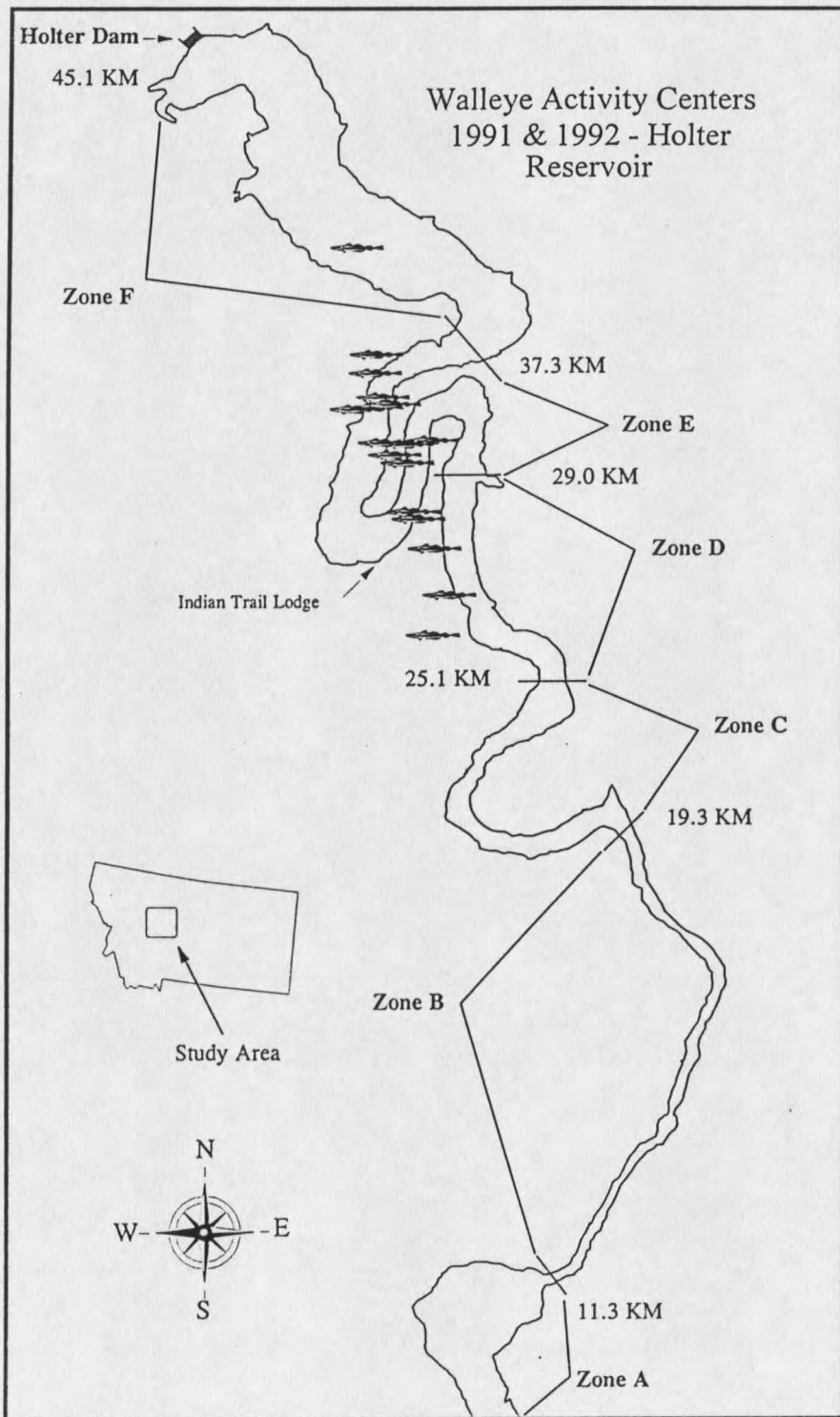


Figure 38. Geographical Activity Centers for individual walleye tracked during 1991 and 1992 within Holter Reservoir.

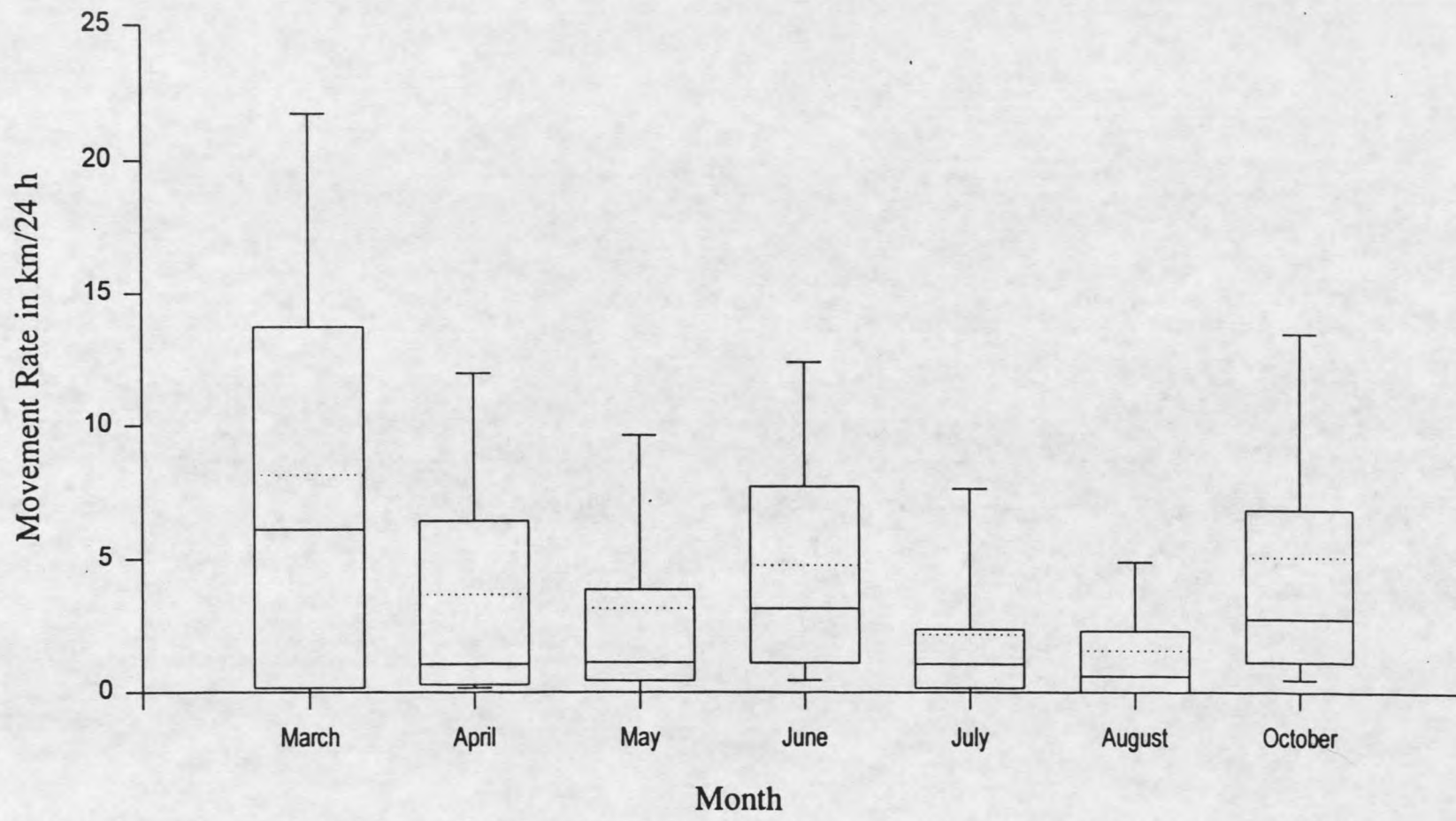


Figure 39. Movement rates (within a 24 hour period) of tagged walleye during the 1991-1992 study period, Holter Reservoir (observations are grouped within months).

averaging 2.2 and 1.6 km/24 h for the months of July and August, respectively (Figure 39). Movement rates during October increased to an average of 5.1 km/24 h (Figure 39).

DISCUSSION

Interpretation of the results of a study of animal behavior requires that the researchers are confident in the validity of the data collected and present assumptions made in the conduct of the study. In my study, as well as other telemetry studies, the long-term effect of the presence of the transmitter on behavior is not known. Several observations during my study, however, suggest that the overall effect of transmitters was minimal: 1) spawning behavior was not suppressed in most of the fish as evidenced by their presence at known spawning areas (EA 1992) soon after the initial recovery period; 2) several transmitter-equipped fish returned to the spawning area 1 year later; and 3) all the fish recovered by angling were reported to have been in excellent condition. Furthermore, inspection of several fish captured by gill net or anglers indicated that tagged fish had grown at normal rates, were feeding actively, and had no obvious inflammation or other problems as a result of the implanted transmitter. However, several tagged fish died within 1 month of surgery, mostly males. These mortalities occurred when fish were implanted with transmitters immediately prior to the onset of spawning. The combined effect of physiological stress related to spawning with that incurred during surgery may have resulted in mortality. Paragamian (1989) reported that several female walleye implanted with transmitters died soon after spawning. No mortalities were evident for fish that had tags implanted well in advance of the spawning season.

The specific locations of tagged fish were defined with a high level of accuracy

during my study. Dead fish, with active transmitters, had their locations consistently pinpointed within a 400 m² area. Signals were identified as coming from dead fish or dropped tags when no movement was evident after numerous tracking episodes.

Although accurate determinations of vertical walleye position were generally not possible, it was assumed that negative phototaxis by walleye would cause the study fish to be located near the bottom of the water column, especially during the day.

Accurate determination of walleye depth (vertical position) was possible on spawning grounds at night through electrofishing and spot lighting (EA 1992). Furthermore, observations of adult walleye conducted while SCUBA diving indicated that walleye were found in close association with the substrate (within 0.5 m). In summary, indications are that the data collected during my study provide an approximation of habitat use and selection by adult walleye within Holter Reservoir.

The results of my study clearly indicate that adult walleye prefer to occupy the lower (northern) portion of the reservoir. This preference is likely attributed to a variety of factors including percentage and absolute amounts of shallow littoral habitats, diversity of depths, current patterns, substrate types, spawning areas, water turbidity, forage fish availability, and other factors.

Seasonal concentrations of fish within the reservoir and individual movement rates provide evidence of habitat preference and spawning behavior. The preference for the lower reservoir was strongest during the summer and fall seasons and weakest during spring (Figure 13 and 17). The relatively greater dispersion of tagged fish during spring coupled with high movement rates (Figure 39), may be related to spawning

behavior, increased water temperature, or increased food availability. Habitat utilization during spring may reflect a pre-spawn foraging behavior, a search for spawning areas, or possibly reflect their distribution during the preceding winter.

The concentration of fish in the lower reservoir and low movement rates observed during the summer months (Figure 13, 17, and 39) provide evidence of a shift in behavior towards utilization of environments where food is most readily available and where feeding efficiency is maximized. This behavioral shift is consistent with other studies across the United States that show that walleye often remain within a relatively small home range which seems to enlarge in the spring (Eschmeyer 1942, Schupp 1972). Schupp (1972) suggested that the mean distance the walleye moved each day was inversely related to the abundance of young-of-the-year yellow perch. He reported that the distance of mean daily movement was large in the spring and fall, and much less during the summer when young-of-the-year yellow perch were readily available. In my study, both rate and distance of movements declined in the summer (Figure 39) corresponding a period starting with the end of breeding activity and followed by probable increased food availability. Eddy and Surber (1960) stated that increasing water temperatures diminished walleye activity and movements during summer.

Ager (1976) noted that spawning was the life history phase which most influenced walleye movement. Spawning behavior in walleye is stimulated by their adaptation to the rising temperatures of spring. Cobb (1923) and Priegel (1970) found that walleye migrated into streams until lake water temperatures became suitable for spawning. Spawning normally begins shortly after ice breaks up on a lake, at water temperatures

of 6.7 to 8.9 °C, but is known to take place over a range of 5.6 to 11.1°C (Scott and Crossman 1973). Initiation of spawning activity at a given location may vary up to 4 weeks among years, depending on yearly variations in spring weather. During the second year of my study (1992), spawning-related movements and associated habitat use appeared to be initiated approximately 1 month earlier than in 1991.

In my study, walleye appeared to stage in upper Holter Reservoir within the Gates of the Mountain area. This behavior may be related to earlier thawing in these areas which could stimulate feeding, or to increased production of food from the outflow of Hauser Dam, or to staging prior to movements into the river section below Hauser Dam for spawning. There are historical accounts of walleye spawning below Hauser Dam. Upstream migrations have been observed within the "rock garden" type habitat 1.6 km below the dam (pers. comm. Frank Pickett (MPC)). This tailwater, riverine area is best described as a relatively deep channel with abundant boulder, and talus slopes and slide areas, which could be favorable spawning habitat for walleye.

Another possible spawning area for Holter Reservoir walleye is also below Hauser Dam, near the mouth of Beaver Creek. During my study, one fish (# 2246) tagged before the spawning season (March 1, 1992) in upper Holter Reservoir disappeared for about 1 month immediately following tag implantation. This fish was later observed in the lower reservoir. The disappearance of fish # 2246 may be indicative of a short term occupancy within the riverine section of Holter Reservoir, below Hauser Dam.

The destination of the initial spawning migration of mature walleye may be guided by currents or the movement of adult walleyes with established movement patterns.

Spawning walleye often migrate short distances between feeding and spawning areas, even though migrations of great distances apparently occur (Colby et al. 1979).

Migration distance is often correlated with the distribution of suitable spawning and feeding areas (Colby et al. 1979). In my study, the distribution of GAC's for all fish are consistent the findings of Colby et al. (1979) as feeding and spawning areas are within relatively close proximity in lower Holter Reservoir (Zones D, E, and F).

The distribution of sonic-tagged walleye during the spring suggested that spawning was concentrated in the Oxbow (Zone E) portion of Holter Reservoir (Figure 14 and 18). While Zone E accounted for only 30.4% of the total reservoir spawning habitat, more fish were located within potential spawning areas in Zone E than in other potential spawning areas, suggesting a preference for habitat available in Zone E, the importance of nearby feeding areas, or perhaps a homing behavior. Suitable spawning habitat is generally not limited for walleye which broadcasts its eggs and utilizes both river and lake shoal environments. Spawning habitat is well distributed throughout Holter Reservoir (Table 5). Olson and Scidmore (1962) report that many walleye marked in the specific spawning runs return to spawn at the same area despite the availability of other spawning areas. In Holter Reservoir, there generally appears to be an abundance of suitable spawning habitat (Table 5). However, certain areas are used more extensively than others, providing evidence that homing behavior may be important for these walleye. Several of my sonic tagged walleye returned to the same general area of the reservoir during the spawning period both years of the study (Figure 14 and 18). Olson et al. (1978) state that homing is probably an adult learned

behavior, influenced by physical characteristics of the environment and strengthened by repeated migrations.

After walleye recover from spawning, they gradually move toward summering areas, dispersing as water temperatures increase. This pattern of movement was evident in my study (Figure 13, 15, 17, and 19). During this period, feeding often becomes the major force dictating their behavior. After spawning, females move away from the shoals and concentrate around points, irregularities on the break line, or the base of off-shore spawning reefs (Sternberg 1986). Adult walleye will spend most of their time in shallow water where prey are plentiful. The tendency towards occupancy of relatively shallow waters was evident in my study (Figure 21). In many mesotrophic lakes, walleye feed primarily on yellow perch, often stalking them at night on shoals less than 1.5 m deep (Galligan 1960, Swenson 1972). Most species of forage fish, including yellow perch, spawn in the spring. The young they produce are usually not consumed by adult walleyes until mid-summer. Because yearling or adult fish are often scarce in spring, most feeding occurs during the summer and autumn and is reduced in the winter, perhaps due to non-availability of forage species in areas frequented by walleyes during winter or reduction of activity by cold temperature (Galligan 1960; Swenson 1972).

Walleye are opportunistic feeders and will prey on any species of fish of suitable size with which it co-occurs on a time-space basis (Ryder and Kerr 1978). If several forage species are available at preferred lengths, walleyes tend to feed on the most abundant species. Analysis of stomach samples extracted from gill netted walleye

indicated that yellow perch comprise a significant portion of the diet of Holter Reservoir walleye (MDFWP 1991, unpublished data). Yellow perch often constitute the primary food of walleye because the perch stay within the preferred forage size range (less than 45% of the walleye length) for a longer period than do such fast-growing forage fishes as freshwater drum, gizzard shad, and white bass which are available as food for only short periods. Yellow perch may therefore not be a preferred food, but only one which is abundant and of suitable size for a longer time than others and therefore predominant in the diet.

While data on perch distribution and abundance in Holter Reservoir were not collected as part of my study, it seems logical to assume that the abundance of young-of-the-year and juvenile yellow perch would be greatest near or downstream of perch spawning sites (EA 1992) or in areas where food resources are abundant. Average abundance of *Daphnia*, a dominant zooplankton in Holter Reservoir and a key component in the yellow perch diet, at the Jackson Limnology Station within Zone F (Figure 1) was 1.5 times greater than that measured at the Cottonwood Limnology Station within Zone D (MDFWP 1992), providing evidence of a more plentiful food supply for forage fish in the lower reservoir. The relative abundance of food in the lower reservoir may partially explain the high degree of walleye utilization in these areas. The percent of littoral habitat, the diversity of depths present, and the presence of turbid water for cover may provide conditions suitable to the production of forage fish.

Depth utilization was highly variable during my study, without significant daily or

seasonal differences. Seasonal trends observed were not consistent between years but significant differences in spring habitat depth were evident. This overall variability is indicative of a broad utilization of depths. Depth selection by adult walleye is usually related to behavior (feeding, spawning) or environmental conditions (light intensity, temperature). Walleye are usually present in 1 to 15 m of water but may occur at depths as great as 27 m (Regier et al. 1969). Bahr (1977) found that walleye in the upper Mississippi River preferred depths < 5 m, and Pitlo (1978) found that walleye had a preference of 2 to 6 m in the summer but went to deeper depths in the fall and spring.

My observations were similar to those of Schupp (1972) who found that walleye moved parallel to the shore and did not show a diel onshore and offshore movement pattern. Schupp (1972) further stated that while there were slight seasonal changes in the extent of the daily movement of test fish, the range of depths used by tagged fish did not change greatly between seasons. I did not detect significant differences in depths of areas used by walleye during day versus night. For a light sensitive species such as walleye, this is unusual. Under turbid conditions, however, lack of diel differences in depth distribution is common (Ryder 1977). In general, the most active feeding times for walleye occur during periods when subsurface illumination is changing most rapidly, usually at dusk and dawn. Nocturnal feeding is common, particularly in clear lakes, and has been shown to be inversely proportional to ambient subsurface illumination which is in turn governed by a variety of exogenous effects, including turbidity, water color, wave action, ambient surface illumination, and other

factors (Ryder 1977). Species normally inhabiting extremely turbid waters intermittently feed through daylight hours as a result of the modified light regime created by suspended matter in the water. Extremely high subsurface light intensities are rarely experienced in these types of environments. The lack of diel change in depth utilization by walleye during my study, may be indicative of strong tendency towards occupancy of shallow, turbid areas during certain times of year.

Diel differences in depth utilization were evident during the spring months in 1991 and 1992. These observed differences were likely related to spawning behavior and localized movements to and from spawning areas during the day. Walleye are essentially nocturnal spawners and usually vacate their shallow-water spawning grounds during the day. It has been hypothesized that as walleyes approach spawning conditions, negative phototaxis may be partially masked through hormonal changes initiated by a photoperiodic control (Ali et al. 1977). Consequently, spawning walleyes may show relatively less negative response to bright light than those engaged in pre-nuptial activity. This decreased negative response continues for about 1 week after completion of spawning and may contribute to good fishing in shallow waters close to the spawning grounds during daylight hours immediately after the eggs have been deposited. The light effect, coupled with the post-spawning physiological need for food can provide improved angling conditions. This effect may be magnified in turbid waters and the successful fishing period extended accordingly (Ali et al. 1977). During the month of May (1991), I located tagged fish during the day in turbid waters less than 3.3 m deep. These fish had been located 3 d earlier on apparent spawning grounds in

close proximity to these feeding areas. The area where these fish were observed was a very popular angling location.

Depths selected by walleye during my study did not appear to be related to thermal conditions within the epilimnion. Ryder (1977) states that walleye are usually found above the thermocline in thermally stratified lakes, although the hypolimnion may be penetrated for feeding forays or to seek shelter in extremely clear lakes. In waters that do not thermally stratify, walleye are less likely to stay at a specific depth. In Holter Reservoir, the high flow-through rate results in weak thermal stratification except in the lowermost portion of the reservoir. These conditions result in the lack of cool-water thermal refugia. Preferred temperatures for walleye are about 20.6 to 23.2 ° C (Hokanson 1977), and such temperatures were widely available in Holter Reservoir.

The morphometry of the Holter Reservoir basin plays an important role in determining habitat use by resident walleye. Habitat structure in the form of woody debris, vegetation, or large boulders is generally lacking in Holter Reservoir. Most suitable habitat for walleye in Holter Reservoir is present either as a result of large areas with favorable depths and/or substrate conditions that create suitable areas for spawning or feeding. In addition to the dominant physical features associated with the general reservoir basin, habitats found along the shoreline are highly influential in determining areas used by walleye.

Habitat suitable for meeting the various life history requirements of adult walleye can be found in both lacustrine and riverine environments. Both of these types of aquatic habitat are accessible to adult walleye residing within Holter Reservoir.

Riverine habitat is present immediately below Hauser Reservoir, lacustrine habitat is present at the northern part of the reservoir near Holter Dam, and habitats displaying intermediate characteristics are found in several narrow, canyon sections of the study area. My study focused on habitat use by adult walleye within impounded areas easily accessible by boat and conducive to the use of ultrasonic telemetry equipment.

However, use of adjacent riverine areas upstream of the impounded areas has been confirmed by MPC personnel (F. Pickett, pers.comm.). In addition, walleye displaced from Holter Reservoir during periods of high outflow, have been captured by anglers in the Missouri River downstream from the reservoir.

Kitchell et al. (1977) proposed that the habitats of walleye in lakes may best be identified by conditions analogous to those found in temperate rivers (Table 8).

Specifically, they contend that the ideal lake habitat may be defined by littoral and sublittoral environmental conditions equivalent to those found in large temperate rivers.

Table 8. Selected criteria of optimum habitat for *Perca spp.* and *Stizostedion spp.* (reprinted from Kitchell et al. 1977)

Variable	Attribute
Lake bathymetry	Shallow-moderately deep
Lake morphometry	Extensive littoral and shoreline area
Substrate	Sand-large gravel, submerged vegetation
Lake size	> 100 ha (<i>Stizostedion spp.</i> only)
Light penetration	Secchi < 2 m (<i>Stizostedion spp.</i> only)
Temp. optimum for growth	< 27-31 ° C (juveniles), < 22-26 ° C (adults)
Temp. optimum for gonad maturation	< 12 ° C during winter
Min. O ₂ at spawning substrate	> 2-4 mg/L

In general, Holter Reservoir does not meet the Kitchell et al. (1977) criteria for optimum habitat for walleye with respect to bathymetry, morphometry, substrate, and light penetration. However, certain characteristics make Holter Reservoir conducive to maintenance of a self-sustaining walleye population. The elongate shape of Holter Reservoir results in habitat characteristics different from many other reservoirs and provides conditions that, in total, are suitable for both lacustrine and riverine stocks of fish [brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), kokanee (*Oncorhynchus nerka*), perch (*Perca flavescens*), and walleye]. The high shoreline development index value for Holter Reservoir is quantitative evidence of its unique shape. Typically, lakes having a lower shoreline development factor support larger walleye populations than those with a higher factor (Johnson and Hale 1963). Holter Reservoir provides diverse conditions that meet varying life history needs of walleye including large areas that approach the Kitchell et al. (1977) criteria for optimal walleye habitat.

Bathymetric surveys indicated that while the percentage of littoral habitat was greatest in upper Holter Reservoir (Zone A), the overall diversity of depths available was low (Table 2). The greatest percentage of littoral habitat in conjunction with the presence of deep water was found in Zone F (Table 2). Littoral habitat for foraging must be found in close association with some form of refuge for walleye during daylight periods of high light intensity. When contrasted with other zones, the habitat conditions within Zone F most closely match the Kitchell et al. (1977) criteria with respect to bathymetry, morphometry, and light penetration.

Substrate conditions within Holter Reservoir are highly variable ranging from silt to boulder talus. While detailed quantification of substrate conditions throughout the reservoir was not completed, a detailed assessment of substrate conditions along the periphery of the reservoir was made. The results of my study, specifically information on depth utilization, indicate that shoreline conditions are often those of greatest importance to adult walleye. The narrow (canyon-like) portions of the upper reservoir typically are composed of firm substrates. In contrast, broad portions of the lower reservoir include littoral areas composed of expanses of clay and silt substrate materials. Over much of their range, walleye appear to generally select clean, hard bottoms with a combination of sand, gravel, and rock substrates rather than bottoms of silt, fine organic sediments, or other soft materials (Olson et al. 1978). I found each of these areas to be important to adult walleye; firm substrates along the shoreline provided spawning areas and the soft substrates often provided areas of diminished light penetration for cover and foraging.

I found walleye to be located over soft bottomed substrates disproportionately more often than these types of substrates were present. Furthermore, consistently more observations were recorded over soft substrates during the day than during the night (Figure 28). These observations are indicative of a preference for occupancy of this type of habitat. Soft-bottomed substrates, comprised largely of colloidal clays, can become suspended by water turbulence at shallow depths and often present conditions where light intensity is conducive to occupancy by walleye. The soft-bottomed substrates present in Holter Reservoir are usually found in close association with

eroding shorelines and provide a temporally stable, turbid habitat conducive to foraging walleye. Areas of enhanced turbidity, associated with eroding shorelines, diminish light intensity in shallow areas occupied by forage fishes. These conditions create a distinct advantage for a light sensitive predator like the walleye as daytime feeding efficiency is maximized. The turbid conditions present in lower Holter serve to lengthen the period of time that optimal levels of light for feeding are available to walleye.

The results of my study indicate that habitat selection is related to water clarity (light penetration). My results are similar to those of Ryder (1977) who stated that light is the principal abiotic variable that determines times and places of feeding and reproduction in walleye. Light conditions are not uniform throughout Holter Reservoir. Areas of more turbid water are most commonly found in the immediate vicinity of clay banks, which occur within the lower portion of the reservoir, downstream of the Gates of the Mountain Recreation Area (Figure 2). The degree of enhanced turbidity and the lateral extent of these turbid "plumes" is variable and dependent on weather conditions, shoreline soil composition, erosion potential, and basin characteristics. These turbid littoral environments typically extend from the shoreline to depths < 10 m, and appear to provide suitable habitat conditions for forage fish species (primarily yellow perch). The amount and location of littoral habitat in a lentic ecosystem typically dictates the availability of habitat for young fishes (i.e. forage for walleye). In Holter Reservoir, most littoral habitat is found in the lower reservoir and often in association with areas prone to increased turbidity.

In my study, the horizontal and vertical distribution of tagged fish was closely tied to water turbidity. The combined presence of erodible shoreline habitat and erosive forces (wind and wave action) resulted in distinct areas frequented by tagged fish. In terms of turbidity, Zone F exhibited characteristics most suitable for walleye. The high percentage (Table 4) and orientation of clay banks in Zone F resulted in highly turbid areas. While fetch was not studied, the predominant wind direction (Figure 8), wind velocity (Figure 9), and reservoir width imply that fetch and associated erosive conditions would be greatest in Zone F.

The results of my study are consistent with those of Ryder (1977) who contends that light levels rather than temperature regulate depth, activity, and feeding for walleye. In clear lakes, walleyes avoid high daytime light levels by a) swimming to deeper water and using the vertical stratum of water as a light filter; b) swimming to a more turbid or usually turbulent portion of the lake; or c) by remaining in shallow water and utilizing some form of physical shelter such as boulders or weed beds to shield themselves from the high subsurface light levels (Ryder 1977). While walleyes may use all three of these methods to avoid high illumination levels, the latter method is more commonly employed, providing that shelter is readily available (Ryder 1977). In Holter Reservoir, there is a general lack of structural complexity and shelter for walleye to escape high illumination levels. As a result, adult walleye must occupy deep or turbid waters to escape conditions of high surface illumination.

In summary, Holter Reservoir provides habitat conditions which meet the various life history needs of adult walleye. Habitat conditions within Holter Reservoir are

highly variable, both spatially and temporally. My study indicated that adult walleye utilize the habitats found within Holter Reservoir in a predictable manner depending on life history needs, with an overall preference towards year-round occupancy of the lower, northern portion of the reservoir.

Management Implications

The fish community of Holter Reservoir is unique as walleye and trout populations co-exist with minimal interaction. The results of my study indicated that the lower reservoir provides habitat conditions most frequently used by adult walleye. In contrast, the upper reservoir may provide suitable conditions for trout and kokanee and a refuge from the potential interactions with walleye. I contend that the combination of the small size of the walleye population and possible spatial segregation between species minimizes interactions between potentially incompatible resources.

The walleye population in Holter Reservoir has remained stable at low density. Colby and Hunter (1989) stated that in certain reservoir situations limited spawning habitat or high flushing rates keep walleye densities low, yet recruitment is sufficient to provide a stable fishery. I found potential spawning habitat to be abundant in Holter Reservoir. I concluded from my study that short retention times impact walleye productivity directly by displacing mature fish and possibly newly emerged fish from the reservoir and indirectly by reducing reservoir productivity. Willis and Stephen (1987) stated that short retention time is not generally considered conducive to the development of large walleye populations.

My study focused on identifying the potential impacts of the MPC's current

operation of Holter Reservoir on walleye habitat and behavior. The MPC's operation of Holter Dam as a run-of-the-river facility results in relatively constant and stable reservoir water levels. However, there have been occasional fluctuations in reservoir levels due to equipment maintenance requirements, short term load control, power peaking requirements, and upstream dam operations. The results of my habitat surveys and telemetry observations indicate that spawning appears to be the life stage most prone to be impacted by fluctuations in reservoir water level. Eggs may be impacted when changes in reservoir water level occur during incubation. Draw downs during the months of March through June should be avoided. In my study, I found that habitat use in Holter Reservoir does not appear to be influenced by current reservoir operations. Furthermore, the current management and operation of Holter Reservoir as a run-of-the-river hydroelectric facility does not appear to alter habitat conditions for adult walleye in Holter Reservoir.

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APPENDICES

APPENDIX A

Soil Erosion Study Results
(Stensatter et al. 1991)

Table 9. Active Erosion Condition site identified along the shoreline of Holter Reservoir (Stensatter, Druyvesten and Associates, 1991).

Zone	Site description	Shoreline length (m)	Bank height (m)		Shoreline slope (%)	Soil type	SCS erosion designation
			Minimum	Maximum			
A	Upper Holter	984	0.6	2.4	6	Silts, fine sands, clays	Moderate
C	Opposite Willow Creek	197	1.2	6.1		Silts and clays	Severe
D	Near Cottonwood Creek	69	1.2	4.6	16	Silts, fine sands, clays	Severe
D	Near Cottonwood Creek	1969	1.5	6.1	8	Silts, fine sands, clays	Severe
D	North of Beartooth Fan	98	0.6	6.1	20	Sands and gravels	Moderate
E	Opposite to Split Rock	886	3.0	9.1	43	Silts and clays	Severe
E	Oxbow Bend	295	0.9	9.1		Silts, fine sands, clays	Severe
E	Near Powerline Crossing	541	1.2	7.6	6	Gravels, sands, silts, clays	Severe
F	Near Boat Loft	30	3.0	9.1	7	Silts, fine sands, clays	Severe
F	Near Boat Loft	344	3.0	9.1	10	Silts, fine sands, clays	Severe
F	Near Boat Loft	197	1.8	4.6	5	Silts, fine sands, clays	Severe
F	Near Falls Gulch	1732	1.2	10.7	12	Silts, fine sands, clays	Severe
F	Near Dam	3465	2.4	10.7	8	Silts, fine sands, clays	Severe
F	Opposite to Log Gulch	1772	1.8	12.2	10	Silts, fine sands, clays	Severe
Total Length (m)		12579					
Total Length (miles)		7.82					

APPENDIX B

Monthly Temperature Profiles

Table 10. Monthly temperature profiles at the Cottonwood limnology station - Holter Reservoir, 1991.

Water Temperature (degrees Celsius)								
Depth (m)	Apr-91	May-91	Jun-91	Jul-91	Aug-91	Sep-91	Oct-91	Nov-91
0.0	6.4	14.4	14.4	19.4	21.1	15.6		5.0
0.9	6.4	13.3	14.4	18.9	21.1	15.6		5.0
1.8	6.4	12.2	14.2	18.9	21.1	15.3		5.0
2.7	6.1	11.7	13.9	18.6	21.1	15.0		4.7
3.7	5.8	11.7	13.9	18.3	21.1	15.0		4.4
4.6	5.8	11.4	13.9	18.1	20.6	15.0		4.4
5.5	5.8	11.1	13.9	16.9	18.9	15.0		4.4
6.4	5.6	10.8	13.6	16.4	18.6	15.0		4.4
7.3	5.6	10.6	13.3	15.8	18.3	15.0		4.4
8.2	5.6	10.3	12.8	15.8	17.8	15.0		4.4
9.1	5.6	10.0	12.8	15.6	17.5	15.0		4.4
10.1	5.6	10.0	12.2	15.6	17.5	15.0		4.4
11.0	5.6	9.4	11.7	15.3	17.2	15.0		4.4
11.9	5.6	8.9	11.4	15.3	17.2	15.0		4.4
12.8	5.6	8.3	11.1	15.0	17.2	15.0		4.4
13.7	5.6	8.3	11.1	15.0	17.2	15.0		4.4
14.6	5.6	8.1	11.1	14.7	17.2	15.0		4.4
15.5	5.6	7.8	11.1	14.4	16.9	15.0		4.4
16.5	5.6	7.2	11.1	14.4	16.7	15.0		4.4
17.4		7.2		14.2	16.1			4.4

Table 11. Monthly temperature profiles at the Cottonwood limnology station - Holter Reservoir, 1992.

Depth (m)	Water Temperature (degrees Celsius)							
	Apr-92	May-92	Jun-92	Jul-92	Aug-92	Sep-92	Oct-92	Nov-92
0.0	8.9	11.7	18.9	18.6	19.4	14.4	10.6	6.7
0.9	8.9	11.7	18.3	18.6	19.4	14.4	10.6	6.7
1.8	8.3	11.7	17.8	18.6	19.4	14.4	10.6	6.7
2.7	7.2	11.7	17.8	18.6	19.4	14.2	10.6	6.7
3.7	6.7	11.7	17.5	18.6	19.4	14.2	10.6	6.7
4.6	6.7	11.7	17.2	18.6	19.4	14.2	10.6	6.7
5.5	6.7	11.7	16.7	18.6	19.4	13.9	10.3	6.7
6.4	6.7	11.4	16.1	18.3	19.4	13.9	10.3	6.7
7.3	6.7	11.4	16.1	18.3	19.2	13.9	10.3	6.7
8.2	6.7	11.4	15.6	18.3	18.9	13.9	10.3	6.7
9.1	6.4	11.4	15.0	18.1	18.9	13.9	10.0	6.7
10.1	6.4	11.1	14.4	17.2	18.9	13.9	10.0	6.7
11.0	6.4	8.9	14.2	16.4	18.3	13.9	10.0	6.7
11.9	6.4	8.6	13.9	16.4	17.8	13.9	10.0	6.7
12.8	6.4	8.3	13.9	15.8	17.2	13.9	10.0	6.7
13.7	6.4	8.3	13.9	15.6	16.9	13.9	10.0	6.7
14.6	6.4	8.1	13.3	15.0	16.7	13.9	10.0	6.7
15.5	6.1	7.8	13.3	15.0	15.6	13.9	10.0	6.7
16.5	6.1		12.8	15.0	15.6	13.6		

Table 12. Monthly temperature profiles at the Jackson limnology station - Holter Reservoir, 1991.

Depth (m)	Water Temperature (degrees Celsius)							
	Apr-91	May-91	Jun-91	Jul-91	Aug-91	Sep-91	Oct-91	Nov-91
0.0	4.7	16.1	14.4	20.6	21.7	15.8		5.3
0.9	4.7	13.9	14.4	20.6	21.7	15.6		5.3
1.8	4.7	13.3	14.4	20.3	21.7	15.6		5.3
2.7	4.7	13.3	14.4	20.0	21.4	15.6		5.3
3.7	4.7	13.1	14.2	19.2	21.4	15.6		5.3
4.6	4.7	12.8	14.2	17.2	21.4	15.6		5.0
5.5	4.7	11.7	14.2	16.7	20.0	15.6		4.4
6.4	4.7	11.1	13.9	16.1	18.9	15.6		4.4
7.3	4.7	11.1	12.2	15.6	18.3	15.6		4.4
8.2	4.7	10.6	12.2	15.6	17.8	15.6		4.4
9.1	4.7	10.0	11.9	15.3	17.8	15.6		4.4
10.1	4.7	10.0	11.7	15.0	17.5	15.6		4.4
11.0	4.7	9.7	11.1	14.4	17.2	15.6		4.4
11.9	4.7	9.4	11.1	14.4	17.2	15.6		4.4
12.8	4.7	9.2	11.1	14.4	16.9	15.6		4.4
13.7	4.4	8.9	10.0	14.2	16.7	15.6		4.4
14.6	4.4	8.9	10.0	13.9	16.7	15.6		4.4
15.5	4.4	8.6	9.4	13.9	16.4	15.6		4.4
16.5	4.4	8.3	9.4	13.6	16.1	15.6		4.4
17.4	4.4	7.8	8.3	13.3	15.6	15.6		3.9
18.3	4.4	7.2	7.8	13.3	13.9	15.6		3.9
19.2	4.4	7.2	7.8	13.3	12.2	14.4		3.9
20.1	4.4	7.2	7.2	12.8	11.7	13.6		3.9
21.0	4.4	6.9	7.2	12.2	11.1	12.5		3.9
21.9	4.4	6.9	7.2	11.4	10.0	11.4		3.9
22.9	4.4	6.9	7.2	10.3	9.4	10.8		3.9
23.8	4.4	6.9	6.7	9.4	8.9	10.0		3.9
24.7	4.4	6.9	6.7	8.6	8.3	9.7		3.6
25.6	4.4	6.7	6.7	8.3	7.8	9.4		3.3
26.5	4.2	6.7	6.7	8.3	7.8	8.9		3.3
27.4	4.2	6.7	6.7	8.1	7.5	8.9		3.3
28.3	4.2	6.7	6.7	8.1	7.5	8.9		3.3
29.3	4.2	6.7	6.7	7.8	7.5	8.9		3.3

Table 13. Monthly temperature profiles at the Jackson limnology station - Holter Reservoir, 1992.

Depth (m)	Water Temperature (degrees Celsius)							
	Apr-92	May-92	Jun-92	Jul-92	Aug-92	Sep-92	Oct-92	Nov-92
0.0	10.6	11.1	18.9	18.9	19.4	14.4	11.7	7.8
0.9	8.3	11.1	18.9	18.9	19.4	14.4	11.7	7.8
1.8	7.2	11.1	18.3	18.9	19.4	14.4	11.7	7.8
2.7	6.7	11.1	18.3	18.9	19.4	14.4	11.4	7.8
3.7	6.7	11.1	17.8	18.6	19.4	14.4	11.4	7.8
4.6	6.1	11.1	17.8	18.6	19.4	14.4	11.1	7.8
5.5	6.1	11.1	17.2	18.3	19.4	14.4	11.1	7.8
6.4	6.1	11.1	16.7	18.3	19.4	14.4	11.1	7.8
7.3	5.8	11.1	16.1	18.3	19.4	14.4	11.1	7.8
8.2	5.8	11.1	15.3	18.3	19.4	14.2	11.1	7.8
9.1	5.6	11.1	14.4	18.3	19.4	14.2	11.1	7.8
10.1	5.6	10.8	14.4	17.2	18.3	14.2	11.1	7.8
11.0	5.6	10.6	14.2	16.7	17.2	14.2	11.1	7.8
11.9	5.6	10.3	13.6	16.7	16.9	14.2	11.1	7.8
12.8	5.6	10.0	13.3	16.1	16.7	14.2	11.1	7.8
13.7	5.6	9.4	13.1	15.0	16.4	13.9	11.1	7.8
14.6	5.6	8.3	12.8	14.7	16.1	13.9	11.1	7.8
15.5	5.6	8.1	11.7	14.2	15.3	13.9	11.1	7.8
16.5	5.6	7.8	10.6	12.8	13.3	13.9	11.1	7.8
17.4	5.6	7.8	10.0	11.4	12.2	13.6	11.1	7.8
18.3	5.6	7.8	9.4	10.3	10.8	13.3	11.1	7.5
19.2	5.6	7.5	8.9	9.7	10.0	13.3	11.1	7.2
20.1	5.6	7.2	8.3	9.4	9.4	13.3	11.1	7.2
21.0	5.6	7.2	8.3	8.9	9.2	13.3	11.1	7.2
21.9	5.6	7.2	8.1	8.9	8.9	13.3	11.1	7.2
22.9	5.6	7.2	7.8	8.3	8.6	9.4	11.1	7.2
23.8	5.6	7.2	7.8	8.3	8.3	9.4	11.1	7.2
24.7	5.6	7.2	7.8	8.1	8.3	9.4	11.1	7.2
25.6	5.3	7.2	7.8	7.8	8.1	8.9	11.1	7.2
26.5	5.3	7.2	7.8	7.8	7.8	8.9	10.0	7.2
27.4	5.3	7.2	7.5	7.8	7.8	8.9	9.7	7.2
28.3	5.3	7.2	7.2	7.8	7.8	8.6	9.4	7.2
29.3	5.3	7.2	7.2		7.8	8.6		7.2
30.2		7.2				8.6		

APPENDIX C

Home Range Statistics
for Individual Fish

Table 14. Geographical Activity Center statistics for individual fish, Holter Reservoir, 1991-1992.

Fish ID number	Sex	Year	Season	Number of observations	GAC (UTM Coordinates)				Mean distance to GAC		Standard diameter
					X	STD	Y	STD	STD	STD	
97	Male	1991	Spring	11	426,201	275	5,197,495	808	749	409	
			Summer	10	426,450	756	5,199,871	1,629	1,635	742	
			Fall	<i>Mortality</i>							
			Mean of Seasonal GAC's	"	"						
			Mean of all observations within year	21	426,320	572	5,198,627	1,736	1,629	829	3,655
97	Male	1992	Spring	<i>Mortality</i>							
			Summer	"	"						
			Fall	"	"						
			Mean of Seasonal GAC's	"	"						
			Mean of all observations within year	"	"						
Mean of all observations during study	"	"									
267	Male	1991	Spring	13	426,720	621	5,198,333	1,627	1,598	694	
			Summer	12	426,555	782	5,198,700	1,681	1,580	969	
			Fall	3	426,238	269	5,199,413	3,086	2,914	1,051	
			Mean of Seasonal GAC's		426,504		5,198,815				
			Mean of all observations within year	28	426,598	686	5,198,606	1,889	1,709	1,058	4,019
267	Male	1992	Spring	12	427,002	570	5,197,669	1,687	1,285	1,232	
			Summer	6	426,341	433	5,198,357	634	684	348	
			Fall								
			Mean of Seasonal GAC's								
			Mean of all observations within year	18					1,194	1,043	3,170
Mean of all observations during study	46	426,670	664	5,198,329	1,769	1,494	1,157	3,779			

Table 14. Continued.

Fish ID number	Sex	Year	Season	Number of observations	GAC (UTM Coordinates)				Mean distance to GAC		Standard diameter
					X	STD	Y	STD	STD	STD	
276	Male	1991	Spring	<i>Mortality</i>							
			Summer	" "							
			Fall	" "							
			Mean of Seasonal GAC's	" "							
			Mean of all observations within year	" "							
276	Male	1992	Spring	" "							
			Summer	" "							
			Fall	" "							
			Mean of Seasonal GAC's	" "							
			Mean of all observations within year	" "							
Mean of all observations during study				" "							
465	Male	1991	Spring	13	427,983	637	5,192,919	5,139	4,970	1,454	
			Summer	13	426,465	1,450	5,201,298	2,374	2,479	1,260	
			Fall	2	426,845	36	5,200,191	548	549	0	
			Mean of Seasonal GAC's		427,098		5,198,136				
			Mean of all observations within year	28	427,197	1,307	5,197,329	5,642	4,478	3,672	11,582
465	Male	1992	Spring	13	427,747	773	5,193,520	4,778	4,445	1,916	
			Summer	4	425,513	1,049	5,203,206	2,014	1,954	1,158	
			Fall	4	427,100	817	5,201,094	806	992	577	
			Mean of Seasonal GAC's		426,787		5,199,273				
			Mean of all observations within year	21	427,198	1,199	5,196,808	5,746	4,451	3,826	11,740
Mean of all observations during study				49	427,198	1,262	5,197,106	5,693	4,484	3,727	11,661

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance		Standard Diameter	
					X	STD	Y	STD	to GAC		STD
2237	Male	1991	Spring	5	426,890	396	5,198,310	920	823	570	
			Summer	6	426,047	767	5,199,191	2,569	2,226	1,493	
			Fall	2	428,000	1,000	5,192,428	5,762	5,848	ERR	
			Mean of Seasonal GAC's		426,979		5,196,643				
			Mean of all observations within year	13	426,672	977	5,197,811	3,730	2,496	2,939	7,711
2237	Male	1992	Spring	7	427,127	907	5,197,045	2,183	1,738	1,602	
			Summer	4	428,250	663	5,195,950	768	947	365	
			Fall	3	426,604	228	5,200,396	611	624	190	
			Mean of Seasonal GAC's		427,327		5,197,797				
			Mean of all observations within year	14	427,336	961	5,197,450	2,284	2,078	1,350	4,956
			Mean of all observations during study	27	427,016	1,024	5,197,624	3,072	2,331	2,247	6,476
2246	Male	1991		<i>Not Deployed</i>							
2246	Male	1992	Spring	7	426,955	931	5,197,595	978	1,198	623	2,701
			Summer	<i>Mortality</i>							
			Fall	"	"						
			Mean of Seasonal GAC's	"	"						
			Mean of all observations within year	"	"						
			Mean of all observations during study	"	"						

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance		Standard Diameter	
					X	Y	STD	to GAC	STD		
2255	Male	1991	Spring	8	426,438	741	5,198,161	1,490	1,511	697	
			Summer	11	426,272	617	5,199,513	2,137	1,968	1,035	
			Fall	1							
Mean of Seasonal GAC's											
Mean of all observations within year				20	426,392	694	5,198,962	1,957	1,833	975	4,152
2255	Male	1992	Spring	<i>Mortality</i>							
			Summer	" "							
			Fall	" "							
Mean of Seasonal GAC's				" "							
Mean of all observations within year				" "							
Mean of all observations during study				" "							
2264	Male	1991	Spring	<i>Mortality</i>							
			Summer	" "							
			Fall	" "							
Mean of Seasonal GAC's				" "							
Mean of all observations within year				" "							
2264	Male	1992	Spring	" "							
			Summer	" "							
			Fall	" "							
Mean of Seasonal GAC's				" "							
Mean of all observations within year				" "							
Mean of all observations during study				" "							

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance		Standard Diameter	
					X	STD	Y	STD	to GAC		STD
2273	Male	1991	Spring	4	426,328	824	5,199,702	1,599	1,660	694	
			Summer	7	427,309	504	5,199,513	1,249	1,237	532	
			Fall	3	425,849	508	5,202,659	1,341	1,333	529	
Mean of Seasonal GAC's					426,495		5,200,625				
Mean of all observations within year				14	426,716	870	5,200,241	1,870	1,827	957	4,124
2273	Male	1992	Spring	14	425,868	1,655	5,202,541	1,792	2,353	644	
			Summer	5	425,728	1,158	5,201,183	2,569	2,575	1,144	
			Fall	4	426,369	1,569	5,201,781	2,156	2,577	683	
Mean of Seasonal GAC's					425,988		5,201,835				
Mean of all observations within year				23	425,924	1,559	5,002,114	2,125	2,472	914	5,272
Mean of all observations during study				37	426,224	1,394	5,201,405	2,226	2,406	1,053	5,253
2327	Male	1991	Spring	7	426,867	595	5,198,095	632	817	292	
			Summer	8	426,780	457	5,199,324	1,535	1,396	785	
			Fall	1							
Mean of Seasonal GAC's											
Mean of all observations within year				16	426,833	513	5,198,716	1,313	1,193	751	2,819
2327	Male	1992	Spring	11	427,124	404	5,198,447	1,037	858	710	
			Summer	5	426,793	271	5,198,598	675	659	308	
			Fall	4	426,706	521	5,198,419	849	888	451	
Mean of Seasonal GAC's					426,874		5,198,488				
Mean of all observations within year				20	426,958	444	5,198,479	925	820	616	2,051
Mean of all observations during study				36	426,902	480	5,198,584	1,120	985	718	2,437

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance		Standard Diameter	
					X	STD	Y	STD	to GAC		STD
88	Female	1991	Spring	10	427,552	717	5,193,228	4,842	4,251	2,427	
			Summer	11	427,132	929	5,200,383	1,704	1,675	981	
			Fall	1							
Mean of Seasonal GAC's											
Mean of all observations within year				22	427,390	883	5,196,888	4,946	4,007	3,030	10,048
88	Female	1992	Spring	11	427,896	1,273	5,193,752	6,013	5,637	2,449	
			Summer	6	425,785	794	5,199,129	2,690	2,535	1,200	
			Fall								
Mean of Seasonal GAC's											
Mean of all observations within year				18	427,194	1,481	5,195,952	5,683	5,005	3,073	11,746
Mean of all observations during study				40	427,302	1,194	5,196,467	5,311	4,462	5,311	10,887
249	Female	1991	Spring	18	427,446	1,004	5,194,216	5,991	5,581	2,399	
			Summer	11	426,887	1,029	5,199,792	1,892	1,630	1,408	
			Fall	3	427,365	909	5,198,183	1,485	1,703	360	
Mean of Seasonal GAC's					427,233		5,197,397				
Mean of all observations within year				32	427,246	1,037	5,196,504	5,343	4,188	3,477	10,886
249	Female	1992	Spring	12	427,226	1,443	5,197,762	4,251	3,333	3,007	
			Summer	6	426,893	482	5,199,619	137	402	299	
			Fall	5	426,948	1,268	5,198,738	3,354	3,183	1,652	
Mean of Seasonal GAC's					427,022		5,198,706				
Mean of all observations within year				23	427,079	1,233	5,198,459	3,536	2,699	2,595	7,489
Mean of all observations during study				55	427,176	1,127	5,197,322	4,772	3,599	3,329	9,806

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)				Mean Distance		Standard Diameter
					X	STD	Y	STD	to GAC	STD	
258	Female	1991	Spring	15	427,379	1,535	5,193,720	6,321	6,159	2,091	13,009
			Summer	<i>Mortality</i>							
			Fall	"	"						
			Mean of Seasonal GAC's	"	"						
			Mean of all observations within year	"	"						
				"	"						
				"	"						
258	Female	1992	Spring	"	"						
			Summer	"	"						
			Fall	"	"						
			Mean of Seasonal GAC's	"	"						
			Mean of all observations within year	"	"						
				"	"						
			Mean of all observations during study	"	"						
285	Female	1991	Spring	15	426,487	485	5,197,651	476	523	434	
			Summer	11	426,069	1,101	5,200,465	2,708	2,738	1,025	
			Fall	3	426,389	1,460	5,200,690	1,727	2,209	483	
			Mean of Seasonal GAC's		426,315		5,199,602				
			Mean of all observations within year	29	426,318	917	5,199,033	2,293	2,100	1,299	4,939
285	Female	1992	Spring	14	426,638	952	5,198,243	1,791	1,619	1,221	
			Summer	4	426,679	633	5,199,494	1,248	1,365	310	
			Fall	5	425,689	1,391	5,202,176	1,533	2,009	503	
			Mean of Seasonal GAC's		426,335		5,199,971				
			Mean of all observations within year	23	426,439	1,095	5,199,316	2,284	2,250	1,164	5,066
			Mean of all observations during study	52	426,372	1,001	5,199,158	2,293	2,180	1,229	5,005

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)				Mean Distance to GAC		Standard Diameter
					X	STD	Y	STD		STD	
294	Female	1991	Spring	12	427,026	635	5,198,302	1,303	1,163	865	
			Summer	12	426,208	944	5,202,046	1,134	1,454	254	
			Fall	3	425,277	303	5,202,183	767	783	259	
			Mean of Seasonal GAC's		426,170		5,200,844				
			Mean of all observations within year	27	426,468	955	5,200,397	2,215	2,239	897	4,824
294	Female	1992	Spring	12	427,627	1,096	5,196,409	2,939	2,357	2,070	6,273
			Summer	<i>Mortality</i>							
			Fall	" "							
			Mean of Seasonal GAC's	" "							
			Mean of all observations within year	" "							
Mean of all observations during study	39	426,825	1,134	5,199,170	3,073	2,619	1,967	6,551			
339	Female	1991	Spring	10	426,836	942	5,199,285	2,470	1,976	1,756	
			Summer	14	426,078	1,190	5,200,542	2,356	2,392	1,115	
			Fall	3	426,000	1,190	5,201,119	2,609	2,741	845	
			Mean of Seasonal GAC's		426,305		5,200,315				
			Mean of all observations within year	27	426,350	1,166	5,200,141	2,521	2,290	1,572	5,555
339	Female	1992	Spring	13	427,092	786	5,198,154	2,335	1,975	1,472	
			Summer	5	425,419	939	5,203,271	1,127	1,316	648	
			Fall	5	425,449	453	5,201,785	1,545	1,361	860	
			Mean of Seasonal GAC's		425,987		5,201,070				
			Mean of all observations within year	23	426,371	1,123	5,200,056	2,969	2,978	1,101	6,349
Mean of all observations during study	50	426,360	1,147	5,200,102	2,737	2,606	1,419	5,934			

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)				Mean Distance		Standard Diameter
					X	STD	Y	STD	to GAC	STD	
348	Female	1991	Spring	10	427,431	469	5,197,950	2,501	2,171	1,327	
			Summer	13	426,688	656	5,198,694	1,357	1,235	864	
			Fall	1							
Mean of Seasonal GAC's											
Mean of all observations within year				24	427,082	755	5,197,875	3,063	2,165	2,295	6,310
348	Female	1992	Spring	8	427,813	921	5,187,597	9,958	7,243	6,896	
			Summer	6	426,188	519	5,198,996	2,069	1,781	1,174	
			Fall								
Mean of Seasonal GAC's											
Mean of all observations within year				14				7,667	5,725	19,138	
Mean of all observations during study				38	427,095	905	5,195,888	6,780	4,507	5,145	13,681
357	Female	1991	Spring	13	426,352	1,070	5,197,778	2,011	1,675	1,544	
			Summer	11	426,145	1,100	5,200,768	2,086	2,093	1,087	
			Fall	2	427,178	1,512	5,195,690	1,238	1,954	ERR	
Mean of Seasonal GAC's					426,558		5,198,079				
Mean of all observations within year				26	426,328	1,154	5,198,883	2,623	2,371	1,608	5,730
357	Female	1992	Spring	12	426,925	860	5,197,304	890	1,153	450	
			Summer	6	427,421	549	5,200,013	804	917	325	
			Fall								
Mean of Seasonal GAC's											
Mean of all observations within year				18				1,531	824	3,477	
Mean of all observations during study				44	426,640	1,092	5,198,606	2,268	2,079	1,420	5,035

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance		Standard Diameter	
					X	STD	Y	STD	to GAC		STD
366	Female	1991	Spring	10	426,160	1,013	5,199,912	1,629	1,757	771	
			Summer	11	426,750	752	5,199,238	1,923	1,521	1,397	
			Fall	3	427,746	749	5,196,579	1,246	1,215	798	
Mean of Seasonal GAC's											
Mean of all observations within year				24	426,624	1,005	5,199,186	2,016	1,813	1,338	4,506
366	Female	1992	Spring	13	426,559	1,407	5,199,168	3,127	3,042	1,582	
			Summer	7	426,380	360	5,198,073	998	1,014	313	
			Fall	4	425,875	1,202	5,201,425	843	1,391	469	
Mean of Seasonal GAC's											
Mean of all observations within year				24	426,393	1,188	5,199,225	2,627	2,467	1,492	5,765
Mean of all observations during study				48	426,393	1,188	5,199,225	2,627	2,467	1,492	5,765
375	Female	1991	Spring	14	426,619	504	5,198,119	1,171	1,072	690	
			Summer	11	426,623	825	5,200,463	1,237	1,349	626	
			Fall								
Mean of Seasonal GAC's											
Mean of all observations within year				25	426,621	665	5,199,150	1,672	1,598	827	3,599
375	Female	1992	Spring	11	427,524	982	5,195,715	2,249	2,368	645	
			Summer	4	426,225	1,205	5,201,794	2,481	2,750	207	
			Fall								
Mean of Seasonal GAC's											
Mean of all observations within year				15				3,052	2,165	7,484	
Mean of all observations during study				40	426,830	939	5,198,470	2,690	2,231	1,772	5,699

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance to GAC		Standard Diameter	
					X	STD	Y	STD	STD		
384	Female	1991	SPRING	<i>Not Deployed</i>							
384	Female	1992	Spring	7	427,623	1,114	5,191,098	5,573	5,581	1,078	
			Summer	3	427,021	1,516	5,198,779	3,345	3,231	1,746	
			Fall	5	426,833	501	5,199,513	1,519	1,545	412	
			Mean of Seasonal GAC's		427,159		5,196,463				
			Mean of all observations within year	15	427,239	1,121	5,195,439	5,836	5,136	2,989	11,885
			Mean of all observations during study								
447	Female	1991	Spring	11	427,091	695	5,198,227	1,304	1,392	495	
			Summer	7	426,996	1,582	5,198,728	3,201	2,957	2,002	
			Fall	4	426,684	2,323	5,198,321	3,849	3,490	2,833	
			Mean of Seasonal GAC's		426,924		5,198,425				
			Mean of all observations within year	22	426,987	1,429	5,198,403	2,618	2,281	1,922	5,965
447	Female	1992	Spring	12	427,066	1,234	5,197,989	2,687	2,484	1,603	
			Summer	4	427,075	843	5,197,463	1,657	1,753	620	
			Fall	4	426,606	908	5,201,763	1,392	1,660	61	
			Mean of Seasonal GAC's		426,916		5,199,072				
			Mean of all observations within year	20	426,976	1,120	5,198,638	2,784	2,594	1,508	6,002
			Mean of all observations during study	42	426,981	1,291	5,198,515	2,701	2,435	1,740	5,986

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)				Mean Distance to GAC		Standard Diameter
					X	STD	Y	STD	STD	STD	
555	Male	1991	Spring	9	426,198	248	5,197,502	480	419	341	1,081
			Summer	<i>Mortality</i>							
			Fall	" "							
			Mean of Seasonal GAC's	" "							
			Mean of all observations within year	" "							
555	Male	1992	Spring	" "							
			Summer	" "							
			Fall	" "							
			Mean of Seasonal GAC's	" "							
			Mean of all observations within year	" "							
Mean of all observations during study				" "							
2228	Male	1991	Spring	11	426,502	299	5,198,143	704	703	301	
			Summer	9	426,942	854	5,199,757	2,035	1,846	1,210	
			Fall	3	426,349	324	5,200,429	1,492	1,367	679	
			Mean of Seasonal GAC's		426,598		5,199,443				
			Mean of all observations within year	23	426,654	630	5,199,072	1,727	1,629	829	3,655
2228	Male	1992	Spring	16	426,247	1,163	5,199,717	1,854	2,010	867	
			Summer	7	426,448	1,172	5,200,584	1,091	1,512	526	
			Fall	1							
			Mean of Seasonal GAC's								
			Mean of all observations within year	24	426,353	1,165	5,199,989	1,671	1,875	797	4,075
Mean of all observations during study				47	426,500	954	5,199,540	1,760	1,752	968	4,003

Table 14. Continued.

Fish ID Number	Sex	Year	Season	Number of Observations	GAC (UTM Coordinates)			Mean Distance to GAC		Standard Diameter
					X	STD	Y	STD	STD	
456	Female	1991	Spring	9	425,823	959	5,200,582	1,699	1,805	742
			Summer	4	425,300	879	5,201,379	2,320	2,189	1,166
			Fall							
Mean of Seasonal GAC's										
Mean of all observations within year				13				2,042	744	4,347
456	Female	1992	Spring	<i>Not Deployed</i>						
			Summer							
			Fall							
Mean of Seasonal GAC's										
Mean of all observations within year										
Mean of all observations during study										

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