Walleye movement and behavior in West Lake Okoboji, Iowa

by

Johannus Marinus Pitlo, Jr.

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
MASTER OF SCIENCE

Department: Animal Ecology
Major: Fisheries Biology

Approved:

Signatures have been redacted for privacy

[illegible]iversity
Ames, Iowa

1978

TABLE OF CONTENTS

ABSTRACT

Nine walleye, five males and four females, were tagged with internal ultrasonic transmitters during late April and May, 1976. The fish ranged from 1.9 to 3.18 kg in weight and from 580 to 660 mm in length. Six of these fish were monitored daily through June, July and August and on weekends during May, September, October and December. During the summer, walleye established well-defined activity centers which ranged from 7 to 77 ha. Five fish selected shallow water (2-7 m) activity centers which included dense stands of rooted aquatic vegetation. One fish selected a deep water (6-15 m) activity center during the summer. Walleye movement was higher at night than during the day, a major movement period occurring from 20:00 to 24:00 and a minor period occurring from 05:00 to 08:00. Walleye were found at shallower depths during nighttime periods than during daytime periods. Evaluation of fish movement and depth with several environmental parameters such as barometric pressure, sky cover, secchi disc depth and wind conditions failed to produce any statistically significant relationships. Shallow water walleye appeared to be scattered in the aquatic vegetation during the summer period and only exhibited schooling tendencies when they moved to deeper water in late fall. When fish were in water greater than about 3 m in depth, outboard motor noise directly over the fish did not appear to affect them.

INTRODUCTION

Knowledge of daily and seasonal behavior and movement of fishes can have important applications in fisheries management and angler harvest. A variety of methods have been utilized to monitor the activity patterns of various fishes.

Visual observation can provide useful information (Regier et al. 1969) but this approach is limited by light intensity and water clarity. Additionally, it is not suitable for long term observations. Hasler and Wisby (1958) attached surface floats to fish to observe movement, but line entanglement, exhaustion from towing, and the unnatural restriction to the fish limited the usefulness of this technique. Conventionally, therefore, mark and recapture methods have been used to discern fish behavior and movement over longer time periods. Such studies have revealed general dispersal patterns, homing tendencies, movement rates and other other behavioral information for numerous species. This procedure is usually inadequate, however, to determine detailed, short term changes in activity. Additionally, it requires extensive recapture efforts which may also interfere with normal fish activity.

The development of biotelemetry techniques has been a major advancement in the study of fish activity. It allows many informational units to be taken on individual fish without extensive recapture efforts and with a minimum of stress on the fish being monitored. Radio and ultrasonic transmitters have been employed in behavioral studies of aquatic animals for over 20 years (Trefethen, 1956). Owing to the large size and brief operational life of earlier transmitters, most telemetry efforts have involved short term studies of larger bodied fishes. The development of miniaturized transmitters with improved operational features now permits long term behavioral studies of a variety of fish species. Stasko (1975) and The Underwater Telemetry Newsletter (1971-1977) provide a bibliography of historic and recent research. Additionally, Stasko and Pincock (1977) discuss ultrasonic telemetry techniques, equipment and biological applications.

Walleye, Stizostedion vitreum vitreum (Mitchill), is an important game fish throughout its native and introduced range. Natural populations are distributed from the Northwest Territories across the Canadian provinces east of the Rocky Mountains into northern Labrador, south along the Atlantic coast to North Carolina, west to northern Arkansas and Nebraska, and north along the Missouri River (Eddy and Underhill, 1974). In the past several decades, many impoundments, especially in the southern and western United States, have been stocked with the species (Eddy and Underhill, 1974).

Walleye generally prefer larger lakes or interconnected small lakes and rivers which contain clean and cold or moderately warm waters (Eddy and Underhill, 1974; Johnson et al. 1977). Walleye are closely associated with the substrate and select gravel bars, stony or rocky points combined with steep gradients and firm substrate such as sand or marl (Regier et al. 1969; Rose, 1969). Although soft bottoms appear to be less suitable, walleye may be attracted to such areas if food resources are adequate (Harlan and Speaker, 1969).

Most investigations of walleye behavioral and seasonal movement have concerned reproductive activities. Many investigators, using conventional mark and recapture techniques, have studied the dispersal from and homing to spawning sites, e.g. Eschmeyer (1950), Rawson (1956), Crowe (1962), Olson and Scidmore (1962) and Ferguson and Derksen (1971). In general, these studies have shown the existence of discrete subpopulations which home to specific spawning areas within a drainage or water body. Most authors believe that extensive intermingling of subpopulations occurs during the summer, but Forney (1963) suggested that most walleye remain in a limited area, and that spawning populations in larger lakes may remain partially discrete throughout the summer.

Diel activity patterns of walleye are known in a general way. Adults tend to be negatively phototropic, seeking out shady areas or deeper waters during daylight hours (Harlan and Speaker, 1969; Regier et al. 1969; Ryder, 1977). Greatest activity tends to occur during nighttime hours, some of this movement being associated with travel to and from feeding areas (Carlander and Cleary, 1949; Sieh and Parsons, 1950; Rawson, 1956). Some authors suggest that the seasonal availability of types and amounts of food may regulate the distance an individual fish travels (Harlan and Speaker, 1969; Schupp, 1972). Daily activity patterns may vary between water bodies according to turbidity (Scott and Crossman, 1973).

A number of recent studies have utilized biotelemetry to observe walleye behavior and movement in various habitats (Table 1). Wrenn, 1974, as cited in Ager (1976), Fossum (1975) and Bahr (1977) worked in large rivers. Reservoir and lake walleyes were studied by Ager (1976), Kelso (1976) and Holt et al. (1977).

The present study was conducted to determine the behavioral patterns, movements, and habitat preferences of mature walleye in West Lake Okoboji, Iowa by means of ultrasonic telemetry. The research focused on several objectives: 1) to determine the normal diel activity patterns and size and nature of activity centers of individual fish; 2) to determine the influence of various environmental parameters such as water temperature, dissolved oxygen concentration, turbidity, basin morphometry, aquatic vegetation and climatic factors upon the behavioral and movement patterns; 3) to ascertain the effect of boating activity upon these behavioral patterns; and 4) to evaluate the usefulness of the technique for expanded behavioral study of the species.

Table 1. Method of transmitter attachment and transmitter longevity of some walleye investigations

Investigator	Type of telemetry	Transmitter attachment	No. of fish studied	Transmitter longevity (days)	Study area
Fossum (1975)	ultrasonic	external	6	2-5	Mississippi River (Pools 3 & 4)
Bahr (1977)	radio	external	12	7-49	Mississippi River (Pools 8 & 9)
Ager (1976)	ultrasonic	surgical	29	4-82	Center Hill Reservoir, Tennessee
Kelso (1976)	ultrasonic	external	8	1	West Blue Lake, Manitoba
Holt et al. (1977)	radio	external	18	2-33	Lake Bemidji, Minnesota
Present Study	ultrasonic	surgical	6	203-379+	West Lake Okoboji, Iowa

MATERIALS AND METHODS

The Study Area

West Lake Okoboji, Dickinson County, is part of a chain of natural lakes in northwestern Iowa known as the Iowa Great Lakes. It is the deepest (42.7 m) natural lake in Iowa and has the second largest surface area (1540 ha). The physical, chemical and biological characteristics of the lake have been well studied. Except in the several major bays, the lake bottom slopes downward rapidly (Bachmann et al. 1966). The substrate is largely gravel, sand and ooze, but areas of glacial boulders are extensive. The lake normally experiences summer thermal stratification. Typically there is hypolimnetic oxygen depletion in late summer, becoming nearly complete below about 20 m (Bachmann and Jones, 1974). Although all of the Iowa Great Lakes are biologically productive, West Lake Okoboji is the least eutrophic. Light penetration is routinely deeper in this lake than in the others, and algal blooms and aquatic macrophytes are rarely more than a local problem (Bachmann and Jones, 1974).

Capture and Release

Tagging operations began in mid-April, 1976. An initial group of nine experimental fish was obtained from Iowa Conservation Commission personnel after use of the fish for artificial propagation purposes. Fish were captured by 160 ft (48.7 m), 2.5 in (6.4 cm) bar mesh gill nets set in spawning areas during evening hours. Shortly after capture, the fish were transported to the East Lake Okoboji stripping station and placed in continuous flow holding tanks. All fish were obtained from West Lake Okoboji, but precise capture locations are unknown as all fish were placed in a common holding tank on the transport vehicle. After stripping the eggs or milt, the transmitters were surgically implanted into the body cavity of the fish. The fish were held for a one week post surgery observation period, during which time all contracted a severe Saprolegnia fungus infection. Treatment with a daily 1 hour bath of 200 mg/l formalin solution was applied. Despite this effort, three fish died. The treatment appeared to arrest the infection among the remaining six fish, however, which were subsequently released at random locations in West Lake Okoboji.

From this experience, it was determined that collecting and tagging procedures should be modified to reduce stress upon the fish. Consequently, three additional experimental fish were handled in the following manner. Collecting was performed by the investigator using nighttime gill net sets. Immediately after the fish were removed from the net, the transmitter was surgically implanted using the boat seat as an operating table. Following recovery from the anaesthesia, the fish were released at the capture site. Using this procedure, study fish were removed from the lake less than one-half hour.

Prior to release, length and weight measurements were taken on each fish, and sex was determined by gonadal observation during the transmitter implantation.

Transmitter Implantation Procedures

For purposes of developing surgical techniques, operations were performed on six walleye in early April, 1976, using dummy transmitters of the same size and weight as functional transmitters. Walleye with dummy transmitters were held for a three month period in a rearing pond at the State Fish Hatchery, Spirit Lake, to observe their condition and healing.

From these efforts, a standardized implantation procedure was determined. Prior to surgery the fish was anaesthetized in a 25 ppm Quinaldine solution. The fish were then placed in a V-shaped trough, ventral surface up, and a wet cloth was placed over the gills. The transmitters were inserted anteriorly into the abdominal cavity through a post-pelvic incision, approximately 10-15 mm to the side of the midventral line and 50 mm anterior to the anal opening. The incision, approximately 25 mm in length, was made by scalpel, using a number 20 blade. The incision was closed using an atraumatic cutting needle trailing 000 silk suture. Three to four individual stitches using overhand knots were required to close the incision. In general, this surgical procedure was completed within 3-4 minutes. The fish was placed in fresh water upon surgery completion. For purposes of external identification, a numbered plastic dart tag was inserted into each fish just below the anterior dorsal fin.

All the surgical equipment was either sterilized in alcohol or boiled in water. The transmitters were sterilized in alcohol. Surgical gloves were worn during the operation. Some investigators, including Hart and Summerfelt (1975), Ager (1976) and Crossman (1977) have injected antibiotics into the body cavity, however, I used no such treatment.

Tracking Equipment and Procedures

The transmitters and tracking equipment were manufactured by Donald L. Brumbaugh, Tucson, Arizona. Transmitters and batteries were housed in plastic capsules measuring 16 mm X 60 mm. The entire unit weighed approximately 8 g in water. Two types of transmitters were used, a temperature transponding type and a fixed signal type. The five fixed signal transmitters were identifiable according to their individual frequency (approximately 76 to 79 kHz) and pulse rate (about 64 to 106 pulses/minute). The four temperature transponding transmitters had fixed frequencies (79 to 84 kHz), but the pulse rate varied directly according to water temperature (Table 2). Prior to use, the temperature transponding transmitters were laboratory tested in water baths of varying temperatures (9-26 $^{\circ}C$). In this manner, a pulse rate was

Table 2. Ultrasonic transmitter parameters

Transmitter No.	Pulse rate/minute	Frequency (kHz)
4	66	78.9
11	106	77.5
13	80	77.3
15	70	76.6
16	64	76.9
T4	71 at 23 °C	79.3
T7	66.5 at 23 °C	82.4
T8	85 at 23 °C	83.3
T9	68 at 23 °C	84.0

obtained for each degree of temperature over the range of temperature tested. When tested at the same temperature, the pulse rates of individual transmitters were different.

The receiving equipment was portable, consisting of three components: a battery powered receiver unit with frequency and volume selectors, an earphone headset, and a hydrophone. The receiver unit converted the sonic signal to an audible signal. An earphone headset was used to aid the observer in the detection of a sonic signal as waves, wind and motor noise obscured the signal from an external speaker. A stop watch was used to determine transmitter pulse rates.

An unscheduled system was utilized to permit tracking at all day and night hours. Tracking was accomplished from an outboard motorboat. Typically, search for a fish would proceed from the point where it was last located. If the fish was not found in that area, a grid search pattern, in which grid lines were approximately 200 m apart, was used to relocate the fish. Weather permitting, tracking was accomplished weekdays during June, July and August, and on weekends during May, September, October and December. Heavy motorboat traffic during the summer months led to abandonment of weekend tracking early in the study due to extensive signal interference from boats and motors.

When a fish was located, the date, time, water depth and pulse rate were recorded. The boat was positioned over the fish and a Lowrance Model LRG 605 Flasher-Graph Recorder was used to determine depth and record the substrate condition, as either clean or vegetated, and hard or soft. Fish locations were determined both by triangulation using a marine sextant, and by a simple visual plot on a detailed contour map of the lake. Prominent land marks such as points of land, silos and water towers were used as sextant triangulation points. Secchi disk readings at fish locations were abandoned early in the study due to inaccuracies resulting from disk and line entanglement in the aquatic vegetation.

Fish locations were plotted on a 1:7920 in scale map by use of a three-armed protractor and triangulation data.

Average hourly movement rates were determined by measuring the straight line distance between successive fixes in a single 24 hr period and then dividing by the elapsed time. This represents the minimal distance of movement possible. For daily movement rates the 24 hour day was arbitrarily divided into a daytime period (07:01 to 20:00) and a nighttime period (20:01 to 07:00).

Measurement of Environmental Parameters

Limnological data were taken periodically at five lake stations (Fig. 1). Dissolved oxygen and temperature profiles were recorded bi-weekly using a Garcia Model 8500 Oxygen Temperature Probe and a Whitney resistance thermometer. Secchi disk readings were also obtained at these stations.

Daily high and low air temperatures were obtained from the first order weather station at the Iowa Lakeside Laboratory, located on Millers Bay, West Lake Okoboji. Barometric pressure readings were recorded at 07:00 and 19:00 (C.D.S.T.) using an Improved Surveying Aneroid Compensated (Keuffel and Esser Company, New York, N. Y.). Morning and evening sky and wind conditions were also recorded daily.

Terminology and Statistical Procedures

Home range concepts and terminology have become well-established in the literature on movements of terrestrial animals. These concepts are relatively new for the aquatic biologist dealing with fishes. I feel that these established

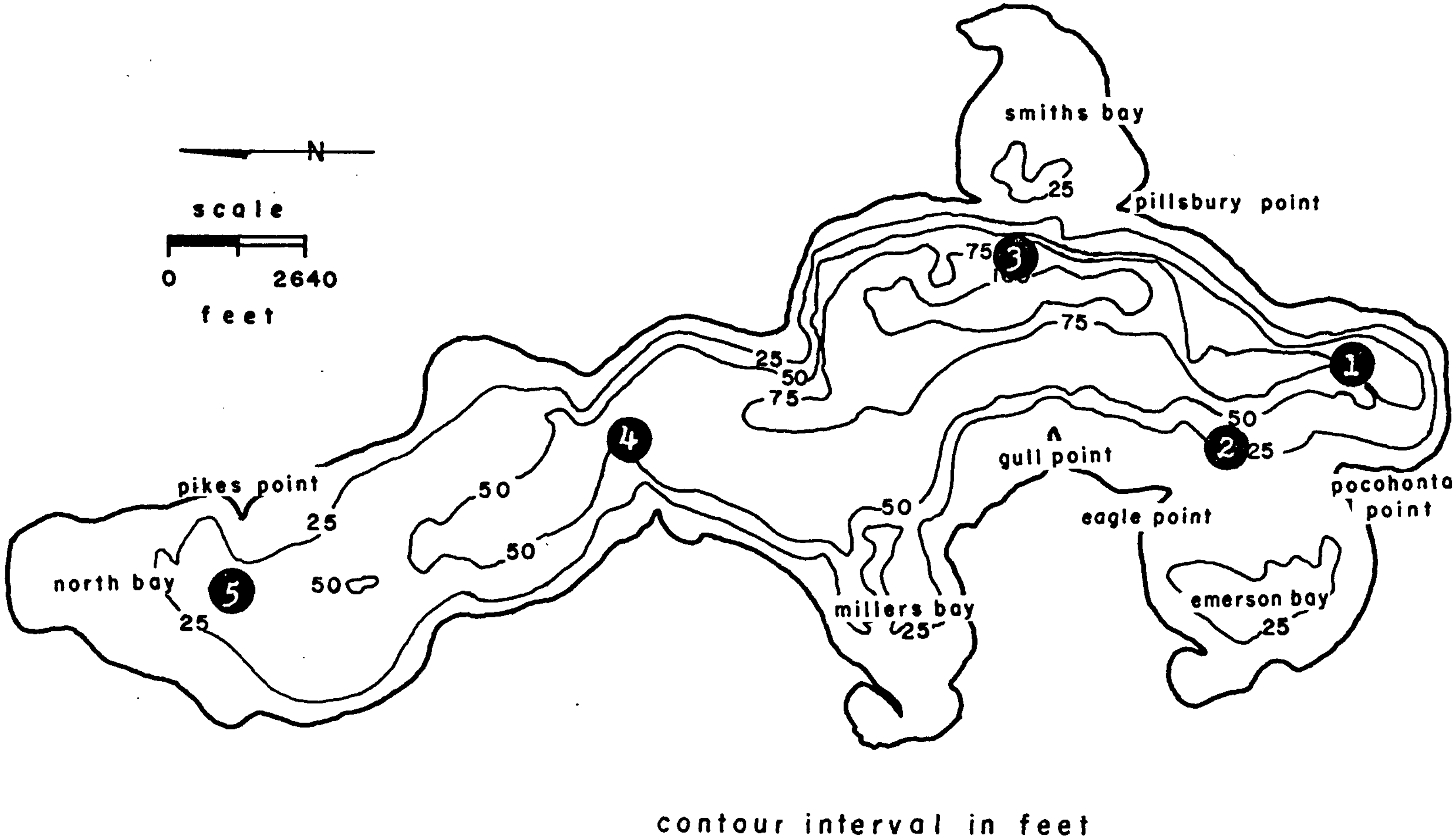


Figure 1. Locations of limnological data stations (●)

concepts should be maintained and modified only when circumstances warrant.

Burt (1943) described the home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young." This definition includes the time interval from one mating season to the next and would encompass one year for most species of temperate regions. Under this definition, home range in the present study may include the entire lake, as present evidence indicates the entire lake is used during the course of a year. I realize that there are seasonal barriers that limit movements such as thermal stratification and anoxic waters, but at some time during the year the entire lake can be utilized, especially during and after spring and fall turnover.

A more useful concept for application to the present study is that of the biological "activity center." This term was used by Ables (1969) to refer to the clumping of position fixes which resulted from unequal habitat use by an individual animal. In the present study, therefore, a concentration or clumping of fish locations in a specific area of the lake was termed an activity center, as there appeared to be other similar habitat which the fish did not utilize. In order to obtain a measurement of area for these activity centers, I used the method described by Odum and Kuenzler (1955) and Winter (1977). Using this method, the extreme outermost position fixes were connected to form the smallest convex polygon which contains all the location points. If a side of a polygon cut across land, the shoreline was used as a boundary. A planimeter was then used to determine the area of the activity center. Certain small areas within the activity center that received heavy daytime usage for one week or more were termed "rest areas."

According to Winter (1977), locations which represent obvious wandering should be excluded from "home range" calculations. In the present study, such wanderings were excluded from activity center dimensions and were termed "exploratory excursions."

Statistical analysis of the data were performed at the Iowa State University Computation Center. Regression and correlation analyses were performed by use of the Statistical Analysis System (S.A.S.).

RESULTS

Three of the nine experimental fish were never relocated after release. The remaining six fish were regularly located throughout the summer and fall periods. Table 3 summarizes the physical characteristics of the fish and their histories of observation.

Summertime Activity Centers

During most of the study period, activity of the study fish was primarily limited to two discrete areas of the lake, the mouth of Emerson Bay and the northern one-third of the lake. Emerson Bay is the largest of several embayments in the lake and is located in the southwest end (Fig. 1). An important feature of the bay is an underwater bar which extends across the mouth from Eagle Point to Pocohontas Point. The bar is approximately 250 m wide and is about 3 m deep at its shallowest point. The bar is flat topped, but drops off rapidly into deeper water on the inside and outside edges. The substrate is largely sand, gravel and marl, with an occasional concentration of rubble and rock. The dominant feature of the bar is the dense growth of rooted aquatic vegetation that occurs over its entire area down to the 5 to 6 m (17-21 ft) depth at the edges. The substrate of the deeper waters has some areas of muck and silt, but extensive zones of rock and boulder are also present. The maximum depth of the bay is about 11 m (32 ft).

Table 3. Physical characteristics of the fish and their histories of observation

Fish No.	Length	Weight	Sex	Capture date	Release date	Date of last contact	Total elapsed days	Total contacts
00[a]	655.1 mm (25.8 in)	3.18 kg (7.0 lb)	F	8 June	8 June	28 Dec. (1976)	203	76
11	621.3 mm (24.5 in)	2.30 kg (4.7 lb)	M	10-16 Apr.	25 Apr.	25 Apr. (1976)	0	0
33	591.8 mm (23.3 in)	2.13 kg (4.7 lb)	M	10-16 Apr.	25 Apr.	25 Apr. (1976)	0	0
44	660.4 mm (26.0 in)	2.22 kg (4.9 lb)	F	10-16 Apr.	24 Apr.	24 Apr. (1976)	0	0
55[a,b]	586.7 mm (23.1 in)	2.22 kg (4.9 lb)	M	15 May	15 May	7 May (1977)	357	81
66[b]	635.0 mm (25.0 in)	2.58 kg (5.7 lb)	F	10-16 Apr.	1 May	7 May (1977)	371	82
77[b]	584.2 mm (23.0 in)	1.90 kg (4.3 lb)	M	10-16 Apr.	1 May	14 May (1977)	379	62
88[a,b]	619.7 mm (24.4 in)	1.90 kg (4.2 lb)	F	6 May	6 May	7 May (1977)	366	73
99[c]	591.8 mm (23.2 in)	1.90 kg (4.2 lb)	M	10-16 Apr.	1 May	25 July (1976)	86	43

[a] Fish capture/release site the same: for other fish, capture site is unknown and release was at random locations

[b] Transmitters that were operational as of late July, 1977

[c] Fish captured by angler, 25 July, 1976

The northern section of the lake is relatively flat-bottomed. It is also the shallowest portion of the lake and is dominated by dense growths of vegetation down to about the 6 m (21 ft) depth. The substrate of the shoreline is predominantly sand and gravel, but rock and boulders are scattered around the major points. The substrate in areas deeper than about 11 m (32 ft) is largely muck and silt.

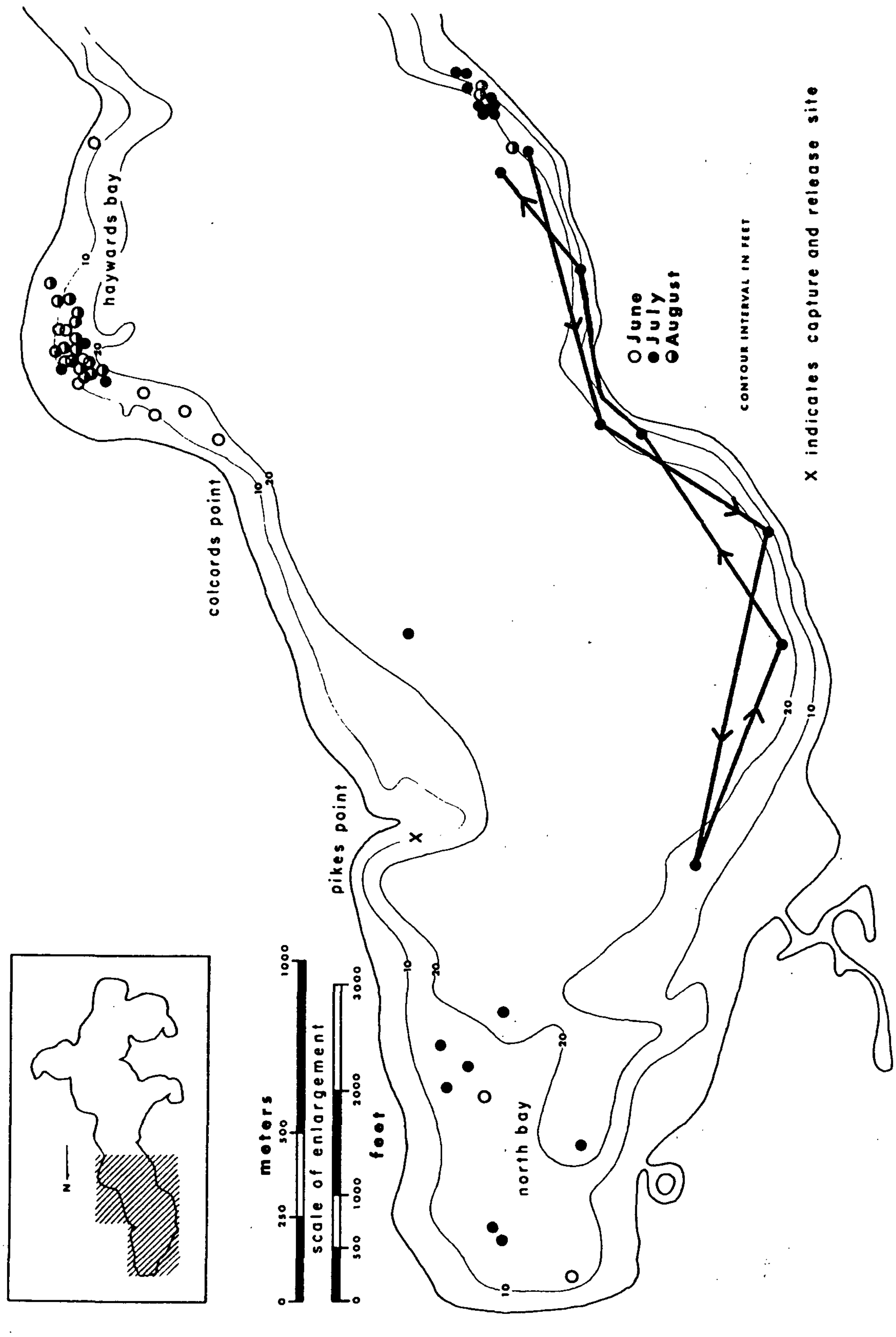
Individual activity centers

General capture and release information and activity patterns for individual fish are given below.

Fish 00 This female was captured at 24:00, 8 June, in 3 m (9 ft) of water off Pikes Point. Transmitter implantation and release at the capture site was carried out immediately.

Fig. 2 shows the shoreline activity centers of this fish. This walleye was different from other fish in that it occupied three widely separate areas of activity. No activity center area measurements were obtained for this fish as the smallest convex polygon method would have included substantial areas of the lake where the fish was never located. Additionally, she was never detected while moving from one center to another so that travel lanes are unknown and could not be included in activity center dimensions. Indirect evidence indicates that movement between the two centers on opposite sides of the lake was in a straight line of travel over deep water. On a number of occasions she was located in both centers within a

Figure 2. Activity center location of fish 00


haywards bay
colcords point
pikes point
north bay
O June
● July
◐ August
CONTOUR INTERVAL IN FEET
X indicates capture and release site
meters
0
250
500
1000
scale of enlargement
feet
0
500
1000
2000
3000
10
20
N

1 to 2 hr period. During this time, normal search was being conducted in North Bay, and a shoreline movement of the fish would have been detected. Also, the distance of a shoreline route was probably too great to be traveled in a 1 to 2 hr period.

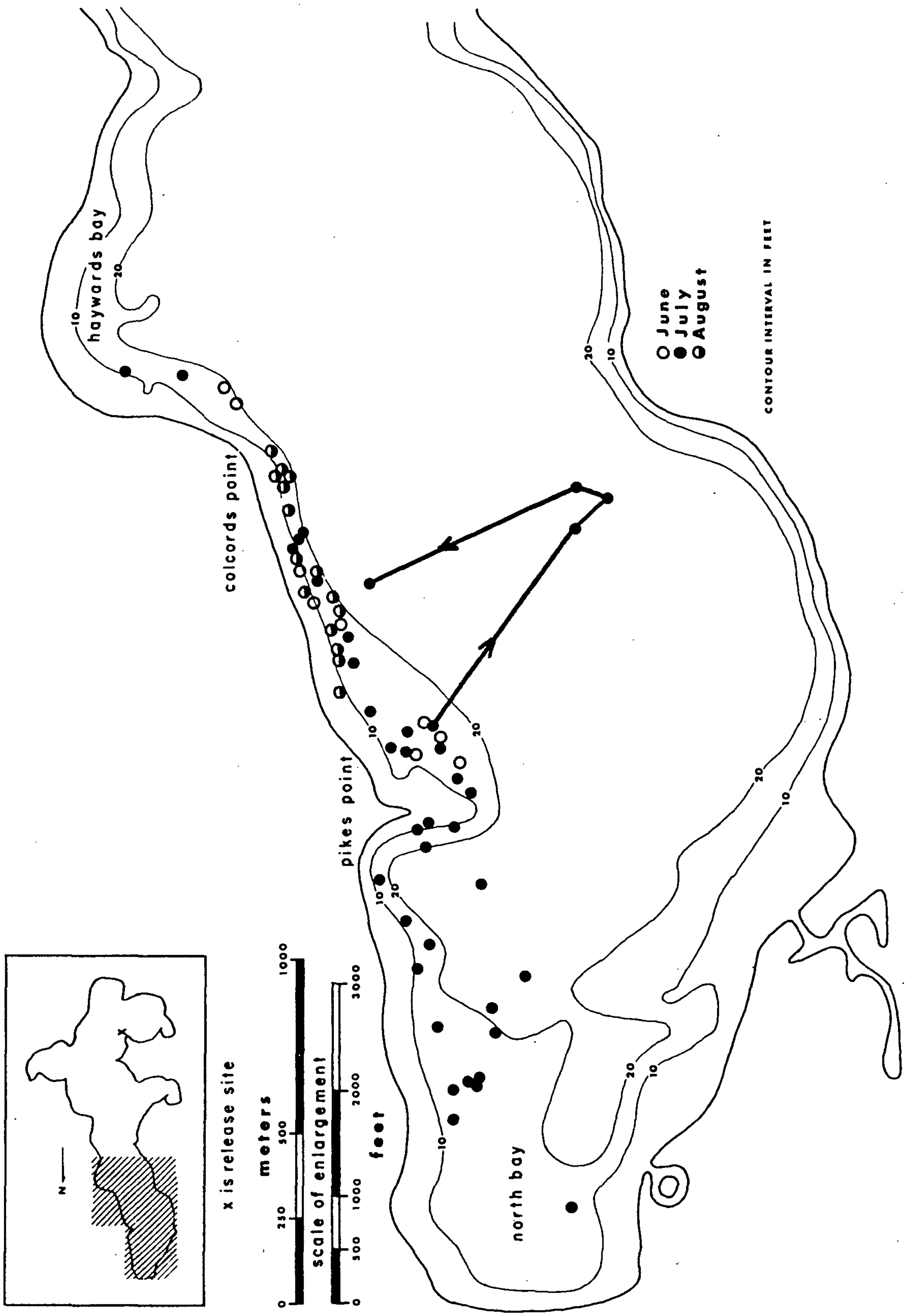
The connected points display an exploratory excursion by this fish when it left the activity center on the west side of the lake and moved northward along the shore for $1\frac{1}{2}$ days. She then returned directly to the same activity center.

Fish 77 Although the early April capture site of this male is unknown, it was released 1 May, off Eagle Point in 2 m (6 ft) of water (see inset, Fig. 3). Upon release the fish moved northward and was relocated 2 June, near Pikes Point in the northern portion of the lake, where it established a shoreline activity center (Fig. 3).

The connected locations near the west shore, shown in Fig. 3, represent a one night exploratory excursion by this fish. Near sundown on 29 July, the fish moved in a straight line from its activity center toward the west shore. It stayed near a rock reef until sunrise when it moved directly back to the general area from which it had started.

Fish 55 This male was captured at 04:00, 15 May, in 3 m (9 ft) of water off Eagle Point. Immediately after capture, the fish was tagged and released at the same site. The capture/release site is included within the activity center near the mouth of Emerson Bay. This area encompassed the bar

Figure 3. Activity center location of fish 77


haywards bay
colcords point
pikes point
north bay
June
July
August
CONTOUR INTERVAL IN FEET
x is release site
N
meters
0 250 500 1000
scale of enlargement
feet
0 500 1000 2000 3000
10
20

between Eagle Point and Pocohontas Point (Fig. 4). Many movements were made to the flat area between Gull Point and Eagle Point.

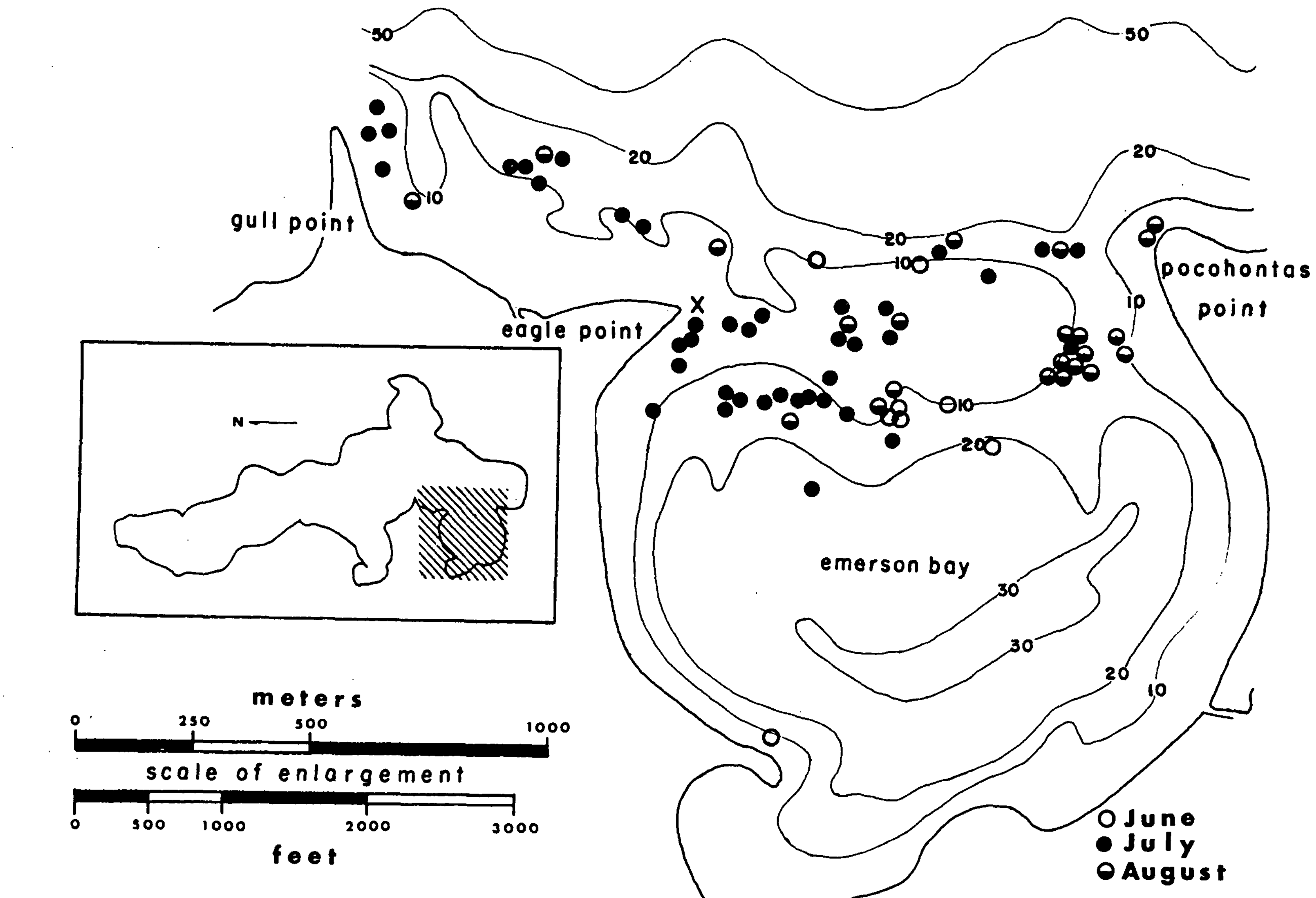
Fish 66 The early April capture site of this female is unknown, but she was released 1 May, in about 5 m (16 ft) of water in Millers Bay (see inset, Fig. 5). After release she moved to North Bay by 7 May, remained there until 4 June, and established an activity center by 9 June in the mouth of Emerson Bay (Fig. 5).

The location plots indicate she utilized both the inside and the outside edges of the southern portion of the bar between Eagle and Pocohontas Points. Extensive use was made of the Pocohontas Point area and a distance of shoreline west from the point.

Fish 88 This female was captured at 23:00, 6 May, in water 3 m (9 ft) deep off Eagle Point. The fish was tagged immediately and released at the same location. The fish established an activity center near the mouth of Emerson Bay, which included the capture/release site (Fig. 6). The center included the bar between Eagle and Pocohontas Point and the flat area between Gull Point and Eagle Point. The activity center of this fish was nearly identical to that of fish 55, and overlapped with a portion of the activity center of fish 66.

Fish 99 Although its early April capture site is unknown, this male was released 1 May, in 3 m (9 ft) of water off Gull Point (see inset, Fig. 7). The fish moved into

Figure 4. Activity center location of fish 55



X indicates capture and release site

Figure 5. Activity center location of fish 66

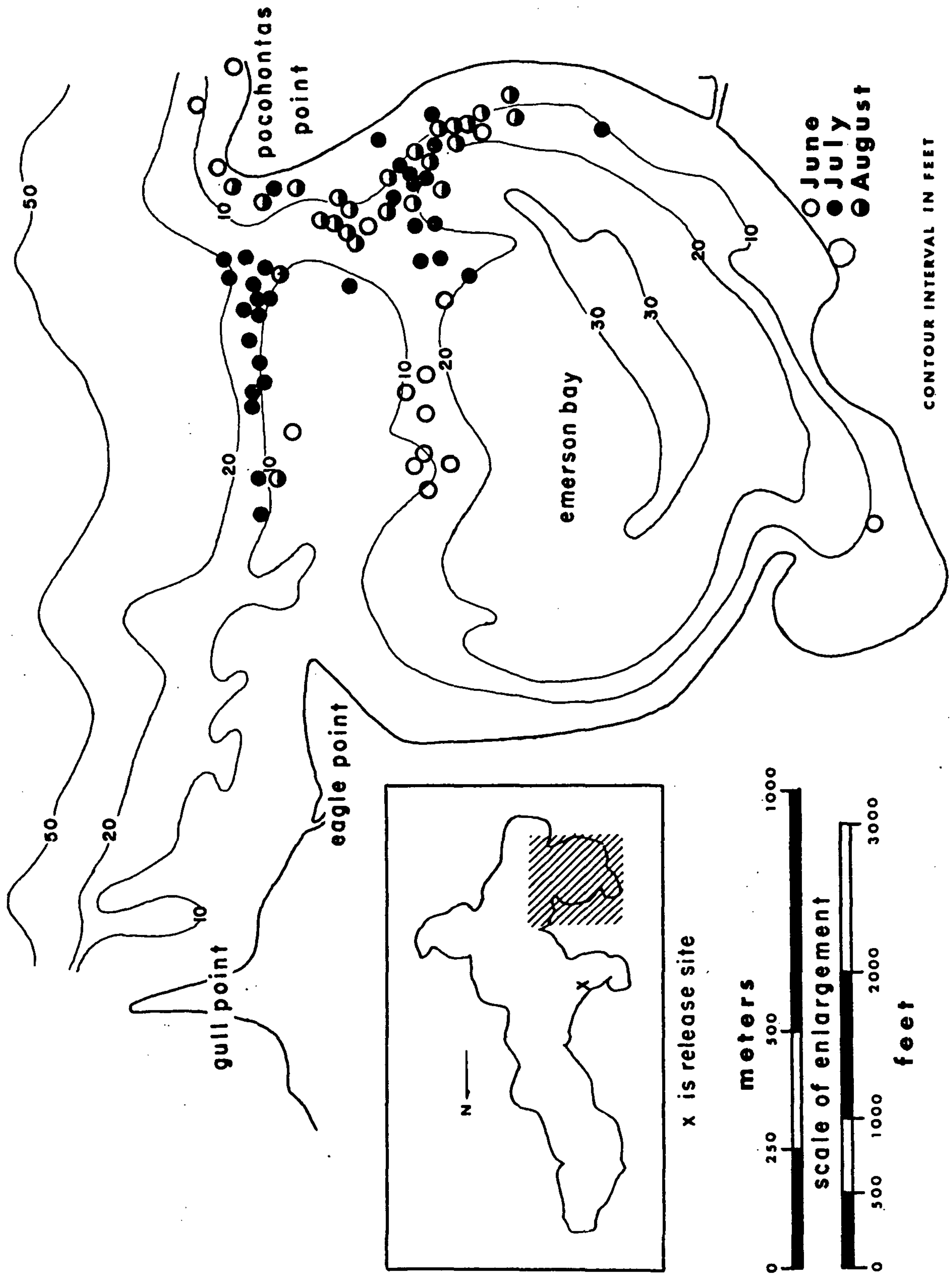

pocohontas point
emerson bay
eagle point
gull point
50
20
10
30
June
July
August
CONTOUR INTERVAL IN FEET
N
x is release site
meters
0
250
500
1000
scale of enlargement
0
500
1000
2000
3000
feet

Figure 6. Activity center location of fish 88

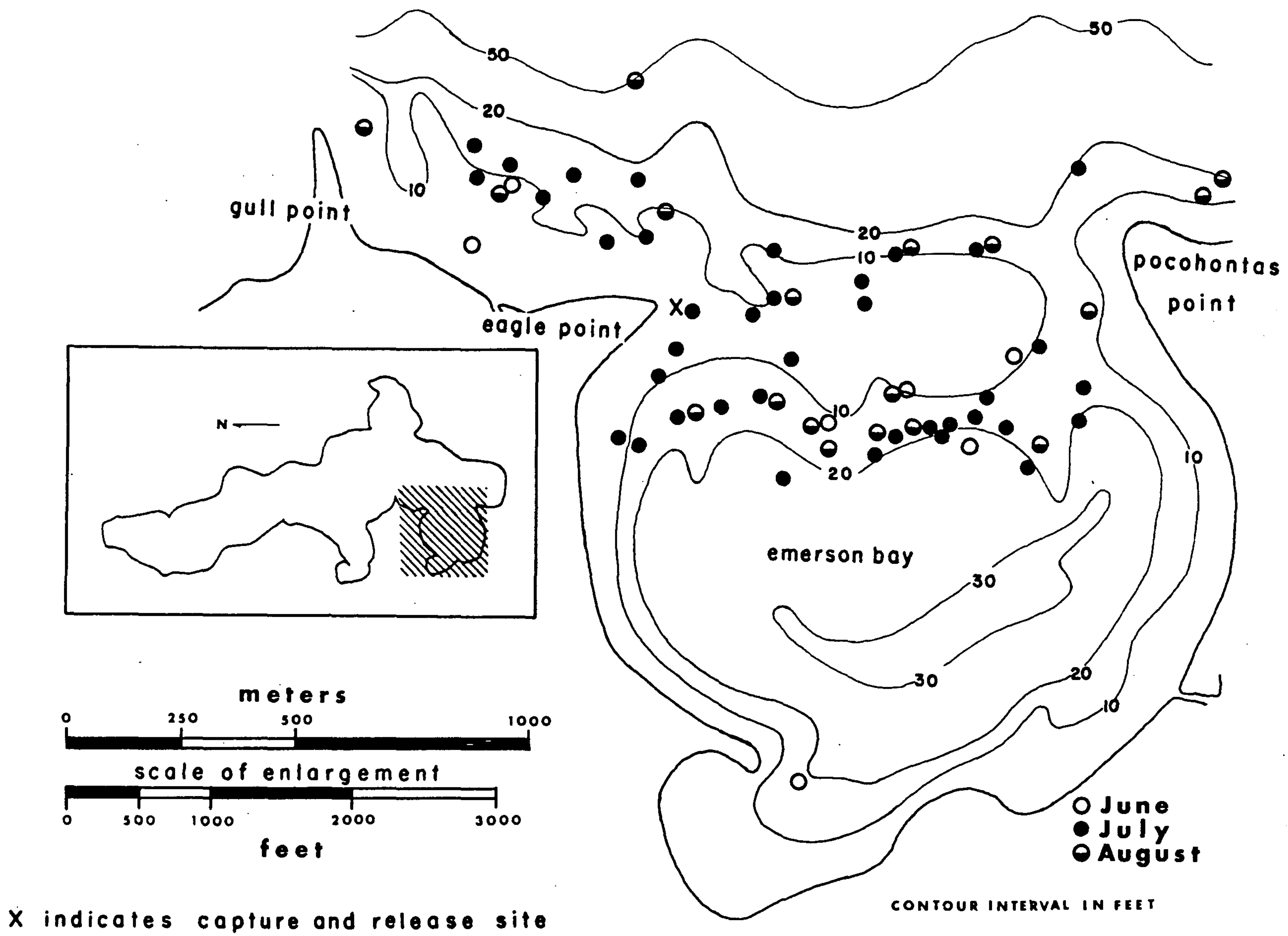
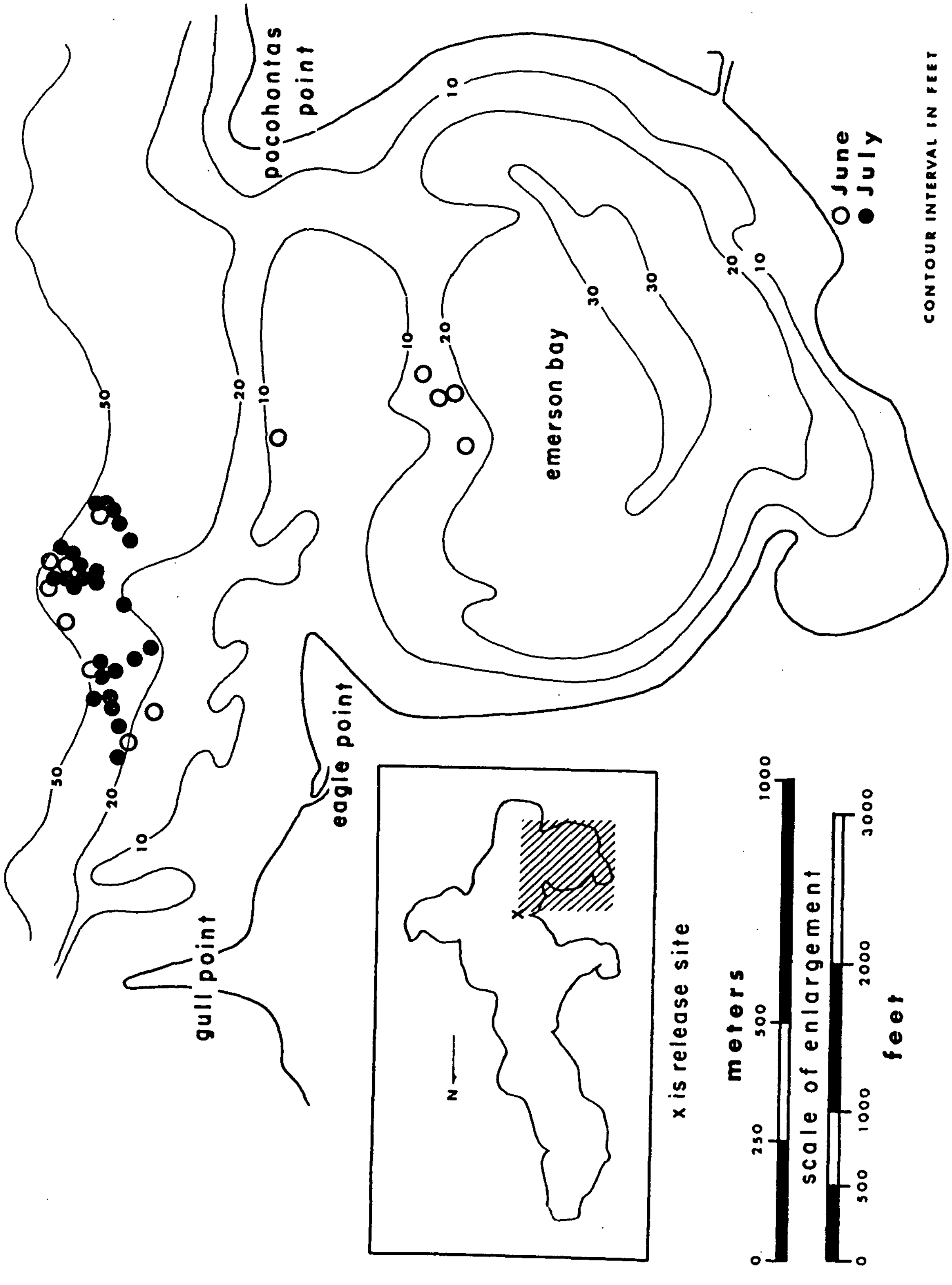

50
50
20
20
10
10
10
20
20
30
30
20
10
gull point
eagle point
pocohontas point
emerson bay
X
N
June
July
August
CONTOUR INTERVAL IN FEET
meters
0
250
500
1000
scale of enlargement
0
500
1000
2000
3000
feet
X indicates capture and release site

Figure 7. Activity center location of fish 99


pocohontas point
gull point
eagle point
emerson bay
50
20
10
30
June
July
CONTOUR INTERVAL IN FEET
x is release site
N
meters
0
250
500
1000
scale of enlargement
feet
0
500
1000
2000
3000

Millers Bay by 7 May and remained there until 1 June. By 4 June it had moved to the inside bar of Emerson Bay. It remained there until 18 June when it suddenly moved into deep water just south of Gull Point and remained there until it was captured by an angler on 21 July (Fig. 7).

This was the only fish that established a deep water activity center. It was also the only fish to be captured by an angler.

Activity center size

Activity center size varied from 7 to 77 ha for those that were calculated. Table 4 shows the activity center size and average daily movement for individual fish. Those fish whose activity occurred primarily along the north shoreline (00 and 77) tended to have larger daily movement rates. The single deep water fish (99) exhibited the smallest daily movement rate and activity center size. There was no obvious relationship between activity center dimensions and average daily movement rate, sex or size of fish. Daily movement also appeared independent of fish sex or size.

Activity center depth

Activity center depth was 2-7 m for the shallow water fish and 6-15 m for the deep water fish. Figs. 2-6 show the concentration of points between the 3-6 m (10-20 ft) contour lines for the shallow water activity centers. Fig. 7 shows the concentration of points between the 7-14 m (23-46 ft)

Table 4. The sex, weight, activity center size and average movement of tagged fish

Fish no.	Sex	Wt. (kg)	Location	Activity center size (ha)	Avg. movement (m/hr)
00	F	3.18	North end	—[a,b]	192
88	F	1.90	Emerson Bay	77	111
55	M	2.22	Emerson Bay	66	103
77	M	1.95	North end	63[b]	305
66	F	2.58	Emerson Bay	43	78
99	M	1.90	South end	7[c]	26

[a] Activity center area not calculated, see page 21 of text

[b] Fish with a shoreline activity center

[c] Fish with a deep water activity center

contour lines for the single deep water activity center.

Activity center habitat features

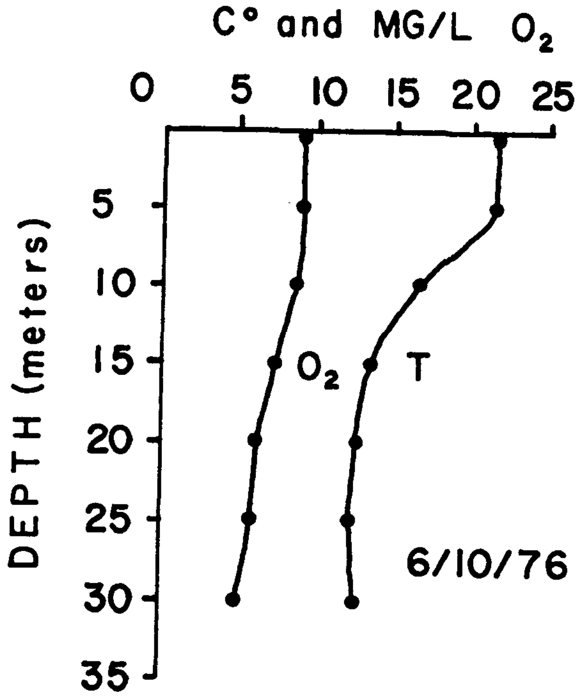
Among the five shallow water activity centers, the most prominent feature was the heavy beds of aquatic vegetation. Grab samples of the submersed macrophytes within the activity centers showed that coontail (Ceratophyllum dimersum) was the dominant plant species and, to a lesser extent, pondweed (Potomageton sp.) and Chara sp. occurred. There was no obvious selection for a specific species or type of rooted aquatic vegetation. The substrate of these activity centers included sand, marl, gravel, rock and rubble and some rock reefs. Fish seldom ventured over muck or silt substrate.

The single deep water activity center did not include aquatic vegetation. The substrate consisted largely of scattered rock and large boulders with some rubble and rock reefs.

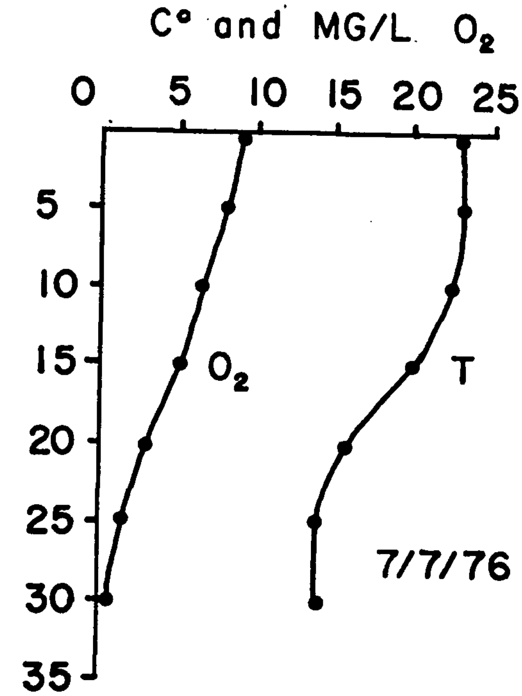
Activity center temperature and oxygen

The thermal and dissolved oxygen profiles during the summer months for station 2 are shown in Fig. 8. The observed thermal and dissolved oxygen values varied little among stations on a specific sampling day. Although these profiles extend deeper than the depths at which most activity centers occurred, they are the same as values observed within the centers. The temperature and dissolved oxygen were fairly homogenous for the shallow water activity centers. At times,

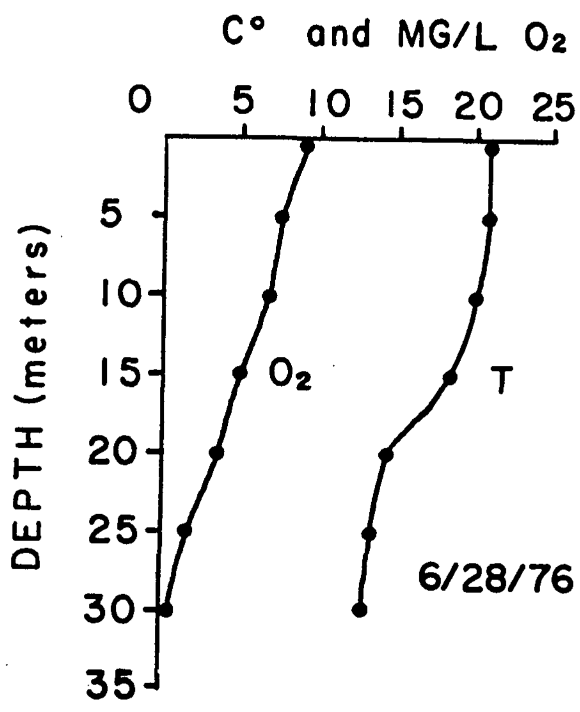
Figure 8. Temperature and oxygen profiles of West Lake Okoboji on selected dates



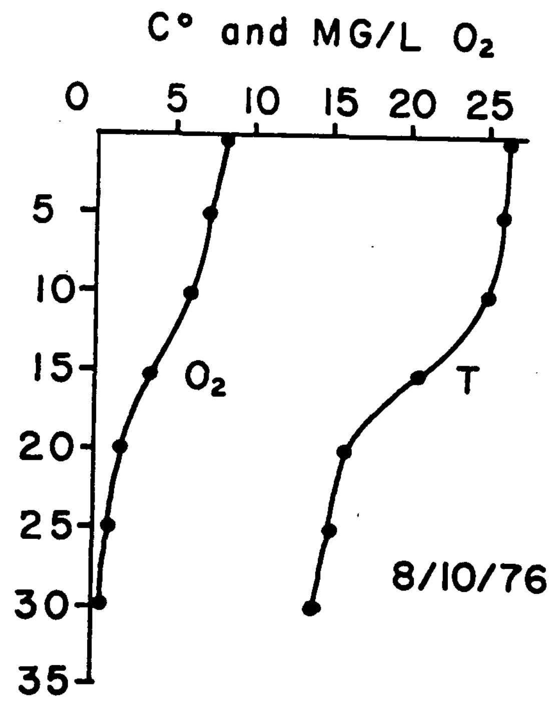
C° and MG/L O_2
0 5 10 15 20 25
DEPTH (meters)
5 10 15 20 25 30 35
O_2
T
6/10/76



C° and MG/L O_2
0 5 10 15 20 25
5 10 15 20 25 30 35
O_2
T
7/7/76



C° and MG/L O_2
0 5 10 15 20 25
DEPTH (meters)
5 10 15 20 25 30 35
O_2
T
6/28/76



C° and MG/L O_2
0 5 10 15 20 25
5 10 15 20 25 30 35
O_2
T
8/10/76

the upper portion of the thermocline was included within the deep water activity center. Generally, temperature and dissolved oxygen were somewhat lower in the deep water center (Fig. 8) when compared to the shallow water centers.

Patterns of Movement within the Activity Centers

Zig-zag and straight swimming

Generally, fish movement, or lack of it, could be determined by the type of signal that was detected. If a fish was stationary, signal strength would remain constant and the signal would eminate from one direction. A signal that fluctuated in strength, and came from somewhat different directions usually indicated active fish.

Two types of swimming behavior became evident during the study period. One was a zig-zag type movement, where fish were either cruising slowly or were stationary and then made sudden rapid bursts in different directions. This movement was distinguished by a strong signal from one direction, then a sudden decrease or momentary loss of the signal only to receive a strong signal moments later from a different direction. Occasionally the monitored fish would move toward and nearly under the search boat. Most examples of zig-zag movements were observed during the nighttime period. The other type of swimming observed was straighter in path direction and at a more uniform travel speed. This movement was distinguished by a strong and somewhat fluctuating signal from one direction with a gradual decrease in signal strength from the same direction as the fish moved away. It was also distinguished by receiving a weak fluctuating signal from one direction, with increasing signal strength as the fish moved toward the search boat, with a corresponding decrease in signal strength as it moved away. Swimming activity with this characteristic usually was observed near sunrise and sundown.

Day and night movements

Comparisons of day and night movement rates showed that significantly ($F = 9.10$, $p = 0.03$) higher movement rates occurred during nighttime intervals (Table 5). The nocturnal activity pattern was bimodal, a major activity period occurring from 20:00 to 24:00 and a minor period occurring from 05:00 to 08:00 (Fig. 9).

Typical daily movement patterns within the activity centers became fairly well established during the summer months. Study fish were usually found stationary in the smaller rest areas during the daytime period and moving toward or within a larger foraging area during the nighttime period. Fish tended to make nightly, daily or two day excursions out of the rest area and then returned. Rest areas within the activity center shifted somewhat during the summer period, but always included heavy beds of rooted aquatic vegetation (except for the deep water fish, 99). For example, Fig. 10 shows the movement in and out of a rest area by fish 55.

Table 5. Comparisons of day and night mean movement rates in m/hr for individual fish

Fish no.	Night	n	Day	n
00	436	6	39	7
55	183	8	23	17
66	128	4	27	15
77	547	6	63	11
88	182	4	41	17
99	39	1	12	9
Total	1425	29	205	76
Grand mean	237 (± 48)[a]		34 (± 48)[a]	

[a] $p = 0.03$, $F_{1,5\ d.f.} = 9.10$

The observation on 9 August was at 05:00 and the fish was moving rapidly southward toward the rest area just north of Pocohontas Point. The observation on 10 August was in the rest area at 09:30. The 11 August observation was at 10:34 with the fish slowly moving northward. The first observation on 12 August was at 01:20 near Gull Point, a foraging area. Observation two on 12 August was at the rest area at 08:45, and observation three on 12 August was at 23:30 back in the foraging area. The observation on 13 August was at 13:55, and the fish was in the rest area. Fig. 11 shows a similar pattern established by fish 88. In this case, the rest area occurred on the inside bar at the mouth of Emerson Bay, and

Figure 9. Combined daily movement rates of monitored walleye

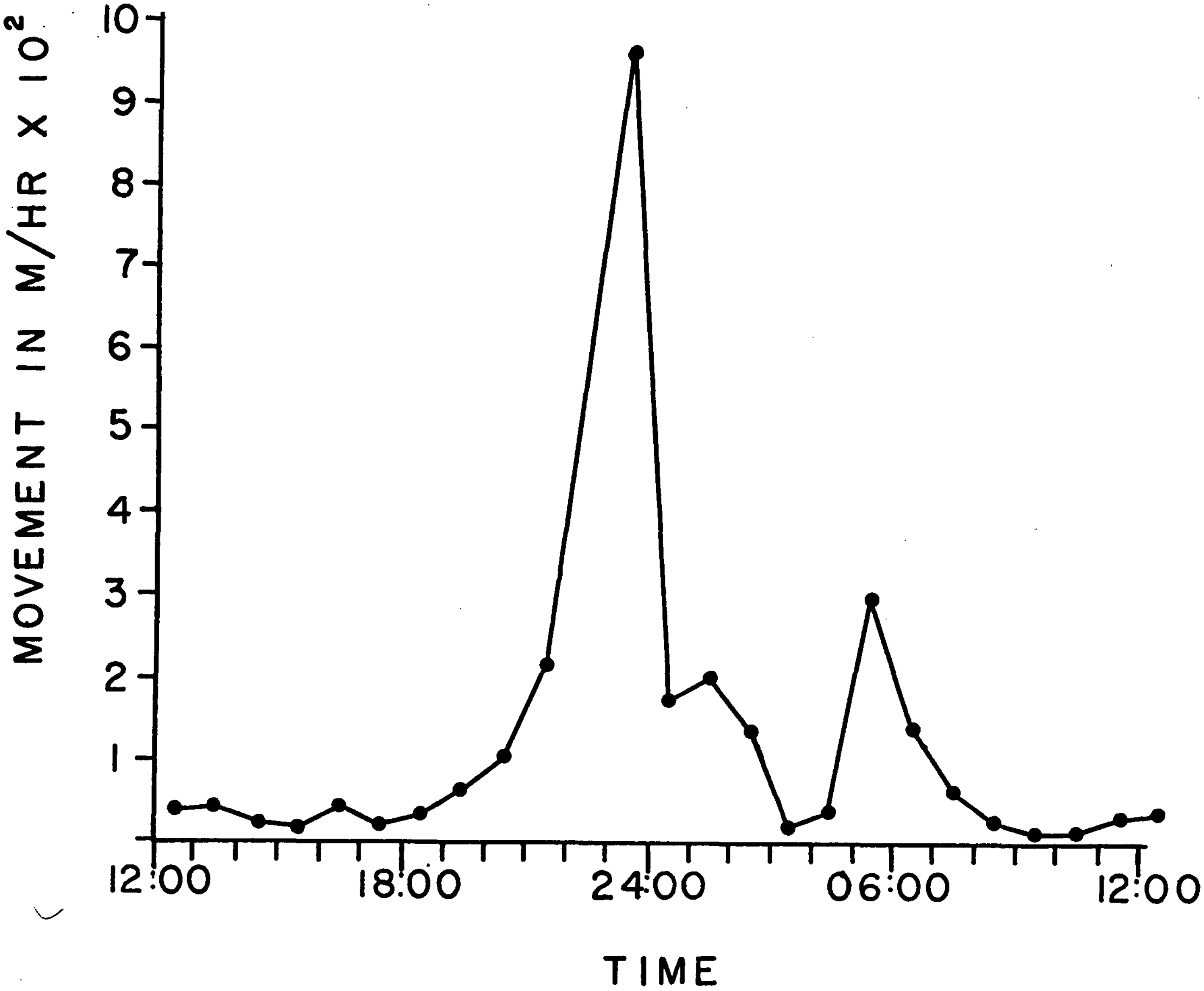

MOVEMENT IN M/HR X 10^2
10
9
8
7
6
5
4
3
2
1
12:00
18:00
24:00
06:00
12:00
TIME

Figure 10. Movements in and out of a rest area for fish 55

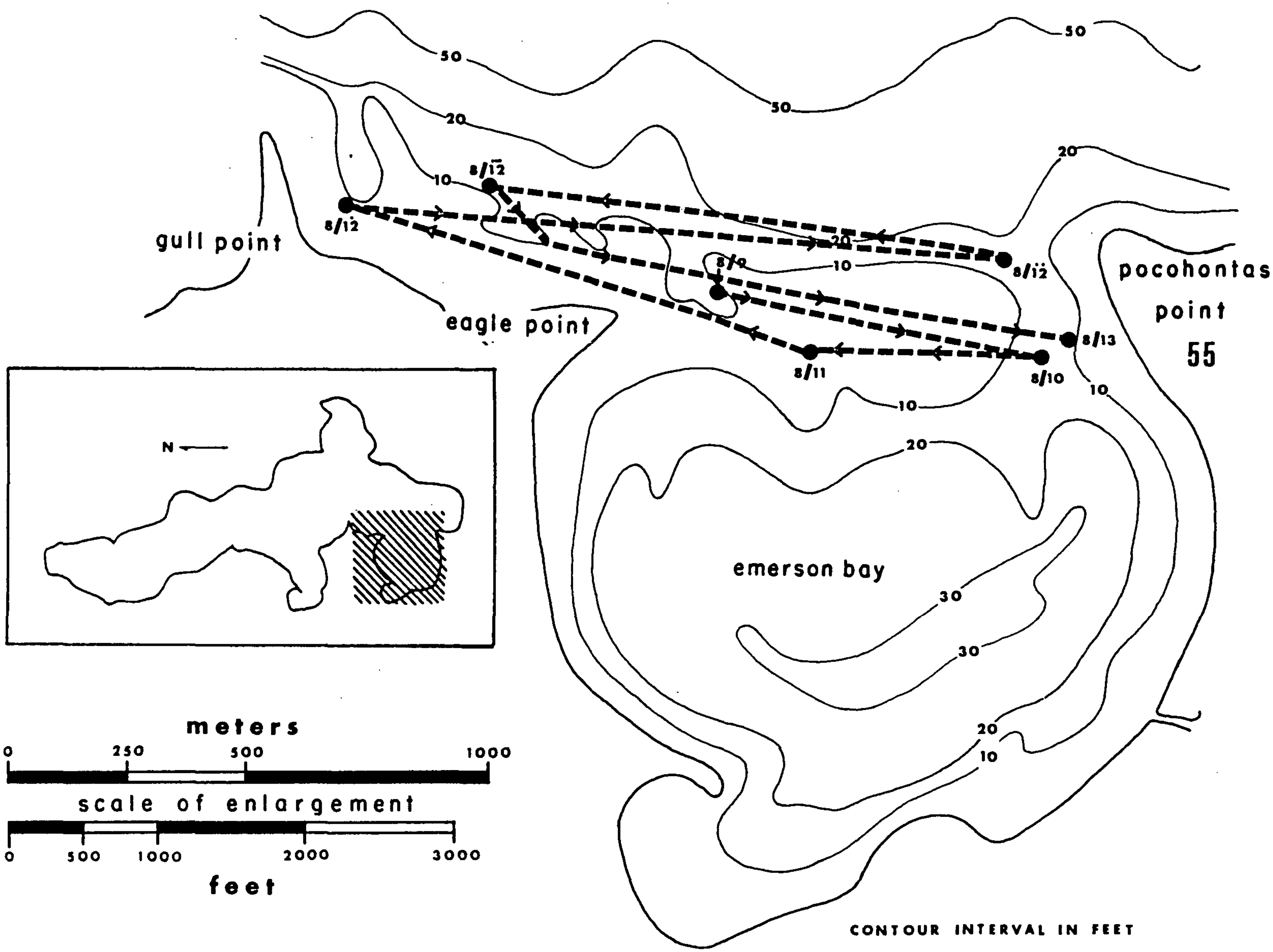
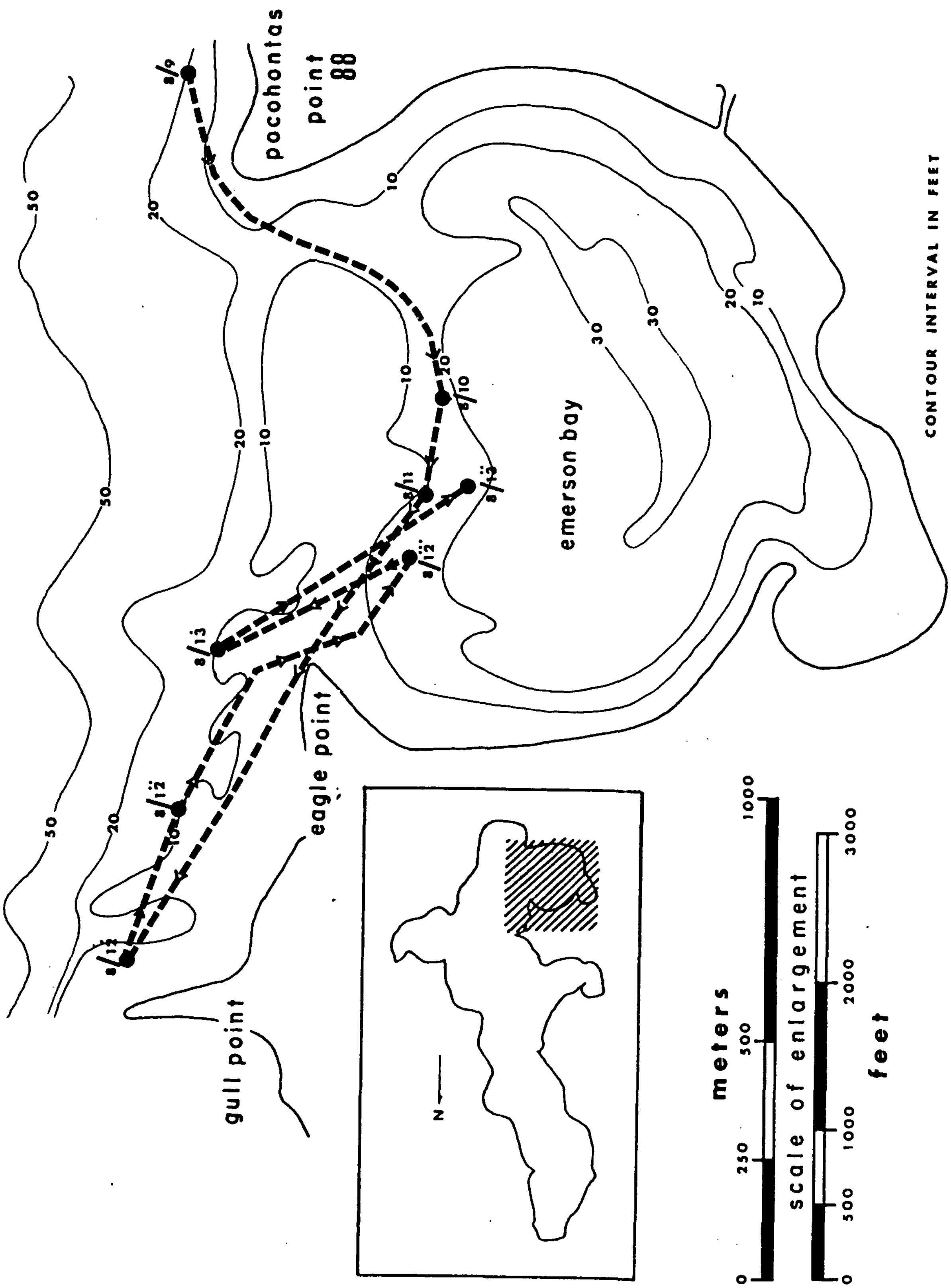

gull point
eagle point
pocohontas
point
55
emerson bay
8/12
8/12
8/12
8/9
8/11
8/10
8/13
50
20
10
30
N
meters
0
250
500
1000
scale of enlargement
0
500
1000
2000
3000
feet
CONTOUR INTERVAL IN FEET

Figure 11. Movements in and out of a rest area for fish 88


pocohontas
point
88
emerson bay
eagle point
gull point
CONTOUR INTERVAL IN FEET
meters
scale of enlargement
feet
N
50
20
10
30
8/9
8/10
8/11
8/12
8/13
0
250
500
1000
2000
3000

the foraging area was between Gull and Eagle Points.

The activity centers of fish 55, 66 and 88 broadly overlapped near the mouth of Emerson Bay as did the centers of fish 00 and 77 in the north end. However, no group movements or schooling of these fish was observed, even when at times tagged fish were in close proximity to each other.

Fish depth and temperature

Fig. 12 shows the water depths that the individual shallow water fish occupied. Grouping of individual depth records for shallow water fish show that 92 per cent of the observations were between the 2-6 m depths (Fig. 13).

To evaluate walleye depth distribution in response to light intensities, I plotted fish depth against time of day, assuming that light intensity would peak near midday and be minimal near midnight. Linear regression analysis of this relationship indicates the slope (b) for both the shallow and deep water fish is significant at the $p = 0.01$ level (Fig. 14). Fish occupied shallower waters during the nighttime periods and deeper waters during daytime periods (Fig. 14). Only data from clear days were used as clouds and waves tended to mask the response.

Individual tagged walleye could usually be recorded on the Grapher-Recorder unless the fish was within a heavy bed of rooted aquatic vegetation. Walleye were usually within 1 m of the lake bottom, many times suspended next to such plant

Figure 12. Depth records of individual fish ($\bar{x}$ is a weighted mean depth)

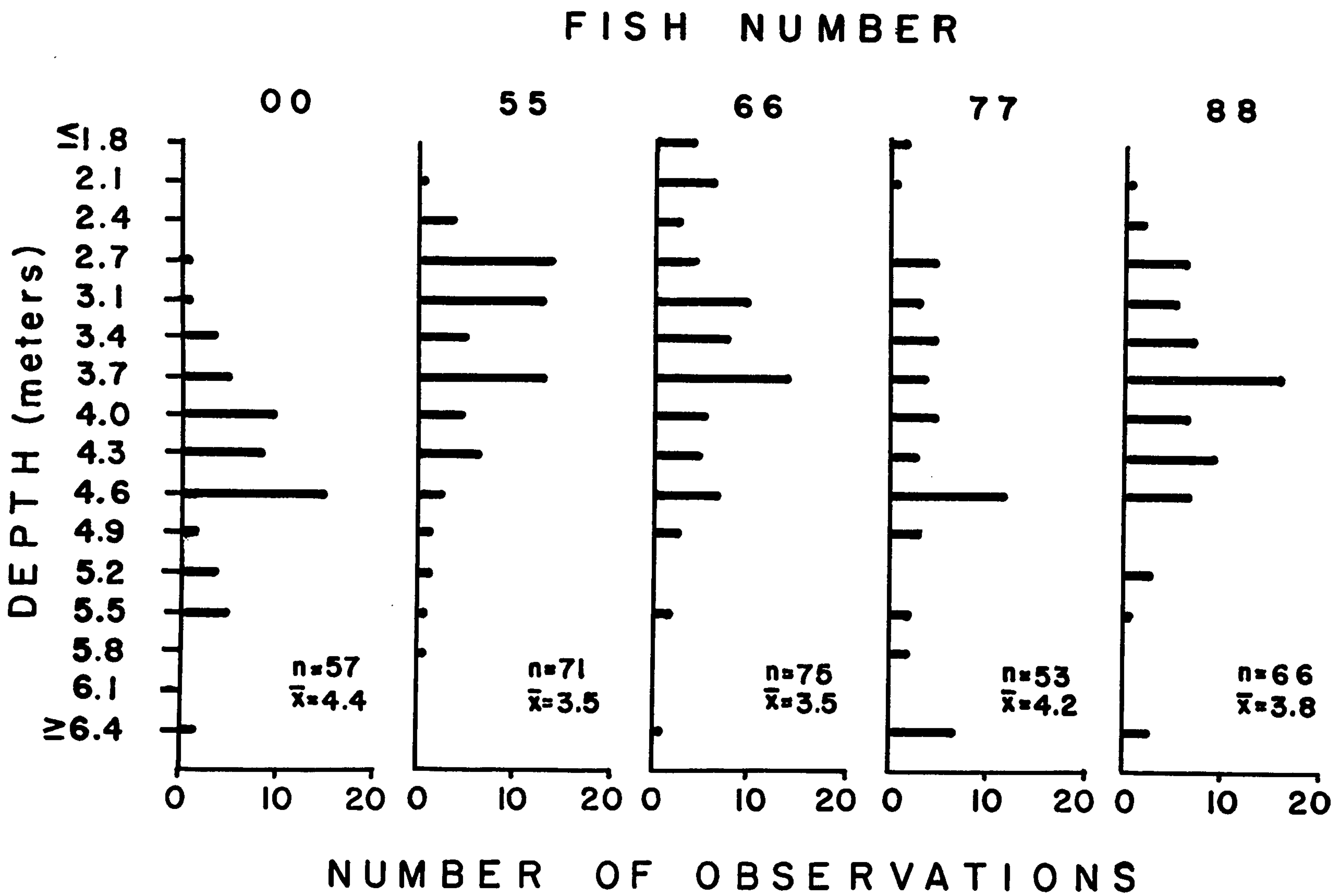

FISH NUMBER
00
55
66
77
88
DEPTH (meters)
≤1.8
2.1
2.4
2.7
3.1
3.4
3.7
4.0
4.3
4.6
4.9
5.2
5.5
5.8
6.1
≥6.4
n=57
x̄=4.4
n=71
x̄=3.5
n=75
x̄=3.5
n=53
x̄=4.2
n=66
x̄=3.8
0
10
20
NUMBER OF OBSERVATIONS

Figure 13. Combined depths of the five shallow water fish

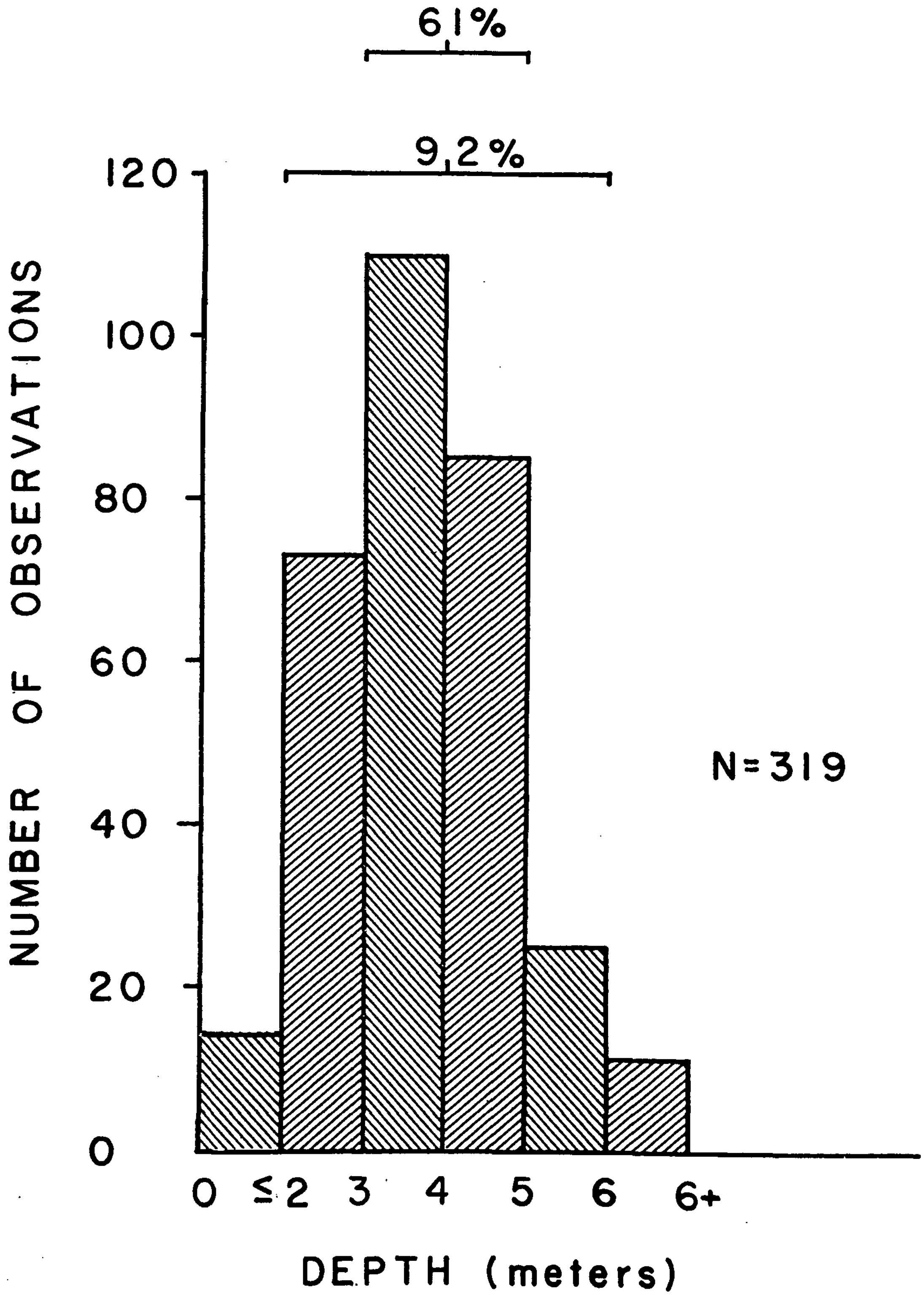
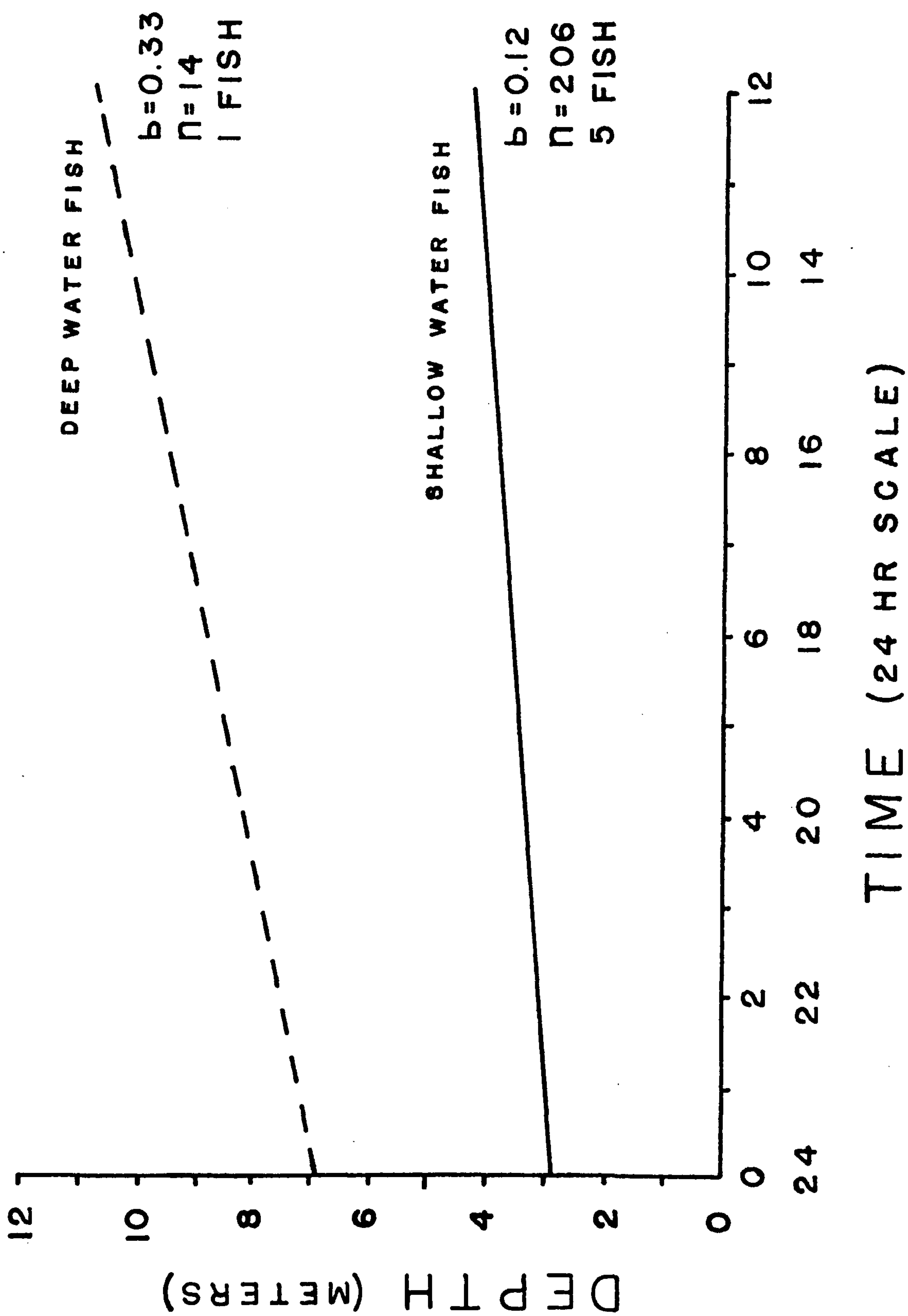

6.1%
9.2%
120
100
80
60
40
20
0
NUMBER OF OBSERVATIONS
N=319
0 ≤2 3 4 5 6 6+
DEPTH (meters)

Figure 14. Linear regression of fish depth vs. time (or light intensity)


DEEP WATER FISH
b=0.33
n=14
1 FISH
SHALLOW WATER FISH
b=0.12
n=206
5 FISH
DEPTH (METERS)
0
2
4
6
8
10
12
0 2 4 6 8 10 12
24 22 20 18 16 14
TIME (24 HR SCALE)

beds.

The average monthly summer body temperature of shallow water fish 00, 55 and 88 as determined from the temperature transponding transmitters is shown on Table 6. Throughout the summer the three fish occupied a narrow temperature range, which was dictated by their depth distribution (Fig. 15). The mean body temperature of the fish was 21.9 °C (71.5 °F), and most observations ranged between 20 and 25 °C (Fig. 15). There were no recorded body temperatures above 25 °C (77 °F), but temperatures below 20 °C (68 °F) were noted both early and late in the season. The warmest body temperatures occurred in July (Table 6).

Other environmental parameters and response to outboard motors

Statistical analysis of fish movement and depth with several other environmental parameters such as barometric pressure, sky cover, secchi disc depth and wind conditions failed to produce any significant relationships.

The tracking boat as well as other outboard powered boats were driven directly over a fish to determine the response to motors. When fish were in waters shallower than about 3 m, motor noise, even at a low idle, caused the fish to move. Movement was not great, however, usually being 3-6 m to either side of the boat's path. If fish were in deeper water, outboard motor noise did not seem to affect them.

Table 6. The average June, July and August fish temperatures as recorded from the temperature transponding transmitters

Fish no.	Transmitter no.	June	n	July	n	August	n	Mean
00	T9	20.0[a]	11	23.3	23	22.5	14	21.9
		68.0[b]		74.0		72.5		71.5
55	T8	20.3	10	23.3	27	22.5	19	22.0
		68.5		74.0		72.5		71.6
88	T7	19.7	8	23.0	29	22.8	19	21.8
		67.5		73.3		73.0		71.3
Mean		20.0		23.2		22.6		21.9
		68.0		73.8		72.7		71.5

[a] Degree Centigrade

[b] Degree Fahrenheit

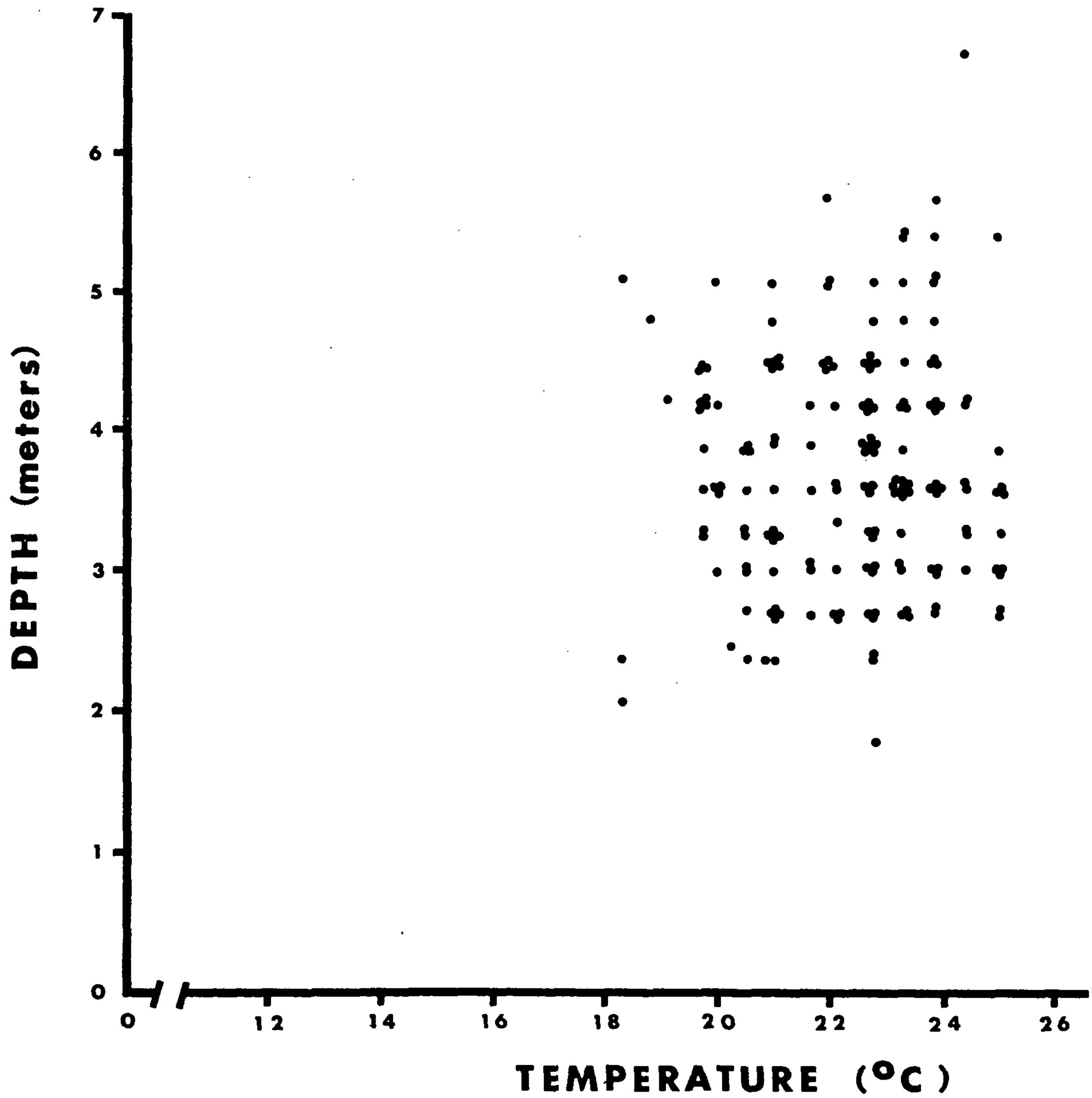


Figure 15. Temperature and corresponding depth for the three temperature sensitive transmittered fish

Exploratory Movements

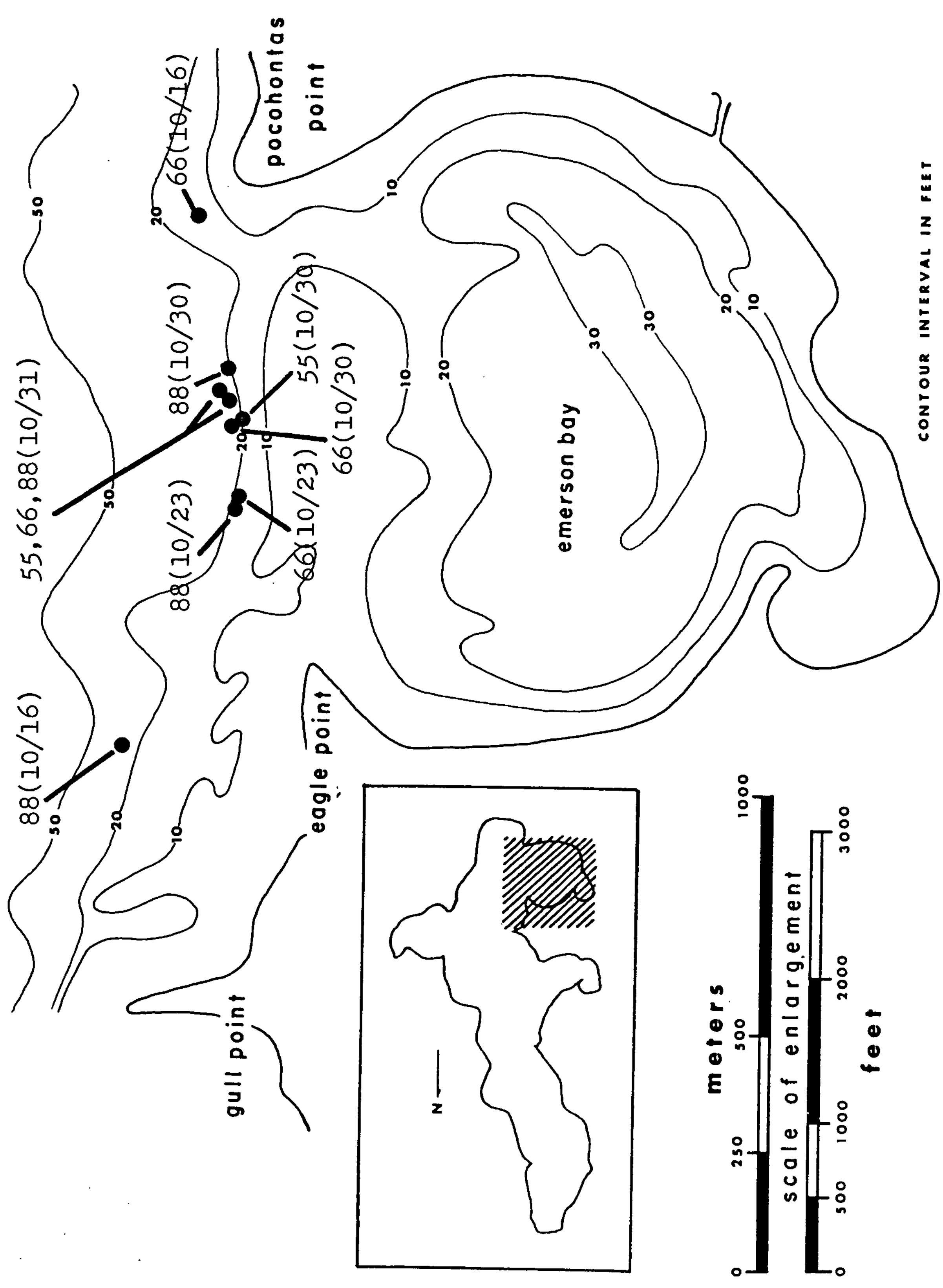
Exploratory excursions involved movement out of the activity center for a period of one to two days followed by direct travel back to the activity center. The distance that fish moved beyond the boundaries of the activity center was substantial, approximately 1500 m roundtrip for fish 77 and 4,800 m roundtrip for fish 00. Environmental parameters were examined, but the stimulus for the behavior remains unknown.

Late Fall and Winter Movements

In late October, as the water cooled and the aquatic vegetation died, the fish began to abandon their shallow water summer activity centers in favor of deeper waters. Fish 55, 66 and 88 were found in close proximity to each other and moving together on the outside bar between Eable Point and Pocohontas Point in 6-7 m (20 to 25 ft) of water (Fig. 16). On a number of October tracking efforts, these fish were so close together that individual signal recognition became difficult. Fish 00 and 77 also moved to deeper water just outside their respective summer activity centers but were not close together at this time.

In late December and early January, fish 00 and 77 were located a considerable distance south of their summer activity centers. Both fish were in close proximity to each other in 9-10 m (30 to 35 ft) of water on a rock reef near Pillsbury Point and the mouth of Smiths Bay. Fish 55, 66 and 88 were

Figure 16. Late fall locations of fish 55, 66 and 88 (October 16,23,30 and 31)



66(10/16)
pocohontas point
88(10/30)
55(10/30)
66(10/30)
55,66,88(10/31)
88(10/23)
66(10/23)
88(10/16)
eagle point
gull point
emerson bay
50
20
10
30
CONTOUR INTERVAL IN FEET
N
meters
0
250
500
1000
scale of enlargement
feet
0
500
1000
2000
3000

not relocated under the ice despite extensive search operations around the mouth of Emerson Bay as well as the entire lake. These three fish were relocated, however, in spring, 1977, after iceout, revealing that transmitters were functional during iceover but were not detected.

Evaluation of Tracking Apparatus

Of the six transmitters regularly monitored during the study period, four were temperature transponding types and two were fixed pulse types. Three temperature transponding transmitters and two fixed pulse transmitters remained functional into spring, 1977. One temperature transponding transmitter (fish 77), recovered from a previous study and refurbished by the manufacturer, ceased to function as a temperature transponding type in June, as its pulse rate became stable, but was utilized as a fixed pulse transmitter. Thus, four transmitters remained functional in fish as of June, 1977, well over one year of operational life (Table 2).

Maximum signal transmission was obtained during early spring and late fall when water temperatures were homogenous and aquatic vegetation was sparse or non-existent. Reception distances in excess of 1.5 km were not uncommon during these time periods. The major problem with reception occurred when the fish were in heavy beds of rooted aquatic vegetation. Under such circumstances, transmission range was reduced to about 50 m. Cold water also reduced reception distances to about 50 m resulting in the inability to find three fish (55, 66 and 88) during the iceover period. Wave action, thermal stratification and external interference also tended to reduce transmission range.

DISCUSSION

Comparison of Fish Tracking Methodologies

A variety of methods have been utilized to attach a transmitter to a fish. The three most common are: 1) external attachment by pins or wire through the dorsal musculature, 2) oral insertion into the stomach, and 3) surgical implantation into the coelom. External attachment is more commonly used for radio transmitters as they need an antenna, however, all three methods have been used to attach ultrasonic transmitters.

Two reports indicate that oral insertion into the stomach is not a satisfactory method of transmitter attachment for walleye. Ager (1976), in evaluating both oral and surgical insertion, reported that all six walleye studied regurgitated stomach inserted transmitters within 24 hours. Morris (1977) found that among 32 walleye with orally inserted sham transmitters, 28 regurgitations occurred in less than a 10 hr period.

The existing evidence for evaluation of external or surgical attachment, however, is not as definitive as that of oral insertion. Fossum (1975), Bahr (1977) and Holt et al. (1977) used external attachment without major problems. One walleye with an external transmitter was at large for 214 days before being recaptured by a commercial gill net (Bahr, 1977). Morris (1977) reported that of 33 walleye with externally attached sham transmitters, none retained the transmitters after six months in a weedy hatchery rearing pond. He also found that of 33 walleye with surgically implanted sham transmitters, only two retained their transmitters after six months in the same pond. According to Ager (1976) one walleye with a surgically implanted transmitter was at large for 190 days and one for 430 days before being recaptured by anglers. This present study has documented four walleye at large over 427 days after surgical implantation (Table 2).

Both external attachment and surgical implantation techniques seem to have advantages and disadvantages. The disadvantages of the former method include hydraulic drag, entanglement, extra weight and external irritation of the harness assembly. The major advantage is that transmitter attachment can be accomplished quickly, with a minimal amount of stress on the fish. The disadvantage of surgical implantation is the initial attachment procedure, which increases stress on the fish. After the wound has healed, however, the surgical method has none of the disadvantages of the external method. Morris (1977) concluded that the benefits of external attachment are outweighed by its undesirable characteristics. Additionally, he reported that once the incision has healed in the surgical method, permanent transmitter attachment has been achieved, whereas an externally attached transmitter might be shed at any time.

In the present study, surgical implantation worked well when performed in such a manner as to remove the fish from the lake only long enough to complete the surgery, followed by immediate release of the fish at the capture site. When handled in this manner, no mortality occurred, their movement upon release was restricted to a local area, and activity centers, which included the capture/release site, were established early. In contrast, fish that were transported, implanted, held for observation, and then released at random locations, wandered around the lake upon release before establishing activity centers and none returned to the release site. Additionally, three *Saprolegnia* related deaths occurred during the observation period, and three fish were never located after release. The increased stress due to transporting, holding and treating can be eliminated with an effective surgical method, increasing the survival of surgically implanted walleye.

The loss of three experimental fish after release could be attributed to: 1) mortality due to the incomplete recovery from the *Saprolegnia* fungus infection, 2) transmitter malfunction, 3) capture by angler and tag not returned, or 4) fish movement into an adjoining water body. Fish mortality appears to be the most likely explanation as: 1) the transmitters were operational upon release and no other transmitter malfunctions were observed, 2) the study received considerable publicity, with many anglers, bait shops, and resort owners aware of it, 3) connecting waters were searched extensively and fish were not relocated. Additionally, gill netting by Iowa Conservation

Commission hatchery crews in the spring of 1977 failed to recapture any tagged walleye in connecting waters while recapturing two tagged walleye from West Lake Okoboji. It is probable that when a fish died, the windblown body was deposited on shore where the transmitter became buried in sand. Consequently, it would have been impossible to detect a signal as ultrasonic signals need to be transmitted through a liquid medium.

Walleye Activity Centers in Different Habitats

Several recent biotelemetry studies have shown conflicting results concerning walleye activity center (home range) establishment. Fossum (1975) stated that Mississippi River walleye did not appear to show preference for a particular locality and did not repeatedly return to a specific habitat or home territory. He found that it was common for walleye to cruise approximately 24 km^2 in a few days and to swim large, circular loops within Sturgeon Lake, a backwater area, before eventual loss of transmittered fish into the main channel of the Mississippi River. Lengths of the tracking periods were short, however, most being two to three days, with a maximum of five days. This may not have been enough time for fish to exhibit or establish a home area.

Similarly, Bahr (1977) did not report establishment of home areas for Mississippi River walleye. Rather, the study fish appeared to move at random, ranging from Lock and Dam 6 downstream to Lock and Dam 8, a distance of 56.3 km. Three walleye which were displaced 11.27-13.68 km from the capture site, a spawning area, all exhibited homing behavior by returning to the spawning/capture site.

Ager (1976) found that of 18 walleye tracked for more than 10 consecutive days, nine established home ranges in Center Hill Reservoir, Tennessee. His definition of home range was that area which was repeatedly traversed by a fish during a monitoring period. He found home range size to be twice as large during winter (29.5 to 75.6 ha) as during summer (11.8 to 33.7 ha). Of the nine fish that did not establish home ranges, seven were tracked during the spring and autumn months, a period when no home ranges were established. Six of the nine walleye that established home ranges were displaced from the capture site a distance of 4.0-9.3 km to determine homing. Subsequently all returned to establish a home area inclusive of the capture site. Three walleye that were not displaced also established a home area which included the capture site.

Holt et al. (1977) found that walleye tended to inhabit particular areas in Lake Bemidji, Minnesota, but individual fish did not establish home areas. They stated that there appeared to be little relationship between the location of the release point and the areas of the lake to which test fish moved after release.

West Lake Okoboji walleye established activity centers from mid-June through mid-October in agreement with the findings of Ager (1976). Three walleye that were released at known capture sites established activity centers which included those sites. In contrast, none of the three walleye that were released at random locations, without knowledge of capture site, included the release site within the eventual activity center boundaries. It is possible, but unresolved, that these fish returned to their original activity centers.

The available evidence suggests that walleye differ in their tendency to establish activity centers according to local habitat. Both Fossum (1975) and Bahr (1977) report random movement patterns among Mississippi River walleye. Ager (1976) and the present study have found that reservoir and lake walleye tend to establish activity centers (home areas). Although Holt et al. (1977) did not report similar behavior among Lake Bemidji walleye, the fish did tend to inhabit particular areas of the lake. Ryder (1977), using SCUBA, observed most walleye swimming in portions of lakes where perceptible currents existed. It is possible that currents, rising and falling water levels, higher turbidity and a generally less stable environment all contribute to the wandering behavior displayed by river walleye.

Establishment of activity centers (home areas) has also been documented for lake or impoundment populations of flathead catfish, Pylodictis olivaris, (Hart and Summerfelt, 1973), largemouth bass, Mictopterus salmoides, (Warden and Lorio, 1975; Winter, 1977; B. W. Menzel, Dept. of Animal Ecology, Ia. St. Univ., Ames, Iowa, personal communications), and muskellunge, Esox masquinongy, (Crossman, 1977). These fish are all predacious, and it is possible that knowledge of a specific area aids the fish to find food, cover and safety.

The establishment and active use of disjunct activity centers by fish 00 has not been previously documented for walleye. However, B. W. Menzel (personal communications) has observed similar behavior among largemouth bass in Big Creek Reservoir, Polk County, Iowa.

Movement Patterns

Seasonal movements

Ager (1976) stated that highest rates of walleye movement were observed during the winter months, and lowest rates were observed during spring and early summer. Holt et al. (1977) found no significant differences in the mean daily distances that walleye moved during three seasons (spring, summer and fall) or between two tracking years. On the basis of gill-net catches Schupp (1972) reported that spring and fall marked walleye of Leech Lake, Minnesota, were recaptured farther away from the release site than summer marked walleye.

In the present case, walleye that were released at random locations in early May moved considerable distances before establishing activity centers by mid-June. It appears that establishment of an activity center reduced wandering since less movement was observed during the summer period. It is possible that greater movements in the spring are a combination of pre- and post-spawning movements and search for or homing to an activity center. Schupp (1972) suggested that daily movement of walleye during the summer months was inversely related to the abundance of young-of-the-year yellow perch (Perca flavescens). He reported that when young-of-the year yellow perch were readily available, summer marked walleye were recaptured closer to the release site than spring and fall marked walleye. Forney (1974) found that walleye in Lake Oneida, New York, began feeding on young perch late in June, and Schupp (1972) reported that young perch did not appear on the shoals and in trawls until late June. If this relationship held true for Okoboji walleye, food abundance may not be related to reduced summer movement as some activity centers had already been established by mid-May and all were established by mid-June. It is difficult to ascertain whether establishment of activity centers during the summer period, and hence, decreased movement, is in response to forage concentration or abundance, habitat availability or to other stimuli.

Abandonment of summer activity centers in late October in favor of deeper waters by Okoboji walleye increased the movement during the fall period which agrees with Schupp (1972) and Ager (1976). I believe that as water temperatures declined aquatic vegetation died and algal blooms decreased, resulting in increased light penetration. With no cover available to decrease light intensity walleye moved to deeper waters in a phototrophic response. It is also possible that the fish were following a forage resource as Eschmeyer (1950) found that Michigan walleye were generally located at the depth of their forage and Rawson (1956) found that Lac La Rounge, Saskatchewan, walleye were most often caught in deep water when ciscoes, the most abundant food item of walleyes, were numerous in the 15 to 20 m depths.

Diurnal movements

Eschmeyer (1950), Rawson (1956), Ager (1976) and Holt et al. (1977) stated that walleye move more at night than during the day. My findings agree with these earlier observations. The bimodal pattern (Fig. 10) of the nocturnal movements observed here has also been documented by Carlander and Cleary (1949), Sieh and Parsons (1950) and Fossum (1975). However Bahr (1977) reported four distinct modes in activity: at 02:30, 16:30, 11:30 and 18:30, with the highest peak at 02:30.

The increased activity of walleye at night has been primarily attributed to food foraging. Sieh and Parsons (1950) suggested that walleye in Clear Lake, Iowa, came into shore at night to feed and Lake of the Woods, Minnesota-Ontario, walleye fed and were most active primarily at night during July through September (Swenson and Smith, 1973). Fossum (1975) visually observed transmittered walleye chasing schools of minnows while displaying zig-zag movement. Although foraging could not be directly observed in the present study, the occurrence of zig-zag movements with increased nocturnal activity suggests feeding behavior. This behavior was observed both close to shore and at the deep water edge of the weedline, indicating that both shallow shorelines and deeper waters were utilized as foraging areas. This agrees with Harlan and Speaker (1969) who stated that nighttime feeding may occur in nearshore shallow water or in deeper water, according to the seasonal availability of food. According to Crum and Bachmann (1973) the outer weedline in West Lake Okoboji varies between 5-6 m.

One method fisheries investigators have used to capture walleye is to set gill nets perpendicular to shore. That this is an effective means of capturing walleye is reflected by a number of telemetry studies. Fossum (1975) stated that walleye spent the majority of the time traveling the shoreline in waters 1.5-3.0 m in depth. Holt et al. (1977) found that test fish moved chiefly parallel to the shore at depths of 1.6-5.0 m. Ager (1976) indicated that walleye remained more than 30 m offshore 60 per cent of the time, but no pattern was established that indicated a depth preference. The results of the present study agree most closely with those of Fossum (1975) and Holt et al. (1977) in that West Lake Okoboji walleye moved primarily parallel to shorelines or to bars that extended between two major land points at 2-6 m depths. Many of the movements along a shoreline or bar were along a specific contour interval. This indicated that the fish either preferred certain depths or that they were using some type of underwater structure such as weedlines as guides for travel lanes.

Exploratory excursions

Exploratory excursions out of the activity center were documented for fish 00 and 77. Environmental parameters were examined, but no factors could be found that would explain this type of movement. Largemouth bass in Big Creek Reservoir have shown similar excursions (B. W. Menzel, personal communications). It is possible that walleye were searching for a more attractive activity center during these exploratory excursions. These excursions also add an unexpected dimension to the aspects of "homing" by fishes. For example, if a fish was captured while on one of these excursions and displaced from the capture site with the assumption that the capture site was within the "home area," the results would be erroneous. I propose that the best method to demonstrate "homing" is to allow the fish some time to establish a "home area" and then to recapture and displace the fish to see if it returns.

Habitat Features

Temperature and depth

The literature suggests that walleye occur over a rather broad range of water temperatures. Dendy (1945) concluded that 21.2-26.6 °C (70-80 °F) was the preferred summer temperature range of walleye in Norris Reservoir, Tennessee. Regier et al. (1969) stated that walleye in Western Lake Erie prefer summer temperatures from 21.1-22.2 °C (70-72 °F).

Temperatures of approximately 12-18 °C (54-64 °F) were preferred by walleye in Center Hill Reservoir, Tennessee (Ager, 1976) over a period of one year. Kelso (1976) showed that walleye chose temperatures between 10.6-11.2 °C (51-52 °F) during September and October in West Blue Lake, Manitoba. Hokanson (1977) stated that the physiological optimum temperature for walleye is 22 °C. The summer body temperature for walleye in the present study ranged between 20-25 °C (68-77 °F), with a mean summer temperature of 21.9 °C (71.4 °F) which compares most closely with Regier et al. (1969) and Hokanson (1977).

A considerable amount of literature has been written concerning walleye summer depth preferences and factors affecting those preferences. Dendy (1945) found temperature to be more significant than light intensity in the depth distribution of walleye. He found that as summer progressed and surface waters warmed, walleye distributed themselves in deeper waters, unless forced into warmer water by oxygen depletion. In contrast, Regier et al. (1969) stated that depth distribution in walleye was determined more by light intensity than by any other factor if dissolved oxygen was not limiting. The preferred summer depths of walleye in some of the recent telemetry studies agree quite closely. Fossum (1975) observed that the most common depth traveled by walleye ranged from 1.5 m to over 3.0 m, and Ager (1976) stated that during summer months, walleye were most often found in shallow waters at the heads of tributary embayments. Kelso (1976) stated that walleye chose depths between 5 m and 10 m during late September and early October, and Bahr (1977) found that walleye had a preference for water depths of less than 5 m. Holt et al. (1977) found that walleye remained chiefly within the littoral zone above the 5 m contour level. Additionally, they stated that turbidity fluctuations appeared to have little influence on the depth distribution of walleye. In agreement with the previous walleye telemetry studies, five walleye studied here were distributed at relatively shallow depths (2-6 m) during the summer period. These fish were observed at deeper depths both in the spring and again in late fall. They did not appear to specifically select the depths and temperatures at which they were observed. Rather it seems that the distribution of rooted aquatic vegetation, which the fish selected to occupy, dictated the observed depths and temperatures.

Eschmeyer (1950) reported that walleye show a strong negative phototropism. Ager (1976) indicated that light penetration was a significant factor governing both the depth and temperature selection of walleye. In contrast, Holt et al. (1977) stated that test fish did not show as strong a negative phototropism as reported by Eschmeyer (1950). Results from the present study indicate that light intensities played an important role in walleye behavior as fish were generally passive in beds of aquatic vegetation during the daytime period and were most active in shallower and unshaded waters during periods of diminished light intensities. This agrees with Ryder (1977) who suggested that diel light regimes govern much of the walleye metabolic activity.

Ryder (1977) noted that walleye can reduce the light intensities that reach them by 1) swimming to deeper water, 2) swimming to a more turbid portion of the lake, and 3) remaining in shallow water and utilizing shelter such as boulders or weed beds. Since establishment of a discrete activity center reduces movement, the option of moving to a more turbid portion of the lake was not observed in the present study. However, both movement to deeper waters and shelter in shallow waters occurred. The increased depth with increasing light intensities (Fig. 15) among Okoboji walleye was smaller (.12 m/hr) for shallow water fish than for the deep water fish (.33 m/hr). It appears that shallow water fish utilized the rooted aquatic vegetation to reduce light intensities. This behavior would keep fish from moving into deeper waters as abundant aquatic vegetation occurred at the 2-6 m depths. The deep water fish apparently depended upon the water column to reduce light intensities and as such, made larger vertical movements in the deeper water.

Although only one fish selected deep water, the selection of two different depth regimes during the same time period raises a number of behavioral questions. It is possible that 1) a shallow water and a deep water group of walleye exist in

West Lake Okoboji, 2) walleye are highly individualistic, with some selecting deep water to reduce light intensities and others selecting shade in shallow waters, 3) some walleye are more sensitive to higher water temperatures and select the deeper, cooler waters, 4) the presence of a transmitter changed the normal behavior of the fish.

Vegetation and substrate

The rooted aquatic vegetation within the activity centers was an important habitat feature. It provided the fish with cover, resting areas, and food.

The distribution of fish locations in relation to lake morphometry also indicates the importance of the aquatic vegetation. Where the lake bottom slopes downward rapidly and the band of vegetation is narrow, the fish locations were also concentrated in a narrow band. Where the lake bottom slopes gently and the aquatic vegetation grows in a wide band, fish locations were much more scattered. Fig. 2 and 3 provide examples.

An interesting aspect of aquatic macrophyte growth became apparent as the summer progressed. The lower leaves and branches died, presumably as a result of shading by new growth as well as by accumulations of marl deposits. As the dead leaves and branches fell from the main stem, a space of up to .6 m (2 ft) was created between the substrate and the lowermost living branches of the plant. This resulted in a habitat comparable to a canopied forest where fish can rest or move about freely in the open spaces and still be protected from light intensities.

Since the littoral zone is largely determined by water clarity, it is probable that in more turbid lakes with shallower growths of aquatic vegetation, walleye may be found at shallower depths and vice versa, other factors not limiting.

Creel surveys indicate that the walleye catch in West Lake Okoboji generally decreases as the summer progresses (Christianson, 1978). It is possible that an inverse relationship exists between aquatic vegetation growth and walleye catch. As aquatic vegetation becomes more dense, lures and baits become entangled and are less visible resulting in decreased catch rates.

Okoboji walleye tended to select hard substrate such as sand, gravel, marl, rubble, rock reefs, and boulders. This agrees with the findings of Eschmeyer (1950), Regier et al. (1969), Rose (1969) and Marshall (1977).

Regier et al. (1969), Dendy (1945), and Ager (1976) indicated that walleye are closely associated with the substrate. The results from the present study agree with those investigators, insofar as depth recorder images suggested that walleye preferred to stay on or within a meter of the bottom.

The results of the present study indicate the importance of the hard bottomed littoral zone in walleye behavior, habitat selection, and movement in West Lake Okoboji. Establishment of an activity center within and including dense growths of aquatic vegetation provides walleye with cover, food, travel lanes at the edges, sufficient oxygen, and a temperature regime within their tolerance range.

Schooling Behavior

According to Harlan and Speaker (1969) and Ryder (1977), walleye associate in loose aggregates or schools. In contrast Bahr (1977) noted that there appeared to be no schooling or congregative behavior of telemetered walleye. Holt et al. (1977) did not record schooling, but indicated that on several occasions tagged fish were seen swimming with unmarked walleye. Fish in the present study appeared to be alone when occupying their summertime activity centers. Although the activity centers of fish 55, 66, and 88 overlapped as did those of 00 and 77, and the fish were at times found in close proximity to each other, no unified movements were observed. Additionally, of the numerous times that tagged fish were recorded on the depth grapher, only rarely were additional large fish also noted. An exception to this was the deep water fish (99). On a number of occasions, up to eight other fish, presumably walleye, were seen in close association with it. This suggests that schooling may occur in deeper waters and that schooling behavior may be partially by sight, as fish in dense weed growth would quickly lose contact with each other.

In late October, fish 55, 66 and 88 were close together in deeper water indicating schooling behavior. In late December and early January, fish 00 and 77 were also in deeper waters and close together. It is possible that schooling among Okoboji walleye occurs only in deeper waters during both the summer and winter periods.

Other Environmental Parameters

Fishermen generally believe that increased fish catches occur with changing barometric pressures, weather changes, and solunar periods. A number of fisheries investigations have tried to correlate fish activity with changing environmental parameters.

Sieh and Parsons (1950) found no correlation between fish activity and barometric changes, wind, sky cover and solunar periods. On the basis of increased gill net catches, Carlander and Cleary (1949), found increased movement at the start of rainstorms. However Ager (1976), noted sharp decreases in walleye activity during thunderstorms. Holt et al. (1977) stated that presence of overcast skies and precipitation coincided with extensive movements of tagged fish, particularly during the spring and fall seasons. Additionally, transmittered fish exhibited a tendency to move in the same direction as the wind, especially when strong winds traveled parallel with the long axis of the lake. Bahr (1977) noted that increasing water levels during spring run-off did not affect walleye behavior. In the present study, correlations between fish movement and barometric changes, wind, sky cover, and water transparencies failed to produce any statistically significant relationships, although some trends were apparent. For example, increased barometric pressures tended to reduce movement and increase fish depth. The failure to find statistical significance in this trend may be due to small sample sizes, or perhaps the relationship is too complex to be revealed by my measurements and analyses. Statistical analysis indicated that walleye are individualistic, as much of the variability in the analysis was due to fish differences and not the tested parameters.

Late Fall and Winter Movements

Ager (1976) found that walleye occupied the deeper channel areas of major tributaries in Center Hill Reservoir, Tennessee during fall and winter months. My findings agree with the results of the Ager (1976) study in that fish were located in deeper water during fall and winter months. Additionally, Okoboji walleye had moved considerable distances from their summer activity centers and were close together, indicating schooling behavior. The nomadic movements observed here during early spring and fall indicate that the entire lake may be utilized during a one year period. Although not documented, it is possible, in the light of these nomadic excursions, that movement in and out of adjoining water bodies occurs.

Transmitter Performance

Fossum (1975), Bahr (1977), and Morris (1977) all indicate that short battery life was one of the disadvantages of ultrasonic transmitters when compared to radio transmitters. I encountered no such problems, as four of the six ultrasonic transmitters that were accounted for lasted in excess of one year, much longer than a number of the documented radio transmitter longevities.

The ultrasonic transmitters used in the present study have performed to manufacturer's specifications, with a longevity that would enable movement and behavior studies to encompass the time period from one spawning season to the next. As such, these ultrasonic transmitters have the capacity for long term behavioral studies on walleye as well as many other fish species.

LITERATURE CITED

Ables, E. D. 1969. Home-range studies of red foxes (Vulpes vulpes). J. Mammal. 50:108-120.

Ager, L. M. 1976. A biotelemetry study of the movements of the walleye in Center Hill Reservoir, Tennessee. M.S. Thesis. Tenn. Tech. Univ., Cookeville, Tenn. 97 pp.

Bachmann, R. W., and J. R. Jones. 1974. Water quality in the Iowa Great Lakes. Iowa Great Lakes Water Quality Control Plan Report. 573 pp.

Bachmann, R. W., R. V. Bovbjerg and J. D. Hall. 1966. The morphometry of West Lake Okoboji. Proc. Iowa Acad. Sci. 73:165-168.

Bahr, D. M. 1977. Homing, swimming behavior, range, activity patterns and reaction to increasing water levels of walleye (Stizostedion vitreum vitreum) as determined by radio-telemetry in navigational pools 7 and 8 of the upper Mississippi River during spring 1976. M.S. Thesis. Univ. of Wis., LaCrosse, Wis. 67 pp.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.

Carlander, K. D., and R. E. Cleary. 1949. The daily activity patterns of some freshwater fishes. Amer. Midland Naturalist 41:447-452.

Christianson, J. 1978. Fishing and boating survey, East and West Lake Okoboji. Project No. 77-I-P-7. 1977 Job Completion Reports, 1978 Management Plan, Fisheries Management Section, Iowa Cons. Comm. 1978:44-67.

Crossman, E. J. 1977. Displacement, and home range movements of muskellunge determined by ultrasonic tracking. Env. Biol. Fish. 1:145-158.

Crowe, W. E. 1962. Homing behavior in walleyes. Trans. Am. Fish. Soc. 91:350-354.

Crum, G. H., and R. W. Bachmann. 1973. Submersed aquatic macrophytes of the Iowa Great Lakes Region. Iowa St. J. Res. 48:147-173.

Dendy, J. S. 1945. Depth distribution of fish in relation to environmental factors, Norris Reservoir. Rep. Reelfoot Biol. Sta. 9:114-115.

Eddy, S., and J. C. Underhill. 1974. Northern fishes. 3rd ed. University of Minnesota Press, Minneapolis, Minn. 414 pp.

Eschmeyer, P. H. 1950. The life history of the walleye Stizostedion vitreum vitreum (Mitchill), in Michigan. Mich. Dept. Cons., Inst. Fish. Res. Bull. No. 3. 99 pp.

Ferguson, R. G., and A. J. Derksen. 1971. Migration of adult and juvenile walleyes (Stizostedion vitreum vitreum) in southern Lake Heron, Lake St. Clair, Lake Erie, and connecting waters. J. Fish. Res. Board Can. 28:1133-1142.

Forney, J. L. 1963. Distance and movement of marked walleye in Oneida Lake, New York. Trans. Am. Fish. Soc. 90:47-52.

Forney, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Am. Fish. Soc. 103:15-24.

Fossum, J. D. 1975. Age and growth, food habit analysis and movement patterns of walleye (Stizostedion vitreum vitreum (Mitchill)) in pools 3 and 4 of the upper Mississippi River. M.S. Thesis. St. Mary's College, Winona, Minn. 144 pp.

Harlan, J. R., and E. B. Speaker. 1969. Iowa fish and fishing. 4th ed. State of Iowa, Iowa Cons. Comm., Des Moines, Ia. 365 pp.

Hart, L. G., and R. C. Summerfelt. 1973. Demonstration of homing behavior of flathead catfish tagged with ultrasonic transmitters. 27th Annual Conf. Southeastern Assoc. Game and Fish Comm., Proc. 27:520-531.

Hart, L. G., and R. C. Summerfelt. 1975. Surgical procedures for implanting ultrasonic transmitters in flathead catfish (Pylodictis olivaris). Trans. Am. Fish. Soc. 104:56-59.

Hasler, A. D., and W. J. Wisby. 1958. The return of displaced largemouth bass and green sunfish to a "home" area. Ecology. 39:289-293.

Hasler, A. D., E. S. Gardella, R. M. Horrall, and H. F. Henderson. 1969. Open-water orientation of white bass, Roccus chrysops, as determined by ultrasonic tracking methods. J. Fish. Res. Board Can. 26:2173-2192.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34:1524-1550.

Holt, C. S., G. D. S. Grant, G. P. Oberstar, C. C. Oakes, and D. W. Bradt. 1977. Movement of walleye, Stizostedion vitreum vitreum, in Lake Bemidji, Minnesota, as determined by radio-biotelemetry. Trans. Am. Fish. Soc. 106: 163-169.

Johnson, M. G., J. H. Leach, C. K. Minns, and C. H. Olver. 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (Stizostedion vitreum vitreum), northern pike (Esox lucius), lake trout (Salvelinus namaycush), and smallmouth bass (Micropterus dolomieui). J. Fish. Res. Board Can. 34:1592-1601.

Kelso, J. R. M. 1976. Diel movement of walleye, Stizostedion vitreum vitreum, in West Blue Lake, Manitoba, as determined by ultrasonic tracking. J. Fish. Res. Board Can. 33:2070-2072.

Leggett, W. C., and R. A. Jones. 1971. Net avoidance behavior in American shad (Alosa sapidissima) as observed by ultrasonic tracking techniques. J. Fish. Board Can. 28:1167-1171.

Marshall, T. R. 1977. Morphological, physiological, and ethological differences between walleye (Stizostedion vitreum vitreum) and pikeperch (S. lucioperca). J. Fish. Res. Board Can. 34:1515-1523.

Morris, W. K. 1977. Evaluation of method of attaching simulated ultrasonic transmitters to adult male walleyes, Stizostedion vitreum vitreum (Mitchill), under adverse environmental conditions. M.S. Thesis. Univ. of Okla., Norman, Okla. 116 pp.

Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk. 72:128-137.

Olson, D., and W. J. Scidmore. 1962. Homing behavior in spawning walleyes. Trans. Am. Fish. Soc. 91:355-361.

Peterson, D. C. 1975. Ultrasonic tracking of three species of black basses, Micropterus spp., in Center Hill Reservoir, Tennessee. M.S. Thesis. Tenn. Tech. Univ., Cookville, Tenn. 129 pp.

Rawson, D. S. 1956. The life history and ecology of the yellow walleye, Stizostedion vitreum, in Lac La Ronge, Saskatchewan. Trans. Am. Fish. Soc. 86:15-37.

Regier, H. A., V. C. Applegate, and R. A. Ryder. 1969. The ecology and management of the walleye in western Lake Erie. Great Lake Fish. Comm. Tech. Rep. 15. 101 pp.

Rose, E. T. 1969. Angling for walleyes. Pages 236-242 in J. R. Harlan, and E. B. Speaker. Iowa fish and fishing. State of Iowa, Iowa Cons. Comm., Des Moines, Iowa.

Ryder, R. A. 1977. Effects of ambient light variations of behavior of yearling, subadult, and adult walleyes (Stizostedion vitreum vitreum). J. Fish. Res. Board Can. 34:1481-1491.

Scherer, E. 1971. Effects of oxygen depletion and of carbon dioxide buildup on the photic behavior of the walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board Can. 28:1303-1307.

Schupp, D. H. 1972. The walleye fishery of Leech Lake, Minnesota. Minn. Dept. Nat. Res., Fish. Invest. Rep. No. 317. 11 pp.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184. 966 pp.

Sieh, J. G., and J. Parsons. 1950. Activity patterns of some Clear Lake, Iowa, fishes. Iowa Acad. of Sci. 57:511-518.

Stasko, A. B. 1975. Underwater biotelemetry, an annotated bibliography. Fish. Mar. Serv. Res. Dev. Tech. Rep. No. 534. 31 pp.

Stasko, A. B., and D. G. Pincock. 1977. Review of underwater bio-telemetry, with emphasis on ultrasonic techniques. J. Fish. Res. Board Can. 34:1261-1285.

Swenson, W. A., and L. L. Smith, Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board Can. 30:1327-1336.

Trefethen, P. S. 1956. Sonic equipment for tracking individual fish. U.S. Fish and Wildlife Serv., Spec. Sci. Rep. No. 179. 11 pp.

Underwater Telemetry Newsletter. 1971-1977. Bibliography of underwater telemetry in biological applications. Charles C. Coutant, ed. Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tenn.

Warden, R. L., and W. J. Lorio. 1975. Movement of largemouth bass (Micropterus salmoides) in impounded waters as determined by underwater telemetry. Trans. Am. Fish. Soc. 104:696-702.

Winter, J. D. 1977. Summer home range movements and habitat use by four largemouth bass in Mary Lake, Minnesota. Trans. Am. Fish. Soc. 106:323-330.

ACKNOWLEDGMENTS

This research was supported financially by the Sport Fishery Research Foundation, Iowa State University Agriculture and Home Economics Experiment Station, the Graduate College at I.S.U. and the Iowa Chapter of the Izaak Walton League, McNurlen Scholarship.

Appreciation is expressed to my committee: Dr. Bruce W. Menzel, major professor, who gave time, consultation, and encouragement; Dr. David F. Cox, I.S.U. Statistics Department, who provided statistical procedures and assistance; Dr. Robert J. Muncy, I.S.U. Cooperative Fisheries Unit, and Mr. James Mayhew, Iowa Conservation Commission, for their interest, encouragement and review of this manuscript.

Appreciation is also extended to Iowa Conservation Commission fisheries biologists Mr. Dick McWilliams and Mr. Wallace Jorgenson for their help in fish capture, transmitter implantation, and the use of their equipment.

Equipment was generously provided by the Iowa Great Lakes Fishing Club and the Iowa Lakeside Laboratory.

The author is also indebted to Jeff Jones for the many long hours of help in data gathering.

Finally, I am extremely grateful to my wife, Vivian, without whom my doing this research would not have been possible. In addition, she has provided encouragement and understanding as well as experiencing many of the frustrating moments of editing and typing.