1
9
8
8

Range of Movement and Daily Activity of Wild Brown Trout in the South Branch Au Sable River, Michigan

Gary E. Regal

Fisheries Research Report No. 1988
July 16, 1992

MICHIGAN DEPARTMENT OF NATURAL RESOURCES
FISHERIES DIVISION

Fisheries Research Report No. 1988
July 16, 1992

RANGE OF MOVEMENT AND DAILY ACTIVITY OF WILD BROWN TROUT IN THE SOUTH BRANCH AU SABLE RIVER, MICHIGAN[1]

Gary E. Regal

PRINTED BY AUTHORITY OF Michigan Department of Natural Resources
TOTAL NUMBER OF COPIES: 350 TOTAL COST: $694.25 COST PER COPY: $1.98
Michigan Department of Natural Resources DNR

[1]This is a reprint of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fisheries, in the School of Natural Resources, The University of Michigan, 1992.

Range of Movement and Daily Activity of Wild Brown Trout in the South Branch Au Sable River, Michigan.

by

Gary E. Regal

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

School of Natural Resources
The University of Michigan
1992

Committee members
Associate Professor James S. Diana, Chairman
Adjunct Assistant Professor Richard D. Clark, Jr., Ph.D.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I thank everyone, unmentioned and the following, who helped me complete this project. Invaluable support was provided by the folks at the Institute for Fisheries Research, Michigan Department of Natural Resources (MDNR). I extend special gratitude to Rick Clark. His contributions were immense, but always offered with subtlety that belied their importance. Long after I forget many details of my own research, I will remember Dr. Clark's approach to research, which recognized that science outside the traditional scope of fisheries may have fisheries applications. Also, thank you: Carl Latta for providing transportation, miscellaneous equipment, and a spacious office; Marlene Bennett and Barb Champion for administrative support; Jim Gapczynski for gastric lavage and graphic support; Paul Seelbach for critical discussions on a variety of topics.

From the University of Michigan, Jim Diana, my major advisor, made certain that my funding and academic needs were always on track. His confidence in me to work with a good deal of independence helped me gain confidence as a researcher. Dr. Diana's editorial support was the carpenter's plane that smoothed the written thesis. Gary Fowler provided thoughtful review of statistical analyses.

A number of people helped with implants, stomach analyses, or habitat sampling in the field. Gerald Casey and company from the Fisheries Station in Grayling (MDNR) graciously supplied me with field equipment and help throughout the study. Bill Merril gave abundant, nonstop assistance during the first summer of field work. Also, Lori Sue Alexander, Rick Clark, John Hudson, Jack Rogers, and Ron Salz gave ample help in the field.

Summer lodging was provided by Michigan State University (for a nominal fee at their Wa Wa Sum research facility) under the direction of Kevin, Brick, and Tex Gardiner.

This project would not have been possible without generous support from the Michigan Fly Fishing Club.

This project would not have been possible for me without a lifetime of support from my parents, Robert and Julie Regal.

In memory of Au Sable's Gold Brick II and his inseparable friend, Ruben.

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Within populations of stream-resident brown trout, there are both mobile and sedentary components. Larger brown trout may range further to reflect a piscivorous, mobile-feeding strategy. Smaller fish may range less to reflect a drift feeding, sit-and-wait strategy. I tested the hypothesis that range of movement increases with fish size in the South Branch Au Sable River, Michigan. I measured range of movement (daily for two summers; biweekly for one fall/winter) and daily activity patterns (one summer) for two- and three-year-old brown trout implanted with radio transmitters. Summer range of movement was significantly greater for larger brown trout, 43 m for fish larger than 30 cm and 13 m for fish smaller than 30 cm. Range of movement was much greater and more variable in fall/winter (950 m average & 0-4500 m range) than in summer (29 m average & 5-110 m range). I believe range increased in fall/winter to reflect life history changes related to spawning or overwintering migrations, and high variability in ranges was a consequence of the timing and duration of tracking. I monitored brown trout only during the day in fall/winter (most movements in summer were recorded at night), and less frequently than in summer. Fish were usually located deep in white cedar log jams during the day and away from cover at night. This behavior pattern suggested brown trout were diurnally inactive and nocturnally active, which was confirmed by brown trout monitored specifically for daily activity patterns. Food availability, predation risk, and water temperature appear to be three factors that influence the daily activity patterns of brown trout in the South Branch Au Sable River, Michigan.

INTRODUCTION

Two fundamental questions of fish behavior are 1) how far do they range and 2) when are they most active? These questions have been asked for brown trout Salmo trutta, but unanimous agreement on the answers has not been established.

Mark and recapture studies have shown that although most stream-resident brown trout move minimal distances, some individuals range much farther (Shetter 1968; Solomon and Templeton 1976; Jackson 1980; Harcup et al. 1984), a dichotomy that Funk (1957) described as sedentary and mobile groups of fishes. Funk (1957) and more recently Bachman (1984) suggested that larger fish might range less than smaller individuals because they are better suited to defending their territory or hierarchical position. However, Clapp et al. (1990) discovered that large (>40 cm total length) stream-resident brown trout ranged extensively, averaging 4.9 km in summer, and suggested that longer movements were related to piscivorous feeding behavior.

Among studies attempting to determine daily activity patterns of brown trout, both nocturnal and diurnal behavior were observed. Swift (1962) demonstrated that wild brown trout caged in a lake were most active during the day. Chaston (1969) found brown trout were most active at night in a laboratory setting. Jenkins (1969a) and Bachman (1984) found brown trout were active during the day from field observations in streams. Priede and Young (1977) measured cardiac rhythms of brown trout in a lake and discovered that activity was greatest during the day, with peaks at dawn and dusk. Clapp et al. (1990) found that large stream-resident brown trout were generally most active at night.

I used radio telemetry in this study to explore the range of movement and daily activity of wild, medium-size brown trout in their natural environment. Mark and recapture techniques, experiments with confined animals, and observational studies are limited in the amount of information they contribute to the fundamental questions of range and activity. Mark-recapture studies delimit range and timing of movements, but only on a gross scale. Interim movements between the time fish are marked and recaptured can not be determined. Confinement studies limit long range movements in an artificial setting. Observational studies effectively answer both questions, but only in the daylight and only in certain habitats where visual observations can be made. Electrocardiogram attachment would be limited to large fish.

I chose to study brown trout from approximately 20 to 30 cm total length because fish that attain these lengths may begin to increase their diet breadth and, therefore, range of movement. Diet studies by Stauffer (1977) and Alexander (1977a) suggest that as stream-resident brown trout grow, they switch from feeding predominantly on aquatic invertebrates to fish. Smaller, drift feeding brown trout may have smaller home ranges that reflect a sit-and-wait (Pianka 1966) feeding behavior. Larger piscivorous fish may have larger home ranges that express a mobile-search (McLaughlin 1989) feeding strategy. Also, brown trout in this size range often make up the bulk of legal catch in recreational trout fisheries, so they are of great interest to anglers and fisheries managers. My study had two specific objectives directed at 20 - 30 cm brown trout: 1) to measure their home range in summer and winter and 2) to monitor their daily activity patterns in summer. Completing these objectives would allow me to compare behavior of medium-size brown trout to that of larger fish Clapp et al. (1990) studied in the same stream, the South Branch Au Sable River.

STUDY AREA

The South Branch Au Sable River is located in the sparsely developed north-central region of Michigan's lower peninsula (Figure 1a). The basin generally has sandy, forested soils above permeable glacial deposits (Hendrickson 1966). Consequently base flow is high and reflected by stable discharges of cold water over much of the river. An exception is the reach above the village of Roscommon (Figure 1a). This reach receives warm surface water inputs from Lake St. Helen and has lower stream gradient, warmer water, and sand, silt, or mud substrates. Pike Esox lucius and mudminnows Umbra lima are common fishes found there (Richards 1973). Below Roscommon, the river has steeper gradient, colder water, and cobble and gravel substrates prevail. The South Branch below Chase Bridge is famous for its brown trout fishery.

From Shetter's (1937) early mark and recapture study to the more recent telemetry work of Clapp et al. (1990), the Au Sable River and its tributaries have been the focus of trout research. The Michigan Department of Natural Resources (MDNR) is currently studying the effects of special fishing regulations on the South Branch fishery and has designated a segment from Chase Bridge to 8 km downstream as "Flies Only, Catch and Release." I implanted fish approximately 1.5 km below Chase Bridge (44°32'30"N, 84°33'00"W). At this location, the summer average stream

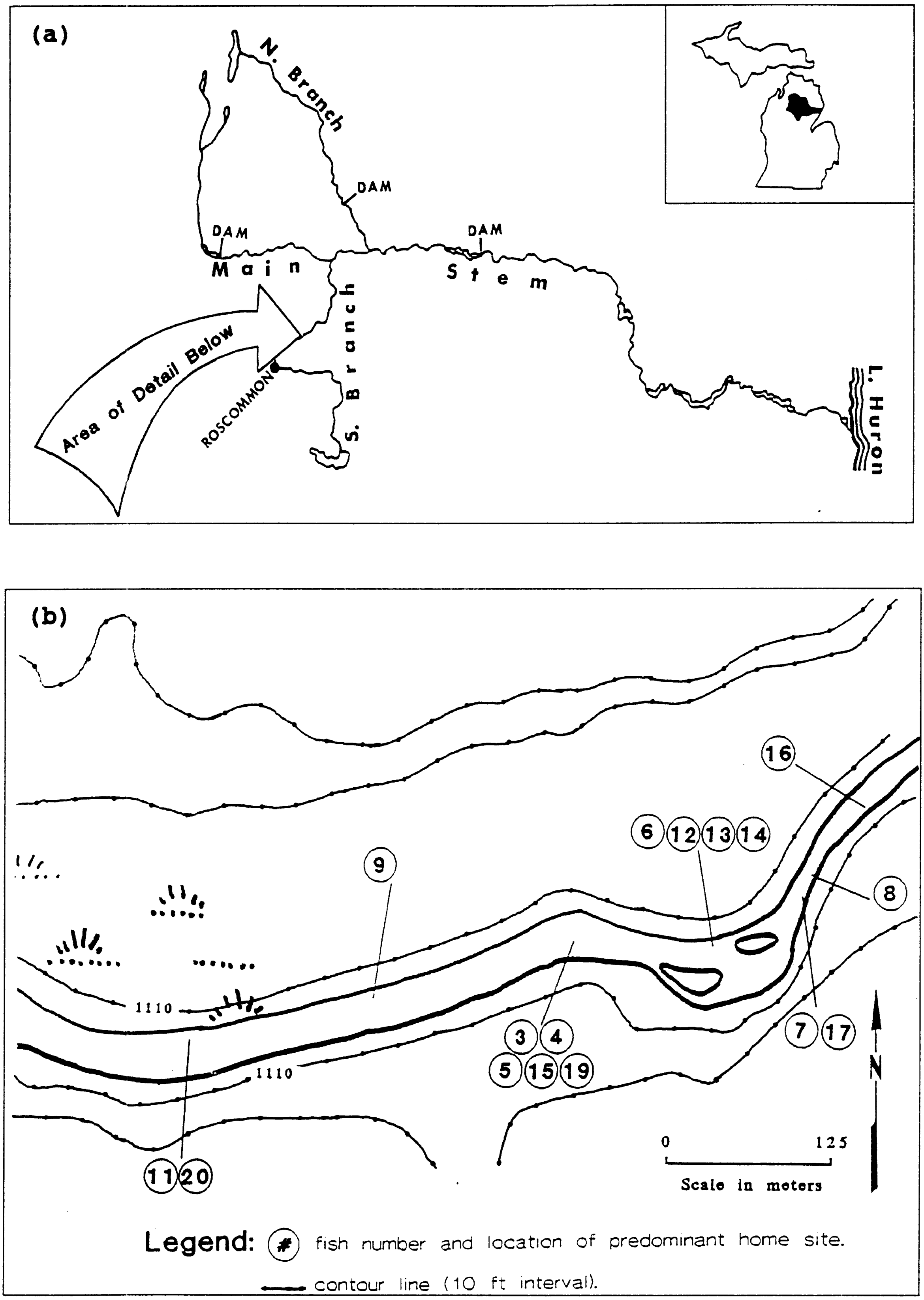

FIGURE 1. Map of the Au Sable River system **(a)**, including the study site on the South Branch in detail **(b)**.

width, depth, and discharge were 23 m, 0.31 m, and 3.87 m^3/sec, respectively. Brown trout outnumber brook trout Salvelinus fontinalis by about 2 to 1 in this section of river (R. Clark, MDNR, personal communication). Mottled sculpins Cottus bairdi and white suckers Catostomus commersoni were the most abundant non-game species.

Methods

Implants

Twenty brown trout from 20 to 34 cm total length were surgically implanted with radio transmitters between 1 May 1989 and 14 July 1990. Age and growth data from Gowing and Alexander (1980) and scales from implanted animals suggested that fish were 2 or 3 years of age. Surgery commenced immediately after fish were captured from the study area (Figure 1b) with DC electrofishing equipment. Each animal was individually anesthetized in a 75 ppm solution of tricaine methanesulfonate and stream water. A 10-20 mm incision was made along the ventral surface of the fish midway between the pelvic and pectoral fins. A transmitter was inserted into the body cavity and the incision was closed with two or three monofilament nylon sutures and a 4-0 needle. Each fish was sprayed with stream water during surgery to keep its body and gills moist. Oxytetracycline (50 mg per kg of fish) was injected into the body cavity with a hypodermic needle to prevent infection before releasing the fish back into the stream.

One challenge of working with small brown trout was to construct a transmitter small enough that it did not adversely affect fish behavior, while large enough to transmit a reasonably strong, lasting signal. I used a length-weight relationship (Clark 1988) derived for South Branch brown trout to estimate the weight of transmitters. My standard was that they should weigh less than 2% of fish body weight, as recommended by Winter (1983). Holohil Systems Limited, Ontario, Canada, custom made the transmitters, which were designed to have an operational life of 90 days. They weighed 1.5 - 4.5 grams and were powered by silver oxide batteries encapsulated in green epoxy. Signals were transmitted at frequencies between 48 and 50 MHz at a rate between 35 and 40 pulses per minute.

Fish were located with a scanning, programmable receiver and a 60 cm directional loop antenna. I monitored fish behavior immediately after tagging to document recovery, but did not otherwise use data collected during two weeks following surgery. Based on behavioral and biochemical responses, Pickering et al. (1982) determined that two weeks was the period brown trout required to completely recover from acute handling stress. Recovery was also documented by recapturing several fish just prior to or after transmitter failure to examine their overall physical condition.

Range of Movement

In summer (24 May - 9 September, 1989 & 1990), I usually located fish on alternate days to determine range of movement and home site use. Range of movement was defined as the linear distance between the extreme upstream and downstream locations at which fish were observed, similar to Clapp et al. (1990). Home site was defined as an area where a fish is normally found inactive, returns to if disturbed, and which provides both overhead and instream cover. Point locations were randomly made day and night by triangulating readings from index stations established along the bank and instream. A point location was defined as one instantaneous sighting that makes no measure of fish activity. To examine the relationship between home site use and time of day, I stratified point locations into day (sunrise to sunset) and night (sunset to sunrise) periods. I exercised extreme caution not to disturb fish when taking point locations. Any observations hinting of bias induced by my movements were discarded. In fall and winter (10 September 1989 to March 1990; 10 September - October 1990), I located fish approximately every two weeks during daylight to determine if range of movement was different by season.

Daily Activity

Daily activity was measured for three fish during the second summer by counting fluctuations in signal strength similar to the method of Clapp et. al (1990). The underlying premise was that signal strength would remain fairly constant for an inactive fish, but would fluctuate to indicate an active fish. Tests conducted by manipulating dead white suckers verified the method was practical; signal fluctuations were detected from movements as small as 0.3 meters. Fluctuations in signal strength were counted each hour over ten equally spaced intervals lasting two minutes each. A 24-hour cycle for one fish was generally completed in seven days by recording activity in blocks of 3, 4, or 8 hours from a concealed position on the bank.

I tried to determine if brown trout activity levels were related to light intensity, water temperature, stream discharge, and fish diet. I also quantified habitat over the range of movement for each fish monitored for daily activity.

I used a sine function to estimate changes in light intensity (LI) over a day:

$$LI = 1 + \text{Sine}\ [\{(Hr - (DlHrs + 2)/2)/(DlHrs + 2)\}2\pi + \pi/2],$$

where Hr was the time of day and DlHrs was the number of daylight hours in one complete day. Light intensity values ranged between 0.00 and 2.00. According to the equation, time of day one hour after sunset to one hour preceding sunrise had a value of 0.00; the zenith hour (midday between sunrise and sunset) had a maximum value of 2.00.

Water temperature (°C) was measured hourly using an automatic temperature recorder positioned 0.4 km upstream from the study site. I compared temperature recordings from that instrument to temperatures measured at the study site with a hand thermometer and found differences were slight, usually $\leq$ 0.5 °C.

Stream discharge was measured weekly during the summer. I measured velocity with a pygmy current meter and calculated discharge according to the United States Geological Survey's midsection method outlined by Orth (1983). Daily flows were determined by regressing staff gage readings against weekly discharge measurements.

An overview of brown trout diet was completed during the first summer. Generally, I collected ten fish weekly with a dc-backpack electrofishing unit (Wisconsin APB-3) and sampled stomach contents using the non-lethal, pulsed-gastric-lavage method (Foster 1977). I collected daytime (1400 - 1530 hrs) samples to begin the study. Ultimately I sampled at night (midnight - 0300 hrs) because brown trout appeared to feed minimally in the daytime. Also I wanted to avoid the warmer daytime water temperatures that may have additionally stressed fish. One fish was sacrificed weekly to test sampling efficiency.

Habitat was quantified from the predominant home site of each fish to approximately 40 m upstream and downstream in 5 m intervals. Along each 5 m transect at 1 m intervals, water depth, velocity at 0.6 depth, substrate, and cover were either measured or categorized using methods similar to Orth (1983).

Statistical Analyses

Nonparametric analyses were generally used because of heterogeneous group variances. Mann-Whitney tests were used to test: 1) if home range was different between the first and second summer; 2) if range was different between small and large fish; and 3) if activity levels were greater at night or during the day. Pearson's Chi-square test was used to examine home site use relative to time of day. Levels of significance were given to the nearest 0.01 and tests were considered statistically significant if $\underline{P} < 0.05$.

Nonparametric tests, regression analyses, correlation coefficients, and measures of central tendency were calculated with SYSTAT (Wilkinson 1989) software and sometimes checked by hand calculations.

RESULTS

Implants

Surgical implants were highly successful based on survival rates. Only one of twenty brown trout implanted with radio transmitters was a confirmed casualty (Table 1). I discovered that animal 6 days after implantation in shallow, open water near the bank. The fish had a fungus infection approximately 30 mm across extending below the lateral line to the incision. I sacrificed the animal and recovered the transmitter. The fish had moved downstream several days in succession after surgery, whereas most animals remained near the implant site in deeper water, often in white cedar log jams. Two fish made significant moves upstream. Two other brown trout may have either been eaten by predators or expelled their transmitters, perhaps because sutures failed. Within ten days of implanting , their transmitters were found on the stream bottom within 0.62 km of the implant site without any evidence of the fish. The original intent was to tag three size groups of fish, 20, 25, and 30 cm long. After losing the two smallest fish soon after the initial round of implants, only animals in the 25 and 30+ cm groups were implanted in subsequent operations.

Range of Movement

Range of movement for medium-size brown trout was 5 to 110 m in summer (Table 2). Only two of fifteen fish observed had more than one home site, and the distance

TABLE 1. Data for brown trout implanted with radio transmitters between 10 May 1989 and 14 July 1990 in the South Branch Au Sable River, Michigan. Transmitter life is the number of days from implant to transmitter failure or loss of fish as indicated under comments. Comments: (A) 24 hr activity monitored; (FW) tracked during fall/winter; (M) mortality; (Mt) transmitter malfunctioned; (R) recaptured and condition assessed; (Ri) reimplanted 1 yr later; (S) tracked during summer; (T) transmitter recovered without fish.

Fish				
number	**size (cm)**	**Implant date**	**Transmitter life (days)**	**Comments**
		1989		
1	19.6	10 May	9	T
2	20.6	10 May	6	M
3	26.2	10 May	127	S,FW,Ri
4	26.9	10 May	259	S,FW
5	33.0	10 May	43	S,R
6	33.3	10 May	99	S,R
7	25.1	21 May	42	S,R
8	32.0	23 May	40	S,R
9	25.6	24 July	40	S
10	32.3	24 July	5	T
11	34.3	30 July	317	S,FW,S
12	23.4	13 Sept	44	FW
13	32.0	13 Sept	38	FW
14	30.7	13 Sept	133	FW
		1990		
15	25.6	7 May	62	S
16	27.7	7 May	46	S
3	29.0	7 May	62	S,A
17	32.0	7 May	90	S,A
18	32.2	6 July	1	Mt
19	30.2	14 July	102	S,FW
20	31.5	14 July	102	S,A,FW

TABLE 2. Number of home sites, range of movement, and tracking period for brown trout followed during summer months.

Fish		Home sites	Range of movement (m)	Tracking period
number	size (cm)			
				1989
7	25.1	1	5	5 Jun - 26 Jun
9	25.6	1	12	7 Aug - 23 Aug
3	26.2	1	20	24 May - 23 Aug
4	26.9	1	5	24 May - 23 Aug
8	32.0	1	15	5 Jun - 26 Jun
5	33.0	1	20	24 May - 9 Jun
6	33.3	1	40	25 May - 16 Aug
11	34.3	1	25	13 Aug - 23 Aug
				1990
15	25.6	2	20	26 May - 5 Jly
16	27.7	1	10	26 May - 18 Jun
3	29.0	1	20	26 May - 5 Jly
19	30.2	1	60	30 Jly - 9 Sep
20	31.5	1	60	30 Jly - 9 Sep
17	32.0	3	110	26 May - 10 Aug
11	34.3	1	15	21 May - 14 Jun

between home sites was 15 m or less. Fish were located in their home site significantly more during the day than at night (P < 0.01; Figure 2).

The average range of movement was 29 m, and 11 of 15 fish stayed within a 25 m range (Table 2). No difference in range of movement was found between the summers of 1989 and 1990 (P > 0.17). Larger brown trout had significantly greater range of movement than smaller fish (P < 0.02). The average range of movement was 43 m for fish larger than 30 cm and 13 m for fish smaller than 30 cm. Although larger brown ranged further than smaller fish, the precise relationship between range of movement and fish size is neither strongly linear or curvilinear (Figure 3).

The seven brown trout tracked during the fall and winter ranged much further on average than fish followed in the summer (950 m compared to 29 m). However, the difference was not statistically significant because fall and winter observations were limited and range of movement was highly variable between individuals (P > 0.82; Figure 4). Four brown trout were tracked during both summer and fall/winter seasons. None had a summer range greater than 60 m, but three of the four had a fall/winter range greater than 249 m (Table 3). In winter, range of movement reflected single long range movements from one home site to another. These fish remained at the new home site until the transmitter apparently expired.

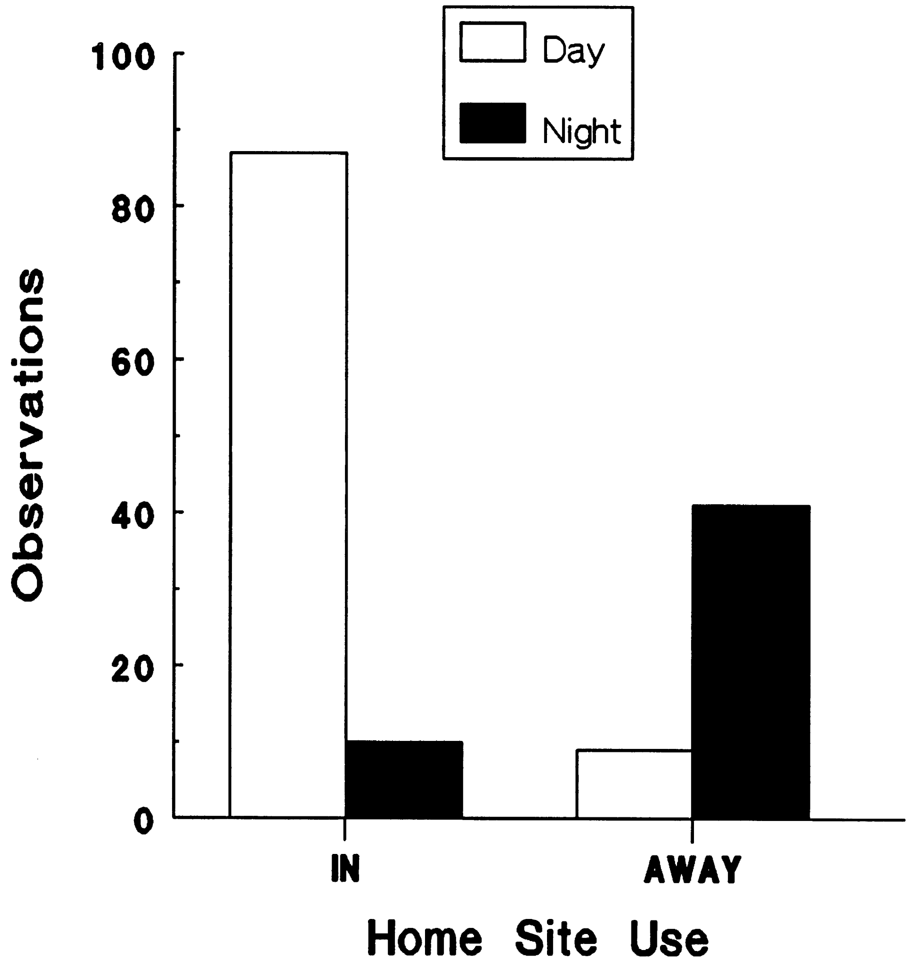

FIGURE 2. Relationship between home site use and time of day (day= sunrise to sunset; night= sunset to sunrise) for 12 brown trout in summer.

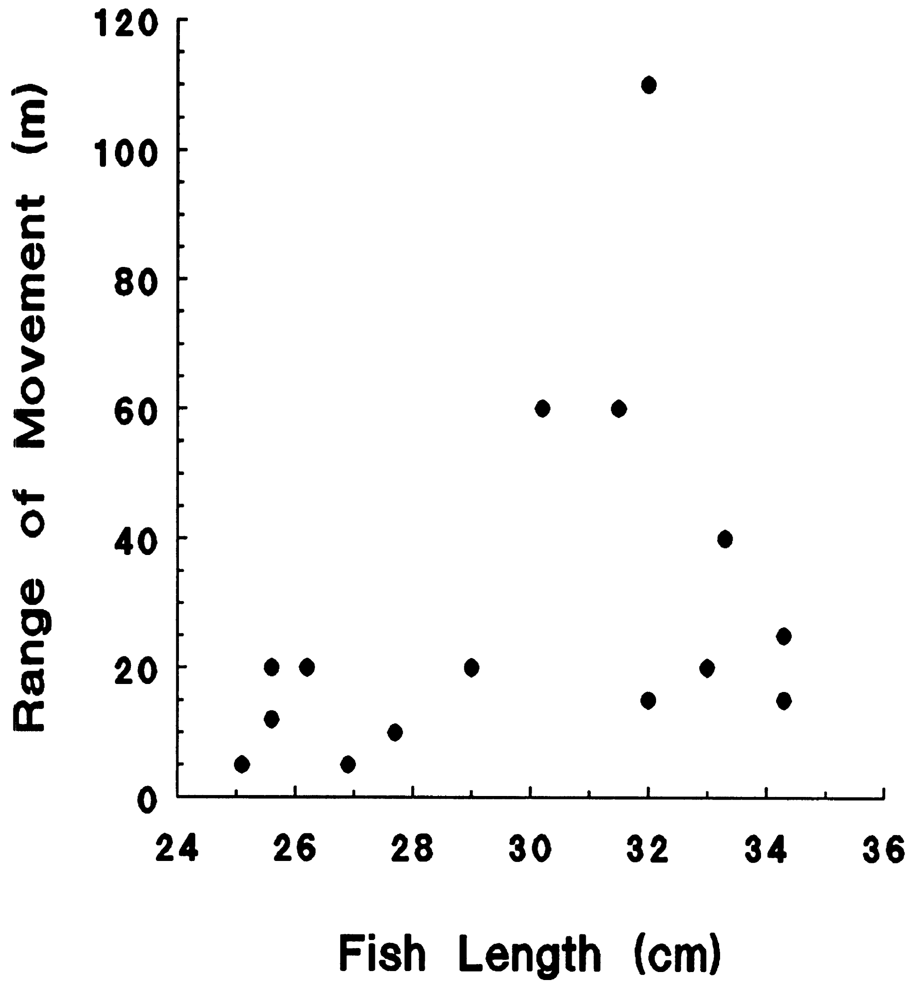

FIGURE 3. Scatter plot of fish length versus range of movement for 15 brown trout monitored during summers 1989 and 1990.

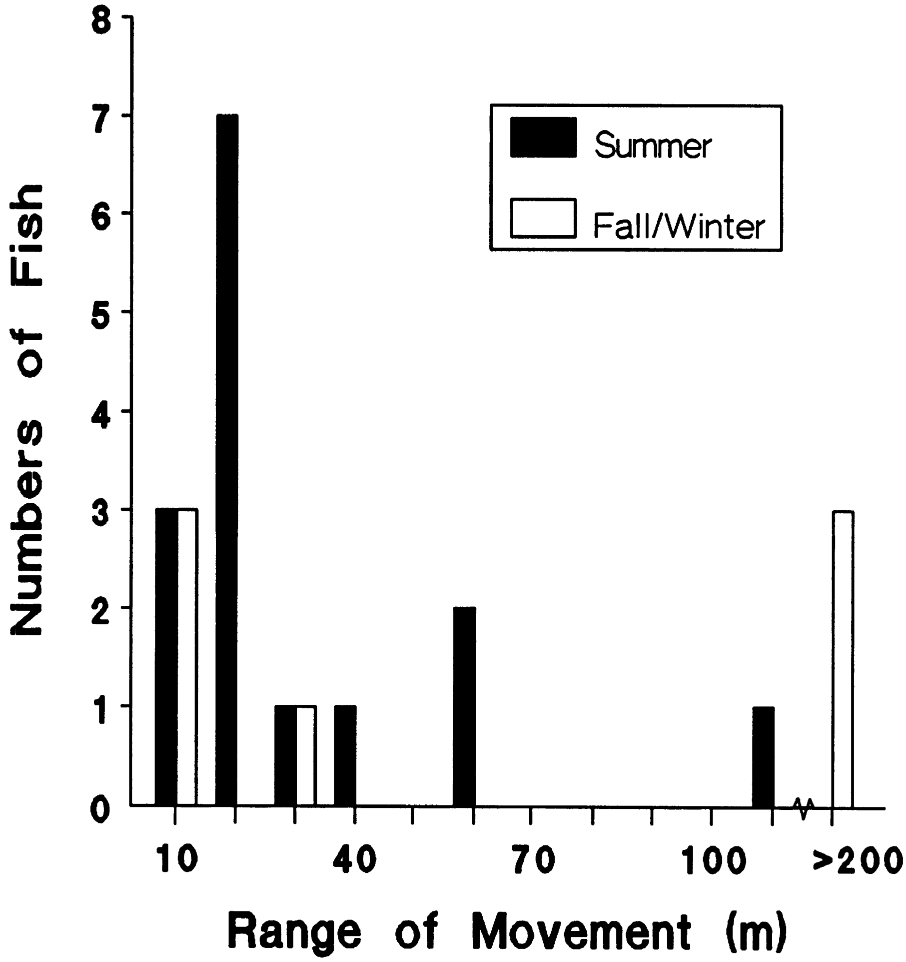

FIGURE 4. Range of movement frequency distribution for brown trout tracked during summer and fall/winter.

TABLE 3. Brown trout range of movement during the fall/winter [FW], and summer [S].

Fish		**Home sites**	**Range (meters)**		**Tracking period**
number	**size (cm)**		**FW**	**S**	
12	23.4	1	0	*[a]	5 Oct 89 - 21 Dec 89
4	26.9	2	4500	5	24 May 89 - 2 Feb 90
19	30.2	2	250	60	30 Jly 90 - 31 Oct 90
14	30.7	2	25	*	5 Oct 89 - 1 Feb 90
20	31.5	1	0	60	30 Jly 90 - 31 Oct 90
13	32.0	1	0	*	5 Oct 89 - 10 Nov 89
11	34.3	2	1875	25	13 Aug 89 - 14 Jun 90

[a] * denotes fall/winter tracking only.

Range of movement was recorded as zero for three brown trout. This could have been a consequence of the sampling schedule. Fall/winter observations were made once every two weeks during daylight, while summer observations were made both day and night. A range of movement of zero in fall/winter might represent a genuine lack of movement or undetected movements because they occurred at night. Most movements in summer were recorded at night.

Daily Activity

Ten 24-hr cycles of daily activity were measured on three brown trout (Figure 5). Fish were more active at night than during the day in 9 of 10 cycles (Mann-Whitney U test, $P < 0.01$; Table 4). Activity levels declined significantly through the summer (Kruskal-Wallis, $P < 0.01$; Figure 6). Fish 3 was the earliest monitored and most active. Fish 20 was tracked last and the least active.

Light intensity was consistently and significantly correlated with activity level ($r= -0.59$ to -0.83, $P <0.05$), but stream discharge and water temperature were not (Table 5). Light intensity explained nearly half of the variance in activity level for each fish based on simple linear regressions ($R^2= 0.47$ for fish 3, $R^2= 0.48$ for fish 17, and $R^2= 0.51$ for fish 20). Although activity levels and water temperature were not linearly related, fish generally remained inactive when water temperatures reached daily lows and highs (Figure 7). Water temperatures fluctuated daily in a consistent pattern during summer and varied only in

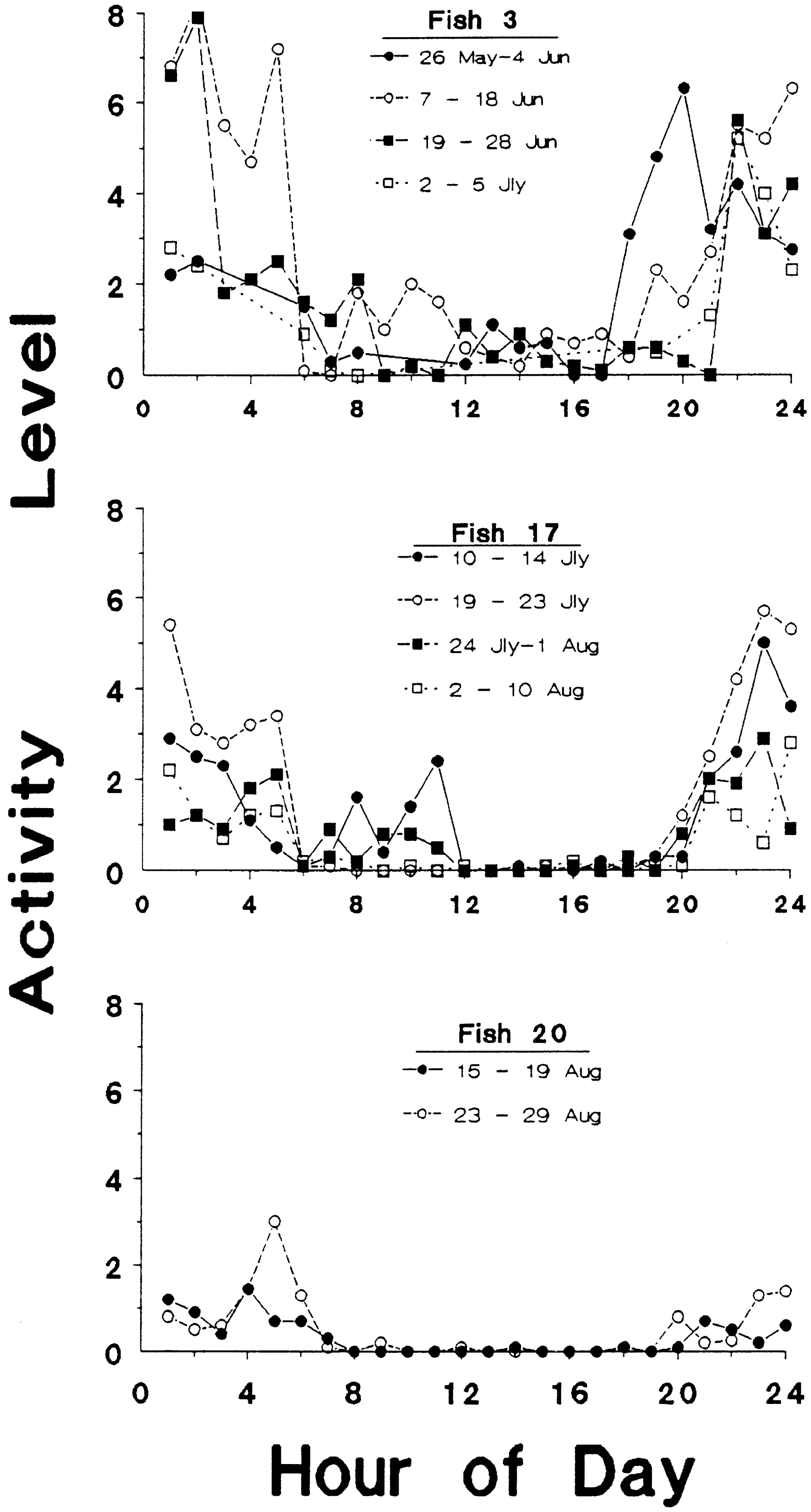

FIGURE 5. Twenty-four hour activity cycles for three brown trout monitored between 26 May and 29 August 1990. Fish 3, 17, and 20 were 29.0, 32.0, and 31.5 cm.

Table 4. Data on brown trout monitored for daily activity between 26 May and 29 Aug 1990. Under activity level, (S) denotes significantly greater activity at night than daytime ($\underline{P} < 0.01$), and (NS) denotes no significant difference at ($\underline{P} > 0.05$).

Cycle	Tracking period	Activity level (day vs night)
	Fish 3	
1	26 May - 4 Jun	NS
2	7 Jun - 18 Jun	S
3	19 Jun - 28 Jun	S
4	2 Jly - 5 Jly	S
	Fish 17	
5	10 Jly - 14 Jly	S
6	19 Jly - 23 Jly	S
7	24 Jly - 1 Aug	S
8	2 Aug - 10 Aug	S
	Fish 20	
9	15 Aug - 19 Aug	S
10	23 Aug - 29 Aug	S

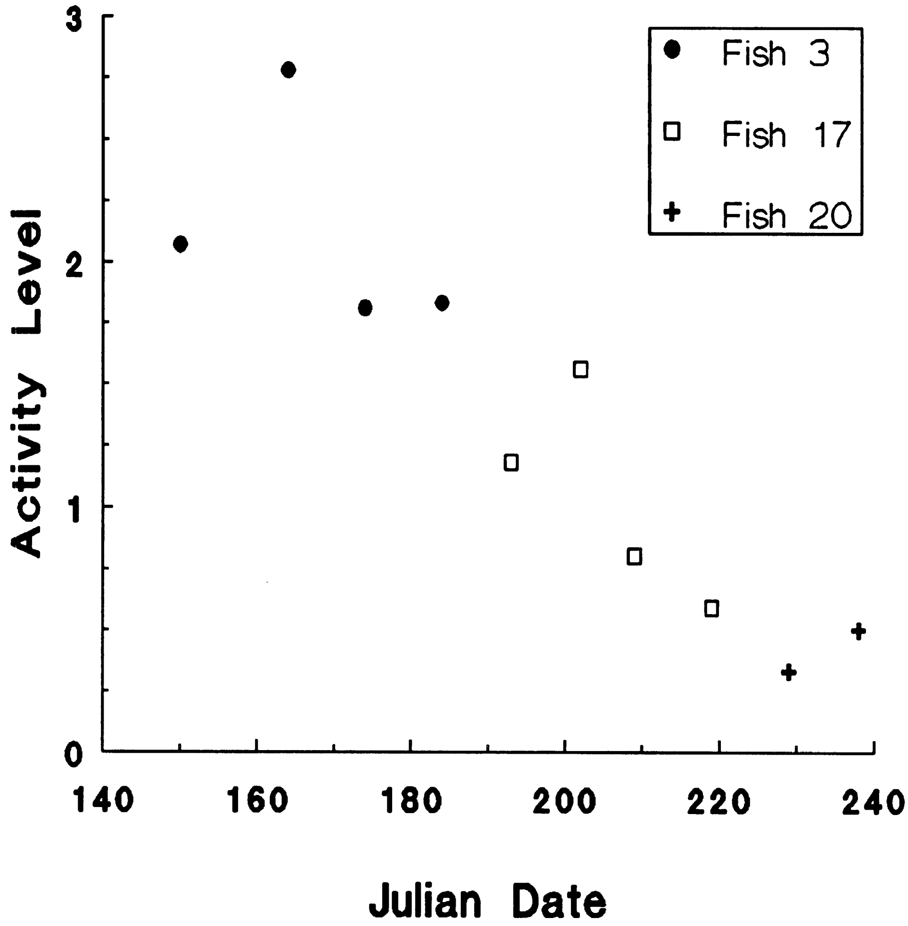

FIGURE 6. Relationship between activity level and time of year for 3 brown trout. Julian dates 160, 200, and 240 correspond to 14 June, 19 July, and 28 August.

Table 5. Zero-order correlation coefficients of activity level with stream discharge, water temperature, or light intensity. Correlations given if statistically significant at $\underline{P} < 0.05$, while NS indicates nonsignificant correlation.

Cycle	**Stream discharge**	**Water temperature**	**Light intensity**
1	NS	NS	-0.69
2	-.078	NS	-0.72
3	NS	NS	-0.68
4	NS	NS	-0.83
5	0.42	NS	-0.59
6	0.44	NS	-0.83
7	0.57	-0.54[a]	-0.74
8	0.48	-0.57[a]	-0.75
9	NS	NS	-0.76
10	NS	0.46[a]	-0.70

[a] correlation is not significant when light intensity is held constant.

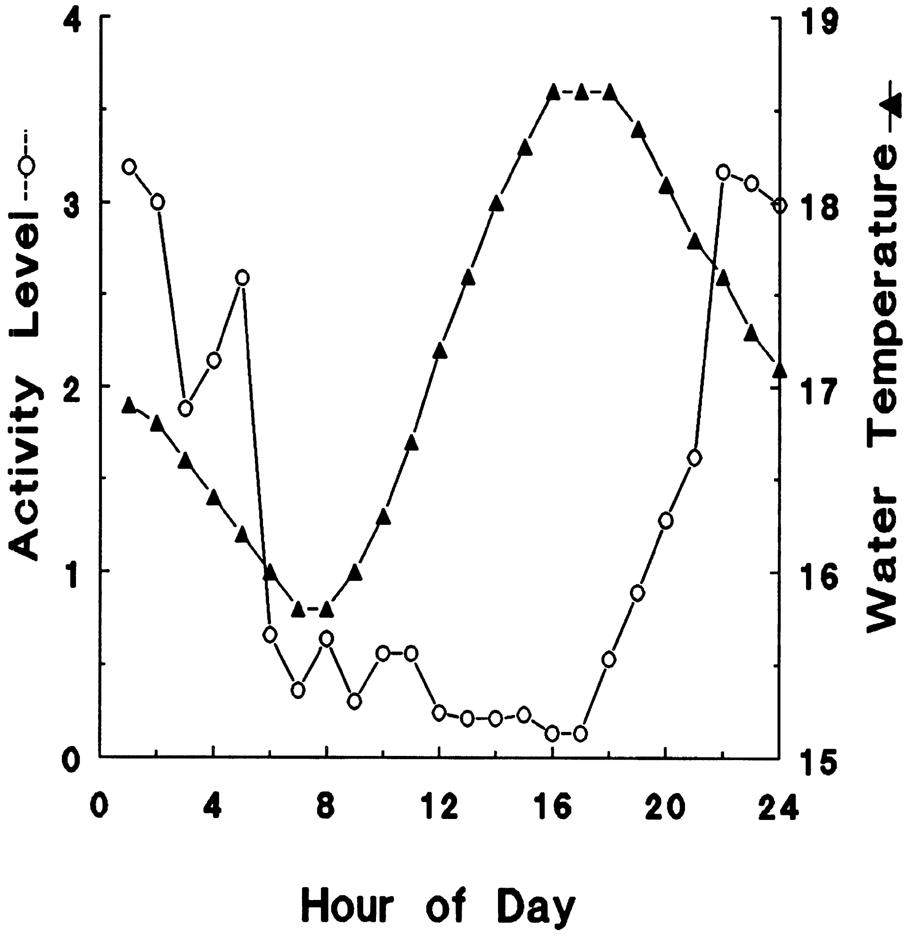

FIGURE 7. Average hourly activity levels for fish 3, 17, and 20 pooled, and average hourly water temperatures during summer 1991.

magnitude with weather (Figure 8).

Nocturnal activity was consistent with diet analyses, which showed that brown trout examined at night generally had greater numbers of food items than fish collected during the day (Figure 9). Of seventy-seven brown trout examined, eight had consumed fish. No relationship was found between brown trout size and presence of fish in the diet. All prey fish were identified as mottled sculpins. The most common food item was a caddis fly larvae of the family Hydropsychidae. Crane fly Tipula sp. larvae were also fairly common. Mulluscs, snails and fingernail clams Psidium sp., were also represented, suggesting that fish were feeding from the stream bottom as well as from the drift. Terrestrial animals were rare in stomachs. They were never greater than 4% of the total number of food items per individual and usually 1% or less. Gastric lavage effectively removed food items from stomachs, based on results from dissecting one out of ten brown trout after flushing.

Habitat measurements verified the visibly obvious, that instream cover was limited and restricted to near the banks. When fish were inactive, they were most often located in white cedar log jams, which were rare (Table 6). The river was between 54 and 85% void of cover. The high percentage of available vegetative cover in the reach Fish 20 held is probably an overestimate. I classified cover as any structure capable of obscuring fish in water ≥ 10 cm

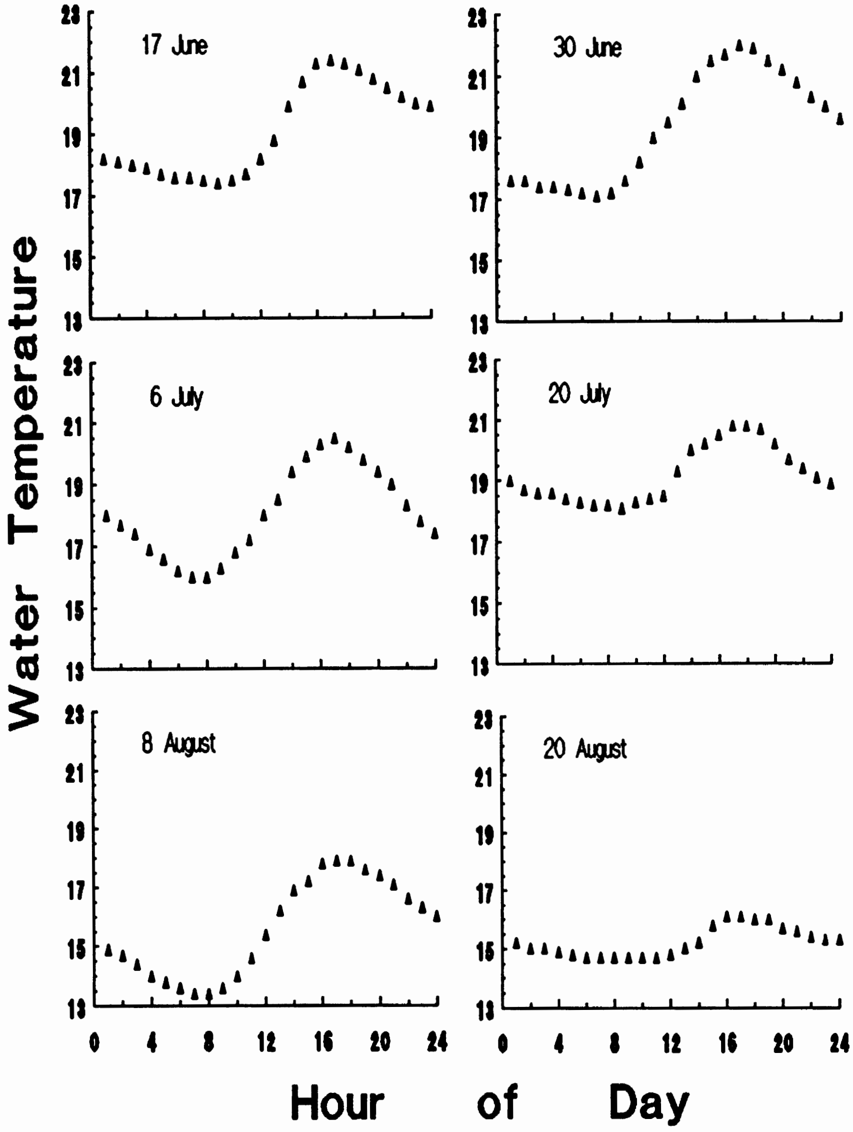

FIGURE 8. Hourly water temperatures in the South Branch Au Sable River, Michigan, for two randomly selected days in June, July, and August 1990. Rain and over cast conditions prevailed on 20 August and the two days preceding.

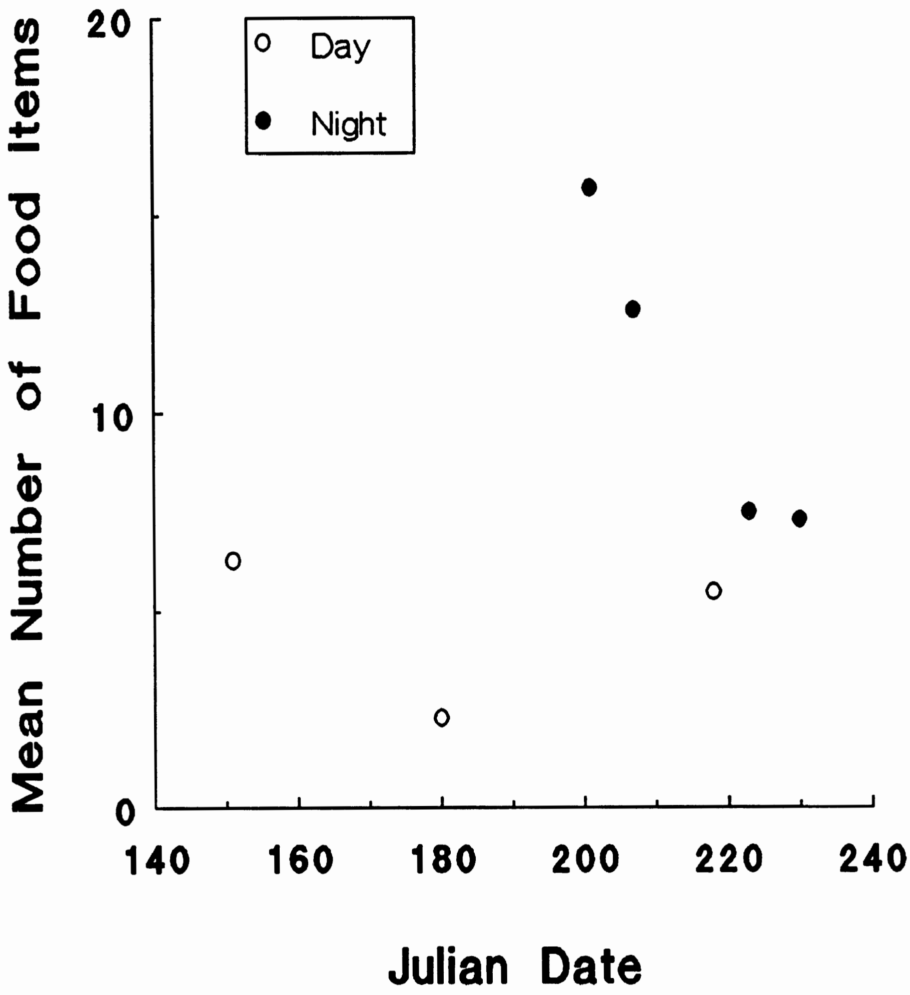

FIGURE 9. Mean number of food items per brown trout stomach versus date and time of capture. Day samples collected between 1400 and 1900 hours; night samples between 2400 and 0330 hours.

TABLE 6. Cover, substrate, and stream parameters summarized over the range of movement for each brown trout monitored for daily activity.

	Fish 3	Fish 17	Fish 20
	Cover Available (%)		
Open	85	92	54
Vegetation	5	0	37
Brush	2	3	4
Log Jam	3	1	1
Single Log	4	3	2
Boulder	1	1	1
	Substrate Available (%)		
Silt	12	6	29
Sand	14	9	18
Gravel	60	67	42
Cobble	13	15	9
Boulder	1	2	1
	[a] Stream Parameters		
Width (m)	23.8(3.8)	15.7(2.5)	27.6(0.8)
Depth (m)	0.29(0.11)	0.35(0.13)	0.35(0.13)
Velocity (m/sec)	0.36(0.23)	0.49(0.24)	0.26(0.19)

[a] Average with standard deviation in parentheses.

with flow present. Vegetation types were predominantly thick mats of Elodea canadensis in shallow water or stands of Sparganium sp. nearshore with barely perceptible flow, unlikely habitat for brown trout. Vegetation was less common at the other two sites, which may reflect higher stream velocities and/or greater overhead canopy. Habitats sampled are representative of the study area because they encompass home sites and range of movement of other brown trout monitored exclusively for range of movement.

DISCUSSION

Range of Movement

The limited range of movement by brown trout in this study is generally consistent with other research. Jackson (1980) and Harcup et al. (1984) found that range of movement was usually less than 75 meters for age 1+ and older stream-resident brown trout. Larsen (1983) discovered that during spring and summer the majority of brown trout between 18 and 33 cm remained in the same area of stream.

Range of movement increased with fish size and is consistent with Shetter (1968) and Clapp et al. (1990). Range of movement was much greater for trophy-size (> 40 cm) brown trout in the South Branch Au Sable River (Clapp et al. 1990). During summer, trophy fish range of movement was on average 4,900 m (the fish in the present study averaged 29 m).

Shetter (1968) postulated that large brown trout range further because they need more living space and food. More expansive range of movements for large brown trout might reflect mobile-search (Mclaughlin 1989), piscivorous feeding. Contracted range of movements for small brown trout might reflect sit-and-wait (Pianka 1966), drift feeding. This dichotomy of feeding strategies was not fully expressed by the limited numbers of brown trout stomachs I examined, but a gradient from one extreme to the other was supported by diet studies that examined greater numbers of brown trout in the South Branch Au Sable River (Stauffer

1977; Alexander 1977a). Feeding strategies are likely influenced by abundance and distribution of food types, as well as by risks associated with competition and predation (Dill 1983). Also, some brown trout might not make a transition from drift feeding to piscivory. These factors may help explain the positive yet variable trend between range of movement and fish size.

Average range of movement was greater in fall/winter (950 m) than summer (29 m) and is similar to the pattern Clapp et al. (1990) observed (11,900 winter; 4900 m summer). Seasonal increase in range of movement is consistent with the life history of brown trout. Solomon and Templeton (1976) and Arnold et al. (1987) have documented fall spawning migrations of stream-resident brown trout. Brown trout number 11 migrated downstream in October into an area with abundant gravel, perhaps to spawn. This fish remained in the vicinity for the duration of tracking, which ended in June because of transmitter failure. Brown trout number 4 migrated upstream in December away from the study area, which had abundant gravel, to an area which appeared to have equal cover and less gravel. This fish may have completed spawning and migrated to more suitable overwintering conditions, where I continued to locate the fish until its transmitter expired the following February. Brown trout (Jonsson 1985; Cunjak and Power 1986) and salmonids in general (Chapman and Bjornn 1969; Chisolm et al. 1987) often migrate in fall and winter into habitats with relatively slower water velocities and greater overhead cover. This migration presumably promotes overwinter survival.

Daily Activity

Brown trout activity decreased from June to August. Seasonal decline in activity is consistent with a decrease in specific growth rates over the same period for brown trout in other systems (Beyerle and Cooper 1960; Swift 1961), which also supports the premise that activity levels predominantly reflected feeding behavior. Clapp et al. (1990), however, found greatest activity in August, with June and July about the same. Perhaps availability of prey for trophy-size brown trout was different seasonally from the availability of prey for medium-size brown trout.

On a daily scale, brown trout in the South Branch Au Sable River were nocturnally active and diurnally inactive, which agrees with some research (Chaston 1969; Clapp et al. 1990), but contrasts other work (Swift 1962; Priede and Young 1977). To avoid confusion, diurnal refers to daylight hours, and diel refers to the 24 hour day with distinct day and night periods. Three factors which might explain diel activity patterns of brown trout include 1) food availability, 2) predation, and 3) water temperature. The nocturnal activity of brown trout in the South Branch Au Sable River may have been a reaction to increased food levels in the form of stream drift. Drift can be defined as the living suspended load of a stream. Although I did not measure temporal changes in drift for the South Branch, other studies have shown that drift abundance follows a daily cycle, with maximum levels at night (Tanaka 1960; Waters 1962; Elliott 1967).

Drift is a key food resource for trout in streams (Nilsson 1957; Elliott 1967; Chaston 1969; Elliott 1970; Cada et al. 1986) and may initiate fish activity. Elliott (1970) found that maximum occurrence of benthic invertebrates in brown trout stomachs (the major peak was at night) corresponded to their increased availability in the drift. Jenkins (1969b) released controlled amounts of ants in an experimental stream channel and discovered that brown trout fed on them over a 24-hour period, but with less success at night. He postulated that night feeding was still profitable because drift of benthic invertebrates increased at night. Chaston (1969) found brown trout were most active between dawn and dusk, but that day activity increased during summer probably in response to terrestrial insects entering stream drift. Cada et al. (1986) discovered in a soft water, southern Appalachian stream that terrestrial drift organisms comprised 50% of the diet in brown trout and was especially important during late summer and autumn.

In contrast to the previous work, Stauffer (1977) found terrestrial invertebrates were a minor (7%) component in the diet of brown trout from the South Branch Au Sable River. Similarly, terrestrial animals were rarely collected from brown trout stomachs I sampled. The low diurnal activity throughout summer of fish in this study may have reflected low abundance of terrestrial drift organisms during the day. The high level of nocturnal activity may have reflected a high abundance of aquatic drift organisms at night. If lower productivity might be assumed to increase the time fish must forage to meet energy requirements, then daytime activity observed in other steams might reflect not only higher levels of terrestrial invertebrates in the drift, but also lower stream productivity overall. However, Bachman (1984) observed daytime activity for brown trout in a productive, limestone stream, so type and temporal abundance of drift does not entirely explain activity patterns.

Brown trout may be prey as well as predator, and diel variability in predation risk might have influenced their nocturnal activity pattern. Alexander (1977b) estimated that avian predators take a substantial number of trout from the North Branch Au Sable River. Considering there are both nocturnal and diurnal predators along the South Branch, I can only speculate that darkness lowers the risk of predation. Although I never observed predators other than human anglers capture fish, I often observed mink Mustela vison, great blue herons Ardea herodias, and belted kingfishers Megaceryle alcyon in the study area, and it was reported that river otters Lutra canadensis killed brown trout nearby (B. Kent, MDNR, personal communication). The deeper water in lakes, compared to shallow rivers, would likely afford brown trout protection from visual predators in daylight, and may help explain diurnal activity of brown trout observed in lakes (Swift 1962; Priede and Young 1977).

Water temperature is a third factor that may help explain the high level of nocturnal activity for brown trout in this study. Although activity level and water temperature were not linear related, there was a pattern of changing activities on a diel cycle which might maximize growth under the constraints of food availability, predation, and water temperature. Such a strategy is shown by sockeye salmon Oncorhynchus nerka that migrate vertically on a circadian cycle in lakes (Brett 1971). By day sockeye remain in cooler, deeper water, and at night ascend to warmer surface water where food is concentrated. Bevelhimer et al. (1990) through model simulation and Diana (1984) in a laboratory study demonstrated that fish can grow faster under varying rather than constant temperatures.

The South Branch Au Sable River does not stratify vertically as some lakes, but water temperature varies on a diel basis. Water temperature was coolest just after sunrise, rose steadily throughout the day and peaked around 1600 hours. This pattern was consistent throughout the summer and varied in magnitude with weather. Brown trout were most active at night, when food was most concentrated in the river, predation risk was reduced, and consumption of food was enhanced by warm temperatures. Such a behavior pattern may have allowed growth maximization under the constraints of water temperature, food availability, and predation risk.

Brown trout were fairly inactive the first few hours after sunrise when water temperature reached daily lows. Assuming that most activity from the previous night was feeding related, brown trout inactivity during the morning may have minimized energetic costs during digestion and maximized food conversion efficiency. Brown trout were also inactive during the day when main flow temperatures were rising, and the analogy with sockeye might end here; however, home sites may have been thermal refuges with cooler groundwater upwellings, as well as resting areas of cover, although water temperature deep within individual home sites was not measured. These early morning and daytime bouts of resting behavior, assuming lower food availability and higher predation risk than at night, again would likely maximize brown trout growth and survival.

Assumptions

The major assumption of this study is that transmitters did not adversely affect fish behavior. The most compelling evidence supporting this assumption was the number of successful implants. Only one of twenty-one was a confirmed mortality. I also recaptured fish from two months to one year after tagging to examine their overall condition. Fish 3 was discovered one year after implanting at the site it was originally captured. This brown trout appeared healthy and had grown approximately 2.8 cm, which is near average growth for this size fish in the South Branch (Gowing and

Alexander 1980). I removed the expired transmitter from Fish 3, replaced it, and monitored the fish for 62 days, during which it appeared to behave normally. Four additional fish were recaptured just prior to transmitter failure. All four appeared healthy. Dissections revealed no infections and three of the four had recently fed.

A second assumption of this study is that the fish sampled reflected the population at large. Because telemetry studies are expensive in time and resources (Morris 1980), not to mention often frustrating (MacDonald and Amlaner 1980-- I concur), sample size is an important consideration. In that three brown trout were monitored for activity, a fair question is, "Are these fish typical?" I believe they are for two primary reasons: 1) each fish showed basically the same pattern of greater nocturnal activity (Figure 5 and 2) the diel pattern of home site use for 12 other fish also suggested they were nocturnally active (Figure 2).

Management Implications

The distinct diel pattern of habitat use by these brown trout may be useful information when applied to the Instream Flow Incremental Methodology (IFIM) model. The IFIM model is used to assess the effect of changes in water flow on habitat use by fishes (Raleigh et al. 1986). Although seasonal habitat preferences have been quantified for spawning and overwintering brown trout, my study demonstrates that fish used different habitat on a daily basis. Brown trout held in low velocity areas of cover during the day and moved to open areas at night, probably to forage. These habitats should be recognized and quantified when applying a model such as the IFIM. A change in a given stream discharge my adversely impact one, both, or neither of the respective habitat requirements.

Brown trout activity levels may also be applied to bioenergetic models which allow fishery managers to better understand fish growth. A cursory look at one particular model illustrates my point. The general equation Kitchell et al. (1977) used is:

$$dB/Bdt = C - (R + F + U),$$

where B = fish weight,

C = consumption,

R = metabolism (standard + specific dynamic action + active)

F = egestion, and

U = excretion.

Thus, the specific growth rate of a fish is the difference between food consumption (energy gains) and the sum of metabolic costs and waste losses. Laboratory studies have provided information for parameters such as standard metabolism, specific dynamic action, excretion, and egestion rates of brown trout (Elliott 1976a, 1976b). However, the activity component of metabolism is often assumed constant because acquiring the necessary field data is difficult (Boisclair and Leggett 1989). Boisclair and Leggett (1989) have estimated that activity costs were major determinants of fish growth. Although some have disputed these estimates, they likewise recognize that activity may have a significant impact on fish growth (Hewett et al. 1991).

LITERATURE CITED

Alexander, G. R. 1977a. Consumption of small trout by large predatory brown trout in the North Branch of the Au Sable River. Michigan Department of Natural Resources, Fisheries Research Report 1855, Ann Arbor, Michigan.

Alexander, G. R. 1977b. Food of vertebrate predators on trout waters in north central lower Michigan. Michigan Academician 10:181-195.

Arnold, D. E., J. T. Nichols, and R. A. Bachman. 1987. Potamodromous spawning migrations of brown trout, with a case study from Pennsylvania. Contribution number 280 of the Pennsylvania Cooperative Fish and Wildlife Research Unit, University Park, Pennsylvania.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Bevelhimer, M. S., S. M. Adams, and L. J. Gross. 1990. Habitat selection by kokanee salmon and smallmouth bass in thermally heterogeneous environments: the importance of growth maximization to diel habitat shifts. Oak Ridge National Laboratory, Environmental Sciences Division Publication No. 3463, Oak Ridge, Tennessee.

Beyerle, G. B. and E. L. Cooper. 1960. Growth of brown trout in selected Pennsylvania Streams. Transactions of the American Fisheries Society 89:255-262.

Boisclair, D., and W. C. Leggett. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Canadian Journal of Fisheries and Aquatic Sciences 46:1859-1867.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (Oncorhynchus nerka). American Zoologist 11:99-113.

Cada, G. F., J. M. Loar, and D. K. Cox. 1986. Food and feeding preferences of rainbow and brown trout in Southern Appalachian streams. The American Midland Naturalist 117:375-385.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 in T. G. Northcote, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, Canada.

Chaston, I. 1969. Seasonal activity and feeding pattern of brown trout (Salmo trutta) in a Dartmoor stream in relation to availability of food. Journal of the Fisheries Research Board of Canada 26: 2165-2171.

Chisolm, I. M., W. A. Hubert, and T. A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society 116:176-184.

Clapp, D. F., R. D. Clark, Jr., and J. S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. Transactions of the American Fisheries Society 119:1022-1034.

Clark, R. D., Jr. 1988. Evaluation of catch-and-release regulations on the South Branch of the Au Sable River, Crawford County, Michigan. Federal Aid in Fish Restoration, Project F-35-R-13, Study 318, Michigan Department of Natural Resources, Ann Arbor, Michigan.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout Salvelinus fontinalis and brown trout Salmo trutta. Canadian Journal of Fisheries and Aquatic Sciences 43:1970-1981.

Diana, J. S. 1984. The growth of largemouth bass, Micropterus salmoides (Lacepede), under constant and fluctuating temperatures. Journal of Fish Biology 24:165-172.

Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Sciences 40:398-408.

Elliott, J. M. 1967. The food of trout (Salmo trutta) in a Dartmoor stream. Journal of Applied Ecology 4:59-71.

Elliott, J. M. 1970. Diel changes in invertebrate drift and the food of trout Salmo trutta. Journal of Fish Biology 2:161-165.

Elliott, J. M. 1976a. The energetics of feeding, metabolism, and growth of brown trout (Salmo trutta) in relation to body weight, water temperature, and ration size. Journal of Animal Ecology 45:923-948.

Elliott, J. M. 1976b. Energy losses in the waste products of brown trout. Journal of Animal Ecology 45:561-580.

Foster, J. R. 1977. Pulsed gastric lavage: an efficient method of removing stomach contents of live fish. The Progressive Fish Culturist 39:166-169.

Funk, J. L. 1957. Movement of stream fishes in Missouri. Transactions of the American Fisheries Society 85:39-57.

Gowing, H., and G. R. Alexander. 1980. Population dynamics of trout in some streams of the northern lower peninsula of Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1877, Ann Arbor, Michigan.

Harcup, M. F., R. Williams, and D. M. Ellis. 1984. Movements of brown trout, Salmo trutta L., in the River Gwyddon, South Wales. Journal of Fish Biology 24:415-426.

Hendrickson, G. E. 1966. Michigan's Au Sable River--today and tomorrow. Michigan Department of Conservation, Geological Survey Bulletin 3, Lansing, Michigan.

Hewett, S. W., C. E. Kraft, and B. L. Johnson. 1991. Consumption, growth, and allometry: a comment on Boisclair and Leggett (1989a, 1989b, 1989c, 1989d). Canadian Journal of Fisheries and Aquatic Sciences 48:1334-1337.

Jackson, P. D. 1980. Movement and home range of brown trout, Salmo trutta Linnaeus, in the Aberfeldy River, Victoria. Australian Journal of Marine and Freshwater Research 31:837-845.

Jenkins, T. M., Jr. 1969a. Social structure, position choice, and microdistribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. Animal Behaviour Monographs 2:57-123.

Jenkins, T. M., Jr. 1969b. Night feeding of brown and rainbow trout in an experimental stream channel. Journal of the Fisheries Research Board of Canada 26:3275-3278.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society 114: 182-194.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Application of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34:1922-1935.

Larson, T. 1988. Exploitation, movement, and growth of tagged brown trout in Rowan Creek, Columbia County, Wisconsin, 1983. Wisconsin Department of Natural Resources, Fish Management Report 135, Madison, Wisconsin.

Macdonald, D. W., and C. J. Amlaner, Jr. 1980. A practical guide to radio tracking. Pages 143-159 in C. J Amlaner, Jr. and D. W. MacDonald, editors. A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford, England.

McLaughlin, R. L. 1989. Search modes of birds and lizards: evidence for alternative movement patterns. The American Naturalist 177:654-670.

Nilsson, N. A. 1957. On the feeding habits of trout in a stream of Northern Sweden. Institute of Freshwater Research Drottningholm 38:154-166.

Morris, P. 1980. An elementary guide to practical aspects of radio tracking mammals. Pages 161-168 in C. J. Amlaner, Jr. and D. W. MacDonald, editors. A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford, England.

Orth, D. J. 1983. Aquatic habitat measurements. Pages 61-84 in L.A. Nielsen and D.L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology 47:1055-1059.

Pickering, A. D., T. G. Pottinger, and P. Christie. 1982. Recovery of the brown trout, Salmo trutta L., from acute handling stress: a time-course study. Journal of Fish Biology 20:229-244.

Priede, I. G., and A. H. Young. 1977. The ultrasonic telemetry of cardiac rhythms of wild brown trout (Salmo trutta) as an indicator of bio-energetics and behaviour. Journal of Fish Biology 10:299-318.

Raleigh, R. F., L. D. Zuckerman, and P. C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: brown trout, revised. U. S. Fish and Wildlife Service Biological Report 82 (10.124).

Richards, J. S. 1973. Changes in fish species composition in the Au Sable River, Michigan, from the 1920's to 1972. Michigan Department of Natural Resources, Fisheries Research Report 1800, Ann Arbor, Michigan.

Shetter, D. S. 1937. Contributions to the natural history of some game fishes of Michigan, particularly brook trout, Salvelinus f. fontinalis (Mitchell), as determined by tagging experiments. Institute for Fisheries Research Report No. 439, Ann Arbor, Michigan.

Shetter, D. S. 1968. Observations on movements of wild trout in two Michigan stream drainages. Transactions of the American Fisheries Society 97:472-480.

Solomon, D. J., and R. G. Templeton. 1976. Movements of brown trout (Salmo trutta) L. in a chalk stream. Journal of Fish Biology 9:411-423.

Stauffer, T. E. 1977. A comparison of the diet and growth of brown trout (Salmo trutta) from the South Branch and Mainstream, Au Sable River, Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1845, Ann Arbor, Michigan.

Swift, D. R. 1961. The annual growth-rate cycle in brown trout (Salmo trutta Linn.) and its cause. Journal of Experimental Biology 38: 595-604.

Swift, D. R. 1962. Activity cycles in the brown trout (Salmo trutta Lin.). Hydrobiologia 20:241-247.

Tanaka, H. 1960. On the daily change of the drifting of benthic animals in stream, especially on the types of daily change observed in taxonomic groups of insects. Bulletin of Freshwater Fisheries Research Laboratory 9:13-24.

Waters, T. F. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology 43:316-320.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois.

Winter, J. D. 1983. Underwater biotelemetry. Pages 371-395 in L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.