

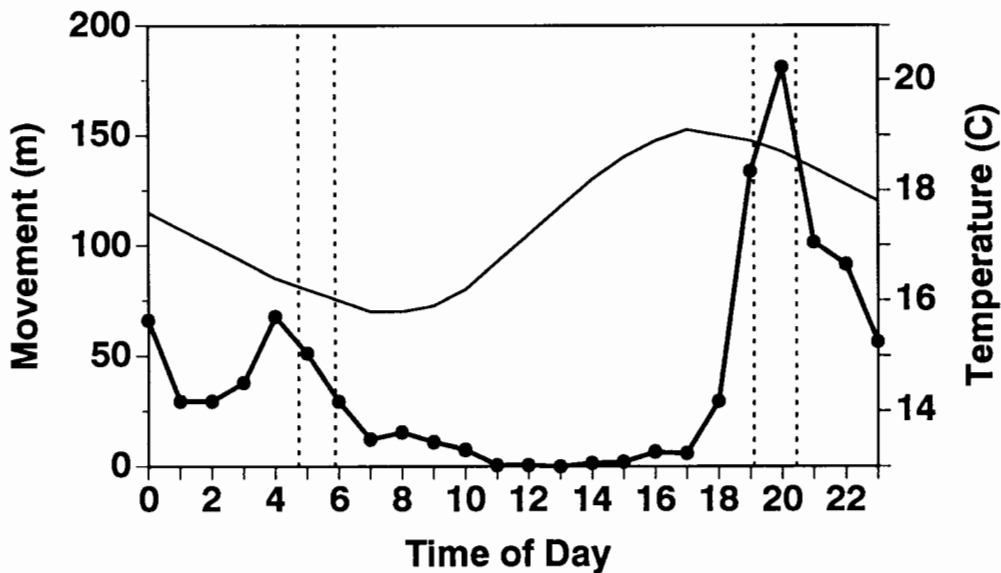
FISHERIES DIVISION RESEARCH REPORT

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May 8, 1993

Seasonal and Daily Movements of Large Brown Trout in the Mainstream Au Sable River, Michigan

John P. Hudson



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STATE OF MICHIGAN
DEPARTMENT OF NATURAL RESOURCES

**MICHIGAN DEPARTMENT OF NATURAL RESOURCES
FISHERIES DIVISION**

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**SEASONAL AND DAILY MOVEMENTS OF LARGE BROWN TROUT IN THE
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John P. Hudson

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Seasonal and Daily Movements of Large Brown Trout
in the Mainstream Au Sable River, Michigan.

by

John P. Hudson

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

School of Natural Resources and Environment
The University of Michigan
1993

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Abstract

Previous studies of stream-dwelling brown trout Salmo trutta indicate that smaller fish exhibit limited range of movement that is likely due to a sit-and-wait, drift-feeding strategy, while greater range of movement exhibited by large brown trout may reflect a piscivorous, active-search strategy. The timing and extent of seasonal and daily movements of large brown trout may vary between streams. Radio telemetry was used in the present study to monitor seasonal and daily movements and home site use of large brown trout in the Mainstream Au Sable River, Michigan and to compare results with a similar study in the South Branch.

Thirteen radio-tagged brown trout (442 - 584 mm in length) were tracked up to 904 d between May 1990 and May 1993. Range of movement varied considerably among fish due to differences in distance between home sites, extent of nighttime foraging movements, and seasonal habitat use. Average range of movement was 1,752 m in summer (May - August) and 4,764 m in winter (September - April). Of eight fish tracked in both seasons, four overwintered in their summer range while four moved to separate overwintering habitats. Eighty-eight percent of brown trout captured in an area protected with catch-and-release regulations remained there during the entire tracking period. Brown trout used from one to five home sites in summer and were found in home sites during 86% of daytime locations and 49% of nighttime locations. Eighty-percent of home sites used by large brown trout were classified as artificial cover, 7% as natural cover, and 11% as pools. Most artificial structures were built specifically for trout cover and 82% of fish used at least one of these structures as a home site. Two fish had home sites over 6,900 m apart, otherwise, home sites were 84 m apart on average.

In summer, most large brown trout occupied home sites during daylight hours, moved into midstream at dusk apparently to forage, and returned to the same or nearby home site at dawn. The extent of nighttime foraging movements away from home sites

suggested individual brown trout were using one of two foraging strategies: sit-and-wait or active-search. Individuals using sit-and-wait held stationary positions in midstream < 30 m from home sites. Fish using active-search moved frequently or continuously and were rarely found within 30 m of a home site at night. Distances moved away from home sites at night varied among fish and were negatively correlated with water velocity. Individual fish that used sit-and-wait generally lived in high velocity areas, while fish that used active-search generally lived in low velocity areas. Factors such as type of prey consumed, prey density, or energetic costs associated with sit-and-wait versus active-search in flowing water may influence the foraging strategy chosen by individual fish.

Three individuals were located hourly over 24-hour periods to monitor their diel movements. Average diel range of movement varied among fish from 78 to 424 m and average total distance moved varied from 143 to 967 m. Movements generally occurred at nighttime, with distinct peaks in hourly movements rates near dawn and dusk. Average distance moved per hour varied among fish from 0 to 8 m/h in daytime and from 7 to 77 m/h at nighttime.

In comparison to Mainstream fish, large brown trout in the South Branch used more home sites, moved between home site more often, and exhibited active-search foraging behavior. Fish in the South Branch also ranged farther in summer and winter and most individuals used separate winter habitat.

Introduction

The movements of stream-dwelling brown trout Salmo trutta have been studied throughout their range using a variety of methods including mark and recapture techniques, direct observation, and radio telemetry. Most studies have focused on small individuals (< 400 mm). With the exception of movements related to spawning (Shuck 1945; Solomon and Templeton 1976; Arnold et al. 1987; Meyers et al. 1992) and overwintering (Meyers et al. 1992; Regal 1992), the range of movement of small brown trout is generally limited. Studies using mark and recapture techniques found the majority (63%-93%) of small brown trout were recaptured less than 100 m from the release site (Shuck 1945; Allen 1951; Solomon and Templeton 1976; Jackson 1980; Harcup 1984; Evensen 1984; Hesthagen 1988). Jenkins (1969) and Bachman (1984) visually observed the social structure and foraging behavior of small brown trout from streamside towers; most fish had small home ranges, occupied discrete foraging sites, and were organized into dominance hierarchies. Although information on the ecology of large (> 400 mm), stream-dwelling brown trout is limited, studies in Michigan's Au Sable River system indicate that size-dependent differences in range of movement may exist. Shetter (1968) used mark and recapture techniques to study movements of brown trout in the Mainstream, South Branch, and North Branch of the Au Sable River; overall, large fish (330-572 mm) moved greater distances than smaller fish. In the South Branch, Clapp et al. (1990) and Regal (1992) used radio telemetry to track movements of large and small brown trout, respectively. Average summer range of movement of large fish (> 400 mm) was 4,900 m (Clapp et. al. 1990) compared to only 29 m for smaller fish (Regal 1992).

Size-dependent differences in range of movement may be related to a diet shift and subsequent change in foraging strategy (Shetter 1968; Jenkins 1969; Bachman 1982). The limited range of movement of small brown trout may reflect a stationary, drift-feeding strategy in which the diet consists primarily of insects and other invertebrates (Bachman

1984). However, as size increases so does the proportion of fish in the diet (Stauffer 1977), with large individuals being more piscivorous (Alexander 1977). Bachman (1982) developed a model which predicted such a diet shift; he believed that as size increased, food limitations, in combination with metabolic constraints, would require a diet transition from invertebrates to fish in order to allow continued growth. A simultaneous transition in foraging behavior from stationary, drift-feeding to actively searching (Eckhardt 1979) would explain the greater range of movement of large brown trout. While there is evidence that brown trout actively search for their food (Shetter 1968; Jenkins 1969; Clapp et al. 1990), factors influencing the timing and extent of such foraging movements may vary among rivers or even within a river system. Clapp et al. (1990) described large brown trout as roving predators that rested within cover by day and hunted for less mobile prey organisms at night; their movements and activity were related to food availability, discharge, water temperature, and light levels. These and other biotic and abiotic factors may vary within a river system resulting in behavioral patterns adapted to a specific set of environmental conditions.

Mark and recapture studies indicate large brown trout in the Mainstream may not range as far as fish in other branches of the Au Sable River. Shetter (1968) found only 19% of large brown trout in the Mainstream moved more than 152 m, compared to 76% and 100% in the North Branch and South Branch, respectively. Favro et al. (1986) found 95% of the larger brown trout in the Mainstream were recaptured within 2 m of a given location, even over a four year period. Differences in range of movement among streams may reflect limitations of the methods used. Mark and recapture studies do not provide information on activities of fish between marking and recapture, especially seasonal or foraging movements that may occur over short time intervals. When recaptures rely on angling, biases may result when efforts are concentrated in certain areas or certain times of the year (Clapp 1988). Unlike mark and recapture techniques, radio telemetry can provide continuous information on the movements of an individual fish. Therefore, telemetry was

used in the present study to obtain more detailed information concerning seasonal and daily movements of brown trout in the Mainstream and to compare results with those from a similar study conducted by Clapp et al. (1990) in the South Branch. The specific objectives of the study were to: 1) determine seasonal range of movement, 2) measure daily movements in summer, and 3) document the number, type and usage of home sites.

Methods

Study Area

The Mainstream of the Au Sable River originates 16 km north of Grayling, Michigan at the confluence of Bradford and Kolka Creeks (Figure 1a). From there it flows 26 km south to Grayling and then east 183 km to Lake Huron. Six large dams on the Mainstream between Oscoda and Mio prevent fish migrations from Lake Huron into the upper Au Sable River. Brown trout in the upper river are free to range throughout the North and South Branches and the Mainstream between dams in Grayling and Mio. Highly permeable glacial drift in the watershed contributes to cool, stable stream flows, and hence favorable conditions for trout.

The study site consisted of four adjacent reaches of the Mainstream between Grayling and Wakeley Bridge (Figure 1b). This division served to identify areas with different biotic and abiotic characteristics that could influence large brown trout behavior and movements. The uppermost reach of the study site extended 1.7 km from a small dam at US-27 in Grayling to I-75. The dam creates a shallow (mean depth < 1 m), 18.6 ha impoundment. Average discharge at the dam is 2.0 m³/s and summer water temperatures there can reach 27°C (Coopes 1974). Between US-27 and I-75 the river is swift, the bottom consists primarily of gravel, and ground water input is relatively high. The East Branch flows into the Mainstream within this reach; average discharge in the East Branch is 1.2 m³/s (Coopes 1974) and summer water temperatures can be 4.5°C cooler than the

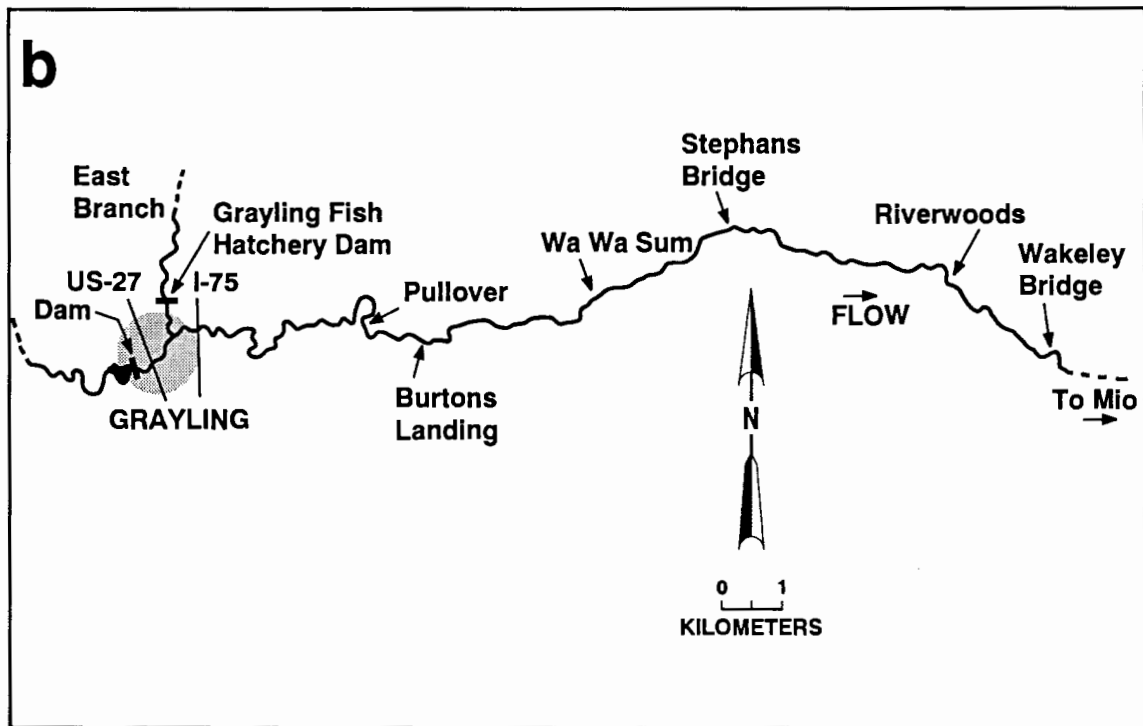
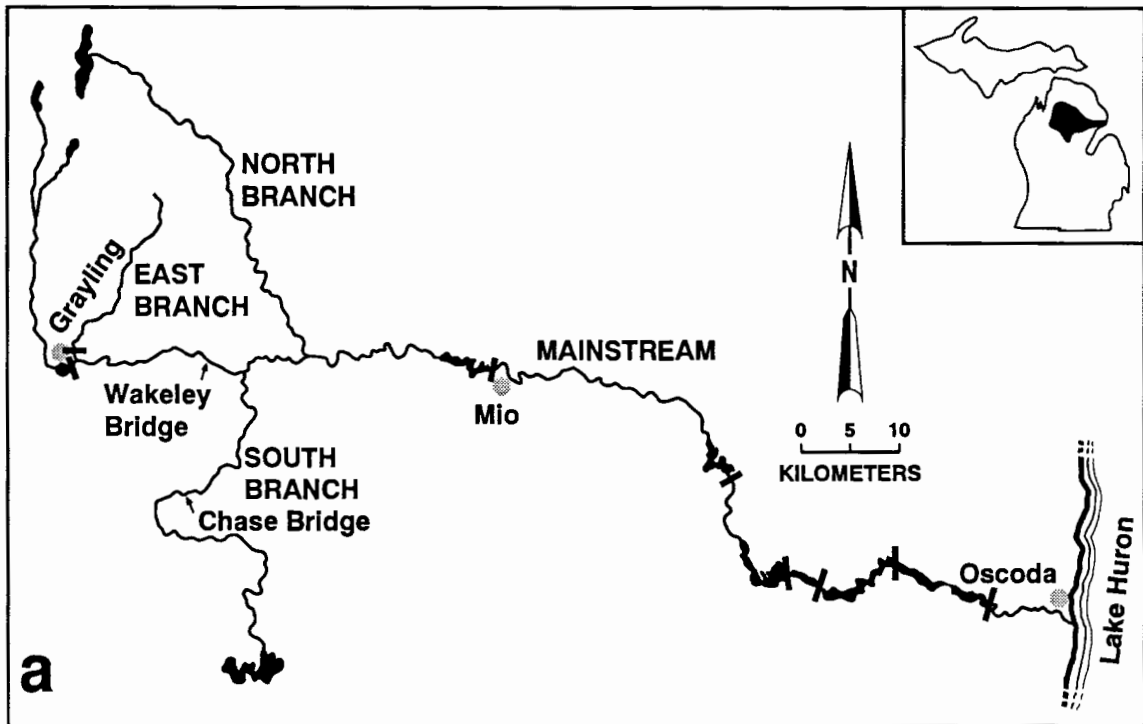


Figure 1.—Map of the Au Sable River system (a). The study site (b) consisted of four stream reaches between Grayling and Wakeley Bridge: uppermost reach, dam in Grayling to I-75; upper reach, I-75 to Burtons Landing; middle reach, Burtons Landing to Stephens Bridge; and lower reach, Stephens Bridge to Wakeley Bridge.

Mainstream. A dam on the East Branch at the Grayling Fish Hatchery restricts fish to the lower 0.8 km of stream. Formerly, the hatchery produced trout for stocking in local streams. It is now operated by the city of Grayling as a summer tourist attraction where the public can view and feed brown trout, brook trout Salvelinus fontinalis, and rainbow trout Oncorhynchus mykiss. Several wild trout living in a pool below the hatchery dam are provided artificial food daily.

The upper reach (I-75 to Burtons Landing) is 8 km long, has a low overall gradient (0.04%), receives little ground water input, and has bottom substrate dominated by sand (Figure 1b). Average stream width is 27 m, and average discharge is 3.2 m³/s (Hendrickson and Doonan 1972). This reach is considered marginal trout water due to warm summer water temperatures, sandy substrate, and limited habitat. At the Pullover area, mean water temperature in July 1991 was 19.7°C and estimates of brown trout and brook trout standing crops in 1982 were 2.3 and 0.03 kg/ha, respectively. Some of the other fish species found in this reach include northern pike Esox lucius, yellow perch Perca flavescens, and white suckers Catostomus commersoni. The river between Grayling and Burtons Landing is under normal statewide trout fishing regulations: live bait or artificial lures may be used between the last Saturday in April to September 30, 203-mm minimum size, and 10-fish daily creel limit.

The remaining 14.5 km of the study site is located between Burtons Landing and Wakeley Bridge (Figure 1b). This section of stream is known as the "Holy Water" due to its exceptional brown trout fishery, and because Trout Unlimited originated along its banks. In 1989 this section was designated as catch-and-release fishing ("no-kill"), flies-only, with no closed season. Compared to the upper reach, the no-kill section has a higher average gradient, more ground water input, bottom substrate composed of gravel and cobble, and greater trout production. Average stream width is 29 m and average discharge is 5.4 m³/s (Hendrickson and Doonan 1972). Resident fishes include brown trout, brook trout, rainbow trout, mottled sculpin Cottus bairdi, blacknose dace

Rhinichthys atratulus, round whitefish Prosopium cylindraceum, and white suckers (Richards 1973). Stephans Bridge divides this section into the middle and lower reaches of the study site, each approximately 7 km in length (Figure 1b). The middle reach (Burtons Landing to Stephans Bridge) has an average gradient of 0.09% and July mean water temperature at Wa Wa Sum of 18.1°C. Estimates of brown trout, brook trout, and rainbow trout standing crops at Wa Wa Sum in 1982 were 30.8, 9.5, and 0.2 kg/ha, respectively. The lower reach (Stephans Bridge to Wakeley Bridge) has an average gradient of 0.15% and July mean water temperature at Riverwoods of 16.0°C. Estimates of standing crops for the above species at Stephans Bridge in 1982 were 77.9, 5.4, and 13.5 kg/ha, respectively. Normal statewide trout fishing regulations resume downstream of Wakeley Bridge.

Implanting Transmitters

Thirteen brown trout were captured using D.C. electrofishing gear and successfully implanted with radio transmitters between 8 May 1990 and 9 September 1991. Three other fish died within two weeks following surgery. Fish were anesthetized immediately following capture in a bath containing 75 mg tricaine methanesulfonate (MS-222) per liter of river water. Transmitters were placed in the abdominal cavity through a mid-ventral incision between the pelvic and pectoral girdles. Incisions were closed using non-absorptive silk or nylon sutures, followed by injection of 2 ml of oxytetracycline solution (50 mg/ml distilled water) to prevent infection. River water was sprayed over the body and gills to reduce stress during surgery and anesthetic solution was sometimes sprayed over the gills to maintain sedation. The procedure required less than ten minutes to complete, after which fish were immediately placed in the stream and allowed to recover at the capture site.

Radio transmitters used in this study (from AVM Instrument Company) were of two designs. Transmitters equipped with hairpin loop antennas (six units) measured 70 x

20 x 20 mm, weighed 21 g, were powered by a mercuric oxide battery, and had an expected life of 690 d. Transmitters equipped with coiled loop antennas (three units) measured 55 x 15 x 16 mm, weighed 18 g, were powered by a lithium thionyl chloride battery, and had an expected life of two years. Each unit was encapsulated in dental acrylic and coated with bees wax to prevent tissue reaction and expulsion (Tyus and McAda 1984). Transmitters emitted a different frequency between 49 and 50 MHz at rates between 60 and 90 pulses per minute. I tried to keep transmitter weight under 2% of body weight as recommended by Marty and Summerfelt (1986).

Locating Fish

I began monitoring the movement and behavior of radio-tagged fish immediately following surgery. However, Pickering et. al. (1982) determined brown trout required two weeks to recover from acute handling stress, so data collected during this time were not used in any analyses. Fish were located from shore by triangulation (two bearings) using a programmable scanning receiver and 60-cm directional loop antenna. When radio-tagged fish could be visually observed from shore or from underwater, I compared the telemetric location with the true position of a fish. From these comparisons, I found that telemetric estimates made from < 30 m were within 1.0 m of the true position.

Fish were located from shore at random times during day and night and were usually found in the same area from day to day. When a fish moved to another section of river, I searched for it by canoeing the Mainstream from Grayling to McMasters Bridge and the South Branch from Chase Bridge to the Mainstream (Figure 1a). In summer 1991, I made brief underwater observations of all fish in their home sites using snorkeling gear to monitor the recovery and general behavior of radio-tagged fish. Otherwise, I disturbed fish as little as possible to avoid influencing their normal behavior.

The number of times I located fish and type of information I collected varied seasonally. In summer (May 1 to August 31), I usually located fish every day or every

other day to quantify range of movement, daily movements, and home site use. In winter (September 1 to April 30), I located fish every two or three weeks to quantify range of movement, daily movements, and to document movements to overwintering or spawning areas. Most fish exhibited a diel pattern of activity in summer, so daily movements and home site use data were grouped into daytime and nighttime periods prior to analysis. I considered nighttime as the period from one hour before sunset to one hour after sunrise. It was not determined whether fish exhibited a diel pattern of activity in winter.

I mapped the summer range of each fish to measure daily movements. Maps included the location of home sites, as well as other instream structures and riparian landmarks. When a fish was located, I used the above features to determine its position on the map, and noted whether or not it was in a home site. Movements beyond the range of maps were measured using aerial photographs.

Seasonal Range of Movement

Seasonal range of movement represented the distance between extreme upstream and downstream telemetric locations in summer and winter (Clapp et al. 1990). Total range was computed the same way for fish tracked during more than one season. A Wilcoxon signed rank test was used to compare mean summer and winter range of movement for seven fish tracked in both seasons. A Mann-Whitney U test was used to compare: 1) mean summer and winter range of movement of all fish; and 2) the average seasonal range of Mainstream and South Branch fish. In the South Branch study, four fish were tracked in each season: summer was defined as the period from May 1 to August 15 and winter the period from August 16 to April 30 (Clapp et al. 1990). Simple linear regression was used to test whether there was a significant relationship between range of movement and number of days a fish was tracked.

Home Sites

Home sites were defined similar to Clapp et al. (1990) as specific cover structures or pools in which a fish was located five or more times in daytime, or to which a fish returned after an extended period of time. Home sites were classified as one of three types: artificial cover, natural cover, or pool. I considered artificial cover as a structure built specifically for trout or some other intended use but used by fish as a home site. Natural cover consisted of aquatic vegetation or submerged riparian vegetation. Pools were areas with slower water velocities and greater depths (both visually estimated) than adjacent areas, and contained little instream cover. Summer home site use was computed for daytime and nighttime periods as the percent of locations in which a fish was found inside a home site. A t-test was used to determine whether home site use varied with time of day for all fish combined.

Daily Movements

Two types of daily movements were measured in this study: active displacement and foraging movements. Active displacement was measured as the change in position between successive daytime locations such as movements between home sites from day to day or movements from summer habitat to overwintering or spawning habitat. Foraging movements represented movements from home sites into midstream areas when fish were believed to be searching or waiting for food. Active displacement represented a minimum estimate of distance moved, because it only included the absolute change in position and not necessarily the total distance moved between locations (Clapp et al. 1990). Average active displacement was computed for each fish by season. Simple linear regression was used to determine whether there was a significant relationship between active displacement and days between successive locations. A Wilcoxon signed rank test was used to compare summer and winter average active displacement of six fish tracked in

both seasons. A Mann-Whitney U test was used to compare: 1) summer and winter average active displacement of all fish; and 2) seasonal average active displacement of Mainstream and South Branch fish .

Two types of foraging movements were measured in summer: foraging displacements and diel movements. I measured foraging displacement for individual fish to quantify the extent of movements away from home sites during daytime and nighttime periods. Displacement was measured as the distance between each random telemetric location of an individual and its nearest home site. Random daytime locations of individual fish were made at least every three days and nighttime locations were made every three to eight days on average. For each fish, I computed median daytime and nighttime and maximum foraging displacement distances, as well as how frequently an individual was found within 30 m of a home site. Fish were divided into two groups based on their foraging behavior and extent of nighttime displacements. Mobile fish (four individuals) appeared to be actively searching for food. These fish were almost always found more than 30 m from a home site and moved frequently or continuously at night. Stationary fish (six individuals) usually held positions in midstream less than 30 m from a home site and appeared to be using a sit-and-wait foraging strategy. Frequency distributions of foraging displacement distances were developed for each group and for daytime and nighttime periods. Distributions were compared by group and time of day using a Kolmogorov-Smirnov test.

Stream velocity was measured within the foraging range (distance between extreme upstream and downstream foraging displacements) of each brown trout to determine whether it was an important factor influencing the extent of foraging displacements. A linear regression model was developed to predict stream velocity from stream gradient by quantifying and relating velocity and gradient along five stream reaches. Mean daily discharge was relatively constant during velocity measurements, averaging $1.8 (\pm 0.4) \text{ m}^3/\text{s}$. Reaches were 82-110 m in length and established in areas

used by fish so that the full range of velocities to which fish were exposed would be included in the model. Stream velocity was measured with a Pigmy Gurley current meter along four equally spaced transects within a reach. Velocities were measured at 0.6 depth at intervals equal to 5% of the transect width. All velocities along a transect were averaged to obtain a mean transect velocity. Average stream velocity (ASV) was computed by averaging the four mean transect velocities. Stream gradient was measured within a reach using a Carl Ziess, Ni-2 level and was computed as the total drop in stream surface elevation (nearest mm) over the mid-channel length of a reach (nearest dm) and expressed as percent slope. There was a significant ($P < 0.01$; $r^2 = 0.98$) positive linear relationship between ASV and percent slope (Figure 2). Stream gradient was measured at 90 m intervals within the foraging range of six fish and converted to ASV using the above model. Average stream velocity was obtained for three fish from direct measurements used to develop the model. Simple linear regression was used to examine whether median nighttime and maximum foraging displacement was related to ASV for ten fish.

The second method used to measure foraging movements involved quantifying the timing, extent, and pattern of diel movements of three fish (4, 11, and 12) during 24-hour monitoring sessions in summer 1991. During a session, I attempted to locate a fish each hour beginning at 0900 h, 1000 h, 1100 h, or 2300 h until that same time the following day. Distance moved from one hour to the next represented the linear (straight-line) distance between locations and not necessarily the total distance moved during the hour. For each session, I computed total linear distance moved (TLD), diel range, and daytime and nighttime hourly movement rates. Total linear distance moved was computed by summing the distances moved between hourly locations, diel range was computed as the distance between extreme upstream and downstream locations, and daytime and nighttime hourly movement rates were computed as the linear distance moved per number of hours in each period. A Wilcoxon signed rank test was used to compare mean daytime and nighttime movement rates for individual fish. The diel movement pattern of each fish was

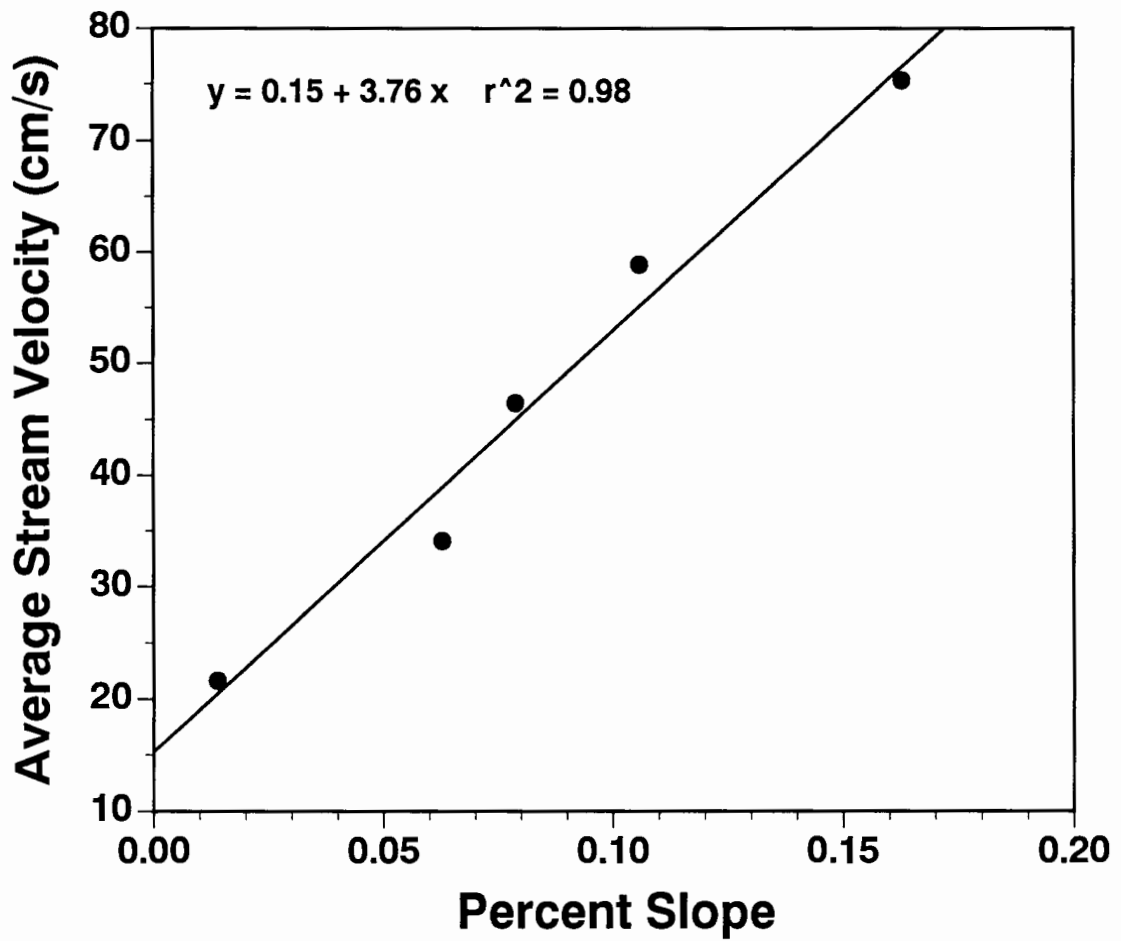


FIGURE 2. Relationship between average stream velocity and percent slope for five stream reaches in the study site.

examined by computing average distance moved during each hour (mean hourly movement) of a session. Simple linear regression was used to determine whether there were significant relationships between: 1) TLD and number of hourly observations, mean daily discharge, and mean daily water temperature; and 2) distance moved per hour and hourly water temperature. A Kruskal-Wallis test, and in some cases a Mann-Whitney U test was used to examine whether TLD, daily range, and daytime and nighttime movement rates varied by month for fish numbers 4 and 11. Discharge data were obtained from the U.S. Geological Survey gauging station at U.S. 27 in Grayling. I predicted hourly water temperatures in areas used by fish from data collected by three continuous temperature recorders located in the study site.

With the exception of t-tests that were calculated by hand, all statistical analyses were performed using Systat (Wilkinson 1989) software and results were considered statistically significant if $P < 0.05$.

Results

Implanting Transmitters

Thirteen fish were successfully implanted with transmitters. Two of these were captured at the Grayling Fish Hatchery, two in the upper reach, and four each in the middle and lower reaches (Table 1). One other fish captured 125 m downstream of Wakeley Bridge was considered a lower-reach fish. The general behavior and movement patterns of most fish before and after the two-week recovery period were similar. Two fish left the area where they were captured within a day following surgery. Fish number 13 moved 5 km downstream less than 24 hours following surgery, then moved 3 km further downstream on the last day of the recovery period. Fish number 5 moved from the Grayling Fish Hatchery to the Mainstream and back in the three days following surgery.

TABLE 1. Summary of radio transmitter implants in sixteen brown trout between 8 May 1990 and 8 September 1991 in the Mainstream Au Sable River, Michigan. Days tracked equal number of days between implant date and last contact. Comments: (W) tracked in winter; (D) tagged downstream of study site; (T) diel movements monitored; (H) tagged at Grayling Fish Hatchery; (L) tagged in lower reach; (LC) lost contact; (M) tagged in middle reach; (Mt) mortality; (R) transmitter recovered; (RR) fish recaptured and reimplanted; (S) tracked in summer; (U) tagged in upper reach.

Fish number	Length (mm)	Weight (g)	Implant date	Last contact	Days tracked	Comments
1	470	850	8 May 90	25 Jul 90	79	S,LC,M,RR
2	452	964	9 May 90	14 Jul 90	67	S,R,U
3	500	1,100	23 May 90	31 Jul 90	70	S,R,L
4	487	1,179	23 May 90	21 Feb 92	640	S,W,T,L
5	566	1,942	23 Jul 90	13 May 91	295	S,W,R,H,RR
6	521	1,602	24 Jul 90	3 Nov 90	103	S,W,LC,M
7	457	1,030	17 Sep 90	1 Mar 91	166	W,R,M
8	442	1,010	6 May 91	14 Feb 93	653	S,W,L
9	457	1,120	6 May 91	8 May 93	736	S,W,L
10	480	1,200	6 May 90	12 Dec 92	588	S,W,D
11	485	1,250	7 May 91	20 Mar 92	319	S,W,R,T,M
12	472	1,110	14 Jul 91	3 Sep 91	83	S,T,LC,U
13	546	----	31 Aug 91	21 Feb 92	175	W,LC,H
5	584	2,120	8 Sep 91	8 May 93	609	S,W,H,RR
14	470	1,148	30 Jul 90	----	----	L,Mt
15	510	1,440	18 Sep 90	----	----	L,Mt
16	514	1,360	6 Jul 91	----	----	M,Mt

Brown trout were tracked from 67 to 904 days between May 1990 and May 1993 (Table 1), however, only data collected through May 1992 were used to compute seasonal range of movement, daily movements, and home site use. Two fish were tracked during more than two seasons between May 1990 and May 1992: fish number 4 for two summers and two winters, and fish number 5 during two winters. Mean values were used for these two fish in computing overall values for range of movement, active displacement, and home site use. I lost radio contact with four fish from 65 to 161 days after surgery. Transmitters in two of these fish exhibited signs of premature failure prior to losing contact. An additional five transmitters were recovered in working condition from eleven to 68 days after the fish's last detected movement and no sign of fish remains were observed near recovered transmitters. The transmitter implanted in fish number 5 was recovered in a pool at the Grayling Fish Hatchery in May 1990, however, the fish was recaptured in the same pool 119 days later in September and reimplanted. The original incision had healed completely and a scar was present near the base of its left pectoral fin where the transmitter was probably expelled. The fish had grown 18 mm in length and 178 g in weight in the 413 days following initial implant (Table 1). Fish number 1 was also recaptured and reimplanted when the first unit began to fail four days after surgery. Three fish died within two weeks of surgery. One died immediately following surgery probably due to high water temperatures (26°C); another fish experienced heavy bleeding during surgery and was found dead two weeks later; and a third fish, that may have been injured during capture, was found dying two weeks after surgery.

Seasonal Range of Movement

Range of movement was documented for eleven fish in summer and nine fish in winter (Table 2). There was no significant relationship between range of movement and number of days fish were tracked ($P = 0.29$). Summer range varied from 33 to 8,330 m, and winter range varied from 206 to 29,030 m. Fish numbers 4 and 10 had total ranges of

TABLE 2. Brown trout range of movement in summer and winter. Distances are in meters. Data from South Branch were from Clapp et al. (1990). (SD = standard deviation, N = number of fish)

Fish number	Summer		Winter	
	Year	Range	Year	Range
1	90	7,875	----	----
2	90	8,330	----	----
3	90	33	----	----
4	90	287	90/91	1,011
4	91	570	91/92	206
5	90	117	90/91	1,210
5	--	----	91/92	1,210
6	90	170	90/91	3,420
7	90	----	90/91	6,300
8	91	160	91/92	571
9	91	67	91/92	244
10	91	160	91/92	870
11	91	1,130	91/92	625
12	91	800	----	--
13	--	----	91/92	29,030
Mainstream				
Mean		1,752		4,764
SD		3,160		9,309
N		11		9
South Branch				
Mean		4,935		11,902
SD		7,938		15,162
N		4		4

1,133 and 975 m, respectively; otherwise, total range was equal to winter range for fish tracked during both seasons. Summer range of movement varied within the study site. Mean summer range of movement was 3,661 m for five fish in the upper and middle reaches and 170 m for five fish in the lower reach. Two fish living at the Grayling Fish Hatchery were rarely found outside of a pool there.

Mean range of movement for all fish combined was greater in winter (4,764 m) than summer (1,752 m), but the difference was not significant ($P = 0.07$; Table 2). Similarly, of seven fish tracked in both seasons, mean winter range (1,078 m) was greater than mean summer range (319 m), but there was no significant difference ($P = 0.09$). For these seven fish, winter range was greater than summer range with the exception of fish number 4 in 1991/92 and fish number 11 (Figure 3). Average winter and summer range of movement for trout in the South Branch (Clapp et al. 1990) was greater than in the Mainstream, but differences between the two streams were not significant ($P > 0.05$; Table 2).

Winter ranges reflected movements during spawning season (October and November) and/or movements to overwintering areas following spawning. During spawning season, eight of nine fish (89%) left areas used in summer or early autumn, moving 75 to 3,250 m (mean = 785 m) from summer home sites to areas where spawning may have occurred. Five fish moved upstream, two (5, 13) moved downstream (both of these fish lived below the hatchery dam), and fish number 4 moved each direction in separate years. Following spawning season, four fish overwintered within their summer ranges while four fish moved 800 to 29,030 m to separate overwintering habitat (radio contact with fish number 6 was lost during spawning season). Two fish (5 and 10) that overwintered outside their summer range, were tracked through May when both returned to areas used the previous summer. Fish number 11 was the only individual that did not leave its summer range during spawning season. However, in November and December it was found 400 m downstream of its usual daytime resting site.

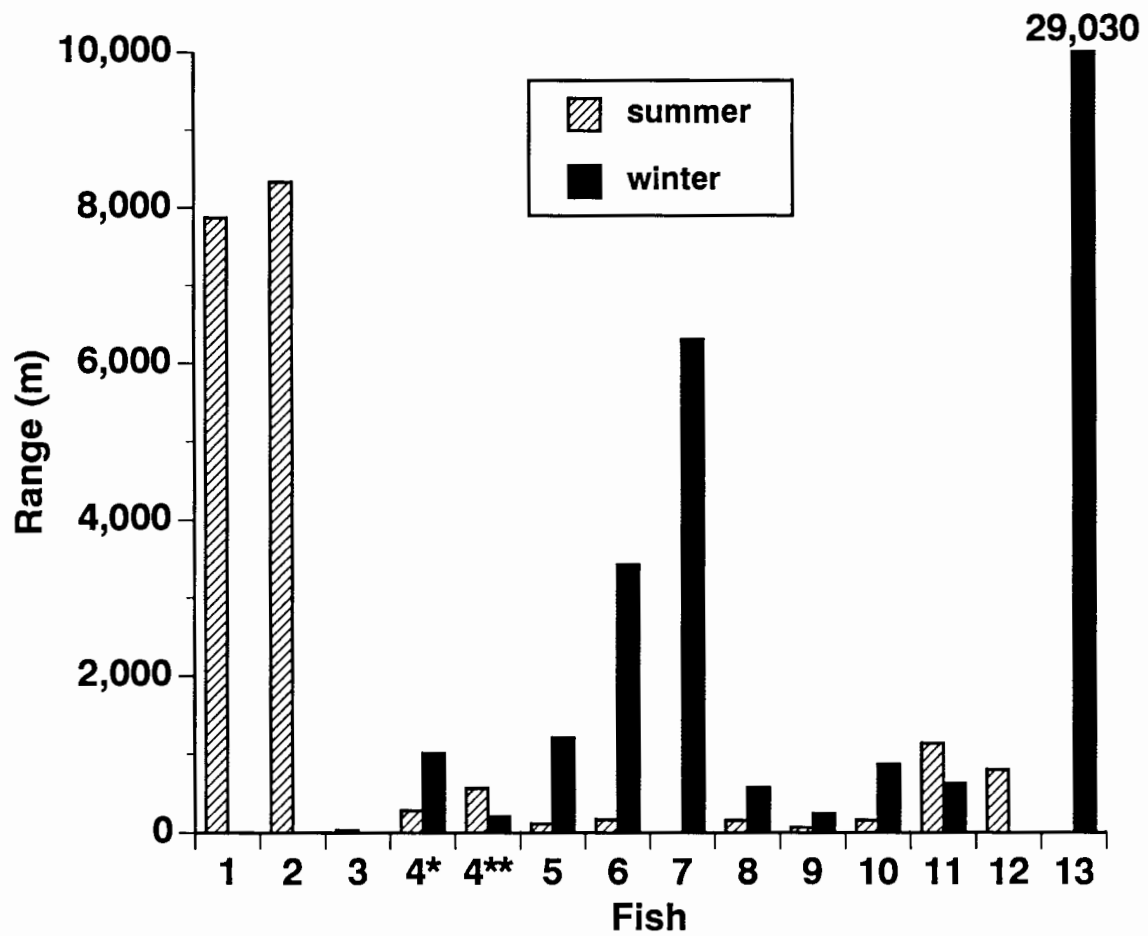


FIGURE 3. Summer and winter range of movement of 13 brown trout. Fish number 4 was tracked in 1990/91* and 1991/92**. Winter range of movement for fish number 5 was the same in 1990/91, 1991/92 and 1992/93.

Seasonal movements and home site use of most radio-tagged brown trout tracked for more than two seasons were similar from year to year. Of five fish (4, 5, 8, 9, 10) tracked during more than one winter, three (8, 9, 10) were found in the same area during October and November, and overwintered within the same 30 m reach of stream in both 1991 and 1992. Fish number 5 moved between a summer home site at the hatchery and a winter home site in the Mainstream six times between July 1990 and May 1993 (Figure 4). Fish number 4 used the same 30-m reach of stream in both autumn-winter 1990/91 and 1991/92, however, its movements during the spawning season varied from year to year. On 3 November 1990, the fish was observed on a redd with three large brown trout 800 m upstream of its summer home sites, and on 3 November 1991, the fish was found approximately 75 m downstream of its summer range. Several redds were present in the area, but no spawning activity was observed.

Radio-tagged fish were found in close proximity to one another on two occasions. Fish numbers 4 and 8 had summer home sites 447 m apart, but were found in the same 100 m reach of stream in late October and early November of 1991. During the peak of the 1990 spawning season, fish numbers 6 and 7 were found less than 10 m apart even though they were tagged 2,724 m apart.

Most fish established summer ranges during nighttime foraging ventures away from home sites or as movements between relatively closely spaced (12 to 535 m apart) home sites. Two fish moved between widely spaced home sites. Fish number 2 moved 8,330 m in a single night from a home site near the Pullover area to the Grayling Fish Hatchery (Figure 1b) where it was observed feeding on artificial food for two weeks until radio contact was lost. Fish number 1 made three trips between home sites that were 6,960 m apart, each trip required two nights to complete.

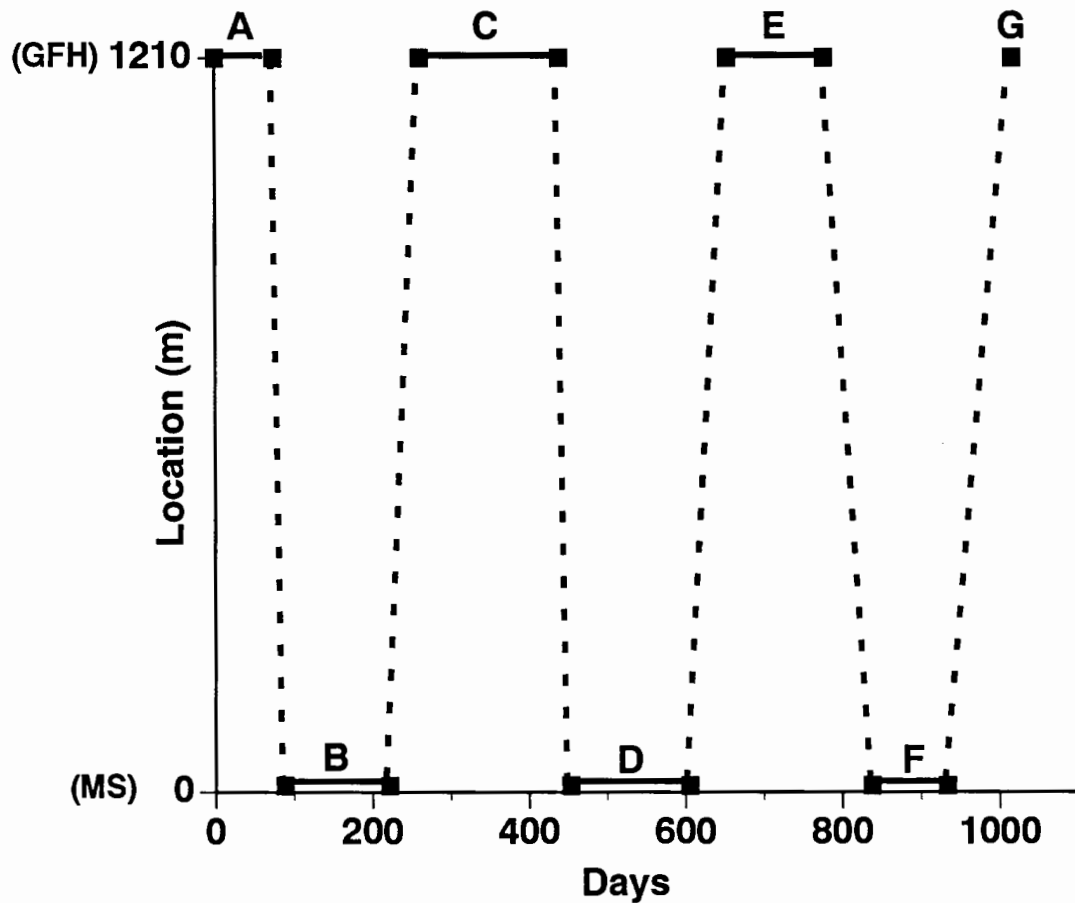


FIGURE 4. Seasonal movements of fish number 5 between Grayling Fish Hatchery (GFH) and Mainstream (MS) from 23 July 1990 to 8 May 1993. Solid lines represent time spent at each site; dashed lines represent movements between sites. (A = 23 July - 6 Oct 1990, B = 20 Oct 1990 - 2 Mar 1991, C = 11 April - 6 Oct 1991, D = 20 Oct 1991 - 20 Mar 1992, E = 8 May - 8 Sept 1992, F = 7 Nov 1992 - 14 Feb 1993, G = 8 May 1993)

Home sites

Eleven fish tracked in summer used a total of 27 home sites (Table 3). Individual fish used from one to five home sites (mean 2.5) with a mean separation of 1,029 m between sites. Mean separation was heavily weighted by two fish mentioned above, otherwise, home sites were 84 m apart on average. There was no significant difference ($P > 0.05$) in mean number of, or separation between home sites used by fish in the Mainstream and South Branch (Table 3). Most fish tracked for more than one summer and winter used the same home site(s) from year to year. Fish number 4 used the same home sites in 1990 and 1991; fish number 5 used the same home site in 1990, 1991, and 1992; and fish numbers 8 and 9 used the same home sites in 1991 and 1992. Fish number 10 used a home site downstream of Wakeley Bridge in 1991 and a home site upstream of the bridge in 1992. Home site use varied from 63% to 100% in daytime and from 8% to 100% at nighttime (Table 3). When data were combined for all fish, the percent of all locations in a home site was significantly greater ($P < 0.05$) during daytime (88%) than nighttime (49%), and daytime home site use was similar to South Branch brown trout (86-97%; Clapp et al. 1990).

Twenty-two home sites (82%) were classified as artificial cover, two (7%) as natural cover, and three (11%) as pools. Twenty-one of 22 (95%) artificial home sites were structures built specifically as trout cover. Four fish (36%) used at least one of these artificial structures as a home site, and five fish (45%) used them exclusively. Artificial cover consisted of log jams, submerged log rafts, stump complexes, or overhanging banks. An undercut retaining wall used by one fish was the only artificial structure not built specifically for trout cover. Pools were used as home sites by three fish, two of which were located at the Grayling Fish Hatchery and were provided artificial food on a daily basis. Home sites classified as natural cover (two sites) included aquatic macrophytes Elodea sp. and partially submerged alders Alnus sp.

TABLE 3. Summer home site use by eleven brown trout tracked between May 1990 and May 1992. Distance between home sites represents mean separation (in m) when number of home sites was greater than three. Home site type represents the number and type of home sites: (A) artificial; (N) natural; (P) pool. South Branch data were from Clapp et al. (1990). (SD = standard deviation)

Fish number	Number of home sites	Distance between	Home site type	Home site use (%)	
				day	night
1	3	3,503	3A	63	26
2	2	8,330	1A, 1P	96	9
3	3	14	3A	97	100
4 (90)	4	42	3A, 1N	91	38
4 (91)	4	42	3A, 1N	78	49
5	1	----	1P	--	--
6	1	----	1P	100	40
8	2	17	1A, 1N	87	71
9	1	----	1A	96	72
10	2	160	2A	91	87
11	3	68	3A	86	8
12	5	166	5A	76	33
Mainstream					
Total	27	----	22A, 2N, 3P	--	--
Mean	2.5	1,029		88	49
SD	1.0	2,598		11	32
South Branch					
Mean	3.3	386		91	--
SD	1.5	628		--	--

Daily Movements

Average active displacement varied from 0 to 485 m in summer, and from 28 to 5,806 m in winter (Table 4). There was a significant positive relationship between active displacement and time between successive locations for two fish (5 and 11) in winter. However, days between locations accounted for less than 30% (r^2) of the variation in active displacement. Mean active displacement was significantly ($P = 0.02$) greater in winter (1,005 m) than in summer (91 m) when all fish were considered, as well as for seven fish tracked in both seasons (winter = 195 m, summer = 17 m; $P = 0.02$). Average active displacement was less than 100 m for all but two fish in summer ($N=10$) and greater than 100 m for all but three fish in winter ($N=7$). Mean average active displacement of South Branch fish was significantly greater than Mainstream fish in summer ($P = 0.01$) but not in winter ($P = 0.09$, Table 4). With the exception of fish numbers 1 and 2, summer displacements generally represented movements between home sites from one day to the next and were therefore a function of the number, separation, and frequency of movements between home sites. Active displacement increased in winter due to movements to and from possible spawning areas and/or overwintering areas. Most of these movements occurred in October and December, after which little displacement occurred between observations until late winter when two fish returned to summer ranges from overwintering areas.

Foraging displacement distances varied between daytime and nighttime periods and among fish (Table 5). Displacement distributions of stationary and mobile fish were not significantly ($P = 0.20$) different in daytime (Figure 5). Fish rarely ventured far from home sites in daytime: median foraging displacement was 0 m for all fish and 86 to 100% of displacements were within 30 m of a home site. Fish that were observed in home sites appeared lethargic and some were found lodged within or resting against debris so that swimming or fin movements were not required to maintain position. Other fish were sometimes observed foraging in midstream during daytime. Daytime home site use was

TABLE 4. Average active displacement of brown trout tracked between May 1990 and May 1992 (* = summer 1990, winter 1990/91; ** = summer 1991, winter 1991/92; SD = standard deviation; N = number of observations minus one). South Branch data were from Clapp et al. (1990).

Fish number	Summer				Winter			
	N	Mean (m)	SD (m)	Max (m)	N	Mean (m)	SD (m)	Max (m)
1	44	485	1,772	6,960	--	----	----	----
2	37	288	1,382	8,330	--	----	----	----
3	33	5	8	33	--	----	----	----
4*	42	44	66	231	20	112	239	977
4**	80	59	93	508	27	28	46	152
6	9	0	0	0	4	855	1,710	3,420
8	52	5	7	17	23	53	137	554
9	53	2	8	37	20	39	67	194
10	55	5	22	160	16	110	281	836
11	76	39	65	270	25	101	150	518
12	40	72	147	575	--	----	----	----
13	--	----	----	----	5	5,806	11,249	25,770
Mainstream								
Mean		91				1,005		
SD		155				2,137		
N		10				7		
South Branch								
Mean		243				3,473		
SD		229				5,206		
N		4				4		

TABLE 5. Summary of daytime and nighttime foraging displacements of ten brown trout tracked between May 1990 and May 1992. N is number of observations, home percent represents the percentage of displacements within 30 m of a home site, and velocity (cm/s) represents average stream velocity. Displacements in m.

Fish number	Day			Night			Maximum displacement	Velocity
	N	Median	Home percent	N	Median	Home percent		
Mobile								
2	27	0	100	9	375	11	1,090	20
6	10	0	100	5	90	20	170	74
11	94	0	91	26	119	23	643	31
12	43	0	86	5	45	40	135	53
Stationary								
1	44	0	98	16	13	88	125	45
3	35	0	100	8	0	100	5	56
4	131	0	94	49	0	94	415	52
8	54	0	100	14	0	86	143	70
9	62	0	98	21	0	100	37	77
10	52	0	100	17	0	88	96	70

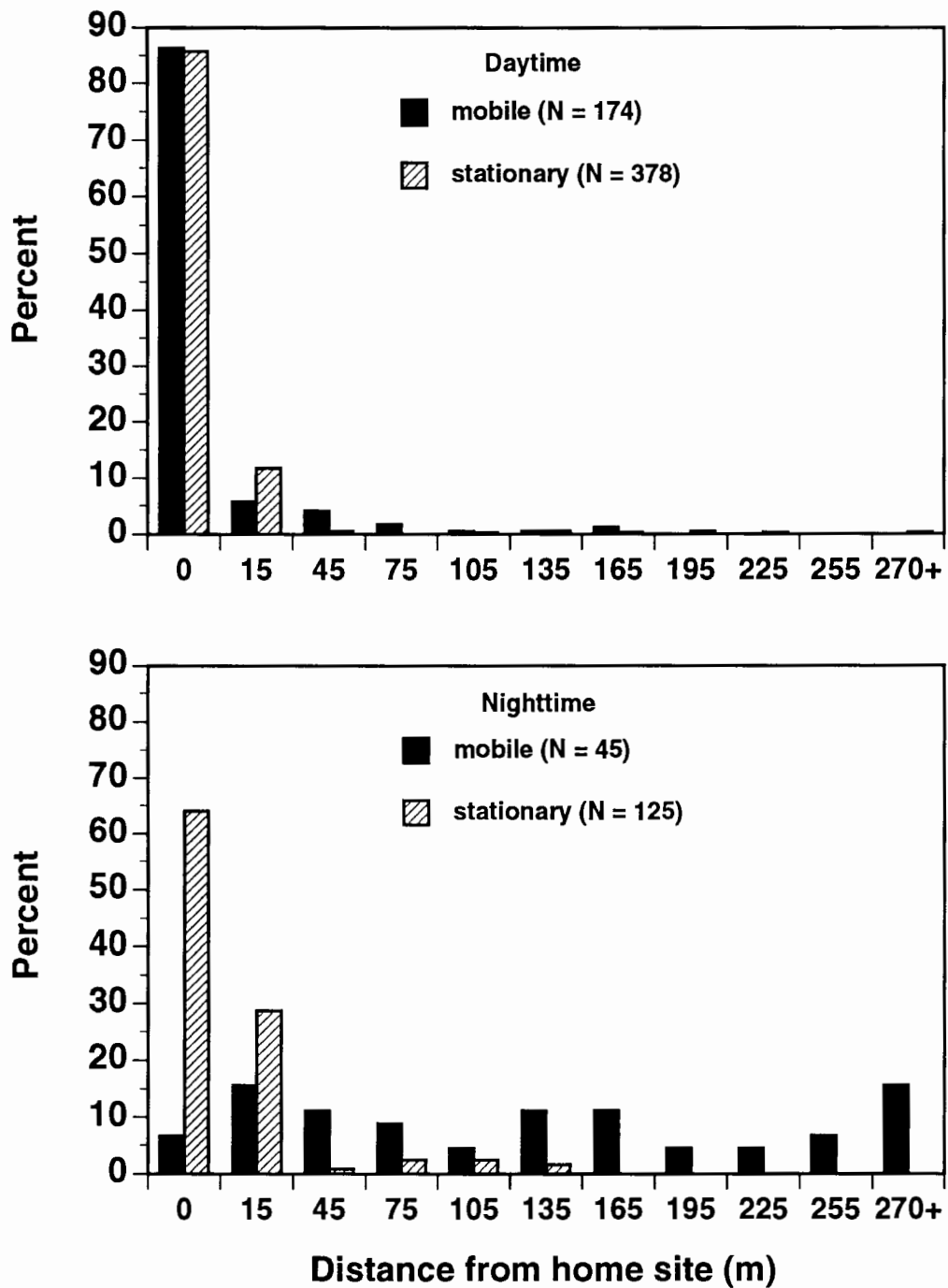


FIGURE 5. Daytime and nighttime foraging displacement distributions of four mobile and six stationary brown trout tracked between May 1990 and May 1992. Distances were divided into 30 m intervals, listed as the mean of each interval.

only 63% for one of these fish (number 1), and on several occasions this fish and two other large brown trout were observed chasing and attacking small prey fish against a retaining wall. Fish residing at the hatchery were also active throughout the day.

Foraging displacement distances of stationary and mobile brown trout were considerably different at nighttime (Table 5, Figure 5). Stationary fish were found within 30 m of a home site 93% (range = 86-100%) of the time and were never found more than 150 m from a home site at nighttime. Mobile fish were found within 30 m of a home site only 22% (range = 11-40%) of the time and frequently displaced themselves more than 100 m from home sites. Daytime and nighttime displacement distributions were not significantly different ($P = 0.42$) for stationary fish and were significantly different ($P < 0.01$) for mobile fish.

Stream velocity appeared to influence the foraging displacements of large brown trout. There were significant ($P < 0.05$) positive linear relationships between the reciprocal of stream velocity and median nighttime ($r^2=0.83$) or maximum ($r^2=0.88$) foraging displacement. That is, as water velocity increased, displacement distances generally decreased (Figure 6). The majority of mobile fish (2, 11, and 12) lived in low- to moderate-velocity (21-53 cm/s) areas in the upper and middle reaches and were regularly observed 50 to 1,000 m away from home sites at night. Fish numbers 8, 9, and 10 lived in high-velocity (70-77 cm/s) areas in the lower reach and were rarely found more than 15 m from a home site at night. Most of the remaining fish were considered stationary and lived in areas with moderate water velocities (45-56 cm/s). However, two of these fish (1, 4) sometimes exhibited behavior similar to mobile fish described above.

A total of 18 diel monitoring sessions were completed for fish 11, fourteen were completed for fish 4, and four were completed for fish 12 (Appendix Tables 1-3, Figures 1-3). With the exception of fish number 4 in August, the majority of movements occurred at nighttime. Peaks in mean hourly movement occurred near sunrise (0400 h) and sunset (1900 - 2100 h) and varied in magnitude from 9 to 68 m/h at dawn and from 22

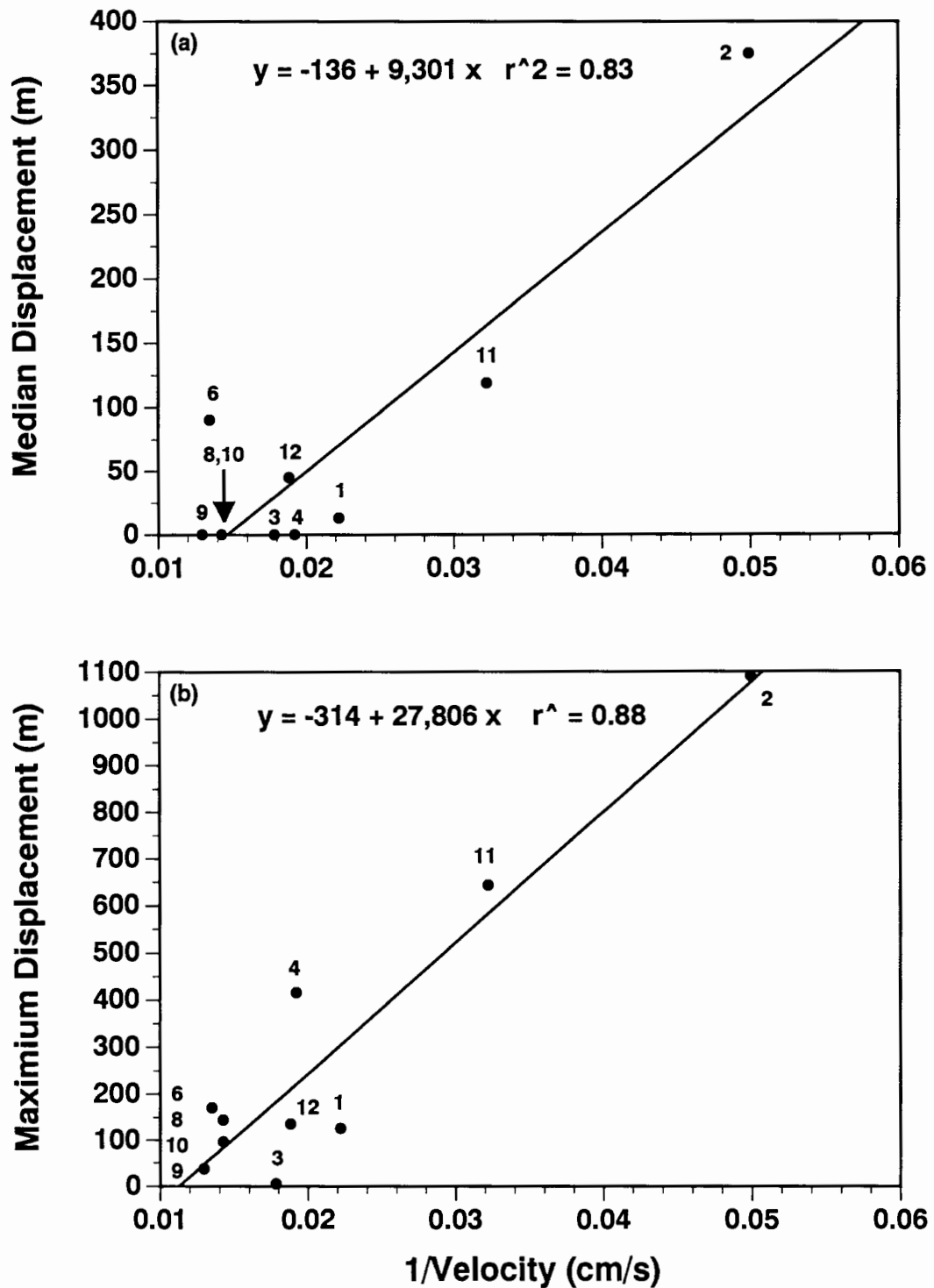


FIGURE 6. Relationship between nighttime median (a) and overall maximum (b) foraging displacement and average stream velocity (reciprocal) for ten brown trout tracked between May 1990 and May 1992. Individual points identified by fish number.

to 181 m/h at dusk (Figures 7a,c,d). Mean nighttime movement rates were significantly ($P < 0.05$) greater than daytime movement rates and varied among fish from 5.1 to 76.7 m/h at nighttime and from 0 to 7.8 m/h in daytime (Table 6). Mean total linear distance moved varied among fish from 143 to 967 m and mean diel range from 77 to 424 m; on average 90 to 100% of the total linear distance moved during a session occurred at nighttime.

Mean monthly TLD, diel range, and nighttime and daytime movement rates were not significantly ($P > 0.05$) different for fish number 11 (Table 6). There was a significant negative relationship between TLD moved and mean daily water temperature ($P = 0.04$; $r^2 = 0.22$) and a significant positive relationship between TLD and mean daily discharge ($P = 0.02$; $r^2 = 0.28$) for fish number 11. Although no significant relationships were found, the diel movements of other fish appeared to be related to water temperature. Fish number 12 moved from 91 to 121 m (TLD) during a session when mean daily water temperatures were $> 19^\circ\text{C}$ (3 sessions), compared to 269 m when temperatures were $< 16^\circ\text{C}$ (1 session). Fish number 4 moved more in August (mean TLD = 232 m) when mean daily water temperatures were 1°C cooler than in June and July combined (mean TLD = 63 m).

There was no significant ($P < 0.05$) difference in mean monthly TLD, diel range, and nighttime movement rates for fish number 4. However, mean daytime movement rates, TLD, and diel range of movement were significantly ($P < 0.05$) greater in August than in June and July combined (Table 6). In June and July, this fish generally made short-range (< 30 m) movements at dawn and dusk between daytime resting sites and nighttime stationary positions in midstream. In August, total linear distance moved and diel range of movement increased due to more extensive and continuous movements especially during daytime (Table 6; Figure 7b). There was no significant ($P = 0.87$) difference between August nighttime (8.5 m/h) and daytime (10.5 m/h) movement rates (Table 6). Two peaks in mean hourly movement occurred during daytime hours in August at 0800 (27 m/h) and 1100 hours (12 m/h), as well as a third peak near dusk at 1900 hours (34 m/h; Figure 7b).

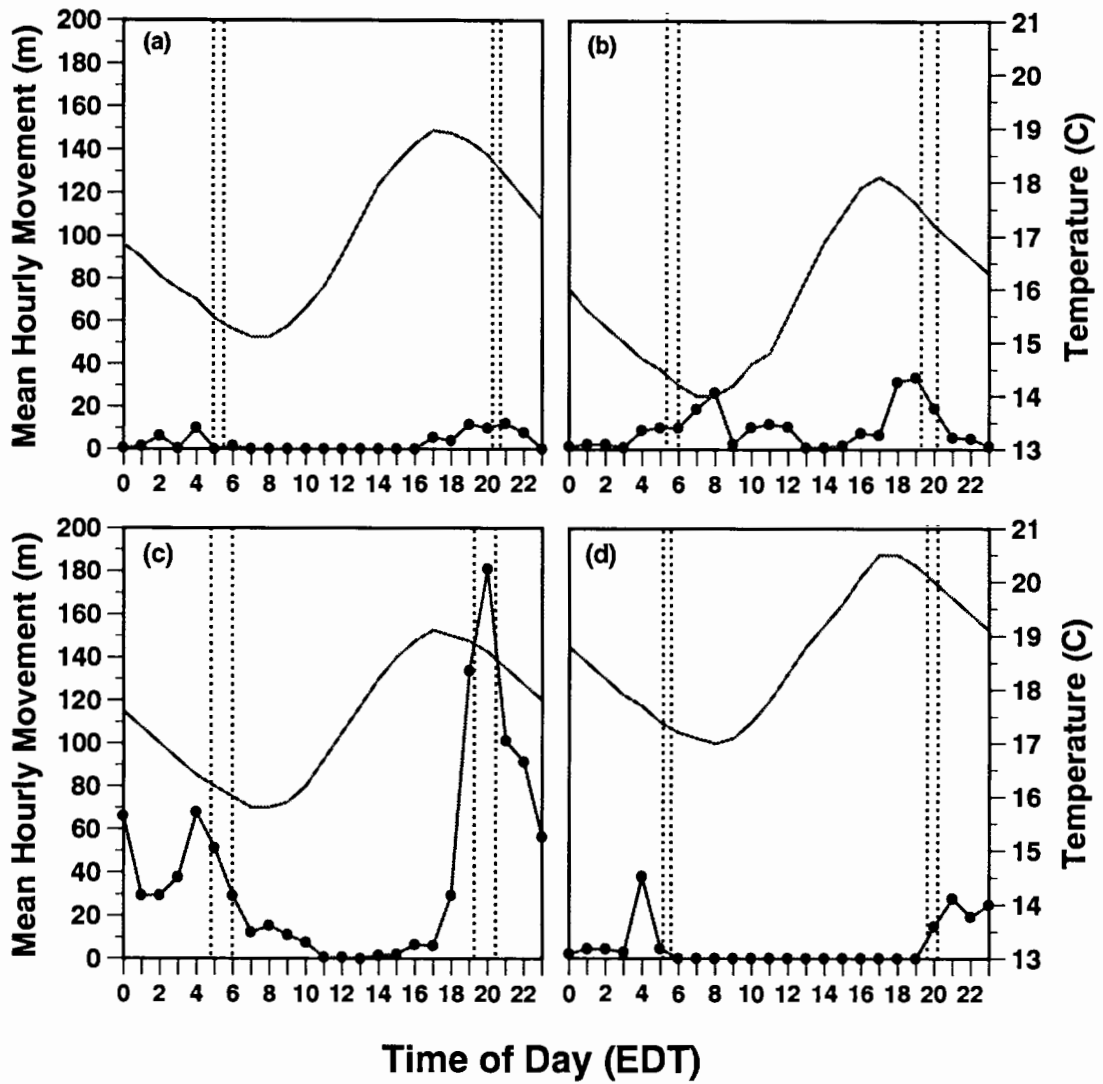


FIGURE 7. Mean hourly movement (line with closed circles) and mean water temperature versus time of day for fish numbers 4 (a = June and July, b = August), 11 (c), and 12 (d). Vertical dashed lines indicate time interval in which sunrise and sunset occurred.

TABLE 6. Summary of diel movements of fish numbers 4, 11, and 12 between 9 June 1991 and 1 September 1991. Asterisks denote significant ($P < 0.05$) difference between mean daytime and nighttime movement rates. Distances are in meters. (SD = Standard deviation)

	Total linear distance moved	Diel range	Linear distance moved (day)	Linear distance moved (night)	Distance moved per hour (day)	Distance moved per hour (night)
Fish 4						
June & July (N=7)						
Range	0-249	0-125	0-65	0-184	0-4.8	0-17.5
Mean	63	31	9	54	0.7	* 5.1
SD	86	43	24	62	1.8	5.9
August (N=7)						
Range	18-581	9-283	0-401	15-290	0-31.7	1.3-25.1
Mean	232	124	131	101	10.5	8.5
SD	224	115	155	99	12.2	8.6
Overall (N=14)						
Range	0-581	0-283	0-401	0-290	0-31.7	0-25.1
Mean	147	78	70	77	5.6	6.8
SD	185	96	124	83	9.8	7.3
Fish 11						
Overall (N=18)						
Range	344-1,760	132-678	0-428	339-1,502	0-35.9	26.4-136.6
Mean	967	424	98	868	7.8	* 76.7
SD	414	165	139	367	11.2	32.8
Fish 12						
Overall (N=4)						
Range	91-269	37-135	--	91-269	--	7.7-24.3
Mean	143	77	0	143	0	* 12.9
SD	85	45	0	85	0	7.8

Discussion

Large brown trout in this study showed considerable variation in both seasonal and foraging movements. Some fish moved long distances while foraging, or when traveling between home sites or summer and winter habitats. Other authors have noted similar long range seasonal movements (Clapp et al. 1990; Meyers et al. 1992) and foraging behavior (Clapp et al. 1990). However, the movements of other brown trout in this study were very different from those described above. These fish occupied relatively small reaches of stream in summer and winter and rarely moved far from home sites while foraging. Differences in range of movement among fish in this study appeared to be related to seasonal habitat use, distance between home sites, and foraging behavior.

Seasonal Range of Movement

Range of movement and active displacement were greater in winter compared to summer most likely as the result of movements to spawning or overwintering areas. Clapp (1988) believed increased movements of large brown trout in fall and winter were associated with spawning or movements to better overwintering habitat. Spawning movements of stream-dwelling brown trout have been described by several authors (Shuck 1945; Solomon and Templeton 1976; Arnold 1987; Meyers et al. 1992). Solomon and Templeton (1976) and Meyers et al. (1992) noted upstream spawning movements of 2,000 m or more. In this study, the average distance moved during the spawning season was 786 m and the majority of fish moved upstream. Distances moved during the spawning season may be related to the proximity of summer habitat to natal areas or areas with suitable spawning conditions. Most fish tracked for more than one winter moved to the same areas in successive years; such repeat homing of brown trout to natal streams has been described for lake-dwelling (Tilzey 1977) and stream-dwelling (Stuart 1957) brown trout.

Use of separate summer and winter habitat by brown trout in this study has also been described by other authors. Large brown trout in the South Branch moved almost 10,000 m between summer and winter habitat (Clapp et al. 1990). Radio-tagged brown trout in a Wisconsin River system moved between spawning and overwintering areas that were 20,000 m apart (Meyers et al. 1992); fish overwintered in a large warmwater river, spent the summer in the mid-reaches of a coldwater tributary, and spawned in the upper reaches of that tributary. Brown trout in the above studies, as well as three fish in the present study, used winter habitat considered marginal for trout in summer due to high water temperatures. Clapp (1988) suggested marginal areas provided critical overwintering habitat with respect to water temperature, ice conditions, and food availability. Meyers et al. (1992) believed the use of large, more productive stream segments in winter and spring were important for production of "trophy" brown trout.

Marginal habitat used by brown trout in this study and in the South Branch (Clapp et al. 1990) appeared to be slower and deeper than summer habitat, and was consistent with findings of Cunjak and Power (1986) that brown trout prefer low velocity areas in winter. In winter, trout may seek habitat that prevents predation (Hartman 1963; Cunjak and Power 1987a; Meyers et al. 1992) and downstream displacement by floods or ice (Hartman 1963; Cunjak and Power 1987a). Brown trout in the study site were not exposed to floods or ice, and predation risk was probably low for fish of this size. Use of low velocity areas may help to conserve energy used in holding station.

While the majority of large brown trout in other studies (Clapp et al. 1990; Meyers 1992) used separate summer and winter habitat, fifty percent of brown trout in this study overwintered within their summer ranges. These areas were relatively shallow, had moderate to high water velocities (30-70 m/s), and had high groundwater input. Individual fish were sometimes located and observed during winter in midstream areas with no cover, even when water temperatures were at or near 0°C. Cunjak and Power (1987a) and Meyers et al. (1992) also reported that brown trout used midstream areas in

winter, but fish were associated with cover. Large brown trout located in midstream in this study may have been feeding. Brown trout continue to feed in winter even when temperatures are near freezing (Needham and Jones 1959; Alexander 1977; Cunjak and Power 1987b).

Range of movement varied among individual brown trout in this study during both summer and winter. The extent of seasonal movements of brown trout may depend upon temperature regime, forage availability, location of winter habitat, and presence of barriers (Meyers et al. 1992). Four fish in this study made long range (> 6,000 m) movements between home sites or between summer and winter habitat. Long range movements indicate the importance of river basin approaches to fisheries management, as well as the need to maintain barrier free river systems (Clapp et al. 1990; Meyers et al. 1992). Many fish, however, occupied a relatively small reach of stream for up to 640 days. The average total range of eight fish tracked in the no-kill section was less than 2,000 m, and several of these fish were tracked for almost two years. Such restricted movement over an extended period indicates this no-kill area is of sufficient size to protect large brown trout. Eight of nine fish (88%) tagged in the no-kill section remained there throughout the entire tracking period, while one fish moved into the upper reach after the fishing season had closed. Seventy-five percent of large brown trout in the South Branch left an area protected with no-kill regulations. However, the South Branch no-kill area was smaller (7.2 km) than the Mainstream area (14.5 km) and most fish left after the fishing season had closed.

Daily Movements and Home Site Use

Range of movement in summer reflected movements between home sites from day to day or nighttime movements that were believed to be related to foraging. Daytime home site use and nighttime foraging movements were similar to those reported by Clapp et al. (1990); that is, brown trout used specific cover structures as bases for nighttime foraging, were relatively inactive during daytime, moved away from cover near sunset, and

returned to the same or nearby home site by sunrise. Two fish frequently covered more than 1,000 m of stream in a single night, and one of these fish moved almost 600 m in a single hour. Extensive nighttime movements were also reported for large brown trout in the South Branch (Clapp et al. 1990).

Three fish monitored over diel periods were active primarily at night, with distinct peaks in hourly movement rates near dawn and dusk. Crepuscular activity in brown trout has been noted by several authors (Chaston 1968; Priede and Young 1977; Swift 1962; Oswald 1978; Bachman et al. 1979). Activity patterns in brown trout may be controlled by absolute light intensity or changes in light intensity (Oswald 1978; Bachman et al. 1979; Regal 1992). Clapp et al. (1990) and Regal (1992) found activity levels were correlated with light levels, but were possibly related to food availability also. Dawn and dusk peaks in hourly movement rates in this study may be related to greater availability or vulnerability of prey at these times. Invertebrate drift densities are known to peak near sunrise and sunset (Elliot 1970; Waters 1962). Large brown trout may be timing their foraging movements in response to greater availability of drift-feeding fish at these times. Diel movements in this study were not well correlated with environmental factors. Fish were generally inactive when water temperatures reached daily lows and highs. Two fish moved greater distances when water temperatures were cooler, and daytime movements of one fish increased with increasing discharge. Clapp et al. (1990) noted increased daytime activity of large brown trout in August may have been related to cooler water temperatures, higher water levels, and possibly reduced food abundance. One fish in the lower reach of the study site moved more during daytime in August than in other months possible due to cooler water temperatures at the time. Long-range movements of two other fish appeared to be in response to high water temperatures. One fish moved over 8,000 m upstream to the Grayling Fish Hatchery in one night when water temperatures at its home site exceeded 20°C for the first time. Water temperatures at the hatchery, where the fish was also fed trout pellets, were 4°C cooler. Another fish moved almost 7,000 m

downstream when water temperatures reached 25°C; temperatures at the downstream home site, where a spring-fed tributary entered the Mainstream, were 10°C cooler. Clapp et al. (1990) and Meyers et al. (1992) also reported long range movements of brown trout that may have been in response to changes in water temperature.

Home sites were qualitatively similar to habitat used by brown trout in the South Branch (Clapp et al. 1990) in that they were used as daytime resting sites, and provided overhead cover and possibly reduced water velocities. Home sites also provided low-light conditions which are favored by brown trout (Devore and White 1978; Fausch and White 1981; Gosse and Helm 1982). The majority of fish in this study used artificial cover which appeared to be more abundant than natural cover in the study site and in some areas was the only cover available. The importance of artificial cover to trout in the Au Sable River is evident from other studies. Nuhfer (1979) found that in the Mainstream more than 50% of brown trout ≥ 150 mm were beneath artificial cover in daytime and that percentage beneath cover increased with trout size. In the East Branch, artificial cover represented 83% of the cover available to trout (Fausch and White 1981) and in the North Branch, artificial cover used by trout represented only 2% of the total stream surface area (Cozad 1992).

The nighttime foraging movements of brown trout in this study suggested individual fish were using one of two search modes. Previous work has classified the search mode or foraging strategy of a predator as sit and wait (Pianka 1966) or active-search (Eckhardt 1979) based on the frequency of moves per unit time (Huey and Pianka 1981) or the probability of moving over a given time period (Peitruszka 1986). I classified the foraging strategy used by individual fish based on the extent of nighttime movements away from daytime resting sites. Stationary fish appeared to use a sit-and-wait strategy, maintaining midstream positions within 30 m of a home site in moderate to high velocity areas (45 - 77 cm/s). The behavior and range of movement of these fish was consistent with that of smaller brown trout in other studies (Jenkins 1969; Bachman 1984; Regal

1992), and it generally agrees with studies in the Mainstream by Shetter (1968) and Favro et al. (1986) in which large brown trout were captured and recaptured in the same general area. Mobile fish appeared to use an active-search strategy characterized by frequent or continuous movements, and they regularly displaced themselves more than 30 m from home sites at night. The majority of these fish lived in areas with low to moderate velocities (20 - 53 cm/s) and were often observed moving 150 to 2,000 m in one night.

The dichotomy between sit-and-wait or active search has been used to predict the optimal diet composition and home range size of a predator (Schoener 1971). If trout forage optimally, they should behave in such a way as to maximize energy intake per energy expended. The foraging strategy used by individual brown trout in this study may reflect the optimal strategy according to type of prey consumed, prey abundance, or the energetic costs associated with a sit-and-wait versus active-search strategy in flowing water.

The foraging strategy used by individual fish may be influenced by prey density. Using model simulations, Norberg (1977) predicted an animal would shift its foraging strategy in response to changes in food availability. Brown trout using a sit-and-wait strategy may live in areas with high prey densities. Three large brown trout, including a radio-tagged fish, were observed initiating attacks on small fish from stationary positions. Brown trout that moved continuously at night may live in areas with lower prey densities and must therefore search larger reaches of stream for food. Jenkins (1969) suggested fish would shift from holding stationary positions in the current to roaming or wandering as a result of decreased food availability. Two fish appeared to use both strategies. An individual may change strategies in response to seasonal changes in prey type or availability.

The foraging strategy used by a predator generally reflects the mobility of prey (Huey and Pianka 1981). The active-search strategy used by some brown trout in this study is consistent with a piscivorous diet whereby relatively sedentary prey (small fish)

are more likely to be discovered by actively searching predators (Ekhardt 1979). Authors have associated the unique behavior and long-range movements of large brown trout with a piscivorous diet (Shetter 1968; Jenkins 1969; Clapp et al. 1990). Sit-and-wait behavior exhibited by several brown trout in this study is similar to the behavior of small brown trout that use a stationary, drift-feeding strategy to feed on invertebrates (mobile prey) in the drift (Allen 1951; Jenkins 1969; Bachman 1984; Regal 1992). Large brown trout using a sit-and-wait strategy may be relying on food in the drift or other mobile prey for all or part of their daily ration. Although fish comprise the bulk of their diet, large brown trout are known to consume insects (Alexander 1977). However, large brown trout may not be able to meet metabolic needs on a diet of insects alone. According to Bachman (1982), the maximum size a fish can attain as a drift-feeder is constrained by the biomass or density of organisms in the drift (energy available) and the costs of swimming in flowing water (energy expended). As size increases the optimal velocity for drift feeding decreases until growth can no longer be sustained, forcing a shift to piscivory. Large brown trout may overcome these constraints using hydraulically efficient foraging sites (Bachman 1982), by living in areas with cooler water temperatures (lower metabolic rates), or by living in highly productive areas (high drift biomass). Most brown trout that used a sit-and-wait strategy lived in the coolest portions of the study site and this area may have been more productive as well.

The energetic costs of searching for prey in flowing water may influence the strategy used by large brown trout. The moment an animal begins to move about in search of food to meet metabolic needs, it suffers an energy drain that must be replaced (Norberg 1977). The energetic costs of actively searching for food in flowing water relative to the potential gains may determine the optimal strategy used by an individual. Median and maximum foraging displacements of large brown trout in this study decreased with increasing water velocity. Brown trout in high velocity areas generally used a sit-and-wait strategy while fish in low velocity areas generally used an active-search strategy.

Velocity dependent activity modes have been described for small rainbow trout and cutthroat trout Oncorhynchus clarki (Johnson et al. 1987) as well as brown trout (Gosse and Helm 1982). Individuals in low velocity water (pools) engaged in random swimming without orienting to the current while fish in high velocity water (riffles and glides) maintained stationary positions by actively swimming against the current. Jenkins (1969) observed wandering behavior to be more common than sitting-and-waiting in the still water areas of his study stream. Clapp (1988) suggested the energetic demands of swimming in fast water may prevent fish from making long range foraging movements.

Previous studies have characterized large brown trout as roving predators that must use large reaches of stream in order to satisfy a piscivorous diet (Shetter 1968; Jenkins 1969; Clapp et al. 1990). This behavior was considered distinct from smaller, stationary, drift-feeding individuals which use limited areas. While roving behavior was evident among some fish in this study, several large fish exhibited limited range of movement and foraging behavior similar to smaller, drift-feeding brown trout. Such behavior agrees with other studies of brown trout movements in the Mainstream (Shetter 1968; Favro et al. 1986). Sit-and-wait behavior may be related to prey type or availability, energetic constraints of foraging in flowing water, or some combination of one or more of these factors. Knowledge of the diet of these individuals would undoubtedly help explain such behavior.

Assumptions

An important assumption in telemetry studies is that transmitters do not influence behavior of radio-tagged fish (Clapp et al. 1990). Brown trout in this study did not appear to be adversely affected by transmitters. Individuals were observed on spawning redds, chasing and capturing prey, and fleeing from predators such as osprey (Pandion haliaetus). However, transmitter expulsion was documented for one fish and several other transmitters recovered in the stream may have been expelled by fish. Studies have shown

expulsion of dummy transmitters occurs rapidly and without infection in rainbow trout (Lucas 1989) and Atlantic salmon (Salmo salar; Moore et al. 1990) and does not affect growth, swimming performance, or maturation (Moore et. al. 1990). The fish that expelled its transmitter in this study appeared healthy and had grown in length and weight since initial implant. In other studies, surgically implanted transmitters did not appear to influence behavior of brown trout (Clapp et al. 1990; Regal 1992) or largemouth bass (Micropterus salmoides, Crumpton 1982; Messing and Wicker 1986)

Management Implications

One objective of no-kill regulations is to increase numbers of trophy-size fish. When considering an area for no-kill regulations or assessing the effectiveness of such regulations, managers should consider the stream's capacity to support large brown trout. Brown trout in the lower reach of the study site spent most of their time in small (≤ 30 m) reaches of stream. This area may support greater densities of large fish than the upper and middle reaches where fish had larger ranges. Areas designated as no-kill should also contain suitable summer, winter, and spawning habitat in order to prevent harvest of individuals that leave protected areas when using these habitats. Managers should also consider the importance of artificial cover to large brown trout in the Mainstream. These structures may be preferred by large brown trout or natural cover may be limited in some parts of the study site. Shoreline development is prevalent within the study site, especially in the middle and lower reaches where removal of shoreline vegetation in the past may have reduced the potential for natural instream cover in some areas. Protecting riparian areas and maintaining the integrity of artificial structures should be considered to ensure adequate daytime resting sites for large brown trout.

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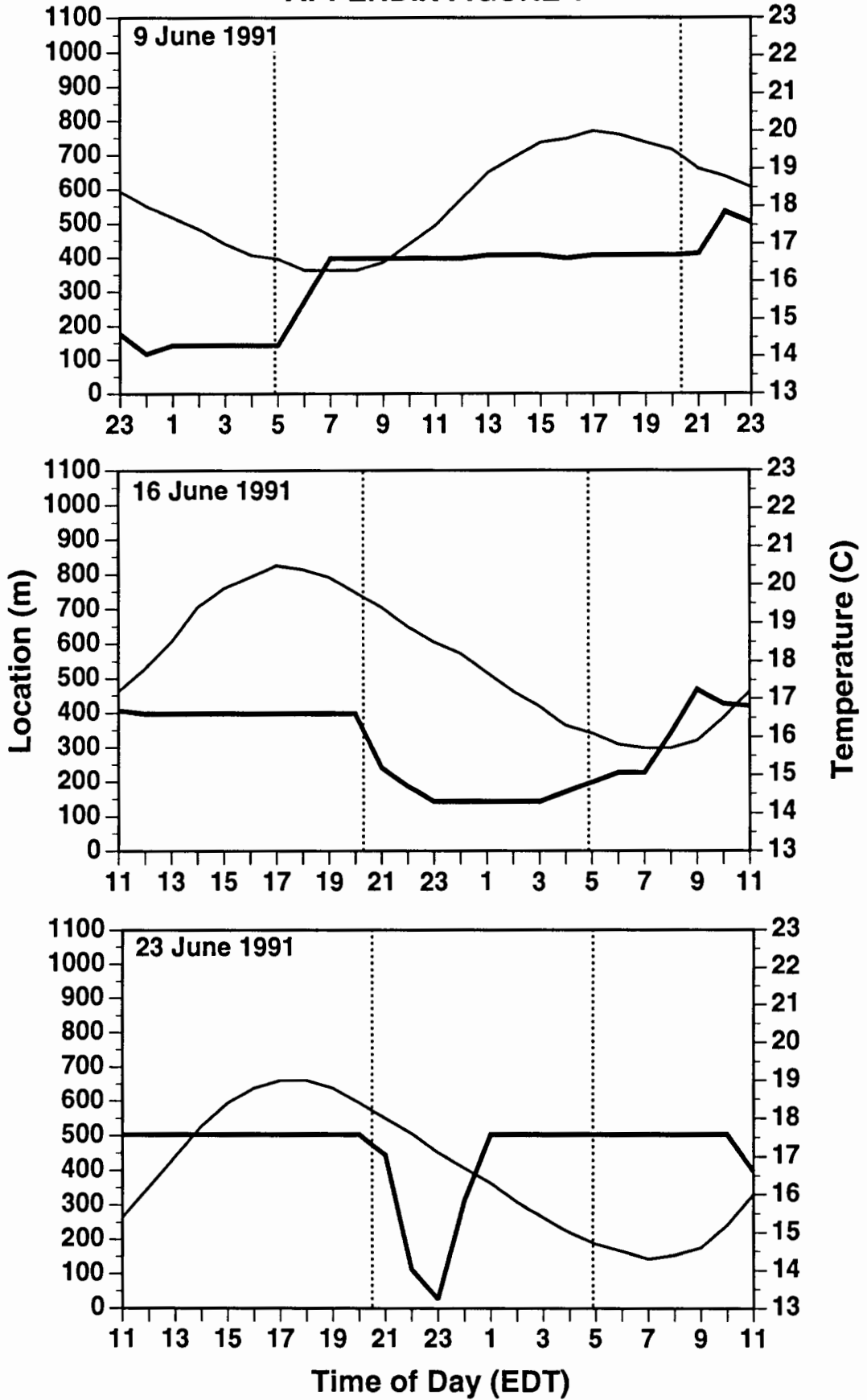
APPENDIX: Summary of diel movements of fish numbers 11, 4, and 12 between 9 June 1991 and 1 September 1991.

APPENDIX TABLE 1. Summary of diel movements of fish number 11 during eighteen monitoring sessions in June (4), July (6), and August (8). Distances are in meters. (SD = standard deviation).

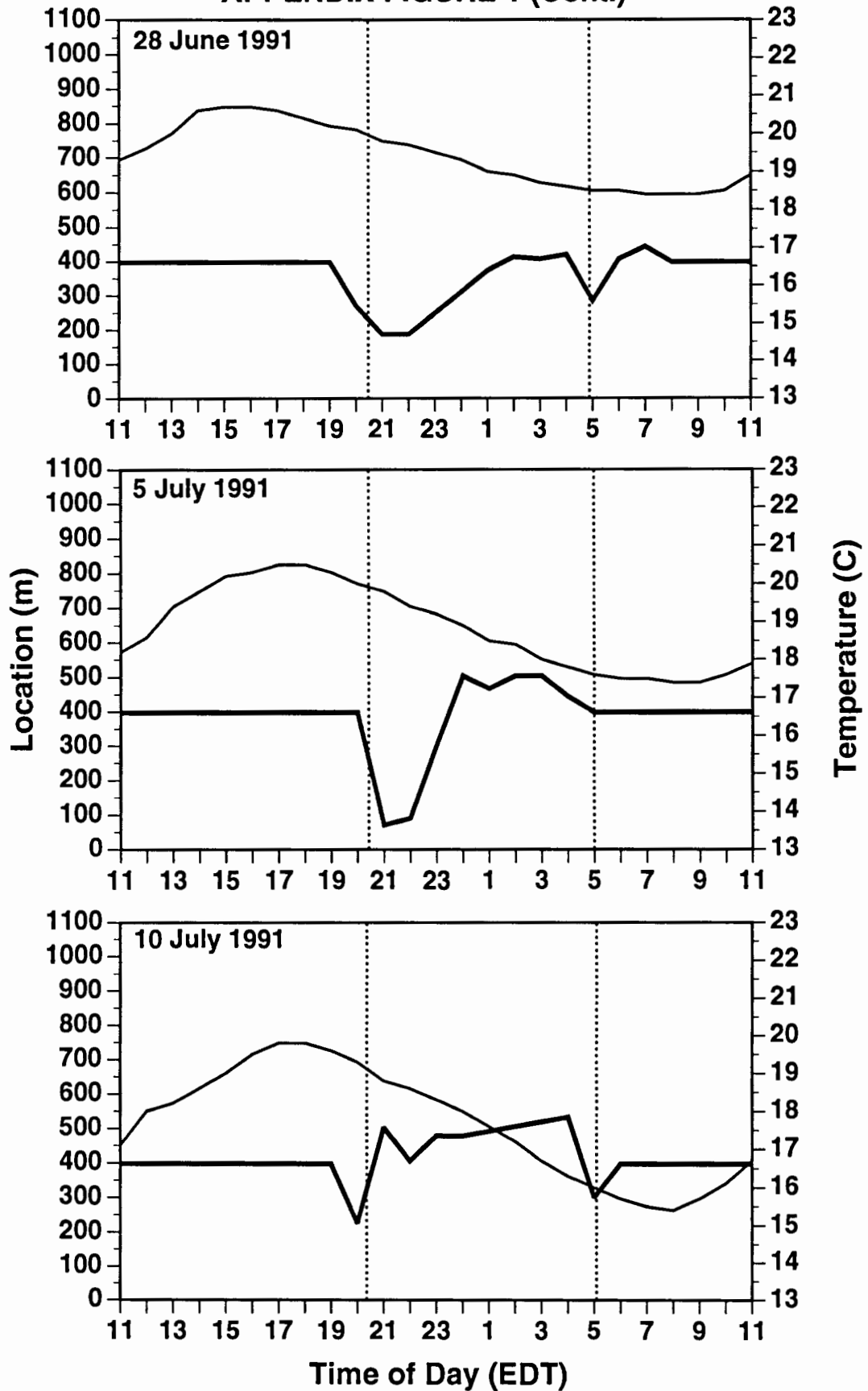
Date	Total linear distance moved	Diel range	Linear distance moved (day)	Linear distance moved (night)	Distance moved per hour (day)	Distance moved per hour (night)
6/9/91	525	416	27	498	2.0	45.2
6/16/91	636	324	296	339	21.9	30.9
6/23/91	1059	477	105	954	7.8	86.7
6/28/91	793	257	82	711	6.1	64.6
7/5/91	937	432	0	937	0.0	85.2
7/10/91	1001	307	0	1001	0.0	91.0
7/13/91	1502	646	0	1502	0.0	136.6
7/18/91	495	248	0	495	0.0	45.0
7/22/91	1473	609	338	1135	26.0	103.2
7/30/91	1319	643	62	1257	4.9	114.3
8/5/91	538	248	22	517	1.7	47.0
8/10/91	766	368	0	766	0.0	63.9
8/18/91	1369	577	428	941	35.9	78.4
8/19/91	1760	678	280	1480	23.5	114.4
8/23/91	1373	587	0	1373	0.0	109.1
8/26/91	344	132	0	344	0.0	26.4
8/29/91	652	326	0	652	0.0	50.2
9/1/91	854	354	127	727	11.3	55.9
Overall						
Mean	967	424	98	868	7.8	76.7
SD	414	165	139	367	11.2	32.8
June						
Mean	753	369	128	625	9.5	59.6
SD	232	98	117	267	8.7	25.6
July						
Mean	1121	481	67	1055	5.1	97.1
SD	387	177	135	340	10.4	31.0
August						
Mean	957	409	107	850	9.1	69.9
SD	490	188	163	398	13.7	32.7

APPENDIX FIGURE 1. Diel movements (thick line) of fish number 11 and water temperature (thin line) during eighteen 24-hour monitoring sessions between 9 June 1991 and 1 September 1991. The thick line represents the fish's location within its foraging range. Vertical dashed lines indicate sunrise and sunset.

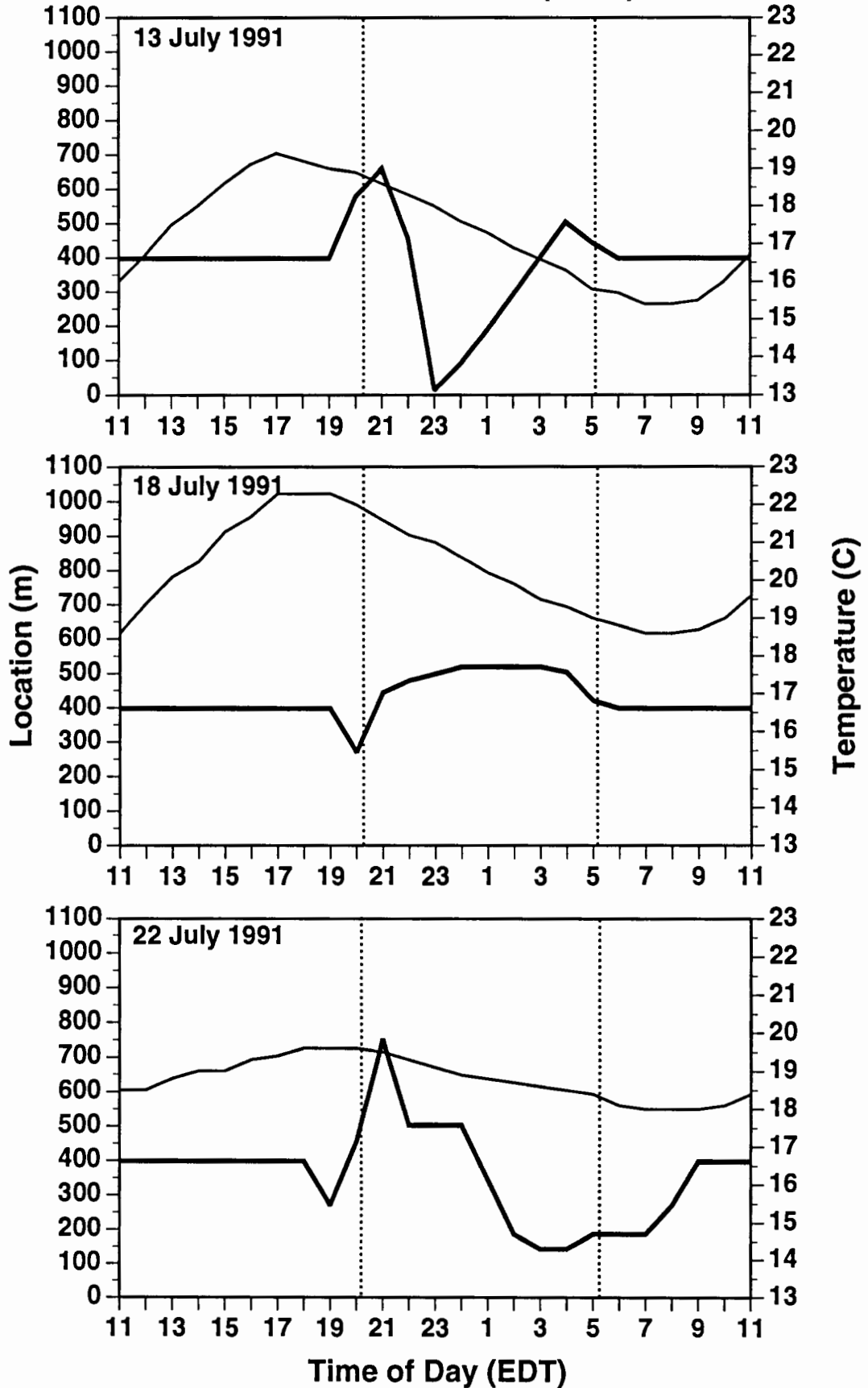
APPENDIX FIGURE 1



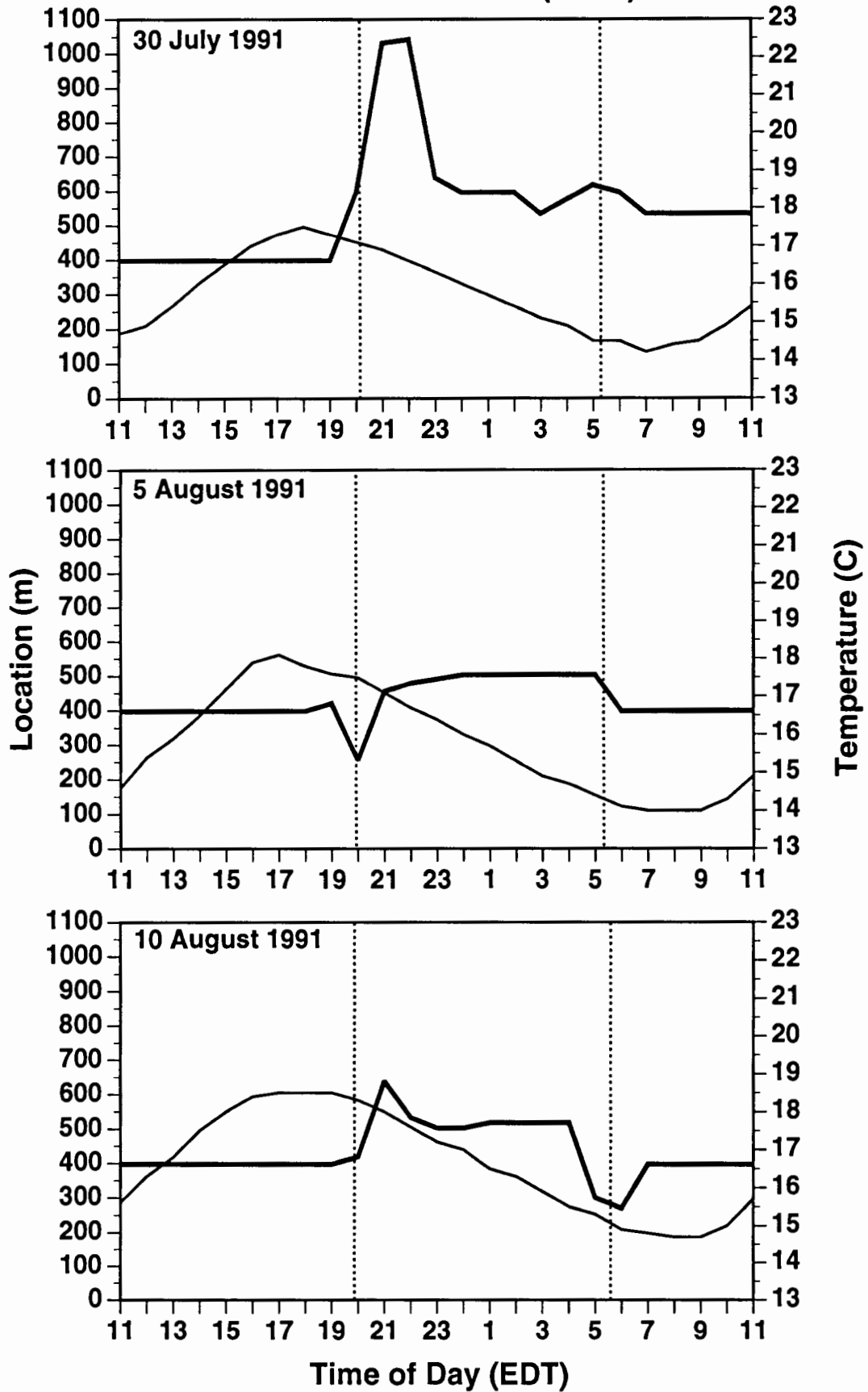
APPENDIX FIGURE 1 (Cont.)



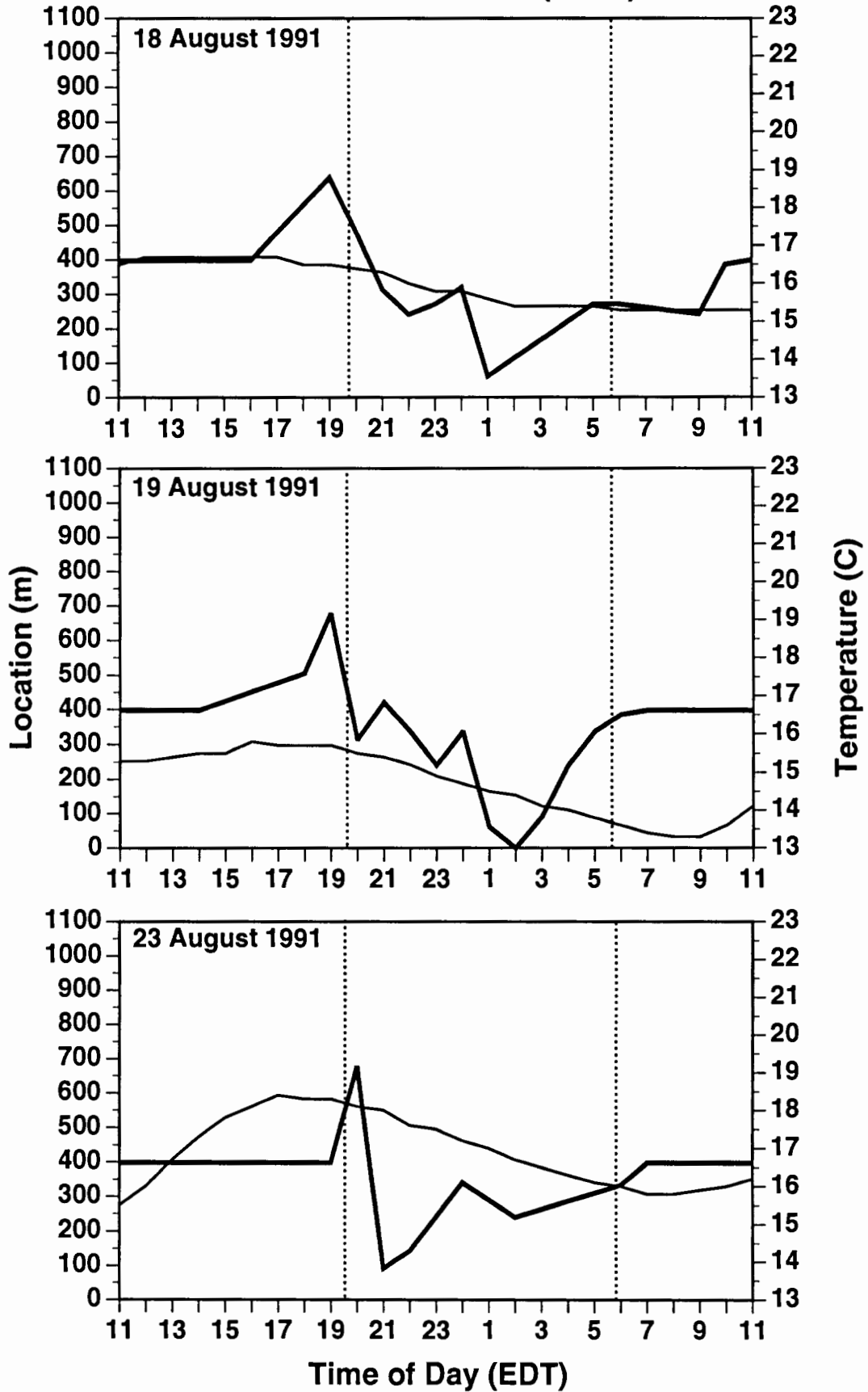
APPENDIX FIGURE 1 (Cont.)



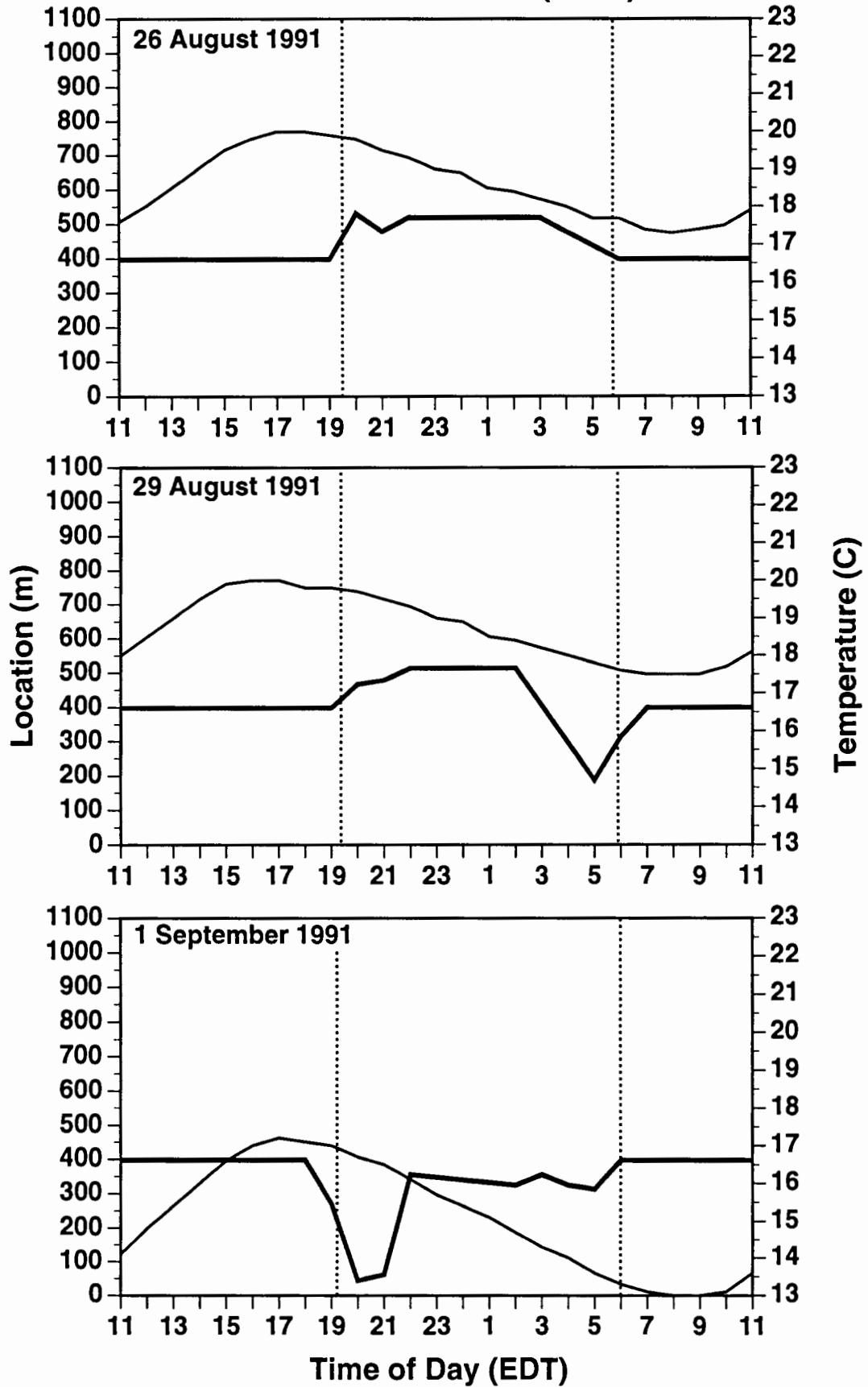
APPENDIX FIGURE 1 (Cont.)



APPENDIX FIGURE 1 (Cont.)



APPENDIX FIGURE 1 (Cont.)

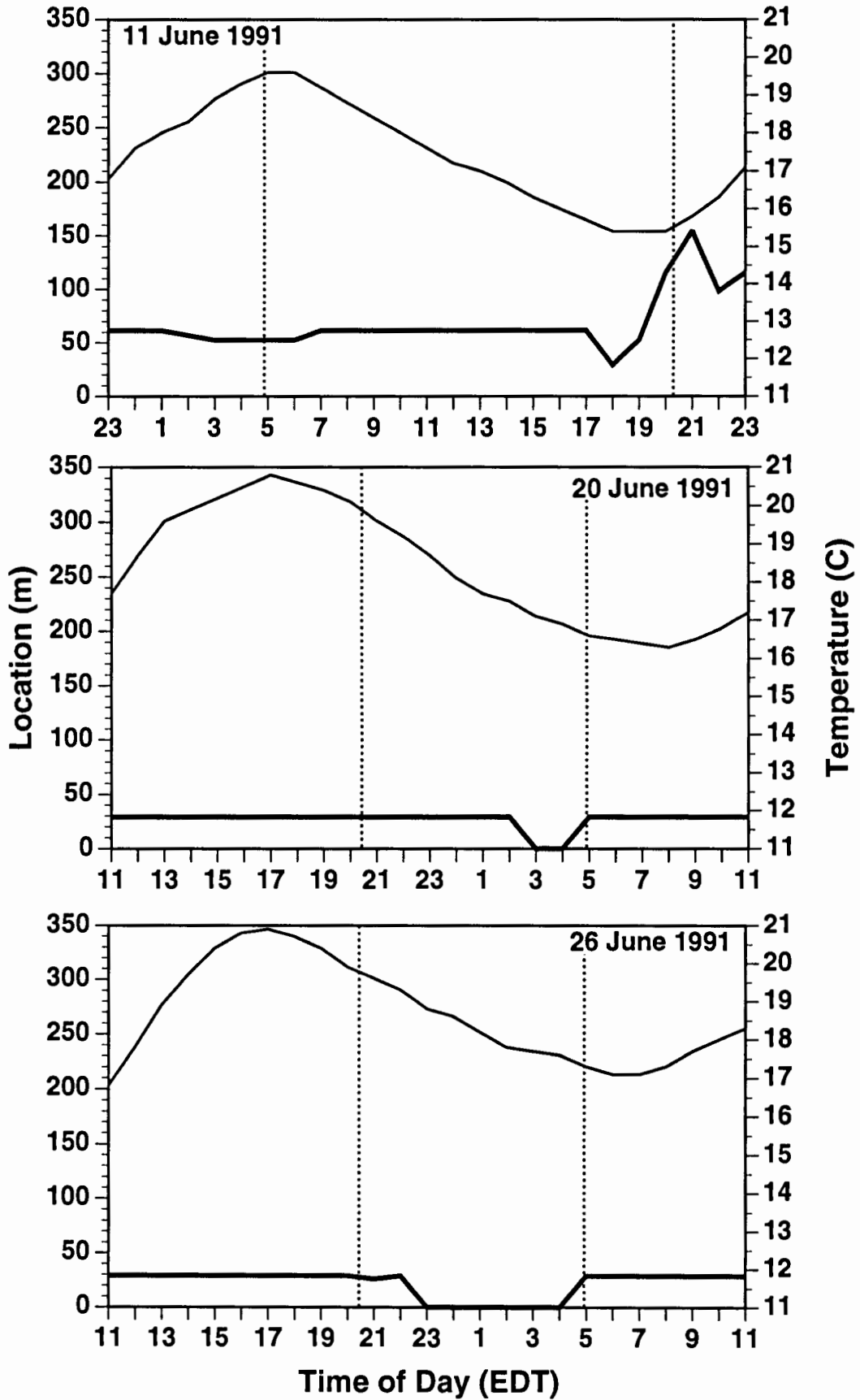


APPENDIX TABLE 2. Summary of diel movements of fish number 4 during fourteen monitoring sessions in June (3), July (4), and August (7). Distances are in meters. (SD = standard deviation)

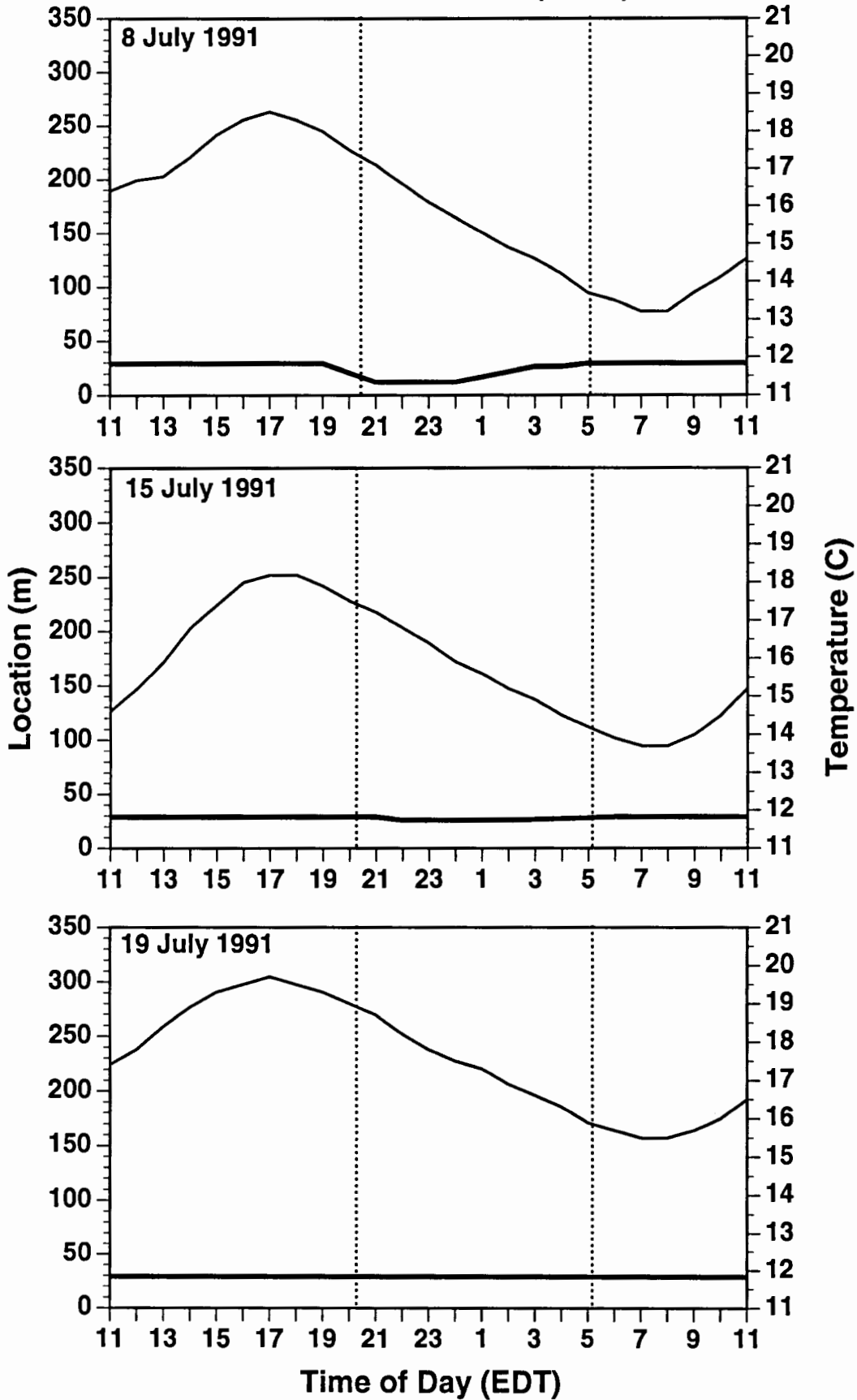
Date	Total linear distance moved	Diel range	Linear distance moved (day)	Linear distance moved (night)	Distance moved per hour (day)	Distance moved per hour (night)
6/11/91	249	125	65	184	4.8	17.5
6/20/91	58	29	0	58	0.0	5.5
6/26/91	64	29	0	64	0.0	6.1
7/8/91	34	17	0	34	0.0	3.2
7/15/91	6	3	0	6	0.0	0.5
7/19/91	0	0	0	0	0.0	0.0
7/29/91	30	15	0	30	0.0	2.7
8/1/91	504	283	401	103	31.7	9.1
8/6/91	581	275	291	290	23.4	25.1
8/8/91	30	15	15	15	1.2	1.3
8/13/91	125	125	106	20	8.7	1.6
8/21/91	219	111	69	150	5.9	12.3
8/25/91	18	9	0	18	0.0	1.5
8/31/91	146	50	32	114	2.9	9.0
Overall						
Mean	147	78	70	77	5.6	6.8
SD	185	96	124	83	9.8	7.3
June						
Mean	124	61	22	102	1.6	9.7
SD	109	56	37	71	2.8	6.8
July						
Mean	17	9	0	17	0.0	1.6
SD	17	9	0	17	0.0	1.6
August						
Mean	232	124	131	101	10.5	8.5
SD	224	115	155	99	12.2	8.6

APPENDIX FIGURE 2. Diel movements (thick line) of fish number ~~1~~⁴ and water temperature (thin line) during fourteen 24-hour monitoring sessions between ~~8~~¹⁴ June 1991 and 31 August 1991. The thick line represents the fish's location within its foraging range. Vertical dashed lines indicate sunrise and sunset.

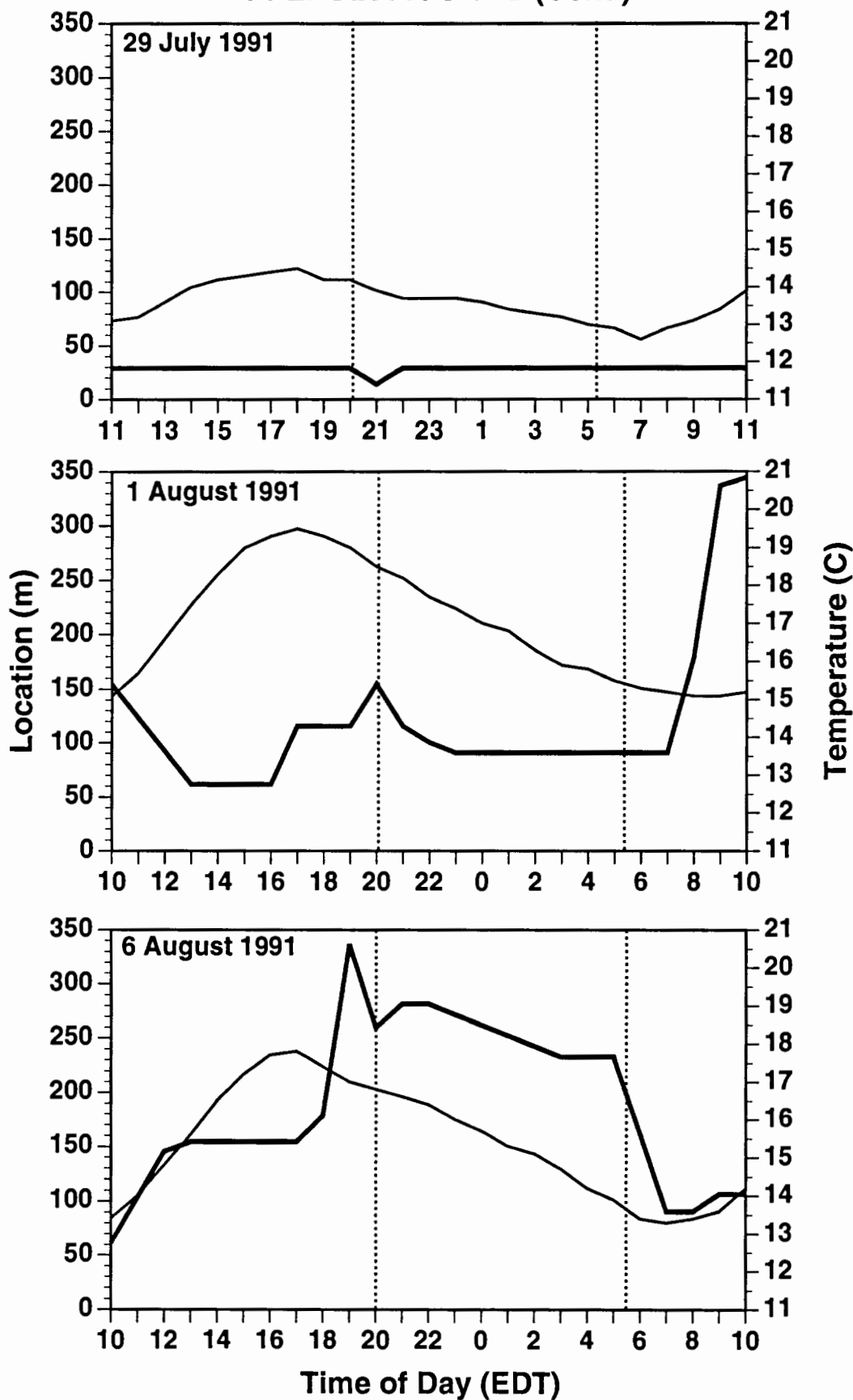
APPENDIX FIGURE 2



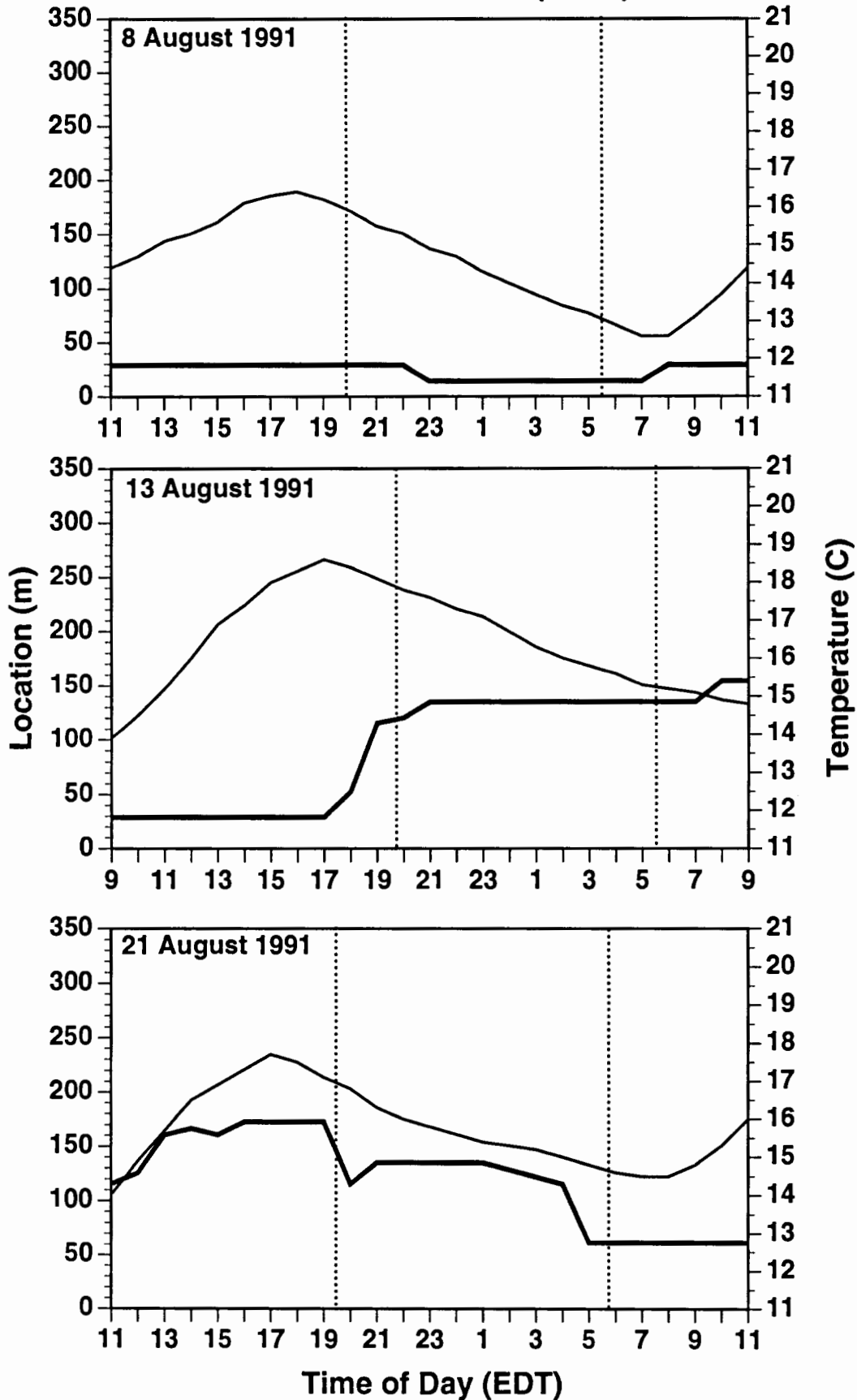
APPENDIX FIGURE 2 (Cont.)



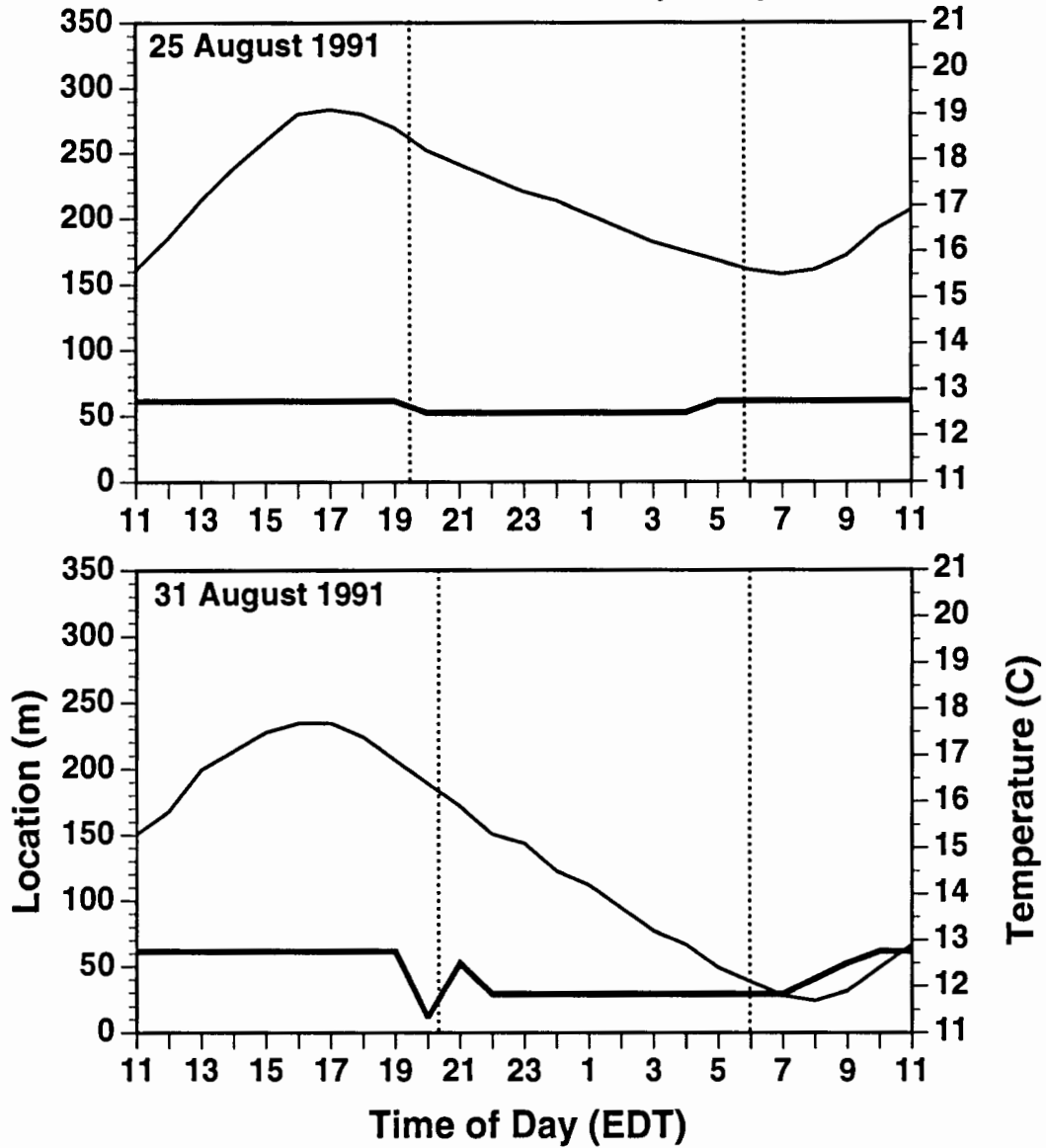
APPENDIX FIGURE 2 (Cont.)



APPENDIX FIGURE 2 (Cont.)



APPENDIX FIGURE 2 (Cont.)

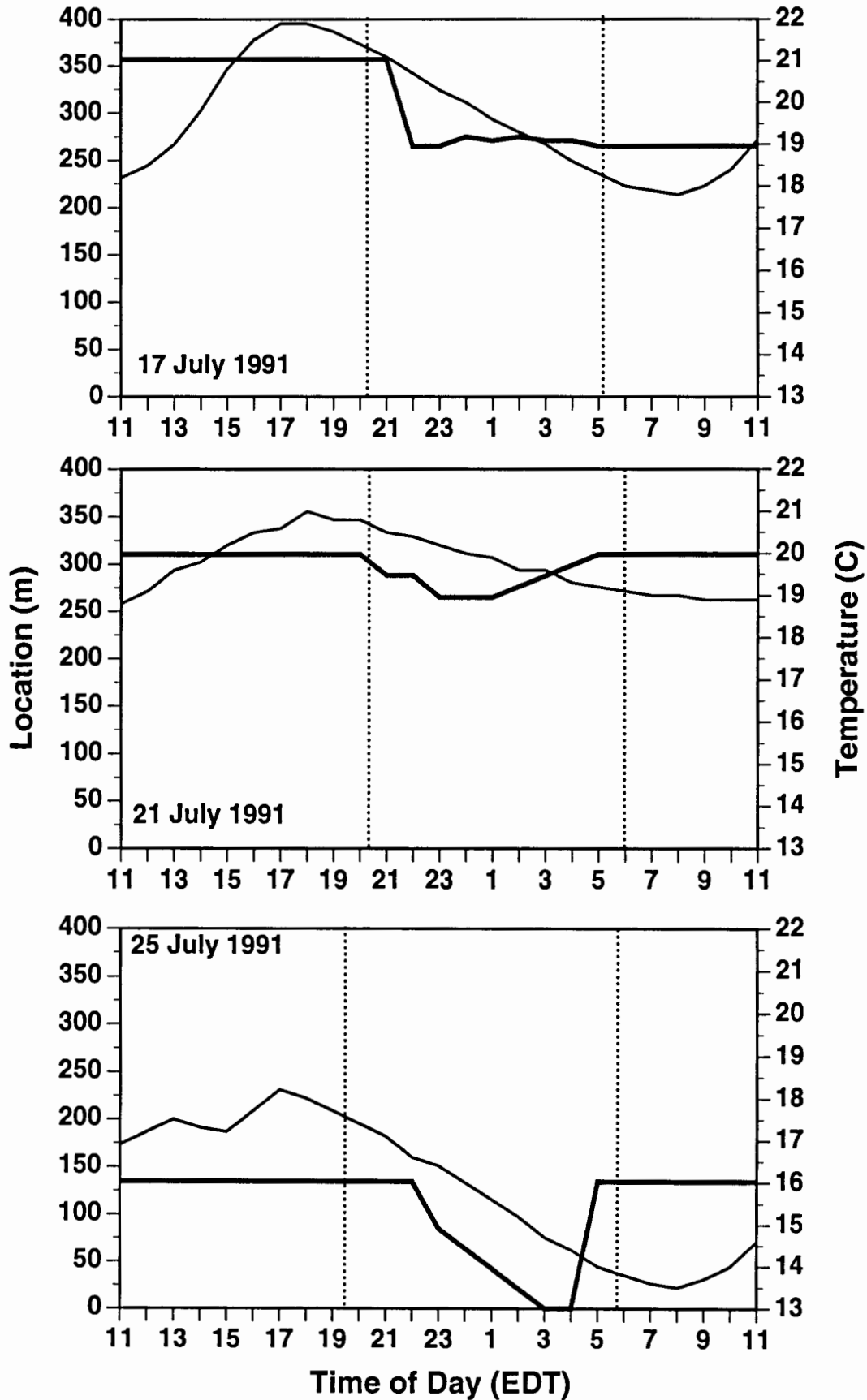


APPENDIX TABLE 3. Summary of diel movements of fish number 12 during four monitoring sessions between 17 July 1991 and 15 August 1991. Distances are in meters. (SD = standard deviation)

Date	Total linear distance moved	Diel range	Linear distance moved (day)	Linear distance moved (night)	Distance moved per hour (day)	Distance moved per hour (night)
7/17/91	121	92	0	121	0.0	11.1
7/21/91	91	45	0	91	0.0	8.3
7/25/91	269	135	0	269	0.0	24.3
8/15/91	92	37	0	92	0.0	7.7
Overall						
Mean	143	77	0	143	0.0	12.9
SD	85	45	0	85	0.0	7.8

APPENDIX FIGURE 3. Diel movements (thick line) of fish number ¹²~~13~~ and water temperature (thin line) during four 24-hour monitoring sessions between 17 July 1991 and 15 August 1991. The thick line represents the fish's location within its foraging range. Vertical dashed lines indicate sunrise and sunset.

APPENDIX FIGURE 3



APPENDIX FIGURE 3 (Cont.)

