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Versatility in habitat use by a top aquatic predator, *Esox lucius* L.

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The habitat selected by northern pike, *Esox lucius*, a solitary top aquatic predator, was evaluated using radio location and ultrasonic telemetry. These predators moved extensively throughout the lake and exhibited a distinct preference for shallow vegetated areas close to shore. Selection of habitat was significantly influenced by meteorological factors. On windy days pike chose habitats which were further from shore, but not necessarily deeper, than those chosen on calm days. On sunny days pike moved into habitats that were close to shore and relatively shallow. Habitat selection of pike was not significantly influenced by rain. Northern pike exhibited a much greater versatility in the range of habitats they utilized than was previously believed. We propose that such versatility is an important feature of the behaviour of top predators.

I. INTRODUCTION

The ecological niche occupied by top predators appears to be similar in terrestrial and aquatic ecosystems. Their diet often appears to be narrow, being dominated by one or two prey species (Errington, 1963; Diana, 1979) even though a wide range of prey species is recorded for the predator. Versatility in behaviour and in habitat utilization is a dimension of predator behaviour which has not received serious attention. Until recently data concerning habitat use were obtained either by direct observation or by analysis of capture success. Both of these approaches are biased in that the animals under investigation are not equally visible in all habitats nor would they be equally susceptible to capture in all habitats. The development of radio telemetry techniques provides researchers with the means to locate the individual under study at any time and hence the ability of examining habitat utilization by individual animals.

Northern pike, *Esox lucius*, are top aquatic predators in north temperate regions. They are solitary, almost entirely piscivorous predators, inhabiting both lakes and slow flowing rivers. Diana *et al.* (1977), using ultrasonic transmitters, found that pike moved extensively but were found most frequently within 300 m of shore and in water less than 4 m deep. They did not determine the distribution of various habitat types in the lake studied so they could not determine whether the fish used one type of habitat more frequently than would be expected by chance.

The objective of the present study was to determine the habitat preferences of northern pike in a lake which presented a range of habitat types.

II. METHODS

This study was conducted in May and June 1980, at Seibert Lake, Alberta. The lake is of moderate size (35 km^2), shallow (maximum depth 11 m), mesotrophic and isothermal

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TABLE I. The observed and expected frequency of use of various habitats by northern pike in Seibert Lake, during May and June. Expected values were calculated on the basis of the assumption that each habitat type was used randomly

Habitat character	Percentage of the lake occupied by each habitat	Expected frequency of use	Observed frequency of use
Depth (m)			
0–3	22	32	61
3–6	26	38	47
6–9	28	41	24
>9	24	35	14
Bottom type			
Silt	60	88	78
Organic	35	51	12
Sand/rock	5	7	10
Distance to shore (m)			
0–500	40	55	73
501–1000	31	42	34
<1000	29	40	30
Vegetation type			
Unvegetated	74	97	79
Scirpus	18	23	30
Potamogeton	1	1	9
Chara	2	2	7
Nuphar	3	4	4

Depth type $G = 16{\cdot}4$; $P < 0{\cdot}005$; d.f. = 3, $n = 146$.
Bottom type $G = 7{\cdot}7$; $P < 0{\cdot}05$ d.f. = 2, $n = 146$.
Vegetation $G = 36{\cdot}0$; $P < 0{\cdot}005$; d.f. = 2, $n = 127$.
Distance from shore $G = 11{\cdot}1$; $P < 0{\cdot}05$; d.f. = 4, $n = 137$.

throughout the summer. It has two shallow bays, representing 2% of the surface area of the lake, containing extensive beds of yellow pond lily, *Nuphar*. There are patches of rooted macrophytes (*Potamogeton* and *Chara*) scattered throughout regions of the lake less than 4 m deep and discontinuous beds of sedge, *Scirpus*, around the margin of the lake. Seibert Lake has been designated as a trophy pike lake because of the very large northern pike caught there.

Fish were captured by angling with barbless hooks and either ultrasonic (74 kHz Smith-Root Electronics, Model SR74) or radio frequency (151 MHz. Telemetry Systems Inc.) transmitters were surgically implanted in the coelom (Diana *et al.*, 1977).

This study was conducted in May and June 1980, immediately after spawning when feeding is greatest (Diana, 1979); thus one would expect that behaviour and habitat use would be geared towards maximizing feeding efficiency. Data concerning habitat selection were obtained from five female fish which weighed between 2·6 and 6·8 kg. No fish died either during surgery or for the duration of the study. The longest lasting transmitter was still operational 49 days after the operation. One fish was caught by a sports fisherman almost 3 months after surgery and he reported that the incision had healed well and there was no indication of infection.

An attempt was made to determine the location of each fish at least once daily, at different times of the day and night. By following this sampling method in a systematic fashion it was possible to construct a profile of the average habitat use over 24 h of the radio

monitored fish. The minimum time between successive locations of a fish was 3 h and the maximum time was several days depending on our ability to locate the fish. In addition to point sampling daily, periodically the location of one individual was continuously monitored for extended periods (3–14 h). The two sampling methods resulted in no apparent systematic differences and for analyses they were considered together, with the location of the fish from the continuous sample only being considered at the beginning of each 3 h period. Three hours was sufficient time to allow a pike to move, at normal swimming speed, the maximum distance between any two habitat types. Based upon this criteria observations taken 3 h apart were considered independent of each other. Every time an individual fish was located five characteristics of the site were recorded. The location of the fish was determined by taking bearings to known land marks with a hand held compass. The distance to the shore was estimated either visually or by using an optical range finder. Visual estimates were used under rough water or low light conditions when the optical range finder could not be used effectively. Both methods are logarithmic with regards to precision, being less precise at greater distances. At distances less than 100 m, the visual estimates were within 5 m of those obtained with the range finder. When both methods were used simultaneously they produced similar results. The depth of the water was estimated to the nearest metre by sounding. It was assumed that pike were always near the bottom and not in the limnetic zone. This was substantiated by SCUBA observations. The vegetation type and bottom type were recorded at each location whenever the bottom could be observed. Normally the bottom was visible when the water was up to 4 m deep. The extent of rooted aquatic vegetation was determined using SCUBA. Little rooted vegetation was found below 4 m. Therefore on those occasions when pike were found in water more than 4 m deep the habitat was considered unvegetated.

In order to assess if the pike exhibited preferences for certain habitats it was necessary to determine the area of each habitat type in the lake. The vegetation distribution and bottom type of the entire lake was surveyed and mapped during the first week of June. The bathymetric map of Seibert Lake we used is shown in Fig. 1. Data were obtained for 147 separate locations selected by the radio tagged pike over 49 days. On certain occasions, particularly when weather conditions were unfavourable, it was not possible to record all habitat parameters. This did not appear to introduce any systematic bias in the final data. The time of each observation was recorded as well as meteorological conditions. Daily weather conditions were also obtained from the unpublished meteorological data of two local fire lookout towers. Heart Lake and Sand River. It was necessary to augment their data with personal observations in order to be able to examine the influence of weather changes involving only small segments of an entire day.

III. RESULTS

The pike we studied moved extensively throughout the lake, resulting in the utilization of the majority of the lake over the period of the study [Fig. 1(a), (b)]. Each individual exploited all habitat types at some time during the observation period.

To test the hypothesis that pike used shallow regions of the lake more often than would be expected if depth was used randomly, we compared the frequency with which the pike were found in water of different depths with the frequency of use one would expect if depth were used randomly (Table I). This comparison revealed that pike may have selected the area of the lake they used on the basis of depth ($G=16{\cdot}4$, $P<0{\cdot}005$; Table I). They were found in shallow regions (0–3 m and 3–6 m) more often than would be predicted from the relative proportion of the lake with shallow depths. This result may be influenced by the close relationship between depth and bottom type. For example below 3 m the bottom type is almost always sand/silt.

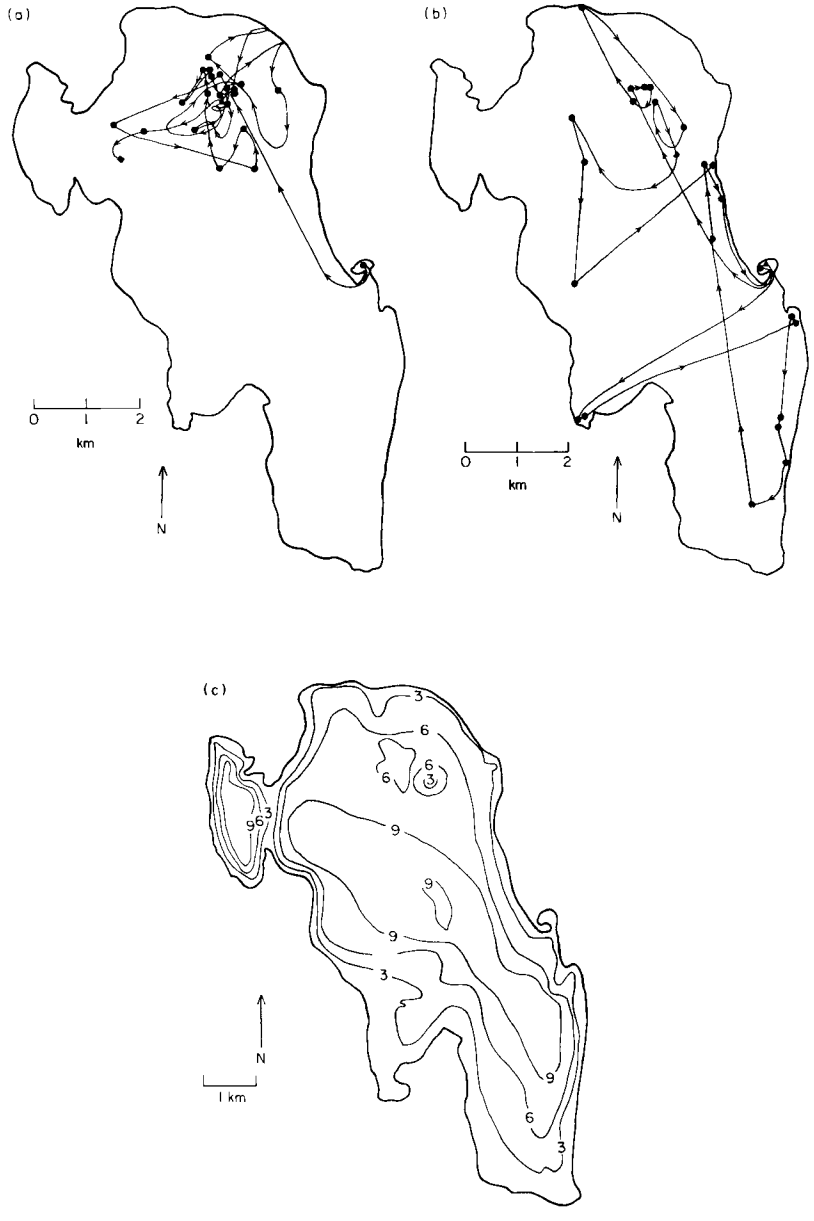

FIG. 1. Regions of Seibert Lake used by (a) a typical northern pike which used only a small portion of the lake and (b) by the pike showing the most extensive movements. Each dot represents the location of that individual on a different day. Lines connecting dots pass through all known locations of the fish. (c) The bathymetric map of Seibert Lake, Alberta. Depths in metres.

When the frequency with which pike were associated with the various bottom types was compared to that expected on the basis of the actual area of each bottom type, our data indicate that the pike may have selected habitats on the basis of bottom type ($G=7{\cdot}7$; $P<0{\cdot}05$; Table I). Pike were found in habitats with a sand/rock bottom twice as frequently as would be expected, but they only utilized areas over organic bottom types a third as often as expected. To test the hypothesis that pike chose habitats close to shore, the lake was divided into three areas, the area of the lake that was within 500 m of shore; between 500 and 1000 m of shore; and greater than 1 km from shore. On the basis of this categorization it is evident that the radio monitored fish may have selected the habitat they used on the basis of distance from shore ($G=11{\cdot}1$; $P<0{\cdot}05$; Table I). Pike were found in those habitats that were closer to shore with a greater frequency than would be expected if they were randomly selecting habitats.

Four genera of aquatic macrophytes *Scirpus, Potamogeton, Chara* and *Nuphar* were common in Seibert Lake. Northern pike were found associated with aquatic macrophytes significantly more than would have been expected if they were choosing habitats randomly ($G=36{\cdot}0$; $P<0{\cdot}005$; Table I). This is not positively influenced by the relationship between bottom type and vegetation. Vegetated areas commonly have organic bottom types, and pike utilized organic bottom types less often than expected by random association.

Pike are not necessarily strongly tied to shallow vegetated areas. This is demonstrated by the fact that on four separate occasions, for periods of time that exceeded 10 days, the radio monitored pike were in areas that were not vegetated.

We tested the influence of wind, rain and cloud cover on depth of water in which the fish were found, distance from shore, tendency to select vegetated areas over nonvegetated areas and bottom type. On sunny days pike were found closer to shore than on overcast days (t-test $P<0{\cdot}005$), while on windy days pike used habitats which were further from shore (t-test, $P<0{\cdot}001$) but not significantly deeper (t-test, $P=0{\cdot}38$) than on calm days. None of the meteorological parameters influenced the use of habitats containing aquatic vegetation nor did they alter the choice of habitats with regard to bottom type. The presence or absence of rainfall did not significantly influence habitat use in any of the four categories we examined (depth, distance from shore, use of aquatic vegetation or bottom type).

A complicating factor to the analysis presented is that the habitat characteristics are not independent of each other, thus the relationship between habitat selection and any one of its characteristics may be influenced by the effect of one characteristic upon another. When interpreting the G tests, the interrelationship between the major environmental features must be considered. One means to illustrate these interrelationships is to preform a principle components analysis of the four major habitat characteristics. Principle component analysis mathematically derives composite variables by taking linear combinations of the original variables and subsequently expresses the 'loading' of each variable on that component (Harris, 1975). By examining the loading of each variable on each component it is possible to illustrate interrelationships between variables. This analysis illustrates a moderate relationship between vegetation and bottom type and one between depth and distance to shore. Any other combinations of variables are not strongly related (Table II).

TABLE II. Loadings of each habitat characteristic on components produced by a Principle Component Analysis of those characteristics

Habitat characteristic	1	2	3	4
Depth	0·036	0·262	0·936	−0·232
Vegetation type	0·962	0·102	0·036	0·258
Bottom type	0·283	−0·046	−0·240	0·928
Distance to shore	0·098	0·965	0·239	−0·039
Eigenvalue	1·74	1·43	0·51	0·30

IV. DISCUSSION

Our data demonstrate that pike are more versatile in the range of habitats they use than was previously thought. The monitored pike were observed to make long distance displacements from one area to another in a period of a few hours. Once in an area the pike would make only short movements staying within one habitat type for up to several days. The pike exhibited a versatile selection of habitats because the areas to which they moved following these long distance displacements were often different from those they left. Our data provide quantitative support for the hypothesis that pike prefer the shallow vegetated regions of the lakes they inhabit (Makoweck, 1973; Scott & Crossman, 1973; Paetz & Nelson, 1976). Our results differ quantitatively from the findings of Diana *et al.* (1977) who reported that 52% of their sightings of radio tagged pike in the summer were in water less than 2 m deep and that 95% of the time they were associated with aquatic vegetation. We suggest the versatile habitat use is advantageous for a top predator because it enables the predator to exploit the food resources in all areas of a lake whenever such exploitation becomes profitable. Pike may show a distinct preference for shallow vegetated regions close to shore because of the high productivity of the area and the proportionately increased availability of prey there, Makoweck (1973) examined the distribution of a number of the organisms preyed upon by the pike of Seibert Lake and suggested that there was a greater number of prey in the littoral zone than in other regions of the lake. The fact that the radio-tagged fish in this study selected habitats further from shore on windy days may be an example of how abiotic factors affect habitat choice. The waves generated by wind create turbidity in shallow areas, and since pike are visual predators (Nursall, 1973, Hoogland *et al.* 1956), this may decrease the desirability of near shore areas.

Our results indicate that relatively large pike (>65 cm S.L.) are versatile in their selection of habitats, moving freely from one to another. This supports Grimm's (1981) report, based on catch records, that large pike (>54 cm F.L.) use both open water and vegetated areas of lakes while small pike (<41 cm F.L.) were restricted to vegetated areas. Our results contradict the previously held view (Ivanova, 1969; Malinin, 1969; Nursall, 1973) that pike are largely sedentary animals inhabiting shallow areas containing aquatic macrophytes. The findings are also in contrast with Diana (1980) who, using a similar telemetric procedure in Lac Ste Anne, Alberta (a medium sized eutrophic lake) found that the monitored pike were

largely sedentary and spent little time or energy in swimming. These conflicting reports suggest that the habitat selection and activity pattern of pike depends on differences between the habitats in which the pike are studied or may reflect differences in the size of pike studied. In one small lake Grimm (1983) studied, the relative proportion of small (< 54 cm F.L.) to large (> 54 cm F.L.) pike increased with increased aquatic vegetation. He suggested that not all habitat areas are accessible to pike of all sizes. Thus one might expect the habitat used to be a function of fish size. These conflicting findings have further ramifications upon how pike are studied. They suggest that broad generalizations concerning the ranging behaviour of pike, commonly used in energy budgets and assessments of the quantity of prey eaten, are prematurely made.

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