Daily and seasonal movements of large brown trout and walleye in an impounded reach of the Au Sable River, Michigan

Michele M. DePhilip
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DAILY AND SEASONAL MOVEMENTS OF LARGE BROWN TROUT AND WALLEYE IN AN IMPOUNDED REACH OF THE AU SABLE RIVER, MICHIGAN

by

Michele M. DePhilip

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science

School of Natural Resources and Environment
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ABSTRACT

Large brown trout and walleye often make long-range movements associated with foraging or spawning. Dams may affect fish movements by presenting physical barriers to migration and by altering habitats available in a reach. Radiotelemetry was used to monitor seasonal and daily movements of eight large brown trout and eleven large walleye in the Au Sable River between Mio and Alcona dams. The purposes of this study were to estimate the long-range movements of both species and to compare specific habitat characteristics for brown trout and walleye.

Eighty-six percent of all brown trout locations occurred within the first 13 km of Mio Dam. Summer (May to August) range varied from 100 to 9,252 m; winter (September to April) range varied from 64 to 8,705 m. Between September and November, three brown trout made spawning migrations of up to six kilometers, then all brown trout tracked during winter remained within their summer range. Brown trout selected low velocity (<0.5 m/s) areas with silt substrates during summer and winter; they selected moderate velocities (0.5-1.0 m/s) during September, October, and November.

Seventy-one percent of all walleye locations occurred within the first 25 km of Mio Dam. Summer range varied from 97 to 36,446 m; winter range varied from 23,266 to 46,629 m. Walleye traveled upriver in April or May and presumably spawned near Mio Dam. In 1996, three of four walleye remained in the river until late August. In 1997, all nine walleye tracked returned to Alcona Pond by early June. Low river temperatures during May and June 1997 may have forced walleye to return to Alcona Pond. While in the river, walleye occupied low velocity areas with silt substrates.
Walleye often occupied the first 25 km below Mio Dam but were seldom found in the lower section. All walleye overwintered in Alcona Pond.

Both species demonstrated regular patterns of daily activity. Brown trout were most active at sunrise and sunset, often moving only short distances between low-velocity resting sites and high-velocity feeding sites during these periods. Activity of riverine walleye increased at dusk and remained high during night. Walleye occasionally foraged 1-2 km away from daytime resting sites. Walleye were often present near stocking sites for fingerling brown trout during May and June, suggesting potential for predatory interactions.

Maximum potential for interactions between these two species occurs within the first 25 km of Mio Dam during summer. In this reach, both species used low velocity sites for daytime resting and increased foraging activity between dawn and dusk. Competition for food and resting sites and walleye predation on small trout may occur in this area.
INTRODUCTION

Dams affect fish populations directly, by presenting physical barriers to migration between habitats and indirectly, by altering the availability and distribution of habitats in a reach. The six hydroelectric dams constructed from 1911 to 1924 altered flow and habitat of the Mainstream Au Sable River. Dams have altered river hydrology by removing high gradient areas and by creating reservoirs that support lentic fishes. Reservoirs trap sediments and release clearer water that scours fine sediments immediately below the dam. Reservoir storage also affects temperature of released water. Regulated discharges tend to have more stable temperatures rather than the daily cycle of warming and cooling typical of unregulated discharges.

Presence of dams may affect distribution and abundance of stream-resident sportfish, particularly brown trout *Salmo trutta* and walleye *Stizostedion vitruem*, which normally show long-range movements in river systems. In north-temperate streams, adult fish experience seasonally favorable periods with rapid growth and unfavorable periods with reduced growth. In response to this temporal variation, adult fish migrate between summer and winter habitats (Schlosser 1991). Additionally, sexually mature fish may migrate to suitable spawning areas. Distribution of feeding, spawning, and overwintering habitats affects long-range movements of stream fishes (Schlosser 1991).

Three previous telemetry studies in the Au Sable River suggested that large brown trout frequently make long-range movements associated with foraging and spawning (Clapp 1988, Regal 1992, Hudson 1993). Range of movement increased with fish size due to a shift in foraging strategy from sit-and-wait to active-search. During night, large
brown trout (>40 cm) regularly foraged up to one kilometer away from daytime home sites (Hudson 1993). In the present study, such long-range foraging movements may be constrained by the presence of dams. Hudson (1993) found that brown trout in low-velocity areas (21-53 cm/s) used active-search strategy, fish in high-velocity areas (70-77 cm/s) used sit-and-wait strategy. Prey density and energetic cost appeared to influence choice of foraging strategy. High velocities (>1 m/s) and stable summer temperatures greater than 19°C may increase energetic costs of movement in the present study site. Clapp (1988), Regal (1992), and Hudson (1993) found that range of movement was greater in winter than in summer due to spawning migrations and movements between summer feeding areas and overwintering sites. Long-range movements of brown trout depend on site-specific differences, including proximity of feeding, spawning, and overwintering habitats (Clapp 1988). By removing high gradient areas and cutting off access to tributaries, dams could limit spawning migrations.

Walleye make long-range movements associated with spawning and foraging in the Great Lakes (Furguson and Dersken 1971, Haas et al. 1988), inland lakes (Holt et al. 1977, Diana et al. 1990), and rivers (Rawson 1957, Paragamian 1989). In impounded river systems, walleye often move to dam tailwaters to spawn (Crowe 1962, Ager 1976, Paragamian 1989). The presence of dams facilitated establishment of naturally reproducing walleye populations in impounded reaches of the Au Sable River. Walleye are known to inhabit Alcona Pond, and observations of walleye congregating below Mio Dam in April (Dave Smith, Michigan Department of Natural Resources, personal communication) suggest that walleye may range throughout the entire reach between Mio
and Alcona dams and that dams may limit the extent of their movements. One hypothesis is that separation of spawning and overwintering habitats could result in long-range movements by walleye in the Au Sable River.

Forced coexistence of these two populations has generated concern that walleye and brown trout may compete for food and that adult walleye prey on juvenile brown trout. The brown trout fishery between Mio and Alcona dams is characterized by a few, trophy brown trout. The fishery is made up almost entirely of stocked fish; natural reproduction is limited. Historic peaking operation of Mio Dam resulted in removal of large woody debris in this reach. Stocked brown trout may be especially vulnerable to predation by large piscivores due to loss of cover. In their native range, rivers and lakes with walleye and salmonids are relatively rare and where they do co-occur, the species have little spatial overlap due to different habitat requirements (McMahon and Bennett 1996). Spatially heterogeneous environments can lead to species segregation (Schlosser 1991). However, channel homogenization characteristic of impounded rivers results in decreased spatial heterogeneity. Such homogenization could lead to overlap of walleye and brown trout in the Au Sable River. Also, restriction of these two species to a 47-km stretch could lead to competition for feeding and resting sites. The Au Sable River between Mio and Alcona dams provided a unique environment to study range and behavior of two large piscivorous fish species.

The purpose of this study was to observe seasonal and diel movements of brown trout and walleye and to relate these movements to Mio and Alcona dams. Radiotelemetry was used because it allowed precise location of fish without affecting
their behavior. Long battery life permitted continuous observation of individual fish throughout the study (Diana et al. 1990). Pinpointing fish locations allowed identification of local characteristics that could trigger movements (Clapp 1988). The specific objectives of this study were 1) to estimate long-range movements of both species associated with spawning or foraging; 2) to compare specific habitat requirements of brown trout and walleye; and 3) to determine how dams affect movement of these two species, either directly or indirectly.
METHODS

Study Area

The Mainstream Au Sable River originates north of Grayling, Michigan and flows east 209 km to Lake Huron (Figure 1a). The major landcover in its 4,660-km$^2$ catchment is forest, which covers 70% of the area (EPA 1997). Highly permeable glacial outwash in the watershed contributes groundwater to the river; eighty-five percent of the flow at Mio is attributable to groundwater (Coopes 1974). Six hydroelectric dams between Mio and Oscoda prevent fish migrations from Lake Huron to the headwaters of the river. Mio Dam, 117 km from Lake Huron, was the upstream boundary of the study site (Figure 1b). From Mio, the river flows approximately 37.8 km to the backwaters of Alcona Pond. Each May this reach is stocked with approximately 11,000 brown trout and 32,000 rainbow trout, *Oncorhynchus mykiss* (MDNR fish stocking records). Alcona Pond makes up the last 4.9 km to the downstream boundary, Alcona Dam. Walleye were stocked in Alcona Pond until 1990.

McKinley Bridge divided the study site into two study areas. The upstream area, from Mio Dam to McKinley Bridge, had higher gradient, more riffle-pool sequences, and more large woody debris than the downstream area. The upstream area had an average daily discharge of 30.5 m$^3$/s, an average width of 46 m, and an average gradient of 0.14%. Gravel and pebble were the dominant substrate types. Coverage by large woody debris was limited in this study area but was more extensive than in the downstream area (Sendek 1994). Most of this area was a single channel with the exception of 0.8 km of multiple channels approximately 6.4 km downstream of Mio Dam. This braided section was formed by deposition of excess sediment during the peaking operation of Mio Dam.
FIGURE 1. Map of the Au Sable River system (a). The study site (b), between Mio and Alcona Dams consisted of two study areas: upstream area, from Mio Dam to McKinley Bridge; downstream area, from McKinley Bridge to the backwaters of Alcona Pond. The quality fishing area extends from 0.75 km below Mio Dam to McKinley Bridge.
The channel was mostly unconstrained with the exception of a 3.75-km residentially developed section downstream of Comins Flats Landing, where seawalls, docks, and concrete riprap were present (Sendek 1994). Special fishing regulations are in effect from 0.75 km below Mio Dam to McKinley Bridge. The size-limit for brown trout is 15” and all other trout is 12” with a creel limit of two trout per day. This area is designated artificial lures and flies only.

The downstream study area, from McKinley Bridge to the backwaters of Alcona Pond, had lower gradient, more run habitat, and less large woody debris than the upstream area. This area had an average daily discharge of 33.5 m³/s, an average width of 51 m, and an average gradient of 0.05% (Sendek 1994). Pebble and cobble were the dominant substrate types. Large woody debris was rare (Sendek 1994). Normal state regulations are in effect in this study area: live bait or artificial lures may be used, the season extends from the last Saturday in April to 30 September, there is an 8” minimum trout size limit and a 10-fish daily creel limit.

Alcona Pond covers approximately 1,075 surface acres and is surrounded by Alcona County Park. Stumps and aquatic macrophyte growth provide structure throughout the reservoir. A maximum depth of 14 m occurs within the old river channel; however, most of the reservoir is less than three meters deep. The deep areas within the channel weakly stratify with respect to temperature and dissolved oxygen between June and September (Jerry Casey, MDNR, personal communication).

Transmitter Implants

In May 1996, DC electrofishing gear was used to capture ten fish between Mio
Dam and Comins Flats Landing. Five brown trout and five walleye (sizes listed in Table 1) were successfully implanted with radio transmitters. Fish were anesthetized using 75 mg of tricaine methane sulfonate (MS-222) per liter of river water. Transmitters were placed in the abdominal cavity through a 2.5-cm mid-ventral incision between the pelvic and pectoral girdles. Incisions were closed with nonabsorbable nylon sutures. Following surgery, 2 mL of oxytetracycline (50 mg/mL) was injected through the incision to prevent infection. The procedure took less than ten minutes to complete and all fish were released at Comins Flats Landing.

In April 1997, DC electrofishing gear was used to capture ten fish from four locations. On 3 April, two female walleye were captured from Alcona Pond. Transmitters were implanted using similar surgical techniques and the two fish were released in Alcona Pond. On 4 April, one male and two female walleye were taken from just below Mio Dam, implanted, and released at Mio Park boat launch, 0.5 km below Mio Dam. Three brown trout were captured between Mio Dam and Perry Creek, implanted, and released at Perry Creek. The remaining two male walleye were captured between Perry Creek and Comins Flats Landing, implanted, and released at Comins Flats Landing.

Two models of radio transmitters (from Advanced Telemetry Services, Isanti, Minnesota) were used in this study. Transmitters used in 1996 were powered by a lithium battery equipped with an internal coil antenna, weighed 17-19 g, and had an expected life of 200-400 days. Transmitters used in 1997 were of similar weight and battery life expectancy but had a 25-30 cm trailing antenna that passed through the body wall instead of the internal coil antenna. A shielded needle technique was used to allow
the antenna to protrude (Ross and Kleiner 1982). All transmitters had identifying labels, including a telephone number to call if the transmitter was found or the fish was caught, and were encapsulated in a biologically inert resin to prevent tissue reaction. Each transmitter emitted a unique frequency between 48 and 48.5 MHz.

Of the two models of transmitters used, the model with an external antenna had superior range. This was especially helpful for locating walleye in Alcona Pond. At depths of six to seven meters, signals could be heard from over 250 m away compared to only 50 m with an internal antenna. External antennas did not appear to affect fish behavior in any observable way, nor did they increase mortality.

Fish Locations

Immediately following surgery, I monitored movement of radio-tagged fish using a programmable scanning receiver (Model R2100) and a 60-cm directional loop antenna (both from ATS, Isanti, Minnesota). I initially located fish by canoeing from Mio Dam to 4001 Bridge. I could detect a signal from approximately 250 m. Once I detected a signal, I located fish from shore by triangulation and marked its position on a set of maps made from aerial photographs. A 15-cm loop antenna was often used to pinpoint locations at close range. Fish were located from canoe or from shore during daylight hours and were usually found in the same area from day to day. Once a fish had established a regular location, I drew site maps with notable instream and riparian landmarks and used these drawings to record fish position. In summer (May to August), I located fish three to four times each week. In winter (September to April), I located fish once or twice each month.
Several walleye moved into Alcona Pond and remained there for 13 to 310 days. In summer, I located fish in Alcona Pond from shore or by boat. When the pond was frozen, I walked on the surface and located fish through the ice. Most locations in the reservoir were made using a 60-cm antenna but a few were made using a 6-foot Yagi antenna. I located fish by triangulating to onshore landmarks and recorded locations on maps made from aerial photographs.

Individual fish locations were used to calculate seasonal range of movement, local range use, and local range size. Data collected during the first two weeks after surgery were not included in analysis since fish may exhibit erratic behavior during this time (Mesing and Wicker 1986). Initially, I plotted all brown trout and walleye locations to determine if fish were evenly distributed throughout the study site or concentrated in certain areas. In summer and winter, the difference between extreme upstream and downstream locations was determined to be the seasonal range of movement for an individual fish. A total range of movement was also calculated for fish tracked in more than one season. Local range was defined as a subset of sites within the total range where an individual fish was commonly located, or as an area to which a fish returned after an absence. I plotted individual fish locations over time and used these plots to determine which locations to include in the local range (Appendix Figures 1-19). Local range size was calculated as the linear distance between the upstream-most site and the downstream-most site included in the local range.

**Daily Movements**

Two types of daily movements were measured in this study: active displacement
and diel activity. Active displacement was measured as the distance between successive
daytime locations. In summer, one to three days separated these observations; in winter
two to four weeks separated these observations. It was a minimum estimate of distance
moved because it only included the absolute change in position but not necessarily the
total linear distance moved between observations.

Diel activity was measured for both species during summer 1996 and 1997. Although walleye occupied river and reservoir sites, diel activity was only measured in
the river. An individual fish was located four times in 24 hours: at sunrise, at mid-day, at
sunset, and during night. At each of the four periods, I spent one hour monitoring activity
of one fish. I divided the hour into 5-minute intervals and listened for changes in signal
strength during each interval. If I detected a change in signal strength during an interval,
I considered the fish to be active. For each species, I calculated the percent of active
intervals at each of the four periods to find peaks in activity. If a fish moved measurable
distances during the observation period, I also estimated total linear distance moved.

Habitat Use

Quantitative habitat data were collected within summer local ranges of seven
brown trout and six walleye. Three transects were used to characterize each local range.
The focal transect was established through the site where the fish was most frequently
observed. Another transect was established 50 m upstream of the focal transect and a
third transect 50 m downstream of the focal transect. In two cases, four transects 50 m
apart were used to characterize large local ranges. Five possible brown trout spawning
sites were also characterized using three transects: one transect through the fall location
of each brown trout, another 50 m upstream, and a third 50 m downstream.

Water depth, surface velocity, mean column velocity, substrate, and cover type were measured at 5 m intervals along each transect. Surface velocity and mean water velocity (at 0.6 of the water column depth) were measured using a Swoffer Open Stream velocity meter. Predominant substrate type was visually estimated at each sampling point along the transect and categorized as silt, sand, gravel (2-16 mm), pebble (17-64 mm), cobble (65-256 mm) or boulder (>256 mm). Predominant cover type at each point was classified as log, brush, vegetation, boulder, overhang, or open (none). Log cover included submerged material >10 cm in diameter; brush included material <10 cm in diameter. Submerged or flooded riparian vegetation, such as *Alnus* and *Cornus*, were included as brush. Vegetation included aquatic vascular plants: often *Ceratophyllum, Potamogeton, Sparganium,* and *Elodea.* Overhang cover shaded fish from direct sunlight; undercut banks were included in this category.

To estimate the degree to which habitat characteristics were available in the study site, I did similar habitat measures on 26 additional random transects at 1.6 km intervals between Mio Dam and the backwaters of Alcona Pond. Using Strauss’ linear index of electivity, I compared habitat use data pooled from the three transects within a fish’s local range to pooled data from the 26 random transects. The index ranges from -1 to +1 with positive values indicating preference and negative values indicating avoidance. I calculated electivity for riverine walleye local ranges, brown trout local ranges, and brown trout spawning sites.

I also separated data from the random transects into two study areas: Mio to
McKinley (17 transects) and McKinley to Alcona Pond (9 transects). I plotted frequency of occurrence for values of depth, mean column velocity, substrate, and cover to determine if variables were evenly distributed throughout the study site or concentrated in either of the two study areas.

**Statistical Analyses**

Nonparametric analyses were generally used because samples were not normally distributed and did not have equal variances. Wilcoxon signed rank tests were used to make paired comparisons; for example, to compare mean summer and winter range size for four brown trout tracked in both seasons. Mann-Whitney U tests were used to make unpaired comparisons; for example, to compare mean summer range size for eight brown trout and twelve walleye. Kolmogorov-Smirnov tests were used to compare frequency distributions; for example, to compare the frequencies of active displacements by brown trout and walleye. Pearson correlation coefficients were calculated to test correlations between habitat variables. Paired t-tests were used to test if selection for habitat variables was significantly different from zero. Wilcoxon signed rank test, Kolmogorov-Smirnov tests, correlation coefficients, and t-tests were calculated using SYSTAT software. Mann-Whitney U tests were conducted using SPSS software. Differences were considered statistically significant if \( p < 0.05 \).
RESULTS

Brown Trout

A total of eight brown trout were successfully implanted with radio transmitters; individual brown trout were tracked between 29 and 426 days (Table 1). In May 1996, five brown trout were implanted. Trout 5 expelled its transmitter after 29 days of tracking. Prior to the expulsion, this fish had moved upstream 4.5 km from the point of its release. The remaining four brown trout were tracked during summer 1996 and winter 1996/97. Two brown trout implanted in May 1996 were tracked during summer 1997. In April 1997, three brown trout were successfully implanted and tracked through October 1997. Only data collected through August 1997 were used to compute seasonal range of movement, active displacement, and local range use.

All brown trout locations occurred within the first 25 km below Mio Dam (Figure 2). No brown trout were ever located in Alcona Pond. Individual summer range of brown trout varied from 100 to 9,252 m; winter range varied from 64 to 8,705 m (Figure 3). There was no significant difference between mean summer range size for five fish tracked in 1996 (4,808 m) and five fish tracked in 1997 (2,836 m). Winter range of movement was calculated for four brown trout in winter 1996/1997. There was no significant difference between mean summer (5,985 m) and winter (4,718 m) range sizes for four fish tracked in both seasons. Summer and winter range sizes for these brown trout were not significantly different from those of brown trout in the middle Mainstream or South Branch of the Au Sable River (Clapp 1988, Hudson 1993).

Eight brown trout used eleven local ranges (Table 2). All brown trout were
TABLE 1. Summary of radio transmitter implants in eight brown trout (Fish number T1-T8) and twelve walleye (Fish number W1-W12) between 2 May 1996 and 4 April 1997. Days tracked equal number of days between implant and last contact.

<table>
<thead>
<tr>
<th>Fish number</th>
<th>Sex</th>
<th>Length (cm)</th>
<th>Weight (g)</th>
<th>Implant date</th>
<th>Last contact</th>
<th>Days tracked</th>
<th>Fate of Fish</th>
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<tr>
<td>T1</td>
<td>----</td>
<td>44</td>
<td>1,134</td>
<td>2 May 96</td>
<td>31 May 97</td>
<td>394</td>
<td>Battery expired</td>
</tr>
<tr>
<td>T2</td>
<td>----</td>
<td>50</td>
<td>1,633</td>
<td>2 May 96</td>
<td>2 July 97</td>
<td>426</td>
<td>Battery expired</td>
</tr>
<tr>
<td>T3</td>
<td>----</td>
<td>55</td>
<td>2,041</td>
<td>2 May 96</td>
<td>27 June 97</td>
<td>421</td>
<td>Battery expired</td>
</tr>
<tr>
<td>T4</td>
<td>----</td>
<td>58</td>
<td>1,452</td>
<td>9 May 96</td>
<td>4 April 97</td>
<td>330</td>
<td>Battery expired</td>
</tr>
<tr>
<td>T5</td>
<td>----</td>
<td>60</td>
<td>2,631</td>
<td>2 May 96</td>
<td>3 June 96</td>
<td>32</td>
<td>Expelled transmitter</td>
</tr>
<tr>
<td>T6</td>
<td>----</td>
<td>59</td>
<td>4 April 97</td>
<td>1 Oct 97</td>
<td>180</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>T7</td>
<td>----</td>
<td>60</td>
<td>4 April 97</td>
<td>2 Oct 97</td>
<td>181</td>
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<td>Still active</td>
</tr>
<tr>
<td>T8</td>
<td>----</td>
<td>56</td>
<td>4 April 97</td>
<td>2 Oct 97</td>
<td>181</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>W1</td>
<td>----</td>
<td>53</td>
<td>1,455</td>
<td>9 May 96</td>
<td>16 May 97</td>
<td>372</td>
<td>Lost contact</td>
</tr>
<tr>
<td>W2</td>
<td>----</td>
<td>54</td>
<td>1,814</td>
<td>9 May 96</td>
<td>8 July 96</td>
<td>60</td>
<td>Angler-caught</td>
</tr>
<tr>
<td>W3</td>
<td>----</td>
<td>50</td>
<td>1,588</td>
<td>9 May 96</td>
<td>9 June 97</td>
<td>396</td>
<td>Lost contact</td>
</tr>
<tr>
<td>W4</td>
<td>----</td>
<td>59</td>
<td>3,039</td>
<td>2 May 96</td>
<td>6 Sept 96</td>
<td>127</td>
<td>Lost contact</td>
</tr>
<tr>
<td>W5</td>
<td>----</td>
<td>47</td>
<td>1,134</td>
<td>2 May 96</td>
<td>6 May 97</td>
<td>362</td>
<td>Angler-caught</td>
</tr>
<tr>
<td>W6</td>
<td>M</td>
<td>51</td>
<td>4 April 97</td>
<td>1 Oct 97</td>
<td>180</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>W7</td>
<td>F</td>
<td>49</td>
<td>4 April 97</td>
<td>4 April 97</td>
<td>0</td>
<td></td>
<td>Lost contact</td>
</tr>
<tr>
<td>W8</td>
<td>M</td>
<td>46</td>
<td>4 April 97</td>
<td>1 Oct 97</td>
<td>180</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>W9</td>
<td>F</td>
<td>68</td>
<td>4 April 97</td>
<td>2 Oct 97</td>
<td>181</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>W10</td>
<td>F</td>
<td>64</td>
<td>3 April 97</td>
<td>1 Oct 97</td>
<td>181</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>W11</td>
<td>F</td>
<td>68</td>
<td>3 April 97</td>
<td>2 Oct 97</td>
<td>182</td>
<td></td>
<td>Still active</td>
</tr>
<tr>
<td>W12</td>
<td>M</td>
<td>50</td>
<td>4 April 97</td>
<td>31 July 97</td>
<td>118</td>
<td></td>
<td>Angler-caught</td>
</tr>
</tbody>
</table>
FIGURE 2. Longitudinal distribution of individual brown trout and walleye locations in the Au Sable River. Data are combined for eight brown trout and eleven walleye tracked between May 1996 and August 1997. Numbers on the x-axis indicate upper limits for inclusion in each category. Distances greater than 40 km represent reservoir locations.
FIGURE 3. Seasonal range of movement by eight brown trout. High and low horizontal bars indicate upstream and downstream limits of fish movements. Eight fish were tracked in summer. Two fish tracked in both summer 1996 and summer 1997 are marked with an asterisk. Four fish were tracked in winter.
TABLE 2. Local range use by eight brown trout between May 1996 and August 1997. Local range use represents the percentage of all observations that were within this local range. Summer was defined as May to August; winter was defined as September to April. Asterisks indicate that a local range was used in summer 1996 and summer 1997.

<table>
<thead>
<tr>
<th>Fish</th>
<th>Total Range (m)</th>
<th>No. of local ranges</th>
<th>Local range size (m)</th>
<th>Local range use (%)</th>
<th>Season used</th>
</tr>
</thead>
<tbody>
<tr>
<td>B1</td>
<td>9,123</td>
<td>2</td>
<td>a) 525</td>
<td>a) 33</td>
<td>a) Summer</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>b) 64</td>
<td>b) 67</td>
<td>b) Summer, Winter</td>
</tr>
<tr>
<td>B2</td>
<td>8,705</td>
<td>1</td>
<td>853</td>
<td>96</td>
<td>Summer *, Winter</td>
</tr>
<tr>
<td>B3</td>
<td>13,918</td>
<td>1</td>
<td>708</td>
<td>85</td>
<td>Summer *, Winter</td>
</tr>
<tr>
<td>B4</td>
<td>5,326</td>
<td>2</td>
<td>a) 227</td>
<td>a) 17</td>
<td>a) Summer, Winter</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>b) 16</td>
<td>b) 81</td>
<td>b) Summer, Winter</td>
</tr>
<tr>
<td>B5</td>
<td>100</td>
<td>1</td>
<td>100</td>
<td>100</td>
<td>Summer</td>
</tr>
<tr>
<td>B6</td>
<td>711</td>
<td>1</td>
<td>711</td>
<td>100</td>
<td>Summer</td>
</tr>
<tr>
<td>B7</td>
<td>3,473</td>
<td>2</td>
<td>a) 5</td>
<td>a) 61</td>
<td>a) Summer</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>b) 5</td>
<td>b) 32</td>
<td>b) Summer</td>
</tr>
<tr>
<td>B8</td>
<td>3,547</td>
<td>1</td>
<td>1779</td>
<td>70</td>
<td>Summer</td>
</tr>
<tr>
<td>Mean</td>
<td>5,613</td>
<td>454</td>
<td>93</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
released downstream of the capture area; six of seven fish established local ranges upstream of the release point. After its release, T6 traveled 3 km upstream and established a local range within 100 m of where it was initially captured (This was the only fish for which I could pinpoint the capture location). Ten of eleven local ranges were located within the first 13 km below Mio Dam. Two brown trout shared one local range for a two-week period in summer 1997. Only one brown trout was ever located outside of the quality fishing area. This fish established a local range in the 0.75-km area between Mio Dam and the upstream boundary of the quality fishing area (Figure 1b). All four brown trout tracked during winter remained in one of their summer local ranges. However, they moved to different cover sites within their local range, often using ice cover in low-velocity areas.

Brown trout were most active at sunrise and at sunset; they often moved between sites within their local range during these periods (Figure 4). They regularly moved from daytime resting positions in low-velocity areas to nighttime feeding positions in high-velocity areas. Brown trout remained in these high-velocity feeding positions during night but I did not observe them displacing long distances or moving continuously to find food. By sunrise, they returned to daytime resting positions within their local range. During several night observation periods, brown trout made quick movements of 10-20 m then returned to their original position.

Brown trout local ranges usually contained low-velocity refuges and silt substrates. Quantitative habitat data were collected for seven brown trout local ranges. Brown trout did not select particular depths for their local ranges. They showed significant electivity for mean column velocities less than 0.5 m/s. Brown trout showed
FIGURE 4. The percent of brown trout active and inactive intervals at four times of day. Y-axis represents the percentage of active and inactive periods during 5-minute observations (N=365 observations). Data are combined for four fish and seven observations dates during summer 1996 and summer 1997.
positive electivity for silt and pebble substrates and significantly negative electivity for gravel. Although brown trout appeared to select overhang, vegetation, and logs, and avoid open areas, none of these electivity values were significantly different from zero.

During the spawning period, brown trout were located within the main channel in riffle or run habitats. No brown trout were ever located in any of the tributaries. Quantitative habitat data were collected for five possible spawning areas. Two possible spawning areas were within local ranges formerly used by other brown trout; and one brown trout spawning area was within a walleye local range. Brown trout did not appear to select particular depths for possible spawning areas. In fall, brown trout showed significant positive electivity for mean column velocities between 0.51 and 1.0 m/s. Brown trout again showed positive electivity for silt and pebble substrates during the spawning period. Brown trout also were more likely to select open areas in fall (October and November) than they were in summer or winter. Vegetation was the only cover type for which brown trout showed significant positive electivity during fall.

Interactions between the four habitat variables were apparent. Significant correlations existed between water depth and mean column velocity, water depth and substrate, water depth and cover, mean column velocity and substrate type, mean column velocity and cover, and substrate and cover. Fine substrate occurred in low-velocity areas and large substrate in high-velocity areas. Most high-velocity areas were open or had very little cover. Substrate and cover were also negatively correlated; log jams, brush, and vegetation occurred in depositional areas with fine substrates. Availability of the four variables measured was not significantly different in the two study areas.
Walleye

A total of twelve walleye were successfully implanted; individual walleye were tracked between 60 and 395 days. In May 1996, five walleye were captured in the river and implanted, presumably after they had spawned (Table 1). Following surgery, they dispersed in the river and established local ranges. Three walleye implanted in May 1996 were located in Alcona Pond during winter and were followed as they returned to the river in April and May 1997. An angler caught walleye 5 during its spawning migration in May 1997.

In April 1997, seven walleye from three different locations were implanted. Two walleye (W10 and W11) captured and released in Alcona Pond were not ripe at the time of surgery. One of the two, W10, moved up the river in mid-May. The other walleye, W11, was never located outside of Alcona Pond although it was missing from early June to early July, when it may have moved into the backwaters of Alcona Pond. Implanting these two fish before they spawned may have delayed or prevented their spawning migration. Three walleye (W6, W7, and W9) captured and released below Mio Dam were exuding gonad products at the time of surgery. Within three weeks following their release, two of these fish (W6 and W9) had traveled over 37 km to Alcona Pond. Two walleye (W8 and W12) captured in the river and released at Comins Flats Landing were also exuding gonad products at the time of surgery. They remained in the river until mid-May then traveled to the reservoir. Five walleye were tracked through October 1997. Only data collected through August 1997 were used to compute seasonal range of movement, daily movements, and local range use.

Summer range of walleye varied from 97 to 36,446 m; winter range varied from
23,266 to 46,629 m (Figure 5). Summer range of movement was documented for eleven walleye. There was no significant difference in mean summer range for five walleye tracked in summer 1996 (4,638 m) and nine walleye in summer 1997 (15,745 m; three of these were implanted in 1996). Winter range of movement was recorded for three walleye. There was no significant difference between mean summer and winter range for three fish tracked in both seasons.

Eight of eleven walleye used both river and reservoir locations. In 1996, three walleye traveled from the river to the reservoir. Once they went to the reservoir, they remained there until they ran upriver in April or May 1997. A fourth fish presumably traveled to the reservoir but I lost contact with it in October 1996. In 1997, all six walleye were located in the reservoir during summer. Two fish (W9 and W12) implanted in the river returned to Alcona Pond in early May and remained there. Three walleye made more than one trip between river and reservoir habitats. W6 and W8, both implanted in the river, returned to Alcona Pond in mid-May, then went back upriver in early June. W10, implanted in Alcona Pond, went up the river in mid-May, returned to the pond in early July, and was back in the river in October. This migration pattern was not observed during 1996.

Walleye established local ranges in both river and reservoir locations. When in the river, walleye frequently used sites between Mio Dam and McKinley Bridge (Figure 2). Few walleye were located between McKinley Bridge and the backwaters of Alcona Pond. Eight walleye used local ranges in the river during summer (Table 3). Five different walleye used local ranges in the reservoir: three fish during summer and two fish during winter. Within the reservoir, locations were concentrated along the old river
FIGURE 5. Seasonal range of movement by eleven walleye. Eleven fish were tracked in summer. Three fish tracked in both summer 1996 and summer 1997 are marked with an asterisk. Three fish were tracked in winter. High and low horizontal bars indicate upstream and downstream limits of fish movements.
TABLE 3. Local range use by eleven walleye between May 1996 and August 1997. Local range use represents the percentage of all observations that were within this local range. Summer was defined as May to August; winter was defined as September to April.

<table>
<thead>
<tr>
<th>Fish</th>
<th>Total Range (m)</th>
<th>No. of local ranges</th>
<th>Location</th>
<th>Local range size (m)</th>
<th>Local range use (%)</th>
<th>Season used</th>
</tr>
</thead>
<tbody>
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<td>W1</td>
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<td>2</td>
<td>a) River</td>
<td>a) 97</td>
<td>a) 78</td>
<td>a) Summer</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>b) Reservoir</td>
<td>b) 467</td>
<td>b) 14</td>
<td>b) Winter</td>
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<td>3</td>
<td>a) River</td>
<td>a) 611</td>
<td>a) 31</td>
<td>a) Summer</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>b) Reservoir</td>
<td>b) 1,041</td>
<td>b) 13</td>
<td>b) Winter</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>c) River</td>
<td>c) 2,132</td>
<td>c) 36</td>
<td>c) Summer</td>
</tr>
<tr>
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<td>1</td>
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<td>998</td>
<td>100</td>
<td>Summer</td>
</tr>
<tr>
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<td>1</td>
<td>River</td>
<td>837</td>
<td>84</td>
<td>Summer</td>
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<tr>
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<td>1</td>
<td>River</td>
<td>1,576</td>
<td>79</td>
<td>Summer</td>
</tr>
<tr>
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<td>1</td>
<td>River</td>
<td>1,544</td>
<td>84</td>
<td>Summer</td>
</tr>
<tr>
<td>W9</td>
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<td>1</td>
<td>Reservoir</td>
<td>630</td>
<td>100</td>
<td>Summer</td>
</tr>
<tr>
<td>W10</td>
<td>25,009</td>
<td>2</td>
<td>a) Reservoir</td>
<td>a) 2,783</td>
<td>a) 60</td>
<td>a) Summer</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>b) River</td>
<td>b) 5</td>
<td>b) 23</td>
<td>b) Summer</td>
</tr>
<tr>
<td>W11</td>
<td>386</td>
<td>1</td>
<td>Reservoir</td>
<td>386</td>
<td>100</td>
<td>Summer</td>
</tr>
<tr>
<td>W12</td>
<td>29,133</td>
<td>1</td>
<td>Reservoir</td>
<td>2,600</td>
<td>73</td>
<td>Summer</td>
</tr>
<tr>
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<td>River</td>
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</tr>
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<td></td>
<td></td>
<td>Reservoir</td>
<td>1,318</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
channel (Figure 6). If an individual walleye was located within the same bay more than five times, I defined this bay as its local range. Observations outside this bay were considered to be outside of the fish's local range.

Walleye activity usually increased about one half hour before sunset and continued through the night (Figure 7). Walleye patrolled short sections of shoreline (5-10 m) for 10-20 minutes at a time, then moved to another section of shoreline and began patrolling there. They would continue this activity throughout the night. Usually they confined this activity to their local range but sometimes would cover 1-2 km in this manner. By sunrise, walleye had returned to their original resting site or had chosen another resting site within their local range.

One walleye was tracked as it traveled from its local range in the river to the reservoir. On 22 May 1997 at 2100, W8 was patrolling shoreline within its riverine local range. At 2240 it began moving continuously downstream. I located it 8 times during a 19.6-km journey downstream that lasted 5.25 hours (Figure 8). During this time, the average swimming speed was 1 m/s, which is about the same as the water velocity. The fish was still moving downstream at 0400 but I was not able to locate it again until 1430 on 23 May. At that time, it was located 11 km further downstream. On 27 May, W8 was located in the reservoir. This was the only return trip to the reservoir that I observed. Walleye return to the reservoir was not synchronous; individual fish returned at different times between May and October. However, walleye did not gradually move downstream. They were located in the river and 1-3 days later they were located in the reservoir. This pattern of sudden disappearance from the river suggests that other fish may have made overnight journeys from the river to Alcona Pond.
FIGURE 6. Walleye locations within Alcona Pond between May 1996 and August 1997 (N= 77 observations). Some points represent multiple observations. The thin line within Alcona Pond outlines the old river channel.
FIGURE 7. The percent of walleye active and inactive intervals at four times of day. Y-axis represents the percentage of active and inactive periods during 5-minute observations (N=648 observations). Data are combined for five fish and nine observation dates during summer 1996 and summer 1997.
FIGURE 8. Locations of W8 as it traveled from the river downstream to Alcona Pond. Times listed are for 23 May 1997 unless another date is specified in parentheses.
Walleye locations were similar to brown trout locations in that they usually contained low-velocity refuges and silt substrates. Quantitative habitat data were collected for six walleye local ranges. Walleye did not select particular depths for their local ranges. They showed significant positive electivity for mean column velocities <0.5 m/s and for silt substrate. Walleye seemed to select vegetation, brush, and logs and avoid open areas but the only significant electivity was for vegetation and brush. Three walleye local ranges occupied in summer 1996 were occupied by different walleye in summer 1997.

**Both species**

Walleye and brown trout had larger ranges in winter than in summer. Mean summer range of brown trout (3,822 m) was not significantly different from mean summer range of walleye (12,042 m). Mean winter range of walleye (36,037 m) was larger than mean winter range of brown trout (4,718 m). Total range for four brown trout tracked through both seasons varied from 5,326 m to 13,918 m; total range for three walleye tracked through both seasons varied from 39,941 m to 46,717 m. Walleye total range was greater than brown trout total range due to the distance separating walleye spawning and overwintering sites.

Most of the time, brown trout and walleye did not move measurable distances between successive daytime locations. Frequency distributions of active displacement for brown trout and walleye were not significantly different (Figure 9). Monthly mean active displacement was always significantly greater for walleye than for brown trout (Figure 10). Mean active displacement of brown trout peaked in September, October, and November. During these three months, brown trout moved from their local ranges to
FIGURE 9. Distribution of active displacement between consecutive daytime observations of brown trout and walleye in the Au Sable River. Data are combined for eight brown trout and eleven walleye tracked between May 1996 and August 1997.
FIGURE 10. Monthly mean active displacement combined for eight brown trout and eleven walleye between May 1996 and August 1997. Data from 1996 and 1997 were included in May, June, July, and August means.
potential spawning sites, then returned to their local ranges to overwinter. Mean active displacement of brown trout was high in June; long-range movements of three fish influenced this peak. In June 1996, T1 moved downstream 8.7 km from a shallow run habitat to an area with several deep pools and log cover. In June 1997, T7 moved 1.7 km upstream from a run habitat to a deep pool near a coldwater input below Mio Dam. In June 1997, T2 traveled upstream 4.7 km, possibly to take advantage of a concentrated hatch of large mayflies that occurred in that area. Mean active displacement of walleye peaked in September, October, and November and again in April and May. During fall, walleye moved to the reservoir. In April and May, walleye returned to the river to spawn.
DISCUSSION

Brown trout

Large brown trout in this study frequently occupied local ranges within the first 13 km of Mio Dam. Fish tracked in summer and winter occupied the same local range in both seasons. Long-range movements associated with foraging were not observed but brown trout often moved to feeding sites within their local ranges during night. During September, October, and November, brown trout moved to spawning areas outside their local ranges. Seasonal range sizes were similar to those recorded in other studies, but foraging movements were smaller than those observed in the middle Mainstream and South Branch of the Au Sable River (Clapp 1990, Hudson 1993).

Eighty-six percent of all brown trout locations were within the first 13 km of Mio Dam, which was also the area of capture. A brown trout will often return to its normal range regardless of whether it has been displaced upstream or downstream (Halvorson and Stabell 1990, Harcup et al. 1984, Armstrong and Herbert 1997). It is not clear whether homing is goal-oriented behavior that utilizes specific cues or simply accidental and results from random movement. If homing were accidental, fish would be as likely to move progressively away from their area of capture as toward it (Armstrong and Herbert 1997). In the present study, only one brown trout (T4) moved away from its area of capture before returning upstream and establishing a local range within the area of capture. Only T8 did not establish a local range within the area of capture. This fish also had the largest local range of any brown trout (1.8 km) and was most frequently outside of it (only 70% occupancy). Although Armstrong and Herbert (1997) observed that homing of brown trout commenced within 65 minutes of displacement, Halvorson and
Stabell (1990) reported that homing took as long as nine weeks. Within four weeks of release, 86% of fish in the present study (N=7) established local ranges within the area of capture. This supports the observation of Armstrong and Herbert (1997) where 86% (N=14) of fish returned to the areas from which they were captured, thus suggesting that homing is a goal-oriented behavior.

Temperature may be an important abiotic factor affecting site selection by brown trout. In the present study, two fish established new local ranges in late June, as the river approached 20°C. Four other fish moved to deeper areas within their local ranges, possibly seeking thermal refuge. In the Au Sable River, mean daily water temperature increased from 13°C on 1 June to 22°C on 30 June. Water temperature reached 19°C for the first time on 10 June then reached or exceeded 19°C 85% of the time until 11 August. Increasing river temperature in June may force brown trout to seek cooler sites within their local ranges or establish new local ranges containing cooler refuges. Since access to coolwater tributaries is limited in this study site, brown trout may seek thermal refuge within the main channel. Clapp (1990), Meyers et al. (1992), and Hudson (1993) also reported long-range movements in response to elevated water temperature. Results from a study in a coolwater reservoir indicate that brown trout used tributaries as thermal refuges once water temperature reached 19°C (Garrett and Bennett 1995).

The third fish to demonstrate long-range movement in late June may have moved to take advantage of a concentrated hatch of large mayflies, *Hexagenia limbata*. T2 moved upstream 4.7 km to a site within the local range of another brown trout. At this site, adult mayflies and surface-feeding trout appeared abundant. T2 may have moved to
feed on available insect prey or on smaller fish concentrated in this area. Within five days, T2 had returned to its local range. This was the only time T2 was located outside of its local range in summer 1996 or 1997. In June 1996, T2 was absent from its local range for one week but I was not able to locate it during this absence. It may have made a long-range movement similar to the one observed in 1997. Increase in active displacement may occur during insect hatches (Clapp 1990). Brown trout may make long-range movements to take advantage of increases in food available at certain sites (Clapp 1988, Hudson 1993).

Three of four fish tracked in winter moved to and from possible spawning areas. T2, T3, and T4 initiated spawning movements in September, October and November, respectively. All three fish had returned to overwintering areas by early December. Prespawning movements appeared to begin in late September and may be related to photoperiod (Meyers et al. 1992) or to temperature (Garrett and Bennett 1995). Generally, sites occupied in September, October, and November were shallower, had higher velocities, and larger substrates than areas used for brown trout local ranges. Since access to small tributaries was limited in the study site, brown trout may seek spawning sites in the main channel with depths, velocities, and substrates similar to those found in small tributaries.

All four fish tracked during winter remained within their summer local range. Within these local ranges, brown trout used ice cover and occupied low-velocity sites, frequently on inside bends, during winter. Clapp et al (1990) and Meyers et al. (1992) observed long migrations (of 10 and 20 km, respectively) to overwintering sites.
However, Hudson (1993) noted that 50% of brown trout overwintered within their summer range. Overwintering habitat described in previous studies is qualitatively similar to the sites observed in the present study. Brown trout use of ice cover and low-velocity areas within their local range during winter was consistent with the findings of Cunjak and Power (1986) and Clapp (1990). Brown trout continue to feed over the winter; and sheltering in low-velocity areas may reduce energy expenditure (Cunjak and Power 1987, Heggenes et al. 1993, Hudson 1993). Distance moved to overwintering habitat may be related to the proximity of suitable summer and winter habitats.

Four brown trout monitored over diel periods showed peaks in activity near dawn and dusk. Crepuscular activity is consistent with findings of several authors (Bachman 1984, Hudson 1993). At dawn and dusk, large brown trout may increase their foraging activity in response to greater availability of drift-feeding fish at these times (Hudson 1993). In the present study, brown trout moved from low-velocity resting areas to higher velocity feeding areas at dusk and remained in these areas during night. Brown trout were observed foraging in open current but not displacing long distances to find food. Fish using a sit-and-wait strategy may move to high-velocity areas and maintain positions near their resting sites; fish using an active-search strategy move frequently or continuously and regularly move long distances from their resting sites (Hudson 1993). Generally, small, drift-feeding brown trout use a sit-and-wait strategy (Bachman 1984, Regal 1992), and large, piscivorous brown trout demonstrate an active-search strategy (Clapp 1990, Hudson 1993). However, individual brown trout have been observed using both foraging strategies (Hudson 1993). Fish in this study appeared to use a sit-and-wait
strategy.

Large brown trout in the present study used a sit-and-wait strategy; large brown trout in the South Branch and middle Mainstream Au Sable were frequently observed using active-search strategy. Site-specific differences in velocity, temperature, and food availability may influence the frequency of the two foraging strategies (Clapp 1988). Energetic costs of searching for prey in running waters may affect the foraging strategy used by large brown trout (Bachman 1984). Hudson (1993) noted that fish in low-velocity areas (21-53 cm/s) were mobile, often foraging 50-1000 m away from resting sites. Fish in moderate to high-velocity areas (70-77 cm/s) were stationary, usually moving less than 30 m from their home site. In the present study, brown trout using sit-and-wait strategy frequently occupied foraging sites with velocities greater than 1 m/s.

Temperature may also affect the energetic cost of swimming in high-velocity areas. Compared to the other two Au Sable River study sites, this site has smaller daily flux in temperature due to regulated discharge. The lack of daily cooling during summer could mean that these fish seldom experience temperatures suitable for active foraging. Brown trout using a sit-and-wait strategy may live in areas with high prey densities; brown trout that move continuously may do so as a result of decreased food availability (Hudson 1993). Lack of long-range foraging movements by brown trout in the present study may also be explained by higher prey density in this study site than in the middle Mainstream or South Branch of the Au Sable River, although prey density in the three areas were not measured.
Walleye

Large walleye in the present study used both river and reservoir locations, and river locations were concentrated in the first 25 km below Mio Dam. In spring, walleye migrated upriver to spawn. Fish moved back to the reservoir between May and October and overwintered in Alcona Pond. Very few walleye were ever located between McKinley Bridge and the backwaters of the reservoir. During summer, individual walleye occasionally made nocturnal foraging movements of up to two kilometers. These results support previous observations of long-range movements by walleye in rivers and reservoirs (Rawson 1957, Crowe 1962, Ager 1976, Paragamian 1989).

Walleye presumably spawned near Mio Dam. In April 1997, five fish captured in the river were exuding gonad products at the time of surgery; two fish captured in Alcona Pond were not. Dam tailwaters often serve as primary spawning sites for walleye (Crowe 1962, Ager 1976, Paragamian 1989, Jennings et al. 1996, McMahon and Bennett 1996). Construction of impoundments degrades riverine environments but produces clean gravel-cobble substrate immediately below the dam, thus creating suitable areas for walleye spawning (Paragamian 1989). Several authors found that walleye home to previously used spawning sites (Crowe 1962, Ager 1976, Olson et al. 1978, Summers 1979, Paragamian 1989, Jennings et al. 1996). In the present study, walleye spawning sites were not pinpointed, thus homing to specific sites cannot be confirmed. However, three walleye captured in the river during May 1996 returned to the river in spring 1997, suggesting that walleye may select riverine spawning sites in successive years.

All walleye tracked had access to both river and reservoir sites, yet apparently chose to spawn in the river. Walleye spawning on riprap in reservoirs has been well
documented (Summers 1979, Prophet et al. 1989). Olson et al. (1978) proposed that the choice of a spawning site is a learned behavior, strengthened by repeated migrations. Jennings et al. (1996) presented evidence for a heritable component to spawning site selection. In their study in the Des Moines River, Iowa, walleye from two genetically discrete stocks, a lake spawning stock and a river spawning stock, were planted into a system where both habitats were available. At spawning time, 86% of walleye collected in the lake were of lake spawning stock; 91% of walleye collected in the river were of river spawning stock. Currently, Alcona Pond has a naturally reproducing walleye population but walleye originally stocked in the pond were from a river spawning stock in the Muskegon River (MDNR, fish stocking records). The fact that the walleye population in Alcona Pond is originally from river spawning stock could explain why these walleye moved upriver to spawn rather than spawning in the reservoir. However, if Alcona Pond supports both a river spawning and lake spawning stock, the present study may have only sampled the river spawners. Attempts were made to collect walleye from the reservoir in February and April 1997 but only two fish were collected. The remaining ten fish were collected in the upstream area during April and May, thus the sample was biased toward river spawners.

Walleye traveled up to 46 km upstream between overwintering and spawning sites. Upstream migrations were made in as few as three to four days. Ager (1976) observed spawning migrations of 3.2-16.1 km in 24 hours. Paragamian (1989) observed upstream migrations of 35 km within three to four days prior to spawning. In the present study, walleye remained in the river for four to twenty-four weeks after spawning. Other authors have noted similar protracted returns from spawning grounds (Rawson 1957,
Paragamian 1989). In 1996, three of four walleye remained in the river throughout the summer. However, in 1997 all eight walleye returned to the reservoir by early June; three walleye came back upriver later in summer. Based on limited temperature data (USGS gauge, MDNR continuous-recording thermometers), the mean daily water temperature was 1-2°C warmer in May and June 1996 than in 1997. Most walleye may have remained in the river during summer 1996 because it warmed quickly after spawning. In spring 1997, cold river temperatures may have encouraged them to return to the reservoir; three returned to the river later in summer when the water warmed. Also, local anglers explained that in warm summers, walleye fishing in the river is good; in cold summers, walleye fishing in the river is poor. Water temperature could have an important influence on how long walleye remain in the river after spawning.

Seventy-one percent of walleye locations occurred in the first 25 km below Mio Dam; less than 2% of locations were between McKinley Bridge and Alcona Pond. In the Cedar River, Iowa, 92% of adult walleye locations occurred within 9.7 km of the dam (Paragamian 1989). In the Cedar River, the reach below the dam was described as having deep intermittent pools and gravel-cobble substrate. Downstream of this reach the river had shallower pools, bank failure, and sandy substrate. Paragamian (1989) also noted that walleye would travel downstream through this degraded reach but did not stay in it. Similarly, walleye in the present study occupied sites in the first 25-km below Mio Dam and traveled through the reach below McKinley Bridge to return to Alcona Pond. Mio Dam may have prevented longer migrations and walleye settled into pools just downstream of the dam. Walleye may have remained in these sites as long as river
conditions, particularly temperature and food availability, were suitable. Once conditions become unsuitable, they quickly returned to the reservoir. However, in 1997, when three walleye made a second upriver migration, they established local ranges in the upstream area. They may have done this because they were familiar with these sites or because thermal conditions and food availability were better in the upstream area.

Walleye used river and reservoir habitats in summer but all walleye tracked used reservoir habitats in winter. In the river, walleye showed positive electivity for low velocities and silt substrate. Walleye may use deep pools to avoid light and river current (Paragamian 1989). The fact that three walleye used river sites in summer 1997 that had been occupied by three different walleye in summer 1996 suggests that suitable riverine sites may be in short supply. Walleye seek analogous habitat in both lentic and lotic environments: low velocities, reduced light, suitable temperatures, and highly oxygenated substrates (Kitchell et al. 1977). Walleye may occupy sites in the upstream area because it has more pools and is more thermally stable around the daily mean. The downstream area has more run habitat and more flux around the daily mean. If conditions in the river are suitable during summer, walleye may use either river or reservoir sites. Movement between river and reservoir sites by three walleye during summer 1997 supports this idea.

Small brown trout (mean length 16.5 cm) and rainbow trout (mean length 15 cm) are stocked in the river in mid to late May, shortly after walleye spawn. This increase in biomass in the river could provide additional forage exploited by walleye. Two walleye established local ranges within 50 m of a trout stocking site in late May; other walleye locations occurred near trout stocking sites during May and early June. In the Seminoe Reservoir, Wyoming, walleye stomach samples indicated that most of the 500,000
fingerling trout stocked annually were eaten within a few weeks after planting (McMahon and Bennett 1996). In spring, stocked trout are particularly vulnerable to predation by walleye because post-spawning walleye have high energy demands (McMahon and Bennett 1996). Post-spawning walleye returning to the reservoir may encounter large concentrations of stocked trout. Exploiting this forage may delay walleye in their return to the reservoir.

Walleye activity increased at dusk and remained high during night. Nocturnal activity of walleye is well documented (Rawson 1957, Ager 1976, Kelso 1976, Prophet et al. 1989). Prophet et al. (1989) describes three types of behaviors: holding station, meander swimming, and cruise swimming. Each behavior is associated with a different activity: resting, foraging, and traveling between sites, respectively. Walleye in the present study demonstrated all three behaviors. During the day, walleye remained in essentially the same location; this was termed holding station. At dusk and during night, walleye apparently changed direction frequently or swam in a zigzag pattern. This meander swimming behavior was associated with foraging movements. When cruise swimming, fish swam for extended periods without changing direction. W8 demonstrated this behavior as it swam downstream from its riverine local range toward Alcona Pond, traveling over 19 km in less than five hours.

**Both species**

The results of this study suggest that maximum potential for interaction between brown trout and walleye occurs within the first 25 km below Mio Dam during summer. Brown trout were probably in this area because they were captured within the first 13 km
and they homed to the area of capture. Walleye were captured from river and reservoir sites before, during, and after spawning, yet 71% of all walleye locations were within the first 25 km below Mio Dam. Brown trout and walleye may compete for feeding and resting sites in this reach. Both species used low-velocity sites for daytime resting and increased their foraging activity between dawn and dusk. Since both species are piscivorous as adults, both probably seek highly productive feeding sites with concentrations of forage fish. Predatory interactions may also be likely. The presence of walleye near trout stocking sites suggests that walleye may be eating juvenile brown trout. Diet analysis within the study site could confirm whether diet overlap occurs between these species and whether walleye feed on young brown trout.

Assumptions

Two basic assumptions accompany telemetry studies: transmitters do not affect fish behavior and the small numbers of fish tracked reflect behavior of the entire population. Three angler-caught walleye were reported to be in good health, thus supporting the first assumption. Since three of twelve walleye were taken, it appears that exploitation is fairly high in the study site and that implanted walleye were feeding actively. Anglers noticed the healed scar in the mid-ventral region but said the fish looked healthy. Fish implanted in 1996 and 1997 demonstrated similar behavior with respect to range, frequency of active displacements, and diel activity. This supports the second assumption. However, this study only sampled a portion of the brown trout and walleye populations in this reach. Large brown trout are present throughout the study site, although they are less common downstream of McKinley Bridge. Distribution of
feeding, resting, and spawning sites is a major determinant of fish movement. Given that differences in the distribution of habitat characteristics in the upstream and downstream areas were not detected, I would expect that brown trout collected from the downstream area would demonstrate similar behavior to those in the upstream area. Also, if the study area supports river-spawning and lake-spawning walleye populations, this study likely sampled only river-spawners. Migrations from Alcona Pond to the Mio Dam tailwaters by river-spawning walleye were the biggest probable determinant of seasonal range; lake-spawning walleye would likely have much smaller ranges.

Two weeks has been considered the proper amount of time to insure that a fish has recovered from the trauma of surgery. Brown trout implanted in 1996 had increased frequency of active displacement during the month following surgery. If data from four weeks post-surgery were used, summer range sizes of two fish would decrease from 5,245 m and 9,252 m to 16 m and 15 m, respectively. Three brown trout implanted in May 1996 and tracked during summer 1997 did not have high frequency of active displacements in May 1997. This suggests that active displacements made after surgery in May 1996 were a result of reorientation and homing rather than normal behavior for this time of year. It may take more than two weeks for displaced brown trout to return to or establish a local range.

One assumption of this study was that walleye spawning activity would not be affected by surgical implants. This was important because the timing of implantation was close to the spawning period for walleye, but not for brown trout. Other researchers had implanted transmitters during spawning season with no adverse effects (Summers 1979). However, some researchers noted that females were more sensitive to surgery (Ager
1976, Paragamian 1989). In fact, Ager (1976) found that a female in advanced stages of egg development reabsorbed her eggs and did not spawn, probably due to the stress of surgery. In another study, all fish that died after implantation were females (Paragamian 1989). In the present study, two females implanted prior to spawning may not have spawned due to the stress of surgery.

**Management implications**

A primary difference between this study and previous studies in the South Branch and Mainstream Au Sable River was that brown trout populations in previous studies were self-sustaining but this population was heavily dependent on stocking. Large brown trout in the present study exhibited daily and seasonal movement patterns similar to large brown trout in previous studies. Brown trout in all three studies made movements associated with feeding, spawning, and overwintering. In this impounded reach, some brown trout survive but their life history patterns may be dramatically altered. They may experience increased mortality, increased age at maturation, or decreased growth rates. Dams may decrease the amount of thermal refugia available during warm summer months. Lack of refugia may limit the number of young brown trout that survive to be adults.

Walleye were initially stocked in Alcona Pond to generate a reservoir fishery separate from the riverine brown trout fishery (Dave Smith, MDNR, personal communication). Stocking walleye from Muskegon River stock, a population of river spawners, may have affected the choice of spawning sites for these walleye within the Au Sable River system. Results of this study suggest that brown trout and walleye range
overlap is most common during late spring and summer. Brown trout and rainbow trout are stocked in mid to late May, a month when walleye occupancy of the river is high. Stocking trout at this time may result in a large proportion of newly stocked fish being eaten by post-spawning walleye with high forage demands.
LITERATURE CITED


EPA. 1997. “Surf your watershed: Au Sable River.”


APPENDIX FIGURE 1. Locations of T1 between May 1996 and May 1997. Closed circles represent locations included in one of the two local ranges. The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 2. Locations of T2 between May 1996 and July 1997.
Closed circles represent locations included in the local range. Locations outside the
local range are represented with an "x." The arrow estimates the release point in
May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 3. Locations of T3 between May 1996 and June 1997. Closed circles represent locations included in the local range. Locations outside the local range are represented with an "x." The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 4. Locations of T4 between May 1996 and April 1997. Closed circles represent locations included in one of the two local ranges. The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 5. Locations of T5 during summer 1996. Closed circles represent locations included in the local range. The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 6. Locations of T6 during summer 1997. Close circles represent locations included in the local range. The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 7. Locations of T7 during summer 1997. Closed circles represent locations included in one of the two local ranges. The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 8. Locations of T8 during summer 1997. Closed circles represent locations included in the local range. Locations outside the local range are indicated with an "x." The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 9. Locations of W1 between May 1996 and May 1997. Closed circles represent locations included in one of the two local ranges. Locations outside of the local ranges are indicated with an "x." The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 10. Locations of W2 during summer 1996. Closed circles represent locations included in the local range. The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 1. Locations of W3 between May 1996 and June 1997. Closed circles represent locations included in one of the three local ranges. Locations outside the three local ranges are indicated with an "x." The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 12. Locations of W4 during summer 1996. Closed circles represent locations included in the local range. The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 13. Locations of W5 between May 1996 and May 1997. Closed circles represent locations included in the local range. Locations outside the local range are indicated with an "x." The arrow estimates the release point in May 1996. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 14. Locations of W6 during summer 1997. Closed circles represent locations included in the local range. Locations outside the local range are indicated with an "x." The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 15. Locations of W8 during summer 1997. Closed circles represent locations included in the local range. Locations outside of the local range are indicated with an "x." The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 16. Locations of W9 during summer 1997. Closed circles represent locations included in the local range. The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 17. Locations of W11 during summer 1997. Closed circles represent locations included in one of the two local ranges. Locations outside of the local ranges are indicated with an "x." The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 18. Locations of W11 during summer 1997. Closed circles represent locations included in the local range. The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.
APPENDIX FIGURE 19. Locations of W12 during summer 1997. Closed circles represent locations included in the local range. Locations outside the local range are indicated with an "x." The arrow estimates the release point in April 1997. The dashed line represents the beginning of the reservoir.