Movement, Habitat Use, and Daily Activity Patterns of Trophy Brown Trout in the South Branch of the Au Sable River, Michigan

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OF THE AU SABLE RIVER, MICHIGAN[1]

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by

David F. Clapp

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Committee members

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Adjunct Professor William C. Latta

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Acknowledgments

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Major funding for this study was provided by the Michigan Fly Fishing Club, based in Livonia. The club members showed tremendous interest in the project; they provide a good example of the positive role that trout fishing organizations can and must play in the conservation of this valuable resource. I would especially like to thank Bill and Fran Merrill. Bill provided a great deal of help to me in the field, and made constructive comments on early drafts of this thesis. Both Fran and Bill showed me

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Abstract

Most previous studies of brown trout <u>Salmo</u> <u>trutta</u> ecology and behavior have focused on smaller fish, or fish in lakes or under controlled conditions. Very little work has been done in investigating the ecology of large, free-ranging, stream-resident brown trout. The present study was undertaken to monitor the movement, habitat use, and daily activity patterns of these fish.

Radio transmitters were implanted in eight brown trout between 437 mm and 635 mm from the South Branch of the Au Sable River, Michigan over a two year period. Daily tracking during summer (May - August), and tracking at two-week intervals during fall and winter (September - April) was used to determine movement, habitat use, and activity patterns of these fish. Range of movement and home site use was defined, and measured for each fish tracked. I evaluated habitat use by comparing habitat in stream quadrats used by fish to that available in quadrats chosen at random from throughout the river. Two measures of brown trout activity were defined; local activity and long-range activity. Local activity was measured by counting fluctuations in radio signal strength over a 24-h period, and long-range activity was measured as the linear distance covered by a fish between consecutive daytime resting locations.

Range of movement for eight fish tracked varied from 370 m to 33.4 km. The average range of movement in summer was approximately 5,000 m, while the average range of

movement in winter was approximately 12 km. Movement appeared to be nonrandom; that is, fish used a few locations often and were seen to return to these sites after movement to other areas of the river. Fish tracked during summer periods used as many as four home sites; the average separation between these sites was 386 m.

Brown trout chose deep, slow areas with heavy log cover. Significant positive electivity was seen for mean and bottom water velocities less than 10 cm/sec, depths between 46 and 60 cm, areas of cover including overhanging branches, vegetation, and logs, and areas with silt substrate.

Distinct peaks in local activity were observed during two summer months. A major activity peak in June occurred at 2200 h, but in July this major peak shifted to 0500 h. No distinct activity peaks were apparent in August. Light intensity accounted for almost 29% of the variance in local activity levels. Seasonal differences in local activity may also have been related to changes in food availability or temperature.

Long-range activity observed in summer was significantly less than that seen during winter. Average summer long-range activity was less than 300 m, while average winter activity was greater than 3000 m. However, extensive nighttime "foraging" activity in summer was much greater than any reported in previous studies. No significant upstream or downstream trends in long-range activity were observed once fish took up residence in an area; however, many of the fish tracked made a long movement to upstream areas in fall, then

remained in these upstream areas over winter. Significant positive correlations were seen for long-range activity with volume discharge and average daily air temperature. Significant negative correlation was seen between long-range activity and groundwater levels.

During the present study, six of eight fish tracked moved out of a catch-and-release section of the South Branch, making them vulnerable to harvest in sections of the river not covered by special regulations. However, four of five fish tracked during the period of peak fishing pressure (May-August) remained in this catch-and-release section. Possibly, increased harvest of trophy fish in areas adjacent to regulated areas could be counted as an additional benefit of these quality fishing regulations.

Introduction

Studies of stream-resident brown trout <u>Salmo</u> <u>trutta</u> have traditionally focused on movement, habitat use, and activity patterns. The results of this research have in many instances been disparate. Some researchers have shown that brown trout move very little. Cobb (1933) found that fish tagged in a number of Connecticut streams showed greater displacement from the site of initial release than brook trout <u>Salvelinus</u> <u>fontinalis</u>, but that the majority of recaptures still tended to occur close to the areas in which brown trout had been tagged initially. Allen (1951) reported similar findings from a mark-and-recapture study of a New Zealand brown trout population. Bachman (1984), using visual observations, found that brown trout in Pennsylvania streams remained close to a single location throughout their entire lives.

Other studies, however, suggest that trout may move extensively, especially during fall and winter. Schuck (1943), using data from fish caught in weirs in combination with tagging, found that brown trout showed little movement during spring and summer, but could be seen to move several miles upstream to spawn during October and November, and then return to their original locations sometime during the winter. Jenkins (1969) observed both a resident and transient segment of brown trout populations in the mountain streams of California. Resident fish generally displayed long-term (50 days) position stability while the transient

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segment of the population was characterized by frequent aggressive displays and the absence of a settled social structure.

Similar disparities can be seen in the results of studies examining brown trout habitat use and activity patterns. The variables thought to constitute ideal trout habitat have been defined (White 1975, Raleigh and Duff 1980), but use of this habitat by trout in streams may vary depending on factors such as lifestage (Raleigh and Duff 1980), activity (Gosse and Helm 1981), competition (Fausch and White 1981), or threat (Bachman 1984). Many studies on the behavior and feeding patterns of brown trout have shown that activity may occur in distinct bouts, but the timing of these bouts may vary considerably. Oswald (1978) recorded three daily peaks in trout feeding activity using an analysis of electromyogram rhythms. Elliott (1970) found midday and evening peaks in feeding activity through an analysis of brown trout stomach contents. Chaston (1969) found that brown trout were most active between dusk and dawn in laboratory experiments.

Disparities between the findings of these studies result in part from differences in the methodologies used and in the size of fish being studied. Mark-and-recapture studies used to investigate movement can only provide limited information. Recapture locations are sometimes known accurately only to within one or two miles (Cobb 1933), so distances moved by fish may be greater than those actually reported. The activities of fish between marking and

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recapture are not known, and dependence on angler efforts for tag returns may bias results to include a relatively large proportion of returns from popular fishing sections and during peak fishing periods. Important fall and winter movements may be missed. Weir captures can provide additional data, but an investigator using weir data still has no information (other than direction) on where fish originated, or what conditions at these original sites may have triggered the movements observed. Direct visual observations, while valuable, place strict spatial and temporal limits on the study of a fish population. For example, fixed shore stations can only be employed in cases where fish are readily visible from above the surface of the water. For this reason, fish which are often under heavy cover may not be observed using this method (Rankin 1986). Underwater (SCUBA) observations have added tremendously to our knowledge of trout behavior and habitat use (Fausch and White 1981, Cunjak and Power 1986), but may still introduce bias by displacing fish from areas actually chosen. Obviously, visual observations cannot be used to investigate nighttime behavior without the aid of specialized optical equipment.

The size of individual brown trout in the studies cited above varied, but few studies specifically included larger stream-resident fish as a part of the population under investigation (the average size of fish in these studies was approximately 250 mm). However, most recounted isolated incidents in which larger brown trout exhibited behavior that

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was strikingly different from that observed in the rest of the fish population under study. Cobb (1933) reported on a brown trout that may have moved 80 km downstream. Shetter (1967) described movements by some large (>330mm) brown trout of up to 65 km from the site of tagging. Jenkins (1969) gave examples of large brown trout periodically leaving areas of cover to roam through a stream section under investigation; at times making attempts to forage on small trout. This roaming behavior, while limited to movements of less than 100 m, was not observed among brown trout of smaller size classes. Bachman (1984) found that the size of a brown trout's "home range" may decrease between age I and age V; after this point, fish may adopt a roaming or migratory lifestyle (Bachman 1982).

Large, stream-resident brown trout appear to show patterns of behavior distinct from smaller fish, and some of the common methods of study may not be appropriate for elucidating these behaviors. The use of radio telemetry overcomes many problems related to the study of brown trout ecology. Telemetry observations allow precise location of fish for documentation of habitat use (Diana et al. 1977), and allow movement and activity to be monitored continually (Diana 1980, Mesing and Wicker 1986). Information on location and behavior of trout at night and in heavy cover can also be obtained. Telemetry is ideal for the study of large fish (which are rarely studied using other methodologies), as large fish are capable of carrying long-lived transmitters without impaired swimming ability (Winter

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1983).

The present study was undertaken to increase the current base of knowledge concerning the movement, habitat use, and daily activity of large, free-ranging, stream resident brown trout. The specific objectives of this study were: 1) to monitor seasonal movement and habitat use by trophy brown trout in the South Branch of the Au Sable River near Roscommon, Michigan; and 2) to evaluate daily activity patterns of these fish during the main fishing season (May-August). In this study, a trophy fish was defined as any brown trout over 432 mm in length.

Methods

Study Area

This study was conducted on the South Branch of the Au
Sable River, near Roscommon, Michigan. The South Branch is a
coldwater river extending from Lake St. Helen in Roscommon
County to its confluence with the Mainstream of the Au Sable
River in Crawford County, approximately 25 km east of
Grayling, Michigan. Six dams along the length of the Au
Sable Mainstream prevent migration of brown trout from Lake
Huron.

The South Branch recieves a stable groundwater input,
and is supplemented by inputs from a number of feeder creeks;
most notably Robinson Creek, just upstream from the town of
Roscommon. The upper reaches of the river flow through low
lying swampy areas and the primary fish present are northern
pike Esox lucius, yellow perch Perca flavescens, suckers
Catostomus spp, and minnows (Cyprinidae) (Shetter 1967).
Quick discharge of rainwater through these low areas into the
river causes increased flow fluctuations in this upper
section of the river (Bosserman and Higgins 1969). Below
Roscommon, the river cools, the gradient becomes somewhat
steeper, and trout species, usually brown trout and brook
trout, dominate (Shetter 1967). I worked primarily on the
area of the South Branch between Roscommon and Smith Bridge
(Figure 1).

Mean annual flow on the South Branch, measured at Smith

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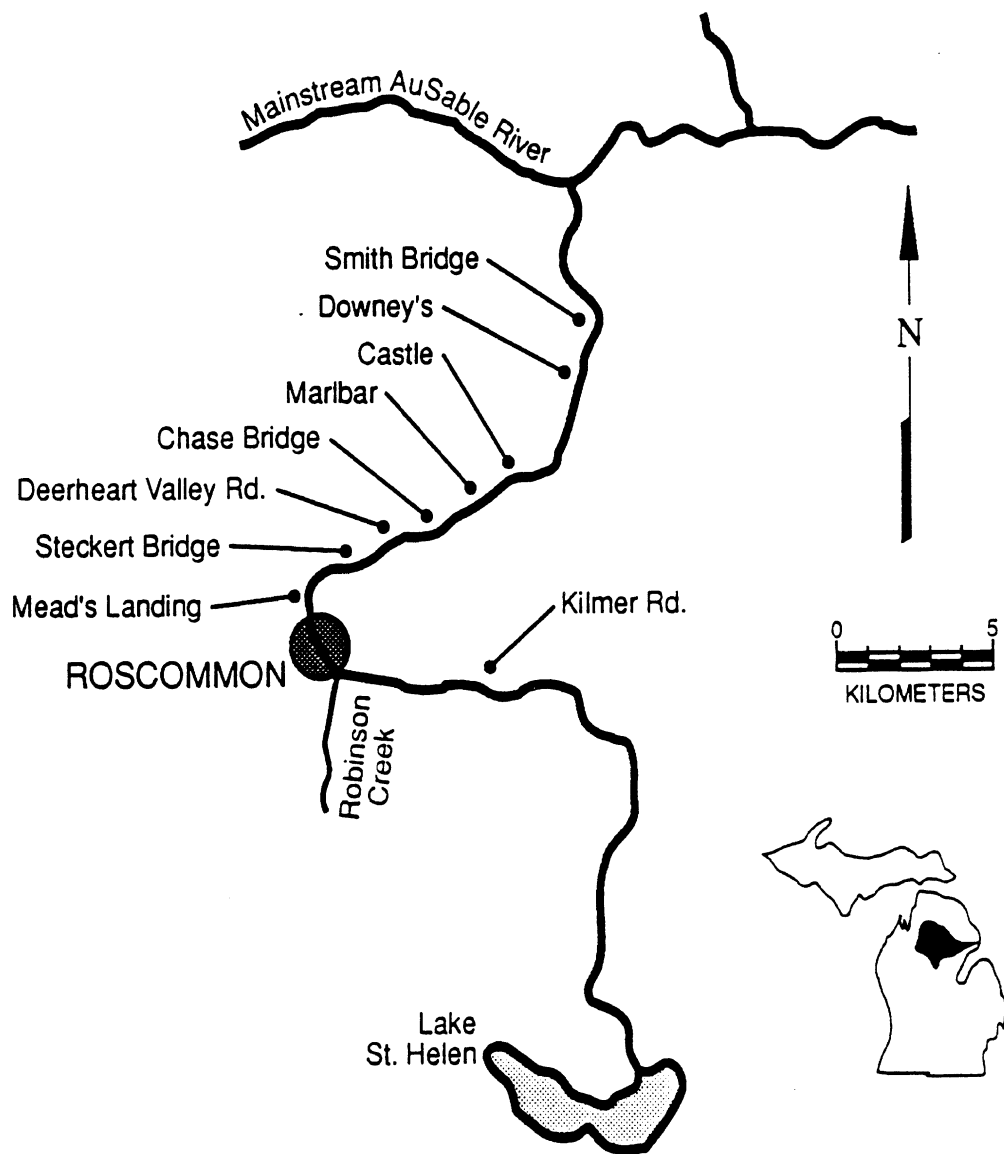
Figure 1. South Branch of the Au Sable River, showing various landmarks in the study area. Fish for implant of transmitters were taken between Chase Bridge and the Castle. Statewide trout regulations were in effect upstream of Chase Bridge. From Chase Bridge downstream to one km below the Castle, a flies-only, zero creel limit regulation was in effect. Downstream from this point to the Mainstream, a flies-only, 5 fish creel limit regulation was in effect.

Bridge, is approximately 6.5 m /sec (Coopes 1974). Average width of the river is approximately 20 m, and average gradient is 0.09% (Shetter 1967). Average minimum water temperature in July is approximately 21 C upstream of Roscommon, and approximately 18 C at Smith Bridge. Average maximum water temperature in these same areas is approximately 26 C and 24 C, respectively (Coopes 1974). This temperature distribution is somewhat unusual. Many streams, particularly those in mountainous areas, have cool upstream reaches and warmer downstream reaches.

Implant of Transmitters

Transmitters were successfully implanted in eight brown trout between May 1986 and June 1987. Another sixteen implants were unsuccessful (Table 1). Fish for transmitter implants were taken using D.C. electrofishing gear. An incision was made into the abdominal cavity either through the lateral body wall or ventrally, anterior to the pelvic girdle. A transmitter was inserted through this incision, and the incision was closed using non-dissolving nylon sutures. Fish were released into the river near the site of capture.

Transmitters used (from Custom Telemetry and Consulting; Athens, Georgia) were approximately 4 cm long, 2 cm in diameter, and weighed approximately 12 g (1986) or 20 g (1987). Transmitter batteries used in 1986 failed earlier than expected, and were replaced with larger batteries in

Table 1. Summary of brown trout transmitter implants performed between May 1986 and June 1987. For Days tracked, NS indicates fish tracked successfully for less than two weeks, and 0 indicates fish dying immediately following surgery.

Date implanted	Temperature (C)	Length (mm)	Weight (g)	Days tracked	Implant site
May 5, 1986	--	488	1112	102	Lateral
		432	810	NS	Lateral
		396	640	NS	Lateral
		396	600	NS	Lateral
		391	570	0	Lateral
		396	610	NS	Lateral
		437	830	52	Lateral
Jul 8, 1986	21	470	1200	0	Lateral
		546	1670	0	Lateral
		541	1710	0	Lateral
		500	1190	0	Lateral
Oct 23, 1986	10	589	1850	80	Lateral
		521	1550	114	Lateral
		569	1570	0	Lateral
		635	2050	93	Lateral
		627	2500	NS	Lateral

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Table 1 (continued)...

Date implanted	Temper- ature (C)	Length (mm)	Weight (g)	Days tracked	Implant site
May 5, 1987	11	470	----	NS	Lateral
		485	----	NS	Lateral
		462	----	NS	Lateral
		419	----	NS	Lateral
Jun 3, 1987	18	505	----	346	Ventral
		488	----	345	Ventral
		510	----	199	Ventral
Aug 8, 1987	20	556	----	0	Ventral

1987.   Each transmitter was encased in surgical wax and bore identifying information, including a telephone number to be contacted in the event one of the fish was found dead, or captured by an angler.   Each fish was tracked on a different frequency between 49 and 50 MHz.

Location of Fish

During the summer months (May - August) I attempted to locate every fish on each day.   When fish moved to widely separate areas this was not always possible.   However, I usually did not go more than two days between locations of a given fish.   During the winter months (September - April), fish were located at approximately two-week intervals.   Data collected during the two weeks immediately following implant of transmitters were discarded, since fish often exhibit erratic behavior during this time (Mesing and Wicker 1986).

I initially located fish by floating the river in a canoe, using a scanning receiver (Model - Challenger 200) and 60 cm loop antenna (both from Advanced Telemetry Systems; Isanti, Minnesota).   Using this system, I could detect fish at a distance of approximately 200 meters.   If a fish had been located recently,   I began searching at the site where I had last found that fish.   After a radio signal was detected, I took bearings from a number of positions on the river bank, upstream and downstream of the estimated position of the fish, in order to more accurately determine that position.   A smaller (15 cm) loop antenna was often used for close-range

work.   When I had determined a fish's location, I waded into the river to verify the position.   I could generally approach to within five meters (sometimes to within one meter) of a fish before it was disturbed, so that verification was by sight of the fish, by maximum signal strength, or in some cases by maximum signal strength followed by a drop in strength (indicating rapid movement by the fish).   Fish were only disturbed to make habitat measurements, and generally they remained near or in cover at the position of location, even as habitat measurements were taken.   I assumed that these disturbances did not significantly influence the movement and activity patterns observed.

The locations of all fish were plotted on maps constructed from aerial photographs and topographic maps of the area.   On these maps, the river was divided into quadrats 10 meters long (thalweg distance) with a width equal to either 1/2 the width of the river, or equal to 10 m (if the river was wider than 20 m).   The size of this quadrat represents an area large enough to include that entire portion of the river in use by a trout at the time of location, and small enough to allow for accurate location and habitat data collection.

In analyzing movement and activity, the data I collected were separated into two groups.   The first group included summer data, collected between May 1 and August 15; the second group included fall/winter data, collected between August 16 and April 30.   This second group will hereafter be referred to as winter data.   Two fish were tracked

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exclusively during a summer period (May - August 1986), three

fish were tracked exclusively during a winter period (October

1986 - February 1987), and three fish were tracked through

both summer and winter periods (June 1987 - May 1988). This

division into summer and winter was not an arbitrary one, but

rather based on observations made in the field. Fish tracked

during this study tended to exhibit much more extensive

movements beginning in mid-August.

Movement

Range of movement is defined in this study as the

distance between extreme upstream and downstream telemetric

locations of each fish. Home sites within this range were

identified for fish tracked during summer periods, and I

compared the average separation between home sites for each

of these fish. A home site was defined as: 1) a quadrat

that was used five or more times by a given fish, or 2) a

quadrat which a fish returned to after moving to a separate

quadrat in the river (thus exhibiting a homing tendency). Two

adjacent quadrats which both fulfilled the requirements of a

home site were considered to be a single home site. I also

plotted distributions of quadrat use for each fish tracked

during a summer period, and compared the average number of

days that each fish remained at a quadrat before moving.

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Habitat Use

Quantitative habitat data was collected exclusively for fish located during summer tracking. This included two fish in 1986 and three fish in 1987. During summer 1986, I measured depth, mean water velocity, substrate type, and cover type at a single point that I took to be the focal location of the fish being tracked. There were two major problems associated with this methodology; 1) radio locations were not accurate enough to be taken as precise focal point values, and 2) because large brown trout were found to move a great deal (as compared to smaller fish), measurements at a single point were not totally representative of habitat being used. To correct these problems, I made some modifications for work during summer 1987. Results reported in this study reflect only habitat data collected in sites used by fish tracked during 1987.

After locating a fish and identifying which map quadrat encompassed its position, I completely characterized the habitat present in that quadrat. Eighteen quadrats used by fish were characterized. Fish often used a quadrat more than once; multiple measurements were taken on six of these eighteen quadrats. I established transects at the upstream edge, middle, and downstream edge of each quadrat, and determined water depth, mean and bottom water velocity, substrate, and cover type present at one meter intervals along each of these transects. These were assumed, from a review of the available literature, to be the five most

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important habitat variables. Approximately thirty
measurements were made in each quadrat, depending on stream
bank morphometry (3 transects x 7-10 m per transect). Mean
water velocity (at 0.6 of the depth of the water column) and
bottom water velocity (from 1-5 cm above the substrate) were
measured using a Swoffer 2000-1 Open Stream current meter.
Predominant substrate type at each meter interval was
estimated by sight as belonging to one of five categories -
silt, sand, gravel (< 2 cm), small cobble (2-10 cm), or large
cobble (> 10 cm). Predominant cover type at each meter
interval was estimated by sight as belonging to one of six
categories - logs, brush, vegetation, boulders, overhang, or
open. Logs provided instream cover for fish, and included
trees, limbs, boards, and combinations of these items with
individual widths or diameters greater than 10 cm. Brush
also provided instream cover for fish but included no
individual items with widths or diameters greater than 10 cm.
This category included primarily tree tops which lay into the
water, as well as some flooded riparian vegetation.
Overhanging cover provided no instream shelter for fish, but
acted only to shade fish from direct sunlight and overhead
disturbance.

In addition to quadrats encompassing brown trout
locations, habitat was characterized for nineteen other
quadrats chosen at random from within the stream sections
used by radio-tagged fish. I used Strauss' (1979) linear
index of electivity to compare habitat use data pooled from
three fish tracked in 1987 to data from these random

quadrats. This index ranges from -1 to 1, with positive values indicating preference and negative values indicating avoidance or inaccessibility. I used a 5% level of significance (t-test, P=0.05) to test whether selection by brown trout for five habitat variables was significantly different from zero.

Only habitat data collected in the five meters of each quadrat closest to the stream bank was used for the analyses reported here, since this was where fish were located in all cases. Analyses using data from the entire quadrat gave similar results.

Daily Activity Patterns

Two measures of activity were obtained during the present study. The first, local activity, reflects fish activity in a limited area within range (approximately 200 m) of a radio reciever and antenna mounted on the stream bank. Observations to determine local activity patterns were made throughout the summer (June - August) during 8 three-hour (1986) or 12 two-hour (1987) observation periods, randomized over a day. A complete 24-h cycle was covered approximately once every two weeks. Two fish were used for observations in 1986, and an additional two fish for observations in 1987. If possible, fish were observed in sequence, one or both fish each day. If the "target" fish could not be located before the observation period in question, the second fish, if it could be located during that period, was used for the

observation.

During these observations, I used a tripod to mount an antenna on the bank of the river within signal range of the fish. It was not necessary to know the exact location of the fish, because I was only monitoring absolute activity levels. I was able to detect changes in the distance from and orientation of a fish to the mounted antenna as fluctuations in radio signal strength. The number and magnitude of these fluctuations reflected three levels (resting, turning, or continuous) of local activity. I determined that fluctuations were caused by fish activity and not simply background "noise" by observing the signal response on a chart recorder to a transmitter placed in a dead fish which was moved manually to simulate swimming activity.

During each observation period, I recorded the number of fluctuations in radio signal strength over a one-minute interval, once every five minutes. Local activity in this study is defined as the number of fluctuations in signal strength per minute of observation. Measures of local activity for fish were stratified by month and year, because I assumed that this activity would vary in response to seasonal changes in day length, water temperature, and food availability. Differences in local activity levels between these strata were investigated using a two - way analysis of variance (ANOVA). I plotted mean hourly local activity levels for each month and year to show 24-h patterns, and attempted to relate the observed variations in activity to metabolic scope for activity, light intensity, and feeding

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rate using a regression analysis. Metabolic scope for activity (the difference between maximum (Q_{max}) and standard (Q_{stand}) metabolism at a given temperature) and feeding rate (in g/hour) were calculated using water temperature data recorded during the present study, and the following equations from Elliott (1975, 1976):

$$Scope = Q_{max} - Q_{stand}, \text{ where}$$

$$Q_{max} = A_1 \times W^{(B_1)} \times e^{((B_2) \times T)}, \text{ and}$$

$$Q_{stand} = A_2 \times W^{(B_3)} \times e^{((B_4) \times T)}.$$

$$Rate = C \times e^{(D \times T)}.$$

A_1, A_2, B_1, B_2, C_1, C_2, D_1, and D_2 terms are temperature dependent constants determined by Elliott (1975, 1976), T is ambient (water) temperature, and W is the fish's weight in grams. Light intensity was included in the regression model as a linear function with a minimum at midnight (0000 h) and a maximum at noon (1200 h).

The second activity measure, long-range activity, was defined as the linear distance, upstream (+) or downstream (-), covered by a fish between consecutive daily resting locations. Yearly and seasonal variations in long-range activity, as well as differences in long-range activity

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between individual fish, were evaluated using a nested ANOVA, or, in some cases, a Kruskal-Wallis test. Frequency distributions of upstream and downstream long-range activity for summer and winter periods were compared using a Kolmogorov-Smirnov test. I also calculated correlations between long-range activity and volume discharge, daily change in volume discharge, groundwater level, daily average air temperature, daily high and low air temperatures, and day length. Discharge and groundwater data were obtained from the United States Geological Survey station in Grayling, Michigan (Crawford County), and the remaining data were obtained from the National Weather Service station at Roscommon County Airport, Houghton Lake, Michigan. I used a 5% level of significance (P = 0.05) for all regression analyses and statistical tests.

Results

Implant of Transmitters

Mortality of brown trout following surgical implant of transmitters was relatively high (67%). Mortality seemed to depend on implant site, as well as water temperature at and following the time of implant. Fish for which transmitters were implanted through incisions in the lateral body wall experienced extremely high mortality (75%). Lateral incisions may have severed connective tissue, causing delays in healing and increasing the risk of infection. Fish

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with transmitters implanted ventrally showed much lower
mortality (25%).   The only mortality following a ventral
implant occurred in August 1987, when water temperatures
reached 20 C (Table 1).   It was apparent that the majority
of mortalities occurred during periods of warm water,
regardless of implant site, and I attempted to avoid these
periods in later surgery.

Movement

Range of movement varied considerably among individual
fish.   The smallest range was 370 m, and the largest was 33.4
km (Table 2).   No seasonal trends in range of movement were
apparent.   The average range of movement in summer was 4.9
km, while the average range of movement in winter was 11.9
km.   Six of the eight brown trout tracked moved out of the
catch-and-release section and into areas of the river under
statewide trout regulations (Figure 2).   However, four of
five fish tracked during summer periods remained in or near
this section of river throughout most of the summer.

Movement by fish, especially in summer, appeared to be
nonrandom.   Trout used a few locations often, and returned to
these sites after movement to other areas of the river.   Of
fifty-seven different quadrats used by trout during this
study, eight were used seven or more times (Figure 3).
Quadrats used by fish tracked in 1986 were also used on three
occasions by fish tracked in 1987.   Overlap in site use

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Table 2. Range of movement and home site use by fish tracked between May 1986 and May 1988. Mean separation refers to average distance between home sites used by a given fish.   Overall values are averages of values for individual fish. Standard deviation in parentheses.

Fish number	Range (m)	Number of home sites	Mean separation	Percent time in home sites
Summer				
1	670	4	40 (22)	86
2	370	4	63 (37)	94
6	16,800	1	--	97
7	1,900	4	1,053 (732)	88
Overall	4,935 (7,938)		386 (623)	91
Winter				
3	470	1	--	33
4	11,610	1	--	25
5	2,110	0	--	--
8	33,420	1	--	40
Overall	11,902 (15,162)		--	33

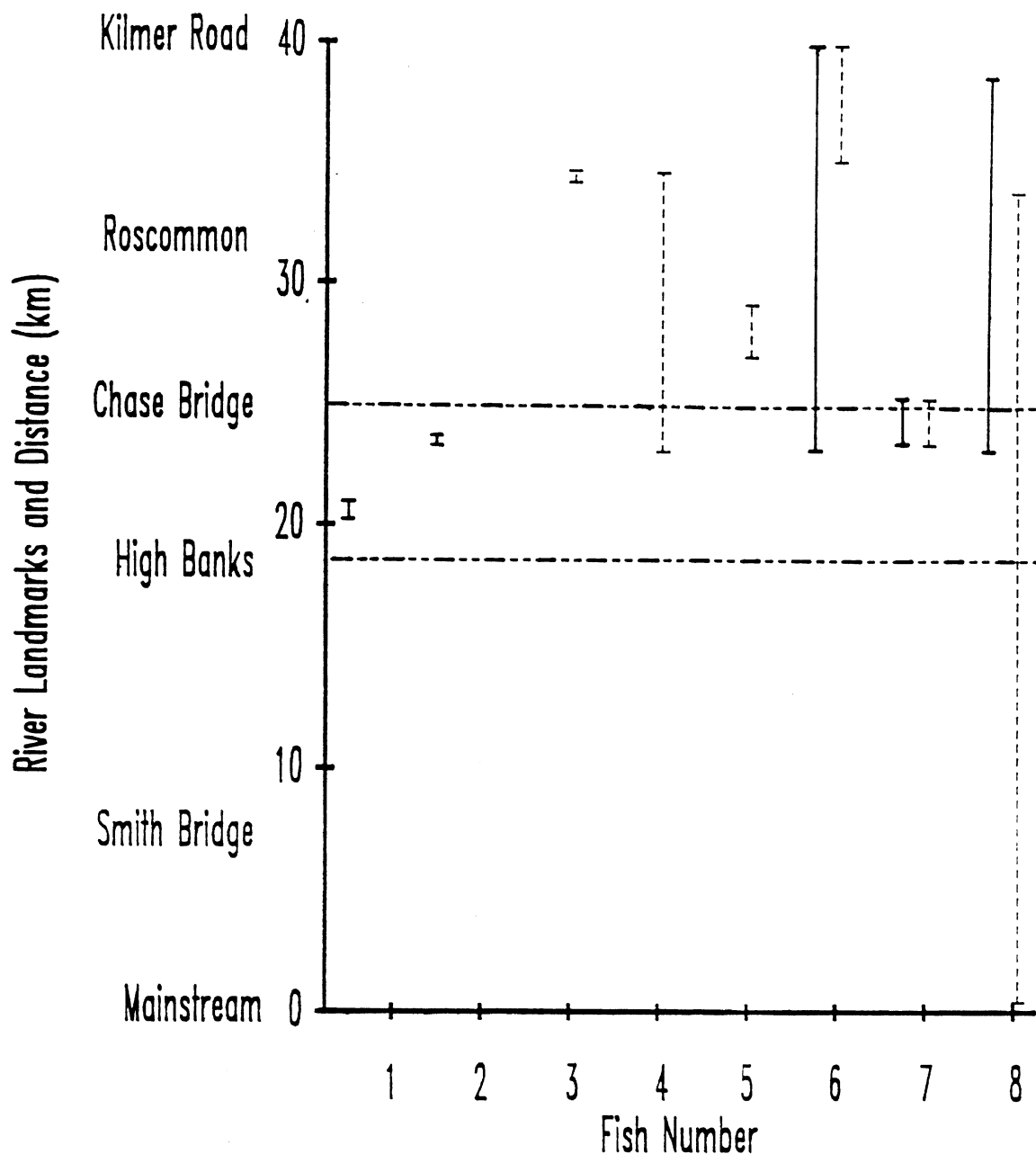Figure 2.   Range of movement by eight brown trout tracked during the present study.   The catch-and-release (flies-only, zero creel limit) fishing area is shown with horizontal dashed lines.   Upstream and downstream limits of fish movements are indicated by high and low horizontal bars. Vertical solid lines indicate summer range of movement, vertical dashed lines indicate winter range of movement.
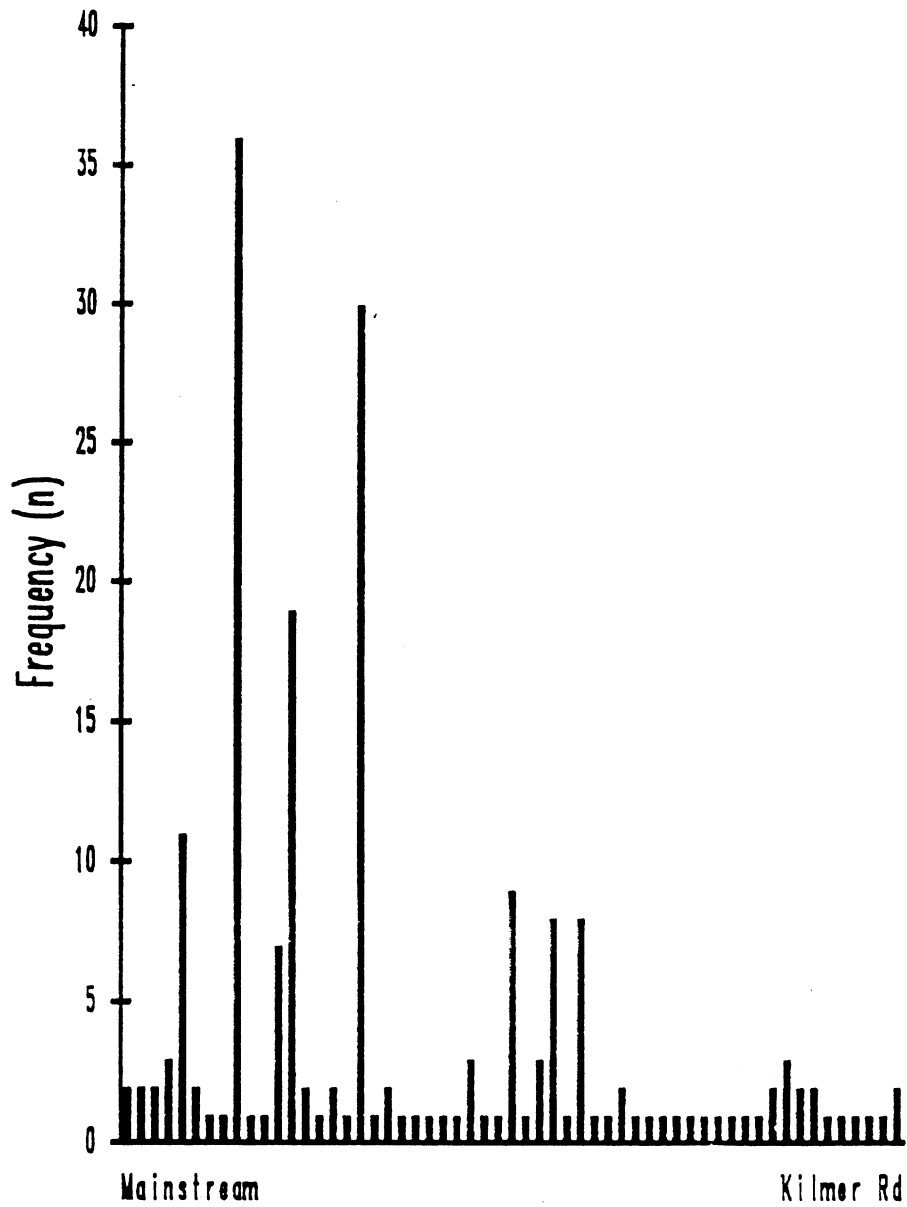
Figure 3. Frequency of use for 57 quadrats occupied by brown trout in the South Branch of the Au Sable River. Joyce Kilmer Road marked the upstream extent of movement, the Mainstream marked the limit of observed downstream movement. Quadrats used were not evenly distributed (in distance) between these two limits.

occurred between two fish tracked in the winter of 1986 and between two fish tracked during 1987-1988.

The number of home sites used by fish tracked during summer ranged from one to four. One fish used a single home site (Figure 4), while three others each used four home sites (Figures 5, 6, and 7). The average separation between home sites for these three fish was 386 m, and these home sites were in use between 86% and 97% of the times fish were located (Table 2). Fish tracked in summer moved between quadrats (not necessarily home sites) about once every three days (mean = 3.15 days), but one fish was observed in a single quadrat for fifty-two consecutive days without displacement.

Habitat Use

Fish appeared to select areas with mean and bottom water velocities less than 10 cm/sec. In quadrants used by fish, 70% of the measures of mean velocity were less than 10 cm/sec, while only 46% of mean velocity measures in random quadrants were less than 10 cm/sec (Figure 8). The corresponding values for bottom water velocity were 79% and 56%, respectively (Figure 9). Electivity indices were significantly greater than zero for both variables (P < 0.05).

Fish consistently used areas with overhang, vegetation, and log cover (Figure 10). Significant positive electivity was seen for all three of these cover types (P < 0.05), while

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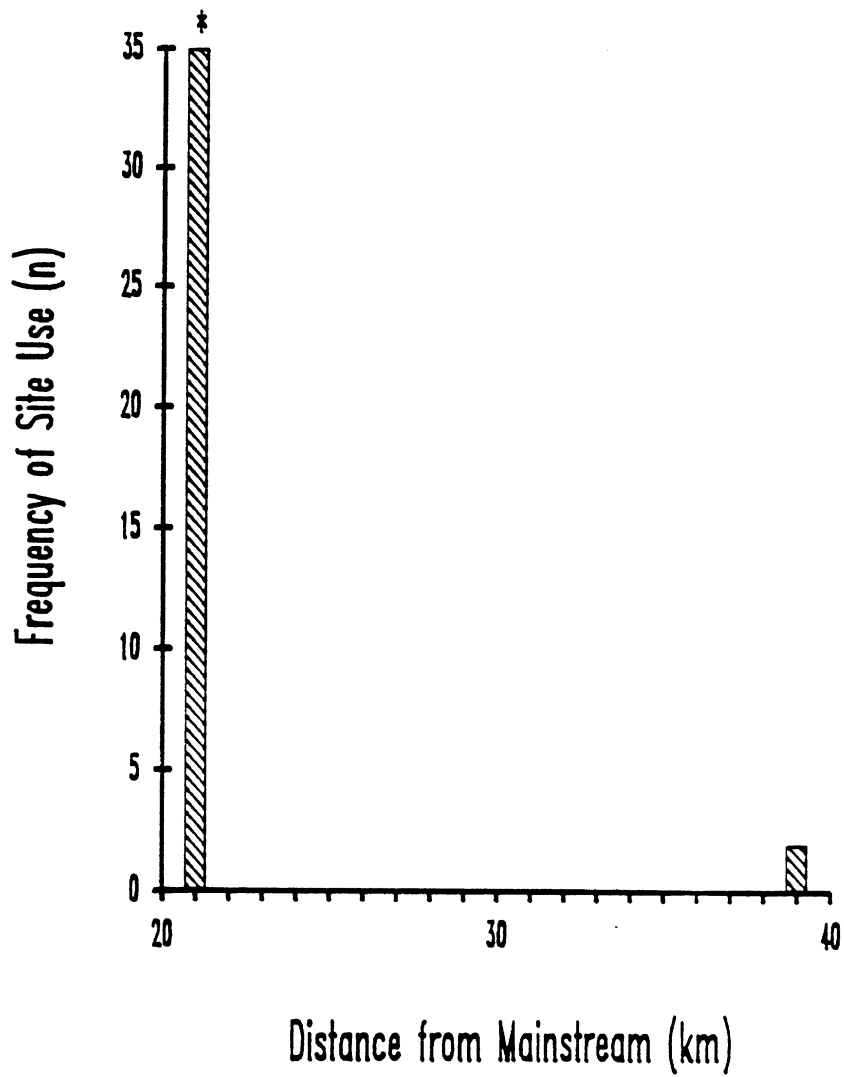
Figure 4.   Summer site use by fish #6,   tracked from June
to December, 1987.   Home sites, as defined in text, are
indicated with an "*".
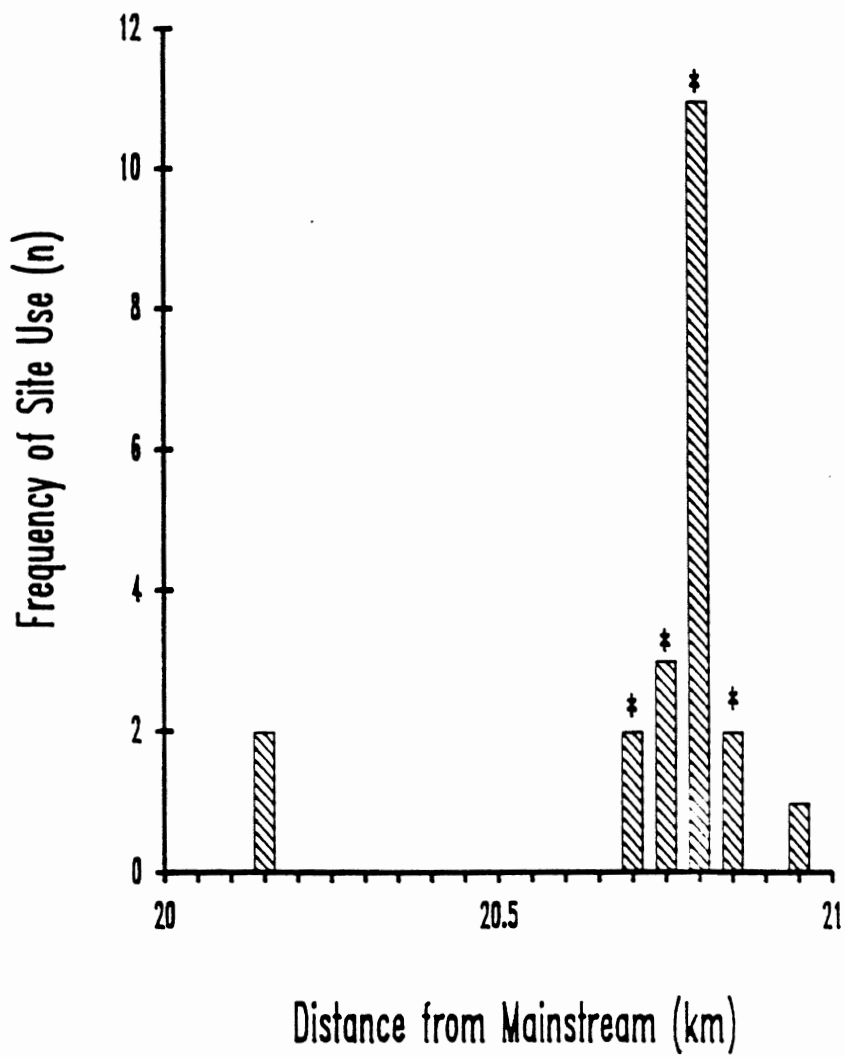
Figure 5. Site use by fish #1, tracked during summer
1986.
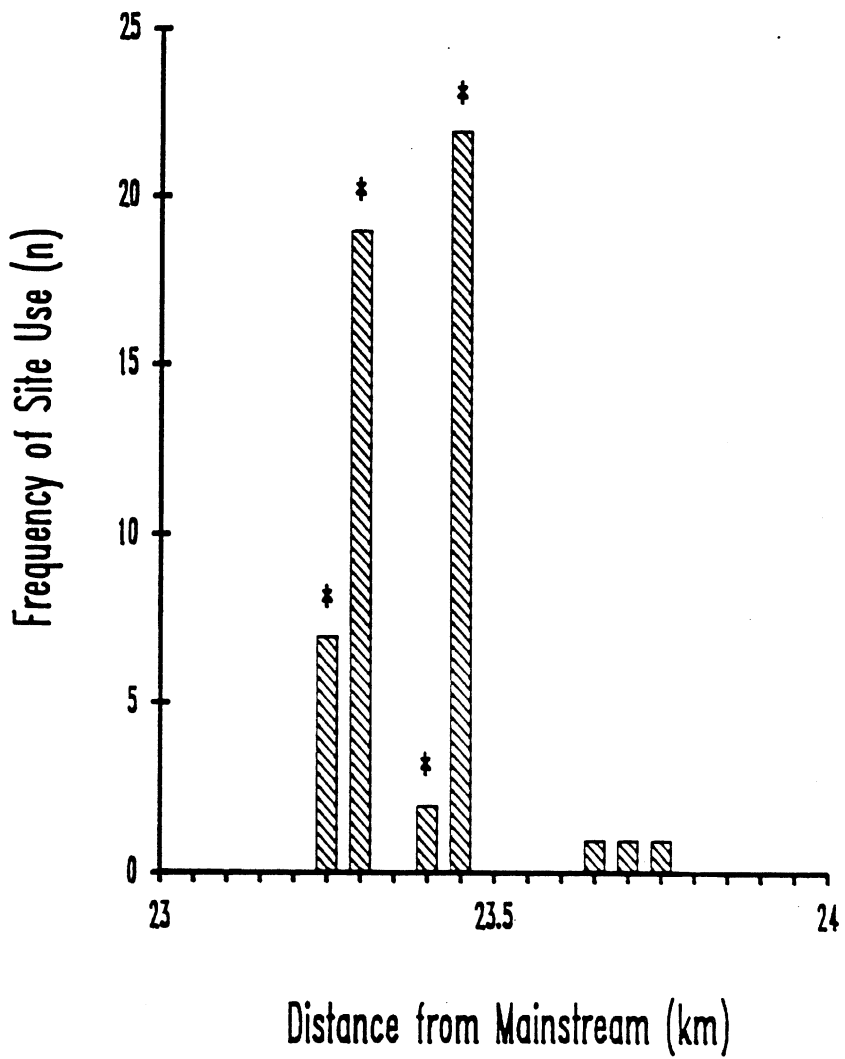
Figure 6. Site use by fish #2, tracked during summer 1986.
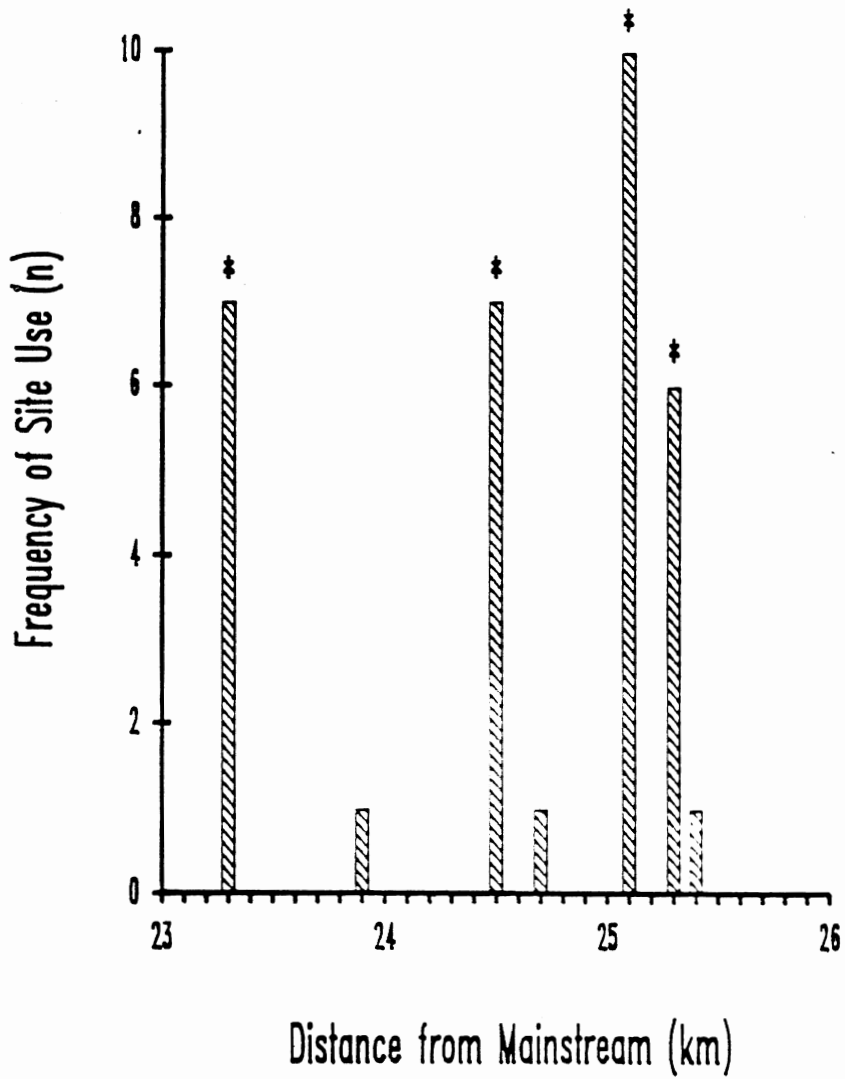
Figure 7.   Summer site use by   :7,   tracked from June
1987 to May 1988.
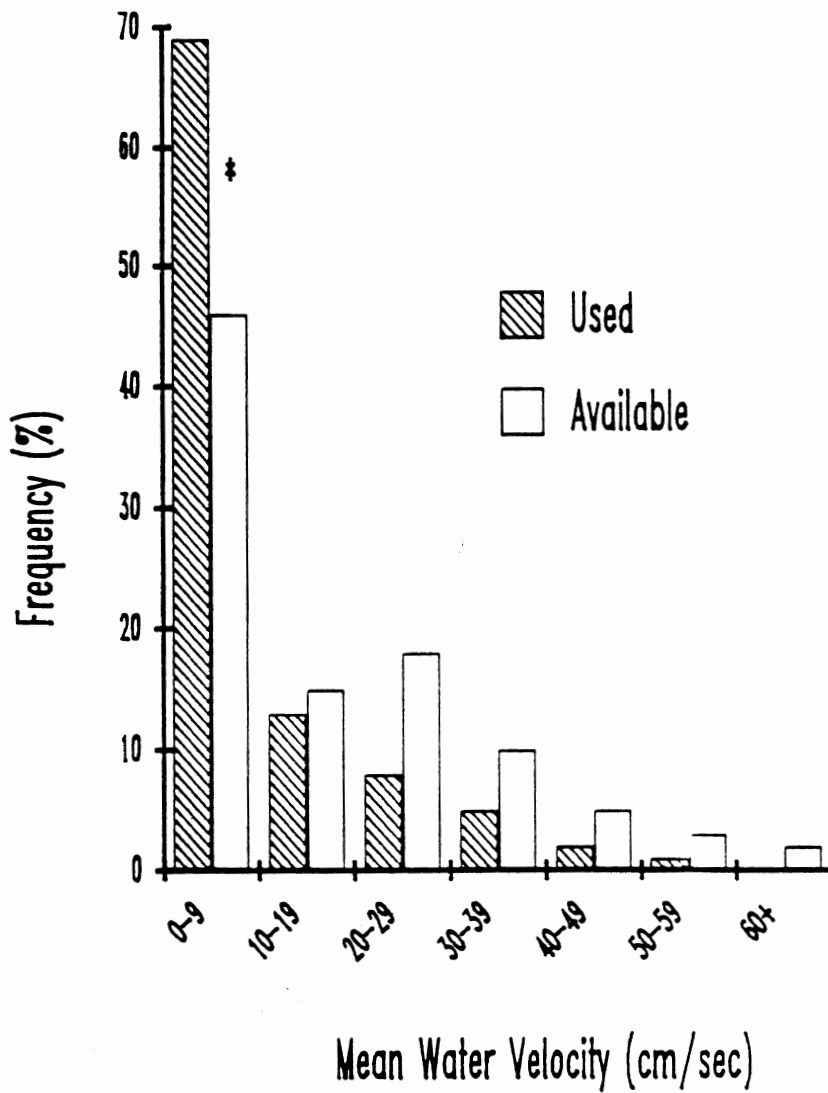
Figure 8.   Comparison of available mean water velocity to
that used by three brown trout tracked during summer 1987.
Velocities for which use was significantly different from
that available (P<0.05) are indicated with an "*".
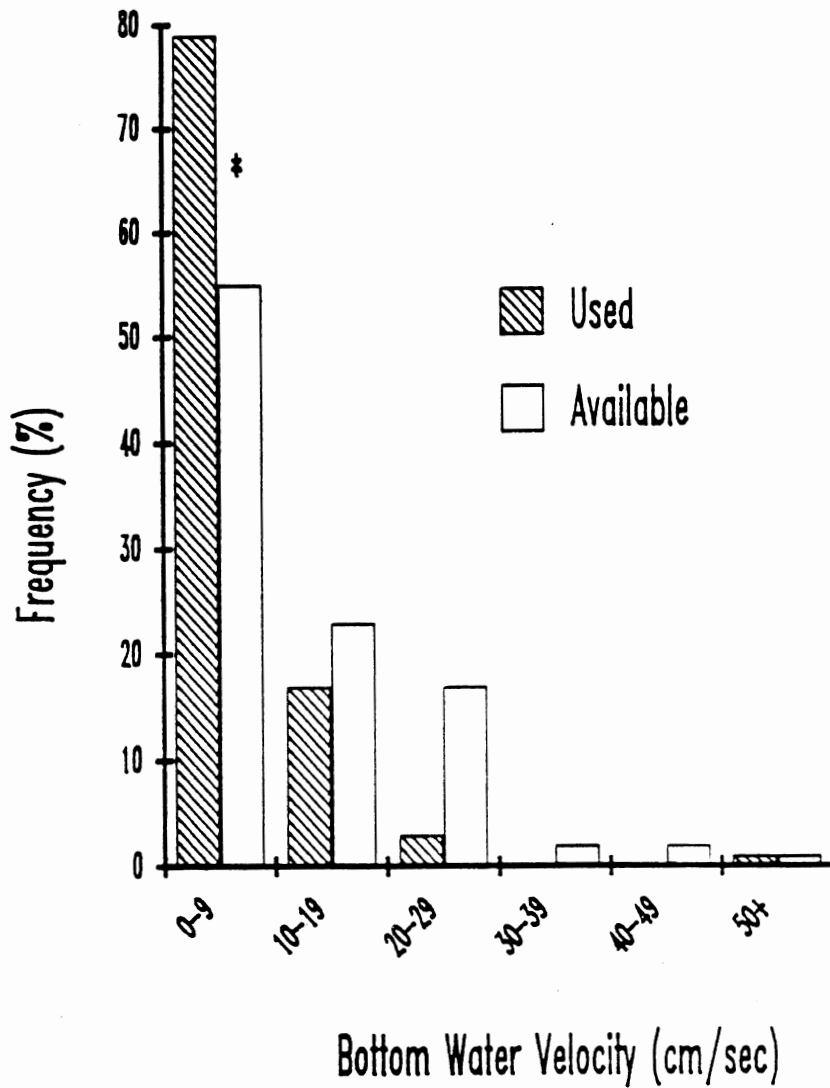
Figure 9.   Comparison of available bottom water velocity
to that used by three brown trout tracked during summer 1987.
Velocities for which use was significantly different from
that available (P<0.05) are indicated with an "*".
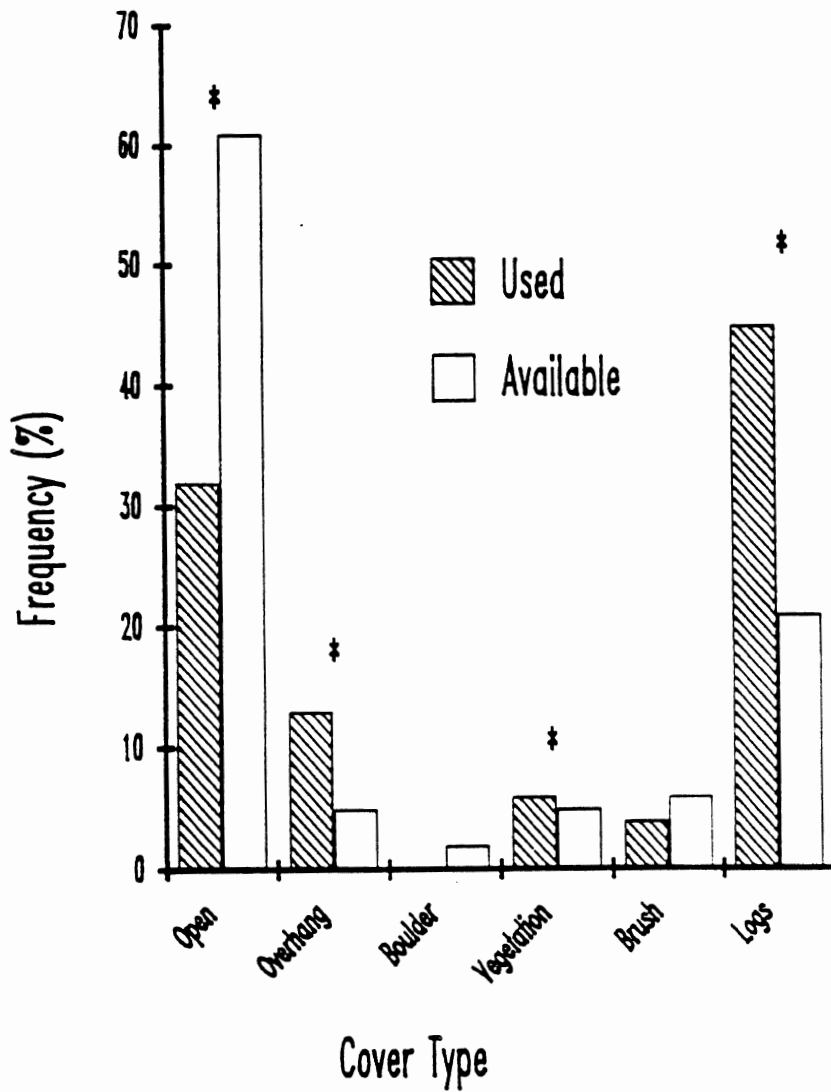
Figure 10.   Comparison of available cover to that used by three brown trout tracked during summer 1987.   Cover types for which use was significantly different from that available (P<0.05) are indicated with an "*".

significant negative electivity (avoidance) was seen for open areas (P<0.05). Fish used predominantly silt and sand substrate (Figure 11), but significant positive electivity was seen only for silt (P< 0.05). Selection was also seen for depths between 31 and 60 cm, and depths greater than 75 cm (Figure 12), but electivity was only significantly greater than zero for depths between 46 and 60 cm (P < 0.05).

An interaction between habitat variables was apparent. Significant correlations were seen between water depth and mean water velocity, water depth and bottom water velocity, water depth and substrate, mean water velocity and substrate, and bottom water velocity and substrate for data from quadrats used by fish (P <0.05; r = 0.28, 0.15, 0.36, 0.60, and 0.43, respectively).

Daily Activity Patterns

Average local activity (signal fluctuations/min of observation) was not significantly different between 1986 and 1987. However, there were significant differences in activity between months within a given year (Table 3). In both 1986 and 1987, local activity in August was significantly greater (P < 0.05) than activity in June or July. There were no significant differences between activity levels in June and July of either year.

There were significant differences between hourly, local activity levels within a given month. In June, major peaks in local brown trout activity were observed at 0100,

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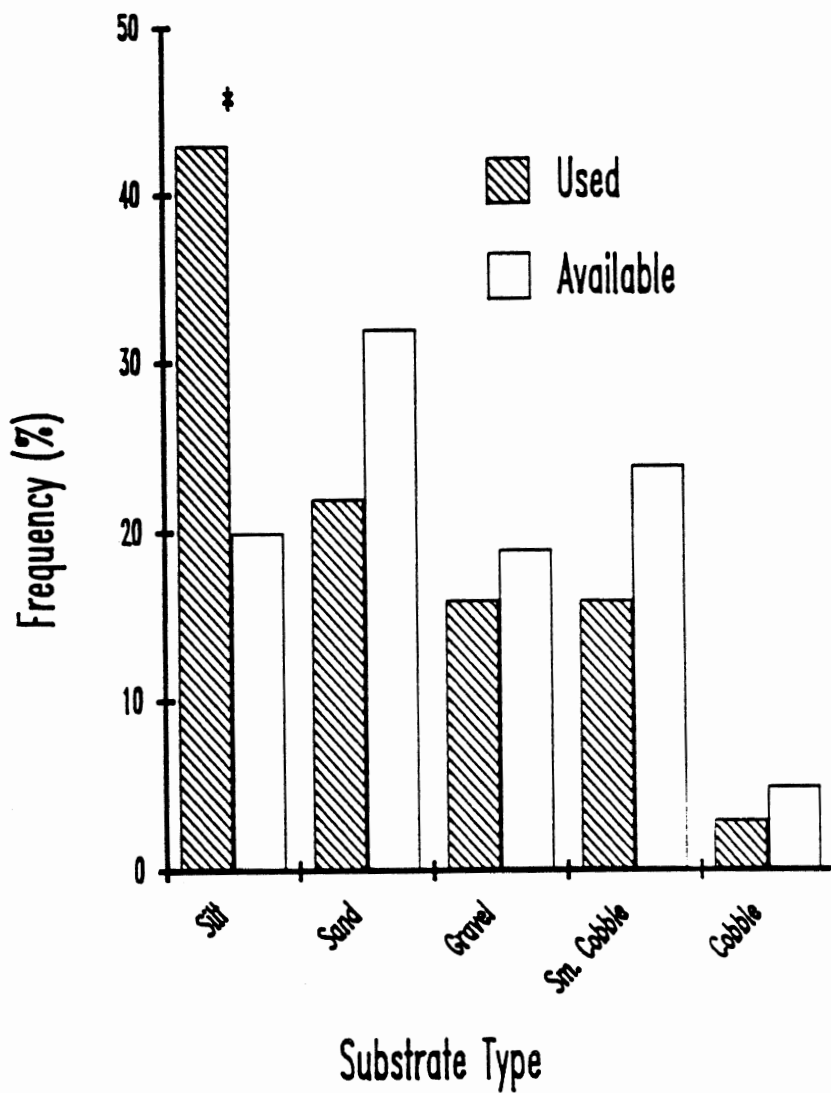
Figure 11. Comparison of available substrate to that used
by three brown trout tracked during summer 1987. Substrate
types for which use was significantly different from that
available (P<0.05) are indicated with an "*".
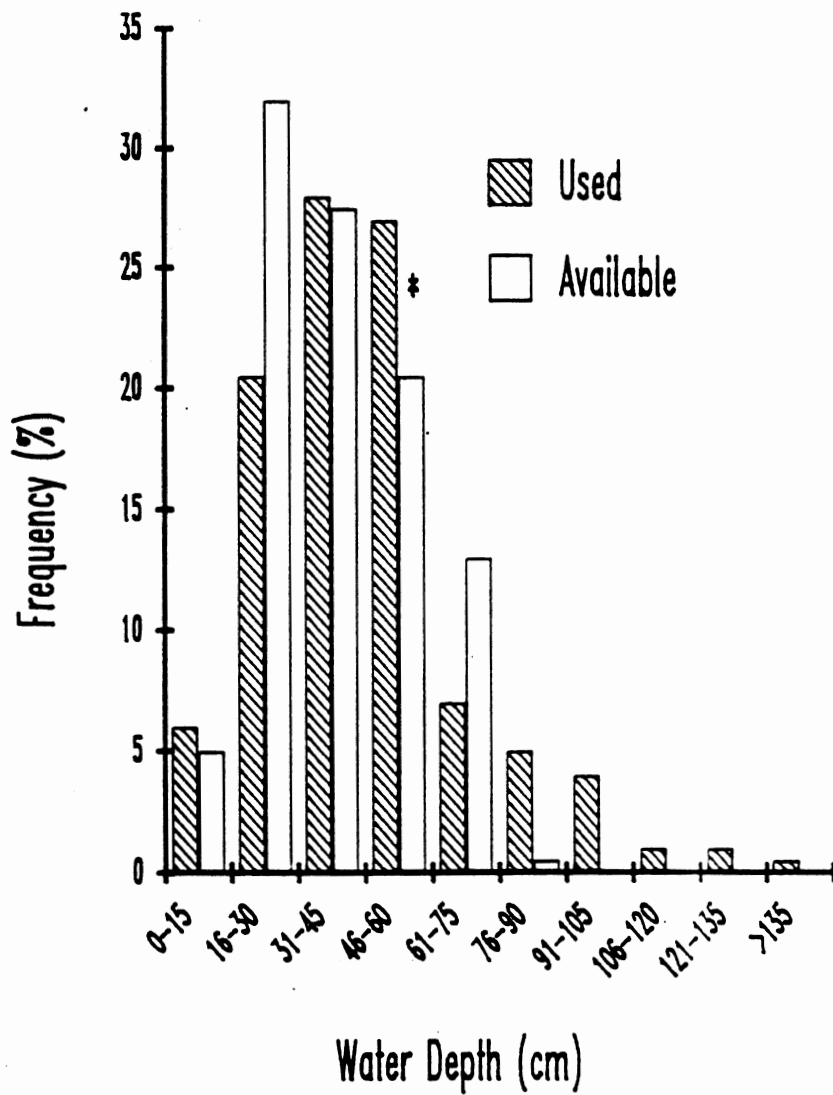
Figure 12. Comparison of available water depth to that used by three brown trout tracked during summer 1987. Depths for which use was significantly different from that available (P<0.05) are indicated with an "*".

Table 3. Mean monthly local activity for brown trout tracked in summer. F/M = fluctuations in radio signal strength per minute of observation, standard deviation in parentheses. N is the number of observations.

	June		July		August	
	F/M	N	F/M	N	F/M	N
1986	5.01 (6.55)	585	4.73 (4.45)	375	6.30 (7.23)	238
1987	5.64 (6.58)	225	5.05 (5.96)	412	6.07 (6.14)	271
Overall	5.18 (6.56)	810	4.90 (5.30)	787	6.18 (6.67)	509

0500, 1430, and 2200 h (Figure 13). Evening (2200 h) was the most active period of the day (approximately 13 fluctuations/min). The 0100 h and 0500 h peaks, at 8-9 fluctuations/min, were of approximately equal magnitude, and secondary to the evening peak. The midday peak (1430) was the third most active period of the day at 7 fluctuations/min.

In July, two peaks in local activity were observed, one near midnight (0000 h) and another at 0500 h (Figure 14). The morning peak (0500) was, at 21 fluctuations/min, the most active period of the day in July, and was more than two times greater in magnitude than the June morning activity peak. The midnight activity peak, at 12 fluctuations/min, was comparable in magnitude to the June evening peak.

In August, no distinct peaks in local activity were apparent (Figure 15). A low point occurred at 1100 h, when activity dropped to 2 fluctuations/min. Before and after this low point, fish seemed to alternate between periods of high and low activity every three to four hours. High points ranged between 6 and 11 fluctuations/min, and low points between 3 and 5 fluctuations/min.

A linear regression model including metabolic scope, light intensity, and feeding rate accounted for 29% of the observed variance in hourly local activity ($P<0.05$). Light intensity accounted for the greatest proportion of this variance.

Long-range activity (the distance covered between consecutive daytime resting locations) of fish tracked during summer was significantly less ($P<0.05$) than that of fish

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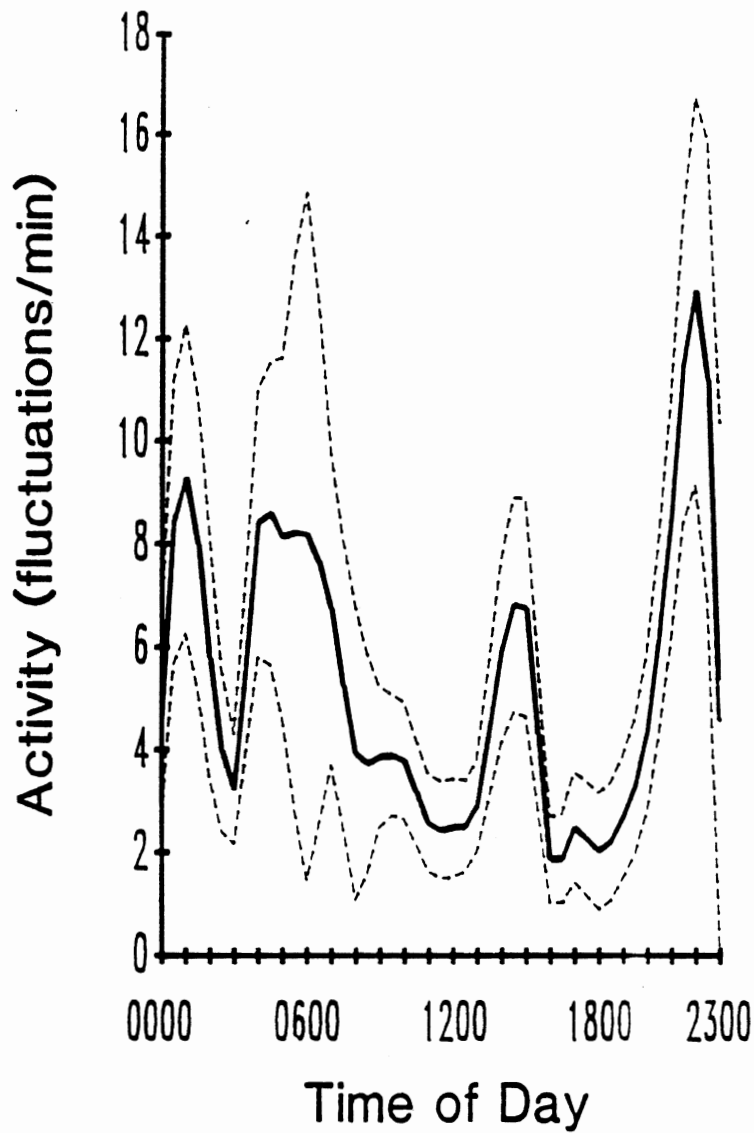
Figure 13. Local activity pattern for brown trout tracked during June. Maximum possible activity = 30 fluctuations/min. Solid line represents mean activity calculated by combining observations for four separate fish, two from 1986 and two from 1987. Dashed lines indicate 95% confidence intervals.

Figure 14. Local activity pattern for brown trout tracked during July. Solid line represents mean activity calculated by combining observations for three separate fish, one from 1986 and two from 1987. Dashed lines indicate 95% confidence intervals.
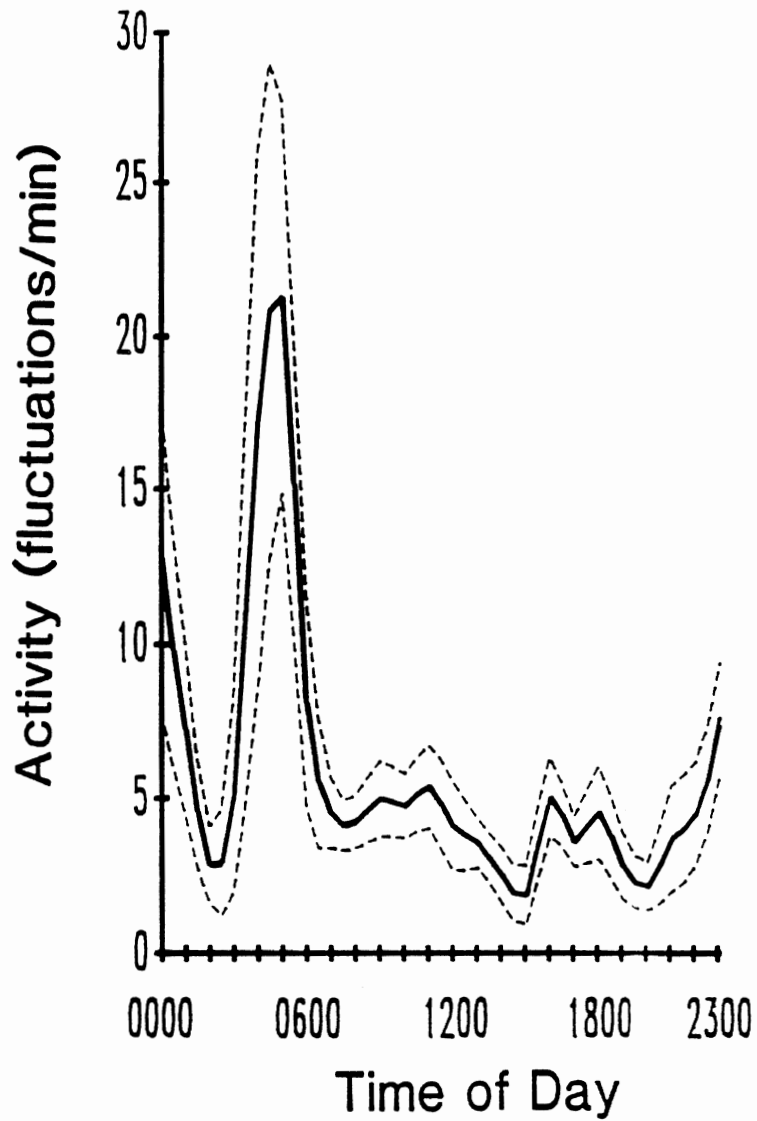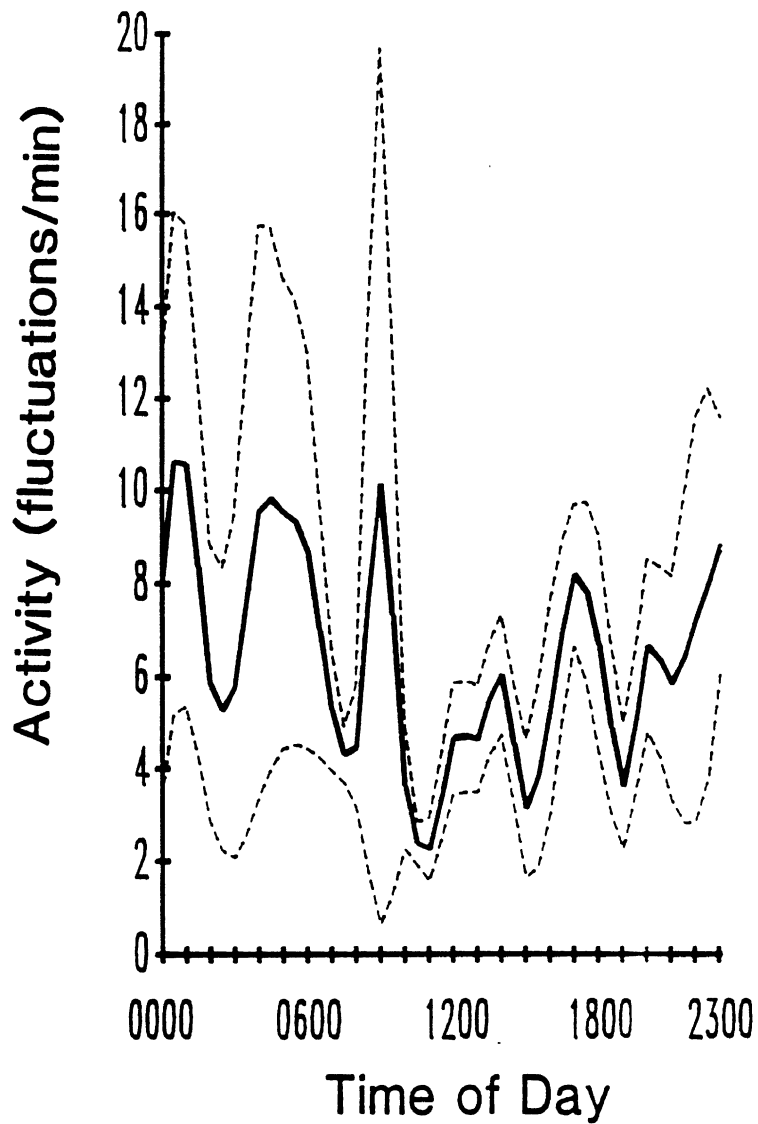
Figure 15. Local activity pattern for brown trout tracked during August. Solid line represents mean activity calculated by combining observations for three separate fish, one from 1986 and two from 1987. Dashed lines indicate 95% confidence intervals.

tracked during winter (Table 4). Mean activity for all fish tracked during summer combined was 239 m, while the mean value for all fish tracked during winter combined was 3,103 m. However, sample sizes (number of observations) were low for winter periods. Two fish tracked during summer showed average long-range activity of less than 100 m, while one fish showed average activity of almost 400 m. A fourth fish showed average long-range activity of 480 m, but was located in the same position for thirty-five consecutive sampling periods. Three fish tracked during winter showed average movements greater than 500 m, and this average movement went as high as 11.2 km for one fish.

Seasonal distributions of upstream and downstream long-range activity were found to be significantly different ($P <$ 0.05). The majority of summer movements were 50 m or less, up or downstream (76%), while only 33% of winter movements were within this range, and 64% were 100 m or more up- or downstream (Figure 16). There were no significant upstream or downstream trends in number of movements observed once fish took up residence in an area; however, many of the fish tracked made a long movement to upstream areas in fall, then remained in these upstream areas over winter.

Significant correlations of long-range activity with abiotic variables varied from year to year and between individual fish. A regression of 1986 activity on average daily air temperature, volume discharge, daily change in volume discharge, and groundwater levels (using data for all fish combined) was significant (P < 0.05), and explained

Table 4. Mean and maximum long-range activity for fish tracked between May 1986 and May 1988. Standard deviation in parentheses.

	Fish number	Maximum (m)	Mean (m)	Number of observations
		Summer		
1986	1	540	48 (120)	20
	2	270	46 (69)	52
1987	6	16,800	480 (2,840)	35
	7	1,895	399 (676)	34
		Winter		
1986-87	3	460	160 (219)	5
	4	8,320	1,750 (3,102)	7
	5	1,760	761 (670)	7
1987-88	8	22,730	11,220 (11,345)	5
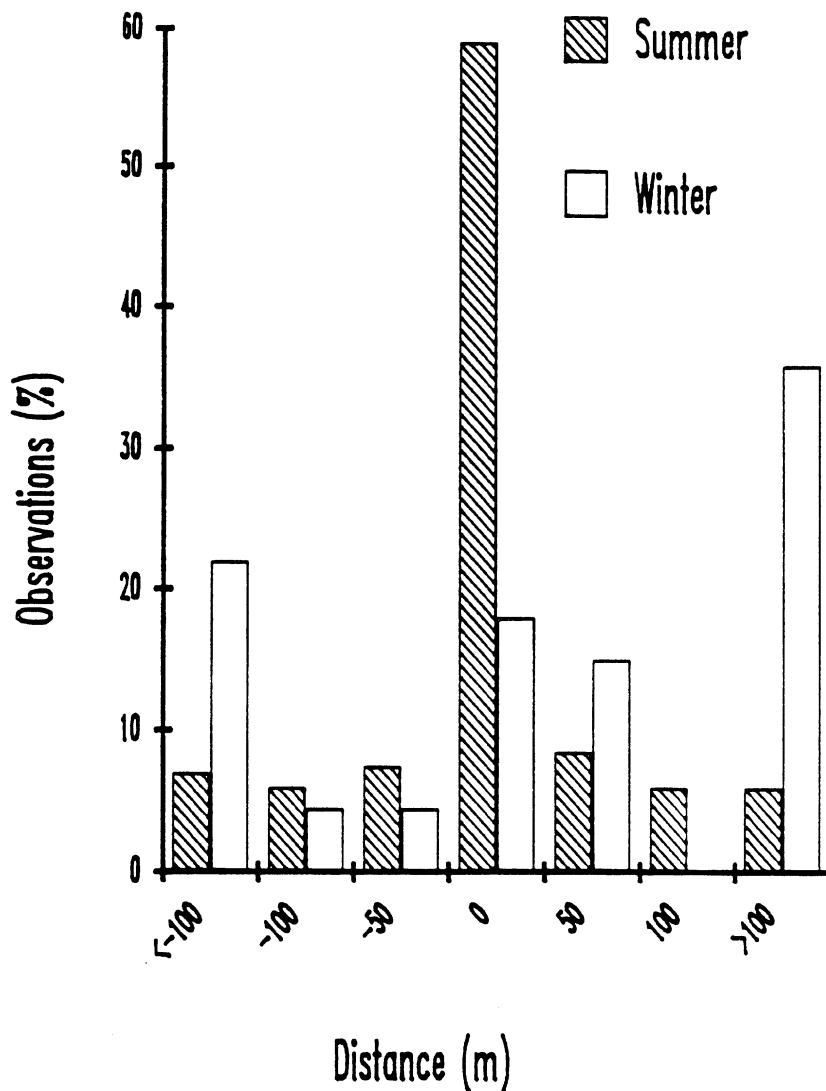
Figure 16. Distributions of upstream (+) and downstream (-) long-range activity. Data combined for eight fish tracked between May 1986 and May 1988. Number of observations was 141 in summer and 24 in winter. Numbers on the abscissa indicate upper limits for inclusion in each category.

approximately 25% of the observed variance in movement (r^2 = 0.24). Average daily air temperature was the most significant variable in this regression. Average monthly long-range activity (all fish combined) was correlated with average monthly air temperature, volume discharge, and groundwater levels. A regression involving all three of these variables was significant (P < 0.05) and accounted for approximately 90% of the observed variance in movement (r^2 =0.91). Volume discharge accounted for the majority of this variance.

Discussion

Trophy brown trout followed in this study had daytime resting sites, but foraged away from these sites at night. The frequency and extent of periodic movements and activity away from and between resting sites was greater than any previously recorded. The following general pattern became apparent: trout showed limited local activity during the day (corresponding to resting or turning activity), then continuous local activity at dusk away from daytime resting sites, sporadic or continuous foraging in midstream throughout the night, and finally continuous activity back to the previous resting site at dawn. This pattern was observed for all fish tracked during the summer periods. One of these fish, tracked in summer 1987, on numerous occasions moved upstream about 1.5 km during the course of this nighttime "foraging", then returned the same distance downstream to its

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previous resting site the following morning. The behavior described is in marked contrast to that exhibited by smaller brown trout, which tend to maintain a single station of limited area where they forage throughout the day (Jenkins 1969, Bachman 1984).

Summer movement and long-range activity by brown trout was limited, as compared to winter movement and activity. This observation is in general agreement with findings by Cobb (1933) and Shetter (1967). The greater fall and winter movement and long-range activity by fish observed in my study was probably associated with spawning, but may have served some other purpose as well. During November and December, many of the brown trout in this study abandoned good spawning habitat below Chase Bridge (where I observed approximately 80-90% of general spawning activity, including one instance of a radio-tagged fish on a redd) to move into what appeared to be suboptimal spawning areas near and upstream of Roscommon. Possibly these large brown trout were moving upstream in search of better overwinter habitat. Cunjak and Power (1986) indicated that space (habitat), and not food, was probably a key resource for brown trout during winter periods. Gosse and Helm (1981) attributed seasonal differences in habitat use to changes in the amount of time spent at various activities during winter periods. While winter habitat use appeared, qualitatively, to be similar to that in summer, the winter areas may have differed with respect to water temperature, ice conditions, or food supply - factors which were not monitored closely in the present

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study. This question concerning the relative importance of spawning versus overwinter habitat in determining fall movements and winter site choice by brown trout is one that needs further investigation.

There are a number of possible explanations for the more extensive movements of large brown trout followed in this study, as compared to those of smaller fish. Many fish species are known to switch food types as they get larger. This switch may necessitate movement over a larger area to obtain this food (Dill 1978, Bachman 1982). Alexander (1977) and Stauffer (1977) have shown that a switch from insects to fish as the primary food items occurs for brown trout in the Au Sable River at about 250-300 mm (age II or III). Prey fish might be more abundant in the warmer, upstream areas of the South Branch. Possibly the large brown trout are moving to take advantage of these prey fish populations when water temperatures allow them to penetrate these areas.

Some evidence exists to support the hypothesis that temperature may influence movement of brown trout in the South Branch. Monthly electrofishing surveys by Michigan Department of Natural Resources (MDNR) personnel in the catch-and-release section of the South Branch between Chase Bridge and the Castle during summer 1987 found 6 brown trout larger than 457 mm in this section in May, 14 in June, 20 in July, 18 in August, 12 in September, and 25 in October (Richard D. Clark, Jr., MDNR, personal communication). Temperatures in the upper reaches of the South Branch are

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warmer than those in the catch-and-release section. Fish numbers may increase in the middle of summer as a result of fish moving from warmer upstream areas into this cooler area of the river with greater groundwater input. Numbers may increase in October as fish move into the catch-and-release area to take advantage of good spawning habitat.

High positive correlation was found for long-range activity with volume discharge, while high negative correlation was found with groundwater levels. Caution should be used in interpeting these results. Correlations were obtained from monthly averages, and there were also high correlations between the independent variables used. While correlations and regression models cannot prove cause-and-effect, the correlations obtained seem logical. Increases in discharge might provide large brown trout with the perception of security and cover, possibly leading to an increase in the amount of fish activity and movement. Also, increases in discharge can wash terrestrial food items into a river. Movement may be greater due to increased feeding activity.

The Au Sable has one of the most stable flow regimes of any trout stream in America (Richard D. Clark, Jr., MDNR, personal communication); the relationship seen in this study between brown trout movement and flow (volume discharge) might be more important in streams where a typical seasonal fluctuation in volume discharge is more apparent. Fish movement might also be related to gradient and water velocity in a given stretch of river. Faster water is harder to swim against. Fish in a high gradient stream may use similar

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physical locations as those used by fish in the Au Sable, but the energy spent in maintaining and foraging from these positions may preclude long range movements.

Fish tracked during the course of this study chose deep, slow-velocity areas with heavy log cover. Habitat utilized by brown trout was quite similar to that described in the literature (Raleigh and Duff 1980, Gosse and Helm 1981, Shirvell and Dungey 1983). There were statistically significant differences between areas used by these fish and areas available to them, but the differences were not extreme. This may be explained by the fact that the South Branch is, on the whole, a stream with many areas of good brown trout habitat along its length. The percentage of usable habitat in the AuSable is probably 15% or greater, the upper limit of the range given by Gosse and Helm (1981). Habitat chosen by brown trout in a marginal stream would probably show a greater contrast to habitat available to them.

Habitat use is generally influenced by factors such as activity (Stalnaker and Arnette 1976), competitive interactions (Fausch and White 1981), and season (Cunjak and Power 1986). Brown trout the size of those I studied are probably the dominant stream-resident fish (Fausch and White 1981, Gosse and Helm 1981). For this reason, and due to the low densities (3/ha: Richard D. Clark, Jr., MDNR, personal communication) of these large fish in this section of the river, I assumed that competitive interactions were not the most important factor determining habitat use.

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The effect of activity on habitat use was apparent in this study. The quantitative data I collected on habitat use was exclusively from daytime resting sites, but habitat use during nighttime feeding and activity periods was obviously different. These trout were often active at night in shallow runs, or simply moved through a large variety of different habitat types during periods of increased nighttime activity.

While quadrats used by fish and characterized in this study probably provide a good description of the type of habitat that is generally used by "trophy" fish, it is important to remember that a diversity of habitat types is necessary. Gosse and Helm (1981) indicate that age 0 brown trout use macrophyte beds not used by juvenilles and adults. Cunjak and Power (1986) saw significant age-specific relationships for depth and velocity use: cover, on the other hand, was used by all age classes in proportion to its abundance in the environment. Appropriate habitat for all ages of brown trout is critical to the maintenance of a healthy fishery.

The number, timing, and size of the local activity peaks exhibited by trophy brown trout changed seasonally from June through August. The large evening peak in June activity seen in this study may have been due to feeding activity by brown trout on large mayflies ("Brown drake" _Ephemera simulans_ and "Michigan caddis" _Hexagenia limbata_) in mid- to late June. However, subsurface feeding activity dominated. I observed surface feeding by radio-tagged fish less than ten times during the course of this study. Fish did not appear

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to take up a feeding lane to feed on drift organisms, as smaller trout do.

The peak activity period in July shifted to the morning (0500 h), and was of greater magnitude than the June evening peak. This shift may have occurred as a result of energetic constraints related to the effect of water temperature on a fish's metabolic efficiency. Daytime summer temperatures above 20 C may have forced fish to feed primarily in early morning, during the coolest portion of the day. While a great deal of work has been done on behavioral thermoregulation by fish species in lakes, the use of behavioral thermoregulation by fish in river systems is an area that warrants further investigation.

August local activity was more evenly distributed throughout the 24-h period than that observed in other months. This may have occurred as a result of higher water levels in August 1986 and 1987, which could have afforded the fish some security and prompted them to feed during parts of the day when they generally would have been under cover. An alternative explanation is that food may have been scarce in August, and fish may have been forced to increase movement in order to search for widely separate food items.

Swift (1962) found that the majority of brown trout activity in lakes occurred during daylight hours, commencing with a sharp rise in activity at dawn. Lab work by Chaston (1969) indicated that fish were most active between dusk and dawn during observations from spring through autumn. Oswald (1978) found three daily peaks in feeding activity by

analyzing the electromyogram rhythms of brown trout feeding in a lake, and indicated that these peaks of activity were closely associated with photoperiod (dawn and dusk). However, he also recorded some subsidiary activity peaks that appeared to be unconnected to photoperiod, and in addition states that night feeding is probably a common occurrence in brown trout. Elliott (1970) found midday and evening peaks in feeding activity through an analysis of brown trout stomach contents.

Just as movement may be site or river specific, so too might activity. Patterns of activity may be based on food distribution and temperature regimes, and these factors vary depending on locality. Because of this, these findings of site-specific and system-specific (lake versus river) brown trout activity patterns should not be surprising.

Oswald (1978) indicated that trout activity patterns may be influenced by variations in the rate of stomach filling and evacuation, and Chaston (1969) stated that pedator-avoidance may be an important consideration. In this study, a model based on metabolic scope, feeding rate, and light intensity explained some of the variation observed in local activity, with light intensity being the most important factor. While there may be some correlation between fish activity and photoperiod, other explanations for fish activity may be just as plausible. Temperature and food availability have been shown to be correlated with light patterns (Chaston 1969, Elliott 1970). Again, these factors, and not necessarily light, may be acting as the primary cues

influencing brown trout behavior and activity.

There were large error bounds on the plots of local activity. This is due in some cases to sample size, but primarily to the nature of the activity pattern of these fish. Because local activity was highly variable (long periods of inactivity followed by short, rapid bursts of high activity; or activity in a localized area followed by extended movements), even a large number of observations would probably not tend to decrease the variance seen in this data.

Mortality of brown trout following surgical implant of transmitters was relatively high, as compared to mortality rates reported in other studies. Schramm and Black (1984) reported an average mortality rate to grass carp Ctenopharyngodon idella following various surgical implant procedures to be 31%, and Mulford (1984) cited various telemetric studies of striped bass Morone saxatilis in which mortality from tranmitter implant ranged from 30-46%. Both Schramm and Black (1984) and Mulford (1984) indicated that high water temperatures have an adverse effect on the survival of fish following surgery.

In telemetry studies, two basic assumptions are made; that transmitters do not adversely affect the behavior of fish, and that the limited number of fish tracked (due to the increased expense of telemetry equipment) adequately and representatively reflect behaviors of the entire population of fish under investigation. Some evidence that the first assumption was met comes from capture of one fish at the end

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of the study. The surgical incision had healed well, and the fish was in excellent condition - able to elude an electrofishing crew for almost one hour with strong upstream and downstream swimming. Agreement between the findings of this study and expectations for behavior of large brown trout based on the current scientific literature provide some evidence that the second assumption was met.

Management Implications

Ideally, research findings will positively influence management decisions. Cobb (1933), upon determining that brown trout displacement was primarily downstream, stressed the importance of stocking brown trout in a location where they could run downstream into "good" water. Knowledge of fish movements can also be of great importance in the assessment of regulations and population estimates. One of the major objectives of the present study was to relate the movement of trophy brown trout in the South Branch of the Au Sable River to a section of the river placed under catch-and-release fishing regulations.

Over the course of this study, six of eight brown trout tracked were observed to move out of the catch-and-release section and into areas of the river under statewide trout regulations. These fish were vulnerable to legal harvest by anglers while outside the catch-and-release section. However, four of five fish tracked during periods of heavy summer fishing pressure (May-August) spent most of their

time inside the regulated area. Also, fish tracked during fall and winter might have returned to this section of the river during June and would again have been "protected".

This study shows that stream-resident trophy brown trout can range over a section of river up to 34 km in length, with the average home range being approximately 8 km in size. Thus, special regulation areas (at least on the Au Sable River) need to be at least 8 km long to ensure that the home range of a single trophy fish is encompassed. When choosing areas to be placed under special regulations, all of the food and habitat requirements for trophy brown trout need to be considered if the aim of the regulations is to produce trophy fishing. Some areas might prove to be unsuitable for trophy brown trout. In the long run though, no matter how large an area we set aside, or how "good" an area it appears to be, there will always be fish that will move out of the area, or whose home ranges will straddle its boundaries. Perhaps increases in the numbers of trophy fish harvested in areas adjacent to these regulated areas could be counted as an additional benefit of these quality fishing regulations.

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