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POPULATION REGULATION OF NORTHERN PIKE (*Esox lucius* L.) IN AN UNEXPLOITED LAKE IN NORTHERN SASKATCHEWAN

by

MICHAEL G. SULLIVAN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1985

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled POPULATION REGULATION OF NORTHERN PIKE IN AN UNEXPLOITED LAKE IN NORTHERN SASKATCHEWAN submitted by MICHAEL G. SULLIVAN in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

..........W.C. Mackay..........
Supervisor

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J.S. Nelson

Date... April 24 ... 85...

ABSTRACT

Populations of northern pike in unexploited lakes exhibit stability in size and structure, which indicates that density-dependent population regulation is operating. To investigate possible mechanisms of this regulation, I studied a population of pike in an isolated lake in northern Saskatchewan.

Four possible mechanisms of regulation were investigated; food limitations, interspecific predation, spacing behaviour and cannibalism.

If pike were food limited, their movements would be related to their large seasonal and sexual differences in food requirements. Using radio-location telemetry, I determined that the home range sizes and displacements of pike remained relatively constant between seasons and sexes and did not fluctuate with respect to their prey requirements. Therefore, I concluded that the pike were not food limited.

Bald eagles were the most important predator of pike at the study lake. By calculating the daily caloric requirement of the eagles and the caloric value of their prey (pike), I determined that the eagle population at the lake may take 400 pike each summer. This represents 5% of the pike population and, therefore, is too minor to result in population regulation.

I investigated spacing behaviour by monitoring the movement of radio-tagged pike. The large size of the home ranges, and prevalence of overlap precluded spacing behaviour from being a proximate factor in regulation.

A year-round collection of stomach contents indicated that cannibalism occurs at sufficient magnitudes to affect regulation. Heavy predation by adults on young pike at the end of their first summer may reduce the numbers of young and thus limit recruitment into the adult population. This mechanism would have a feed-back effect on numbers of young and adults and would result in the observed stable population size.

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For the research and production of this thesis, I am indebted primarily to my mother, who took it upon herself to worry about thin ice, frostbite, food supplies, costs, computers and writing, and thusly alleviated me from that wearisome responsibility.

The field work was made enjoyable and, in many cases, possible through the support of my father, whose experience and expertise in field situations were of invaluable assistance. The Jack Endall family of Pelican Narrows, Saskatchewan provided companionship, knowledge and experiences in a traditional Cree lifestyle which will long be with me.

My sled dogs, Sporkeau, George, Tara, Fudge, Beep, Pancake and Bozo, taught me much of bush life, got me into and out of several bad situations and provided many fond memories. My lead dog, Sheba, deserves special recognition for her skill, obedience and companionship.

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Numerous academic colleagues and personal friends assisted in a multitude of ways, and my heartfelt thanks go out to you all.

Financially, the project was supported by grants from the Boreal Institute, the Natural Sciences and Engineering Research Council and the Max Ward Scholarship for Northern Studies. Thanks, guys.

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1. GENERAL INTRODUCTION

The Canadian North provides many opportunities to study animal populations which exist in natural states, unexploited by man. Through such studies, knowledge may be gained about the basic processes which affect these populations, serving to increase our understanding of the ways in which man's activities can affect them and thus enhancing our ability to manage these species.

One such species is northern pike (<u>Esox lucius</u>), found throughout much of the Northern Hemisphere, in both heavily exploited southern waters and undisturbed northern areas. Pike are harvested by commercial, native and sports fisheries and form an important economic and cultural resource. An understanding of the processes which regulate pike populations is of considerable importance in fisheries management.

Studies of exploited pike populations indicate that they have large year to year fluctuations in population size. These fluctuations are further shown to be correlated with fluctuations in spring water levels and summer water temperatures and not correlated with the size of the breeding population (Johnson 1956, Franklin and Smith 1963, Forney 1968, Hassler 1970, June 1970, Kipling and Frost 1970). However, this form of density independent population regulation fails to account for the stable population sizes observed in unexploited lakes. Such stability is exhibited by a number of northern fish species (Grainger 1953, Kennedy 19 53, Johnson 1972, Dunbar 1973, Johnson 1976), and has been suggested for pike, although conclusive evidence is lacking.

In exploited populations, the size of the breeding population will generally be lower than in a natural population (Goedde and Coble 1981). As Busch et al. (1975) suggested for walleye (Stizostedion vitreum vitreum) populations, a density-dependent regulatory mechanism would only be expected in a population whose size was at its natural level and not artificially suppressed by human activities. In unexploited populations, the number of pike would be expected to be at or near the carrying capacity of the habitat and some form of density-dependent population regulation would be operating to maintain the observed stability (Johnson 1976).

The mechanism of density-dependent population regulation may operate in two basic, although closely related fashions. Limitations may be imposed which act on the adult pike to directly limit the size of the breeding population, such as limitations due to food or predation, or indirect limitations may be imposed through regulation of the recruitment of juvenile pike into the breeding population, through cannibalism, exclusion from suitable habitats or territoriality of adults.

Little work has been done to determine the mechanism of regulation of pike populations. Snow (1974) speculated that competition between adults for food and space limited a pike population which was near the carrying capacity of its environment. However, Johnson (1976) proposed a general model for unexploited fish populations which suggests that juvenile recruitment may be limited through the action of adults (either by cannibalism or by forcing the juveniles into shallow, shoreline areas where they would be vulnerable to avian predation).

I studied an unexploited population of pike in a small, isolated lake in northern Saskatchewan and investigated several possible types of population limitations. Two mechanisms which may directly regulate the adult pike population size, food and predator limitations, and one indirect mechanism, social limitations through spacing behaviour, were found to be of insufficient magnitude to account for population regulation. A fourth mechanism, cannibalism, although investigated to a lesser degree, would appear to be a likely regulatory mechanism for unexploited pike populations.

2. Study Site Description

Neagle Lake, Saskatchewan (54° 46'N., 102° 25'W., Figure 1) is a small lake located in spruce-jackpine boreal forest on the Precambrian Shield. It has an area of approximately 700 ha, with many islands and bays. It is relatively shallow, having a maximum depth of 11 m. Neagle Lake does not stratify during the summer. Surface temperatures reach a maximum of about 23° C, whereas bottom temperatures are 2° C to 3° C cooler. The open water season lasts from late May to late October. From early November to early May, ice cover is constant with a maximum thickness of approximately 1.2 m.

The conductivity of Neagle Lake is very low, less than 50 mS, likely due to its location on the Precambrian Shield and to its relatively high flushing rate as a result of active inlet creeks and a major outlet creek. The turbidity is fairly high (1.5 m to 2.5 m summer Secchi disc reading) compared to other lakes in the area. This appears to be due to a high level of organic particulate matter suspended in the water.

The shoreline areas are a heterogenous mixture of bare rock, sand beaches, <u>Scirpus</u>, <u>Typha</u> and <u>Carex</u>. <u>Nuphar</u>, <u>Potamogeton</u> and <u>Sagittaria</u> are common in shallow protected areas.

Fish species found in the lake include northern pike (<u>Esox lucius</u>), lake whitefish (<u>Coregonus clupeaformis</u>), white suckers (<u>Catostomus commersoni</u>), yellow perch (<u>Perca flavescens</u>), emerald shiners (<u>Notropis atherinoides</u>), fathead minnows (<u>Pimephales promelas</u>), spottail shiners (<u>Notropis hudsonius</u>), longnose dace (<u>Rhinichthys</u>

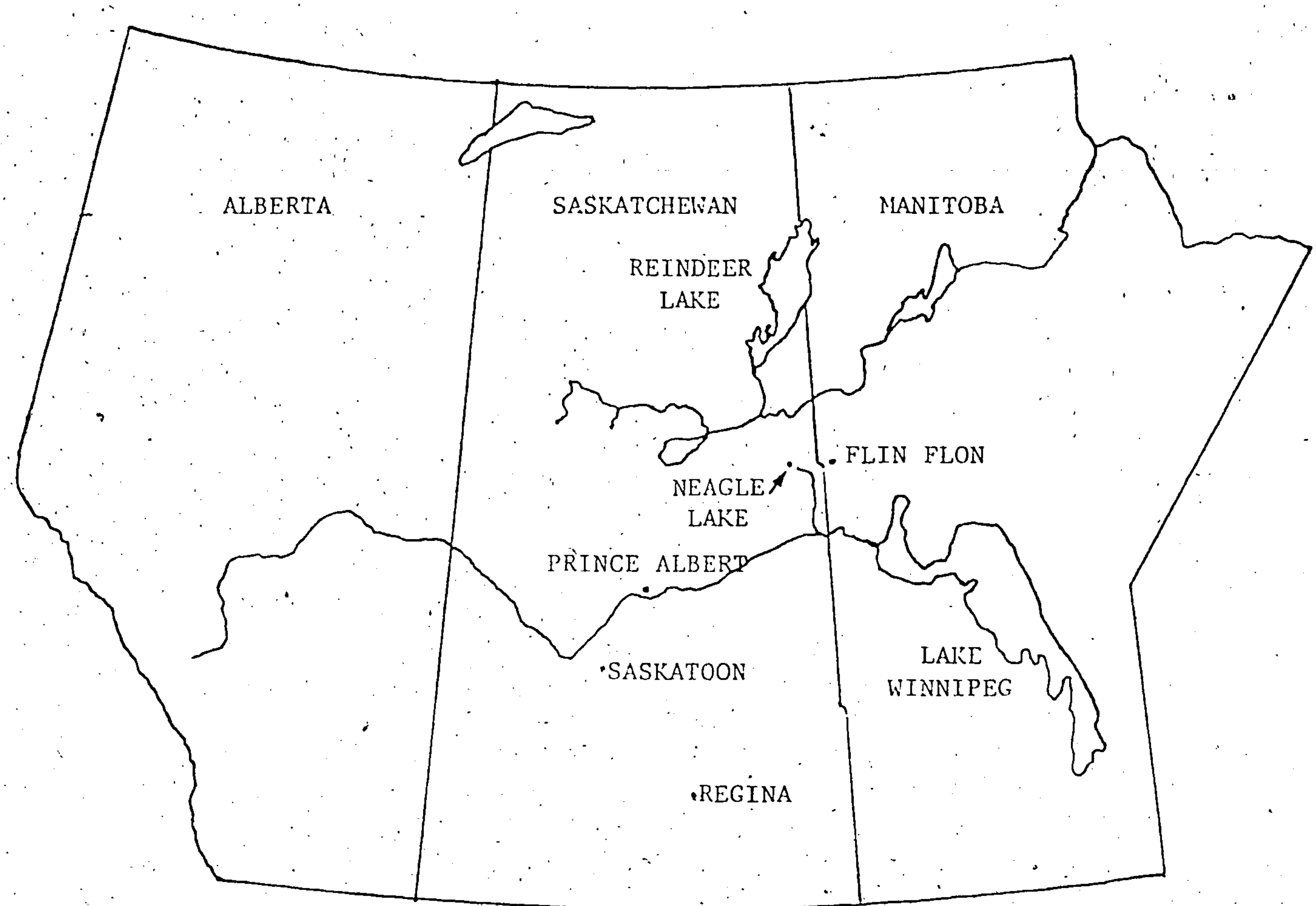


Figure 1. Map of western Canada, showing location of Neagle Lake.

cataractae), trout-perch (*Percopsis omiscomaycus*), slimy sculpins (*Cottus cognatus*), and several other small fish which I observed but was unable to capture and identify. Animals which may potentially prey on pike (either young or adults) and were commonly found at Neagle Lake include bald eagles (*Haliaeetus leucocephalus*), ospreys (*Pandion haliaetus*), kingfishers (*Megaceryle alcyon*), common loons (*Gavia immer*), great blue herons (*Ardes herodias*), mink (*Mustela vison*), otters (*Lutra canadensis*), foxes (*Vulpes vulpes*), wolves (*Canis lupus*), and black bears (*Ursus americanus*).

Neagle Lake has been relatively free of human disturbance as it has no road access, very difficult canoe access, and does not contain locally desirable gamefish (lake trout, *Salvelinus namaycush*, or walleye, *Stizostedion vitreum*). It is located about 20 km from the nearest road and about 50 km from the nearest float plane base. The boundary of two traplines bisects Neagle Lake and as a result of personal animosities between the particular trappers who operate these lines, neither regularly visits the lake.

A local outfitter occasionally flies a party of sports fishermen to Neagle Lake. However, in the period I was associated with the lake (1973-1982), only one party [illegible] flown in. Geological survey crews were based at the lake three or fo[illegible]mes during this period, with occasional sports angling bein[illegible]ducted by crew members. I estimate that fewer than 50 pike per yea[illegible] taken out of Neagle Lake by humans (not including the sampling for this study) between 1973 and 1982. Frequently, the pike population of Neagle Lake would experience no human exploitation pressure during the course of a year.

3. Pike Population Description

During the study, 267 pike were collected by angling, gill-netting or snaring. I recorded the stomach contents of all 267 pike and for each of 107 of the pike I recorded the standard length (to the nearest 0.5 cm), weight (to the nearest 50 g), gonad maturity and weight (to the nearest g) and removed the left cleithrum (for aging purposes). The ages of these fish were determined by counting the annuli on each cleithrum. The birth-date for pike from Neagle Lake was assumed to be 31 May. Thus, a pike having a cleithrum with three annuli which was caught in September would be classed as 3+ (3 years of growth plus an undetermined amount since 31 May).

The age-class composition of the population was determined for three separate periods, 15 March 1981 to 31 May 1981 (1980 sample), 1 June 1981 to 31 May 1982 (1981 sample) and 1 June 1982 to 15 March 1983 (1982 sample)(Appendix 1). Although the sample sizes may be too small to draw accurate conclusions, there does not appear to be obvious strong or weak year classes present. This tends to support the principle that unexploited populations have stable age class distributions (Johnson 1976).

The growth curve of pike from Neagle Lake is similar to that of pike from other northern Canadian lakes (Figure 2), as is the weight-length relationship (Figure 3, Appendix 12). The age at first maturity of pike from Neagle Lake was identified by examining their gonads and determining whether or not the pike would spawn the following spring. Of the 107 pike necropsied, the single 1+ pike was immature, two

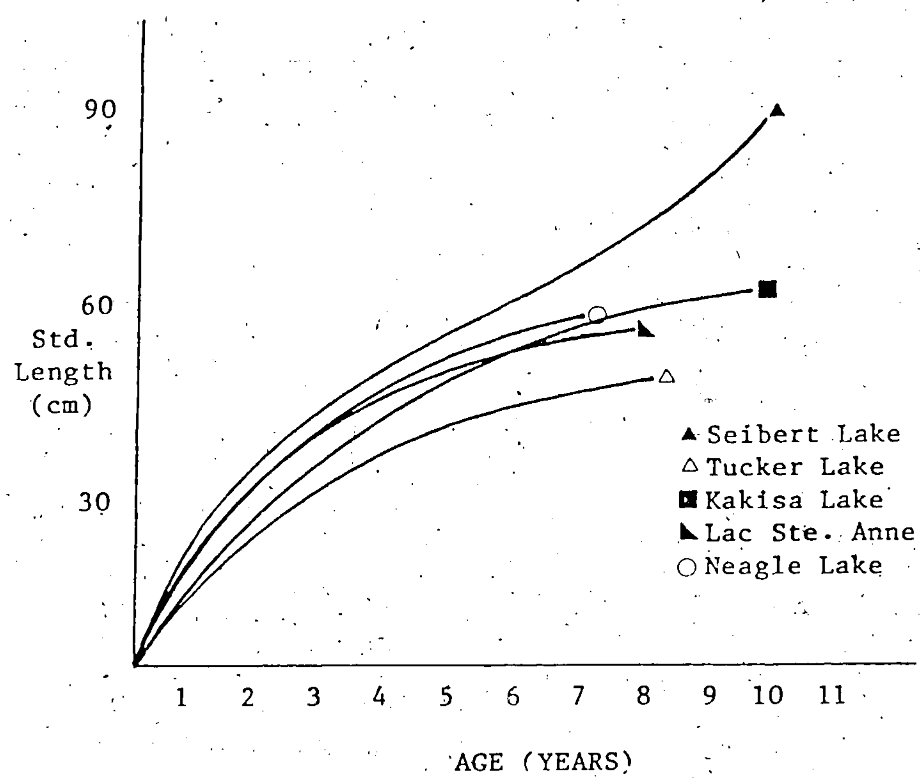


Figure 2. Growth rates of northern pike from several Canadian lakes. Data from Mackay (personal communication), except for Neagle Lake.

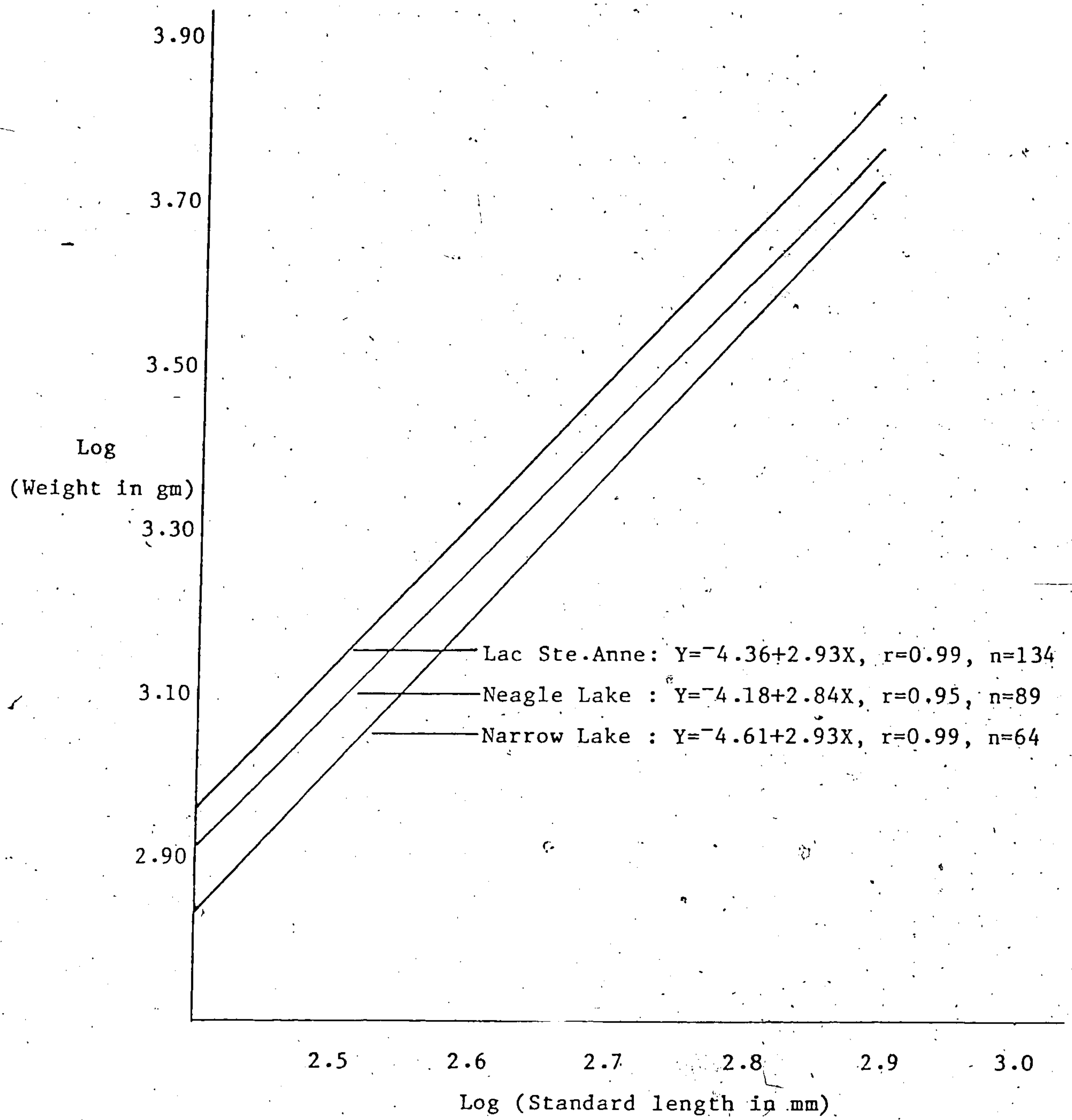


Figure 3. Comparison of weight - length relationship of pike from three Canadian lakes. Data from Mackay (personal communication), except for Neagle Lake.

out of the three 2+ pike would have been mature at the end of their third year and all older pike were mature.

The stomach contents of the pike sampled indicates a diet composed of a variety of fish and invertebrates (Table 1). The unidentified fish may have included the aforementioned shiners and dace found in abundance in the lake, but as my identification of the stomach contents relied on undigested pieces of large bone or flesh, most of the fish identified were fairly large. This partially explains the stomach content data appearing to indicate a preference for the larger species (perch, whitefish, and white suckers). The invertebrates found in the stomachs were mainly <u>Gammarus</u>, crayfish (<u>Oronectes</u> sp.), and dragonfly nymphs (O. Odonata).

Table 1. Stomach contents of northern pike from Neagle Lake, Sask. March, 1981 to December, 1982. Number under stomach contents indicates number of pike stomachs where prey items of that species were found.

			STOMACH CONTENTS					
SEASON	N	NO. FULL	UNIDENT. FISH	YELLOW PERCH	WHITE-FISH	WHITE SUCKER	INVERT.	PIKE
Spring	40	17	2	5	1	0	8	1
Summer	118	31	17	12	3	2	18	2
Autumn	44	21	8	8	8	1	0	2
Winter	65	33	7	2	3	2	6	14
Total	267	102	34	27	15	5	32	19

4. Are Pike Food Limited?

4.1 INTRODUCTION

One of the most obvious regulatory mechanisms for populations is food limitation. This is often assumed to be a proximate factor of major importance in governing population size and behaviour of fish (Snow 1974, 1978, Dombeck 1979, Fish and Savitz 1983) but it is seldom objectively tested. Grimm (1981a) tested the hypothesis that pike are food limited. He compared biomasses of stocked pike and prey fish in artificial ponds during a five month period and found that changes in biomass of pike and prey fish were not correlated. Grimm (1981a) concluded that pike were not food limited. However these results may have little relationship to natural situations where reproducing populations of pike and prey fish have interacted over many generations.

In this study, I tested the hypothesis that the size of a natural, unexploited population of adult pike was limited by the constraints of food availability. If adult pike are food limited, their home range size or degree of movement should vary inversely with the level of prey availability. This relationship has been observed in a wide variety of animals, including many species of mammals (McNab 1963, Zimen 1976, Singer *et al*. 1981), various birds (Schoener 1971), rainbow trout (Slaney and Northcote 1974), iguanid lizards (Simon 1975) and limpets (Stimson 1973). Conversely, in animals which are not food limited, such as *Microtus* (Krebs and Delong 1965, Krebs *et al*. 1969) and blue grouse (Zwickel and Bendell 1972), the home range size does not vary in response to food availability (Abramsky and Tracy 1980, Zwickel -

personal communication).

It would be extremely difficult to accurately quantify changes in the availability of prey items of pike in a natural situation as they feed on a great diversity of prey (Frost 1954, Lawler 1965). However, the prey or food requirement of pike shows large seasonal fluctuations (being highest in spring and declining to a low in mid-winter; Weithman and Anderson 1977, Johnson 1966, Diana and Mackay 1979). Additionally Diana and Mackay (1979) found that the food requirement of female pike is nearly twice that of male pike.

Therefore, from the hypothesis that food availability limits pike populations, one may predict that pike will optimize their activity with respect to food requirements by varying their home range size or activity levels in response to seasonal changes in their prey requirements.

To test this prediction and its corresponding hypothesis, a radio-location telemetry study was conducted to measure seasonal and sexual differences in pike space use and activity at Neagle Lake, Saskatchewan during 1981 and 1982.

4.2 MATERIALS and METHODS

A total of 21 sexually mature northern pike (9 males and 12 females, all between 45 and 59 cm standard length, Appendix 2) were surgically implanted with radiolocation transmitters (49 MHz, AVM Instrument Co., Dublin, Ca.) following a modification of the method of Crossman (1977). A pike to be radio-tagged was captured by angling using barbless lures and immediately transferred to a holding tank where it was anaesthetized with MS 222 (tricaine methanesulfonate, 1:10,000) and measured to the nearest 0.5 cm of standard length. A 4 to 5 cm incision was made posterior to the pelvic fins, to one side of the ventral midline. The transmitter was coated in beeswax, sterilized in 95% ethanol and inserted into the body cavity. The incision was then closed with 5 or 6 sutures of 4-0 silk. A 10% solution of oxytetracycline was injected subcutaneously into the area of the incision and the fish was transferred to a recovery tank containing fresh water. When it responded vigorously to a light touch, the fish was released at the site of capture. The entire process took between 20 and 30 minutes. Handling of the pike was kept to a minimum.

Tagged fish were located using an AVM Instrument Co. La 12 receiver and a 3 element YAGI mast antennae mounted in an 5.5 m aluminum boat during the summer and mounted in a dog sled during the winter. The open boat was powered by a 15 hp outboard motor and proved to be a fast, manoeuvrable and safe tracking platform. Radio interference from the outboard engine was kept to manageable levels through frequent replacement of spark plugs and regular maintenance of all electrical connections. Snowmobiles were initially used for winter tracking, but excessive radio interference from the engine and the difficulty in simultaneously operating a snowmobile and radio receiver severely limited their usefulness. The preferred winter tracking platform was a Yukon freight sled pulled by 5 to 11 Siberian huskies hitched in tandem. The lead dog was trained to respond to voice commands for speed and direction which allowed me to concentrate on operating the radio receiver. Additionally, the sled dogs instinctively avoided areas of thin ice and slush. The dog sled provided efficient and very reliable transportation during the entire winter, including during the severest weather (radio-tracking with the dog team was conducted at temperatures as low as -47 °C). Drawbacks to this system included lack of manoeuverability in deep snow and maintenance of the dogs during the summer months.

I determined the location of the radio-tagged pike by travelling along a gradient of increasing signal strength. This was accomplished once the signal had been received, by travelling in a straight line until a definite peak in signal strength was recognized. At that point, the approach was altered 90° and a second straight line was travelled. This procedure was repeated until the signal was audible at the lowest gain setting on the receiver. Trials with radio transmitters in known locations indicated that this method allowed the location of the transmitter to be determined to within 2 or 3 meters. Triangulation of radio signals was not used to determine pike locations as the antennae used proved to lack sufficient directionality.

Maximum ranges of radio signals varied with respect to individual transmitters, water depth and ice conditions. Generally, signal ranges during summer were between 200 and 300 m. During winter, maximum ranges were usually under 100 m. Ice, snow and especially slush drastically attenuated the radio signals.

The location of the radio-tagged pike was then plotted on a grid coordinate map of the lake (1:10,000 scale) via triangulation to visually superimposed landmarks of known grid coordinates. Checked with a surveyor's transit, this method proved accurate to within 10 m when less than 200 m from shore (greater than 99% of all locations).

Radio-tagged pike were located once every five daylight hours during a tenday sample period. This resulted in each fish being located three times per day during the spring and summer and twice per day during the autumn and winter. For example, if a fish was located two hours before dark, it would be relocated three hours after dawn. Although these two locations may have been up to 21 hours apart during winter, only 5 hours of daylight would have elapsed. As pike are essentially inactive at night (Mackay and Craig 1983), this method ensured that pike were located over equal time spans during each season and enabled accurate comparisons of activity to be made.

The area used by each fish in a 10 day sample period was termed its area of use and was optimally represented by 20 (winter and autumn) or 30 (spring and summer) radio locations.

The sizes of the areas of use were determined using a modification of the grid square method of Rongstad and Tester (1969). Grid squares of 1 ha were used as this area is larger than the limitations imposed by the accuracy of the tracking system , yet small enough to be influenced by most displacements of pike between locations. Squares were included in a pike's area of use if they were separated by no more than 3 unoccupied squares. This method allowed a minimum of 70% of the locations to be included in the area of use.

The minimum polygon method of Mohr (1947) was also used to determine the sizes of the areas of use during spring, summer and autumn. This method was not used to analyze the winter data. During the winter, radio-tagged pike were lost on many occasions (due to poor signal transmission through ice and snow), especially if they moved more than 200 m from the last location. As the area determined by the minimum polygon method is strongly influenced by excursions and distant locations (Voight and Tinline 1980) , I felt it would provide a biased estimation of the areas of use during winter, compared to the other seasons. The grid square method is obviously not strongly influenced by these outlying locations and is therefore more suitable for comparisons between seasons. The minimum polygon method was used as much as practical due to its objectivity and wider familiarity.

Activity of pike was also analyzed since it is possible to maintain a constant size of area of use, yet vary the amount of movement within that area. Displacement of radio-tagged pike was calculated as meters moved between radio-locations (which were 5 h apart) and also as multiples of body lengths moved between radio-locations. The latter calculation was done in order to reduce variation in displacements caused by variation in body sizes.

Comparisons between sizes of areas of use and between displacements were made using the Wilcoxon Two-Sample Test and the Kruskal-Wallis one way analysis of variance and medians are reported with quartiles. Results were considered significant if $P < 0.01$.

4.3 RESULTS

My original intention of tracking the same individual pike during all seasons could not be realized because of numerous unforeseen radio failures. Data were therefore gathered from samples of fish during each season which were neither completely dependent nor independent of each other. However, the variation within individual fishes home range sizes and rates of movements were equal to or greater than the variation between fish (Appendices 10,11). For this reason, I treated each group of observations as independent samples.

The variation in size of areas of use did not follow the expected pattern of being largest during spring and decreasing to a low during winter. Sizes of the areas of use, as determined by the grid square method, were significantly different (Kruskal Wallis Test, H=34.25, df=4, P<0.001) between the seasons examined (Figure 4). However, pairwise contrasts based on ranks indicated that the only differences were that areas of use during autumn (1982) (16;13,19, median; Q1, Q3, n=14) were significantly different (P<0.001) from areas of use during winter (3; 2, 5, n=17); and summer (6; 2, 8, n=11) was significantly different (P<0.001) from autumn (1982). The size of the areas of use as determined by the minimum polygon method were not significantly different (H=5.206, df=3, P=0.15) between the seasons examined (Figure 5).

The rates of movement within these areas did not follow the expected pattern of being highest during spring and lowest during autumn. Displacements, measured as meters moved during 5 h were significantly different between the seasons examined (H=41.69, df=3, P<0.001) with displacements during autumn (1981) (80; 30, 200, n=472)

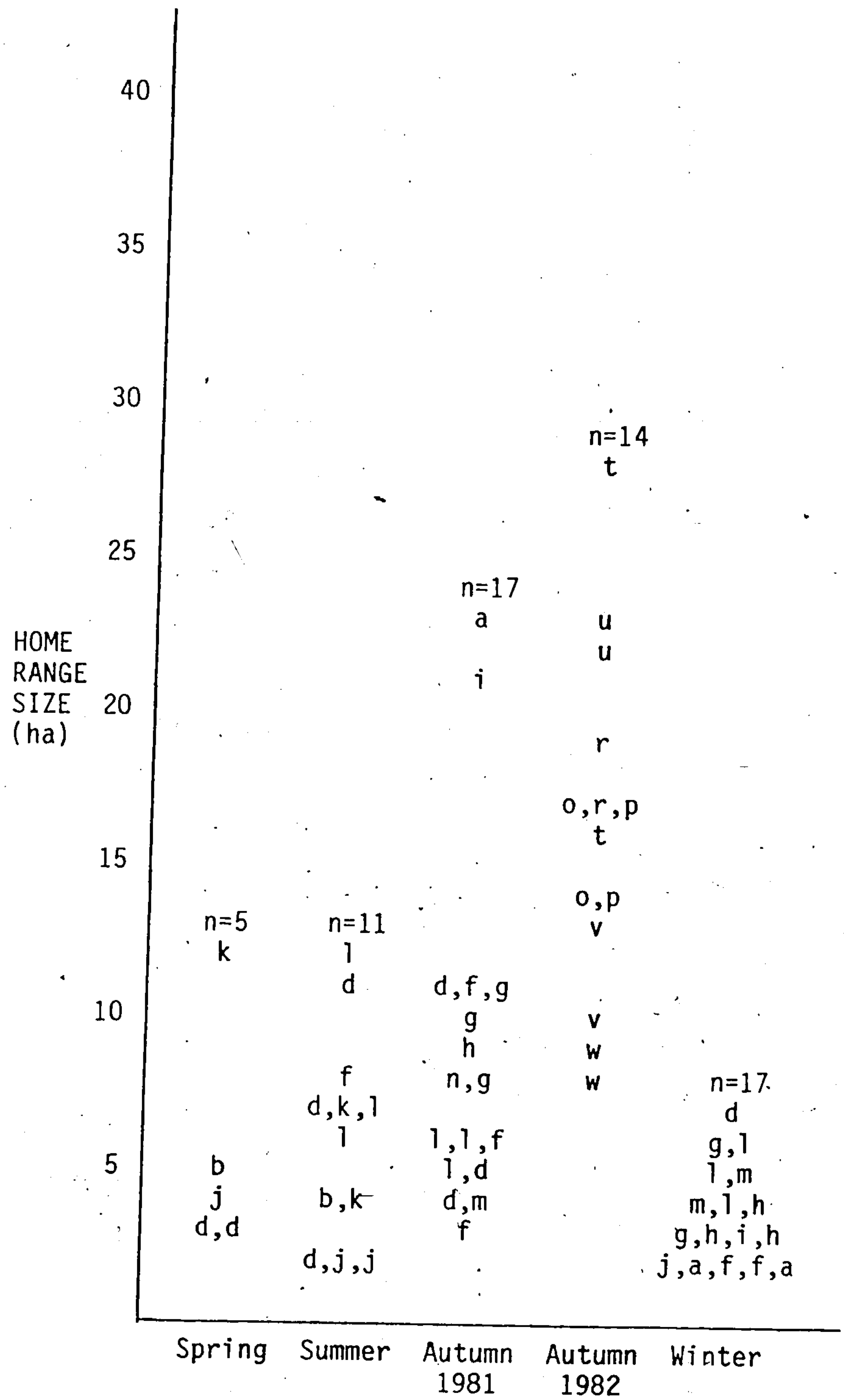


Figure 4. Variation in size of home range of radio-tagged pike as determined by the grid-square method. Letters indicate identification number of individual pike (a=01,b=02,c=03,etc.)

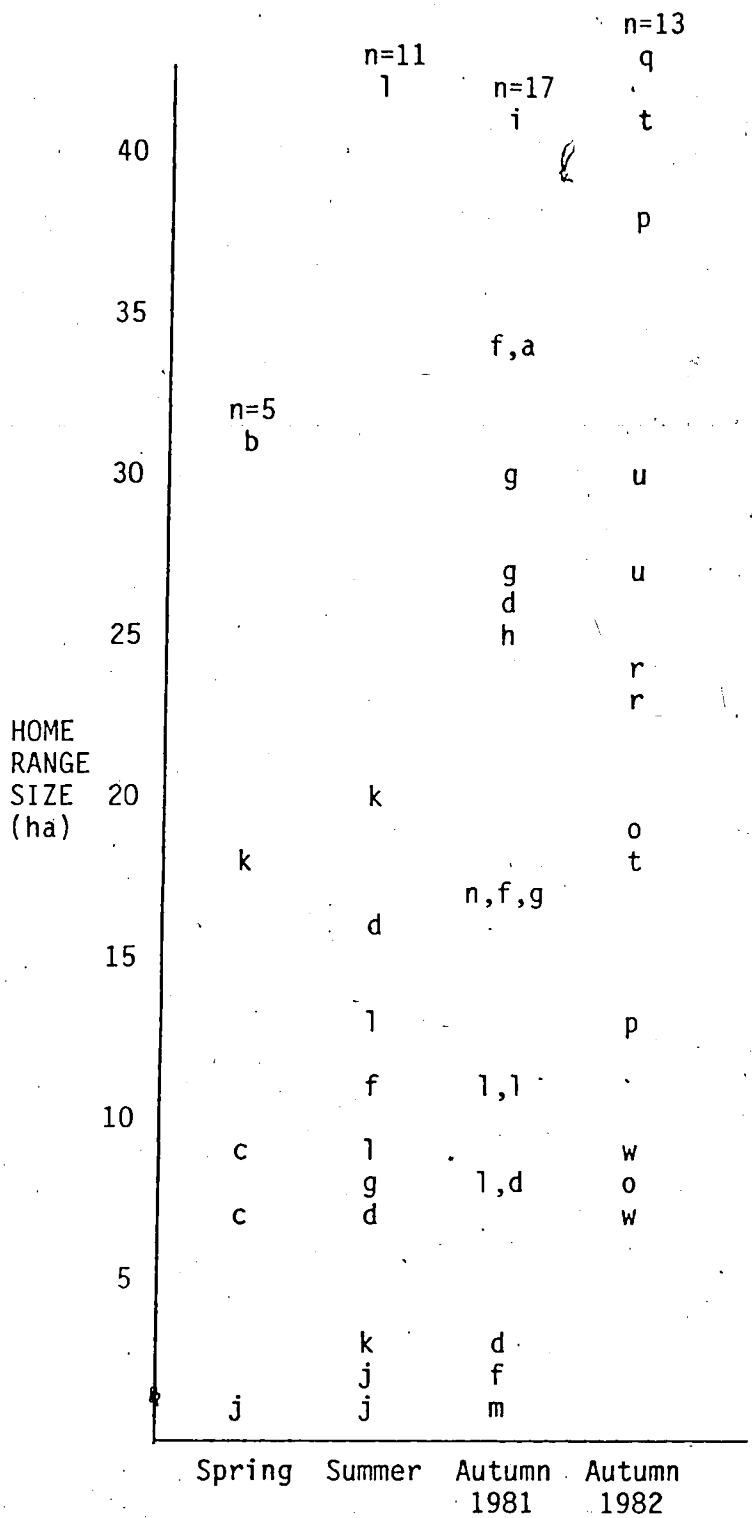


Figure 5. Variation in size of home range of radio-tagged pike as determined by the minimum polygon method. Letters indicate identification number of individual pike (a=01,b=02,c=03,etc.).

and spring (106; 53, 224, n=127) being similar, and both being significantly different (P<0.001) from displacements during summer (53; 22, 155, n=294) and from displacements during autumn (1982) (150; 69, 277 , n=419) (Figure 6).

Displacements as measured in body lengths (bl) moved during 5 h were also significantly different between the seasons examined (H=92.10, df=3, P<0.001) with displacements during autumn (1981) (158; 59, 395, n=472) and spring (206; 103, 433, n=127) being significantly different (P<0.001) from displacements during autumn (1982) (306; 141, 565, n=419) and summer (108; 45, 316, n=294) (Figure 7).

The sizes of the areas of use, determined using the grid square method, were not significantly different (Mann-Whitney U-Test, U=504.0, P=0.70) between male pike (7; 4, 12, n=26) and female pike (7; 3, 11, n=41) with areas during all seasons combined. There were no significant differences between the sizes of the areas of use of males (6; 2, 12, n=9) compared to females (4; 4, 8, n=7) during spring and summer (combined) (U=23.0, P>0.05), during autumn (1981) (median size of area of use of males =6; 4, 8, n=5, median size of area of use of females = 13; 9 , 7, n=15, U=25.5, P>0.05), during autumn (1982) (median size of area of use of males =17; 14, 19, n=6, median size of area of use of females =13; 9, 17, n=8, U=20.0, P>0.05) or during winter (median size of area of use of males =5; 4, 6, n=6, median size of area of use of females =3; 2, 3, n=11, U=16.5, P>0.05).

The sizes of the areas of use, as determined using the minimum polygon method, were not significantly different between males and females during all seasons (median size of area of use of males =11; 2, 20, n=22, median size of area of use of females =17; 8, 30, n=26, U=217,

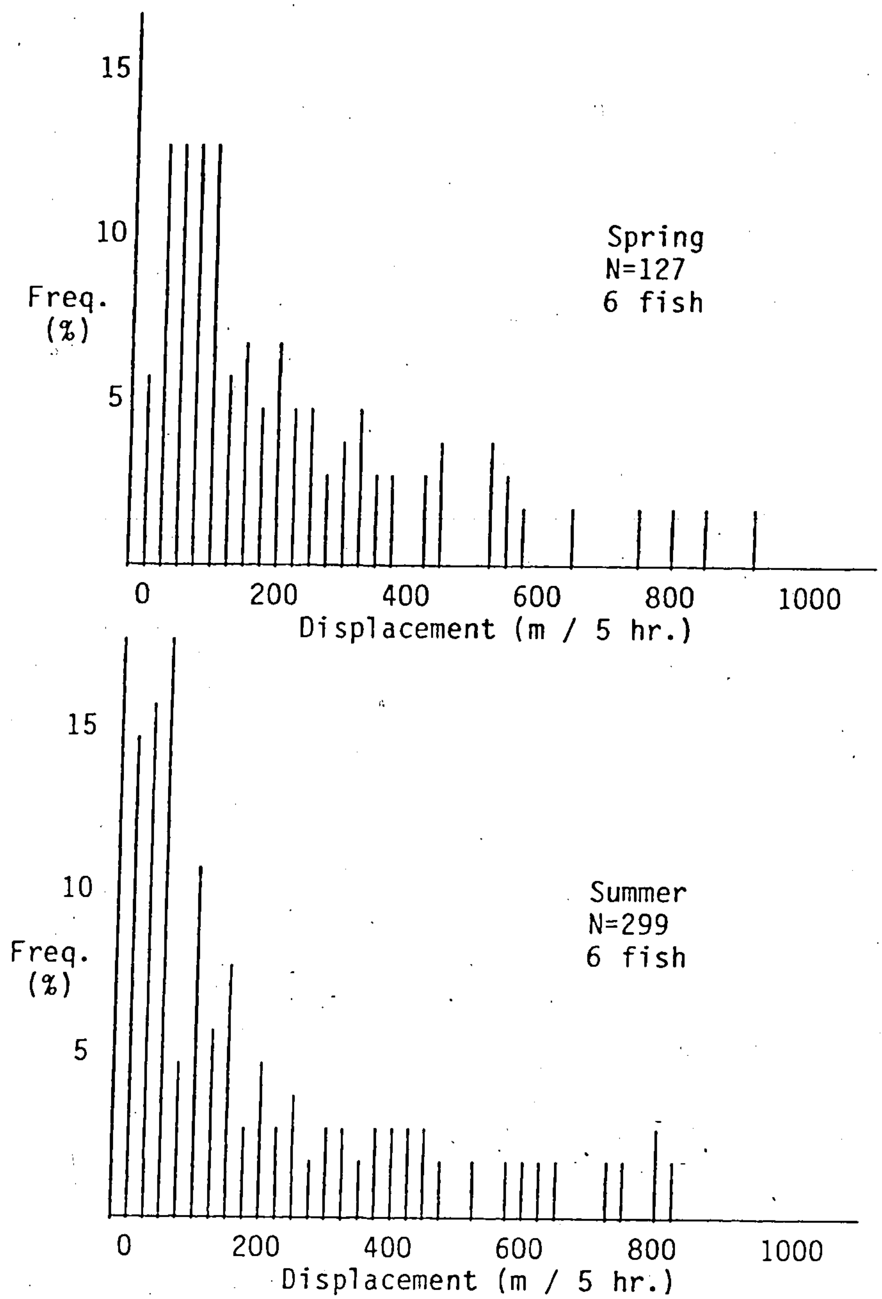
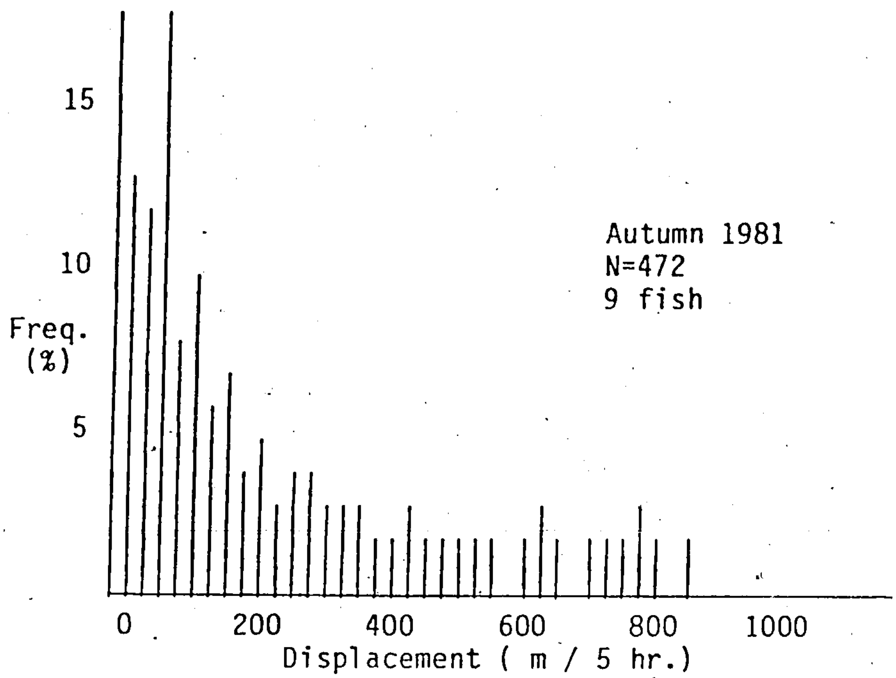
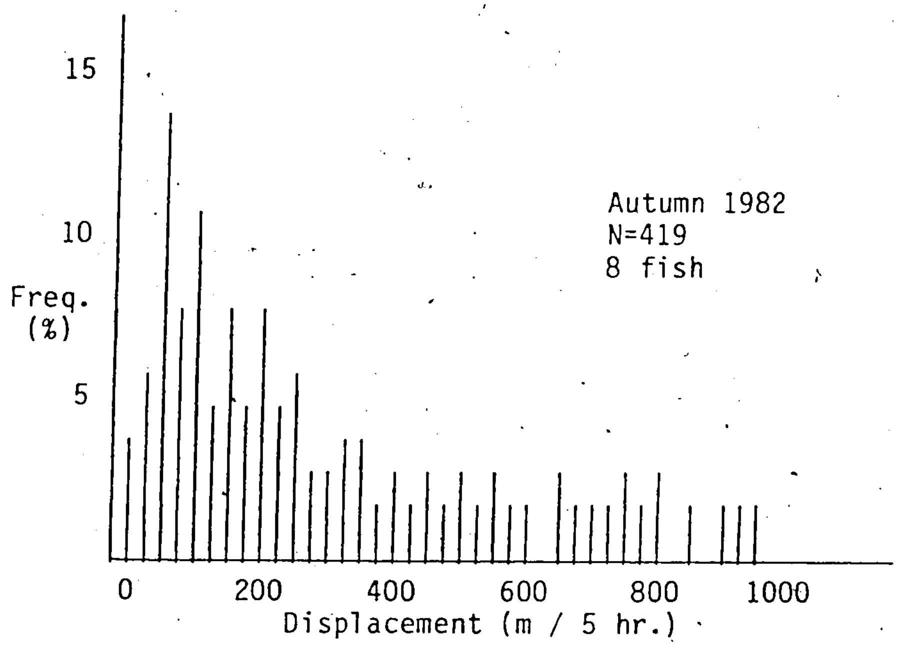


Figure 6. Displacement of radio-tagged pike measured in meters moved during a 5 hour period. Neagle Lake, Sask.





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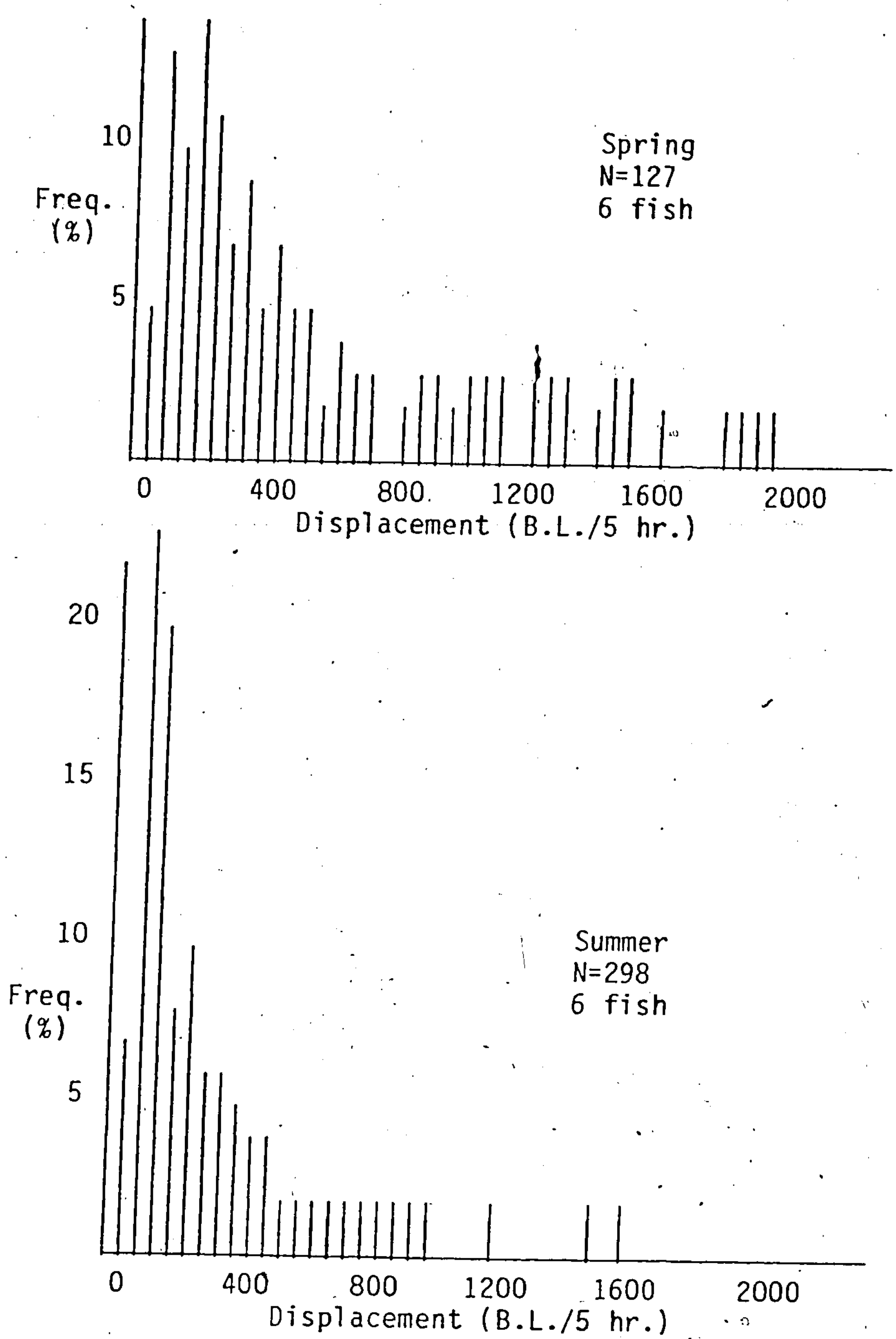
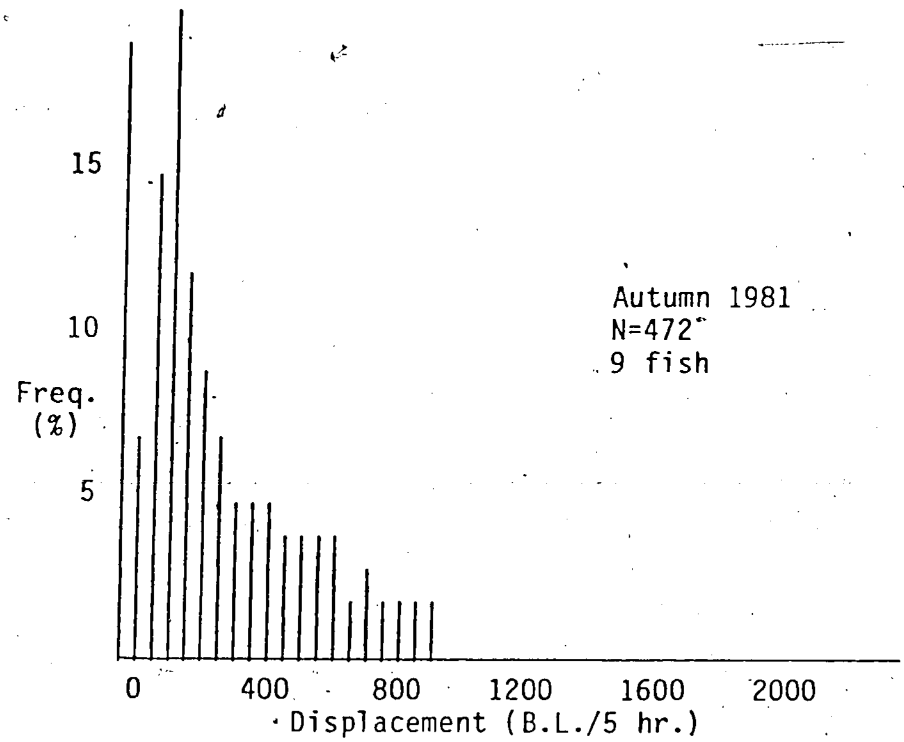


Figure 7. Displacement of radio-tagged pike measured in body lengths moved during a 5 hour period. Spring 1981, Summer 1981. Neagle Lake, Sask.



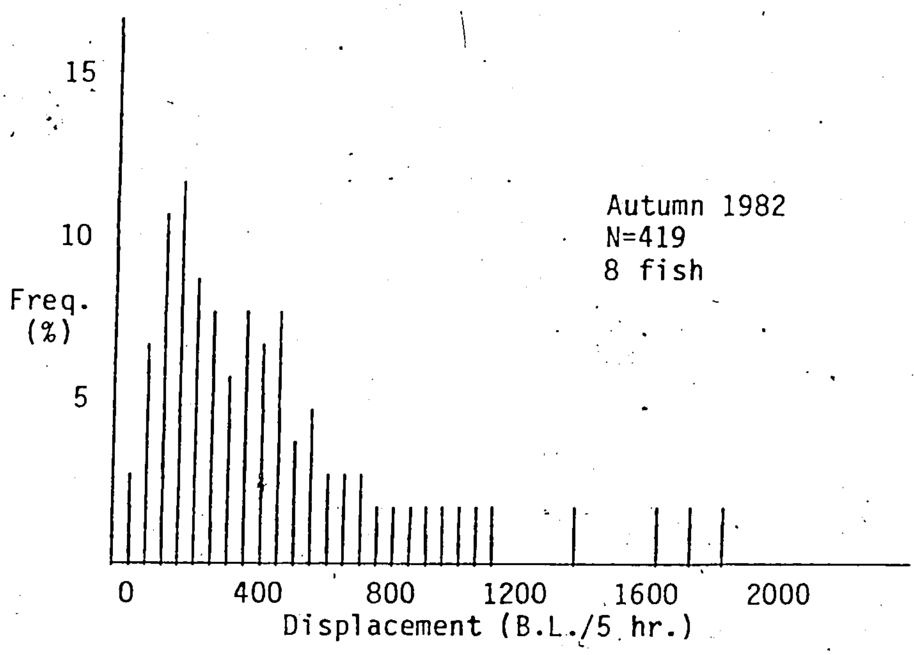


Figure 7. (CONTINUED)

P=0.15). The sizes of these areas of use were not significantly different between males and females during spring and summer (combined) (median size of area of use of males =9; 2, 20, n=9, median size of area of use of females = 9; 7, 11, n=7, U=27.5, P>0.05), during autumn (1981) (median size of area of use of males =11; 1, 11, n=5, median size of area of use of females =25; 8, 30, n=12, U=12.0, P>0.05) and during autumn (1982) (median size of area of use of males =19; 8, 24, n=8, median size of area of use of females =27; 9, 30, n=7, U=25.0, P>0.05).

The displacement of radio-tagged pike, measured as meters moved during 5 h, was significantly different (U=18578, P=0.007) between males (median displacement =82; 31, 199, n=589) and females (median displacement =110; 39, 235, n=723). These displacements were not significantly different between males and females during spring (median male displacement =126; 63, 228, n=50, median female displacement =102; 39, 214, n=77, U= 1667.5, P>0.203), during summer (median male displacement =49; 20, 136, n=188, median female displacement =63; 25, 161, n=6, U=9199.5, P=0.274) or during autumn (1981) (median male displacement =58; 20, 147, n=135, median female displacement =89; 36, 223, n=337, U=19653, P=0.021) but were significantly different between male and female during autumn (1982) (median male displacement =120; 60, 250, n=216, median female displacement =186; 90, 322, n=203, U=16824, P<0.001).

Movement may be related to body length (Minor and Crossman 1978) and as males were significantly smaller than females (Appendix 2, mean standard length of males =48.6 ± 2.53 cm, n=9; mean standard length of females =52.8 ± 0.88 cm, n=12, t=-3.453, P=0.003), variation in displacements may simply be the result of variation in body size.

Although the relationship between pike body length and mean 5 h displacement in meters (during autumn 1982) was not significant (r=0.228, P=0.586, n=8), I transformed displacements in meters to displacements in multiples of body lengths for each fish's movements to reduce any variation in displacements from this source.

The displacements of pike, measured as body lengths (bl) moved during 5 h, were not significantly different between males and females during all seasons combined (median male displacement =168; 64, 408, n=589, median female displacement =209; 74, 447, n=723, U=1984160.0, P=0.034). Displacements between males and females were not significantly different during spring (median male displacement =252; 126, 456, n=50, median female displacement =181; 69, 380, n=77, U=1560, P=0.071), during summer (median male displacement =99; 40, 275, n=188, median female displacement =122; 48, 311, n=106, U=9370.0, P=0.396) and during autumn (1981) (median male displacement =122; 42, 310, n=135, median female displacement = 173; 70, 434, n=337, U=20385.5, P=0.078). Displacements in body lengths were significantly different between males and females during autumn (1982) (median male displacement =245, 122, 510, n=216, median female displacement =349; 169, 604, n=203, U=18578, P=0.0007).

4.4 DISCUSSION

Although the prey requirement of pike shows seasonal and sexual differences, the sizes of their areas of use and their rates of movements in this study did not fluctuate in conjunction with these differences. This suggests that pike were not optimizing their activity with respect to food acquisition and were therefore not food limited. However, similar results in a food limited population would be expected if prey availability and abundance had fluctuated with the level of the prey requirement of pike. It is unlikely that this situation occurred during this study. Yellow perch, the most common item in the diet of the pike of Neagle Lake, would likely be most available to pike during the late summer and autumn when the young of the year perch formed large, inshore aggregations along with large numbers of spottail and emerald shiners. If the expected pattern of space use fluctuations did not occur as a result of the effects of changes in prey availability, one would expect the areas of use and magnitude of movements to be smallest during autumn, when prey availability appeared to be highest. This was not observed, with space use and movements during autumn generally being larger than during other seasons.

Lack of seasonal fluctuations in space use was also noted by Diana et al. (1977), who determined that there was no difference in the extent of pike movements between the summer and winter during short-term observation periods. These results and my results contrast with those obtained for the closely related muskellunge (Esox masquinongy) by Minor and Crossman (1978) and Dombeck (1979). Their studies revealed that muskellunge show seasonal variation in their home range sizes, being largest in the spring, decreasing during summer, slightly increasing in the autumn and being smallest during winter. If muskellunge have a seasonal pattern of prey requirements similar to that of pike, their fluctuations in area of use may indicate that they are food limited. This seems reasonable because muskellunge have a growth rate twice that of pike (Scott and Crossman 1973) and would presumably have a much higher prey requirement. This may partially explain the limited geographical range and competitive ability of muskellunge when compared to northern pike (Scott and Crossman 1973).

My observations and conclusion that the pike of Neagle Lake are not food limited provides behavioural evidence in support of the similar conclusion drawn by Grimm (1981a), based on quantitative evidence of population fluctuations. Although my study was conducted on a population of pike much different from those studied by Grimm (1981a), the similarity of our conclusions indicates that they are applicable to many populations of pike. If a species was to be generally food limited over its range, this condition would be most prevalent where the local population was at a high, unexploited level. The population of pike in Neagle Lake would appear to meet this condition as commercial and sports fishing pressure is virtually non-existent and the lake is locally reputed to have a large population of pike. As my results indicate that these pike are not food limited, it is reasonable to assume that exploited populations of pike (having lower densities than unexploited populations) would not be food limited.

5. Influence of Predation on the Pike Population

5.1 INTRODUCTION

Predation may be a density-dependent regulatory mechanism. As a population of prey animals increases, predators may immigrate to the area of abundance or through increased birth or survival rates increase their numbers. Mortality rates of the prey then rise, reducing their population size and resulting in a concomitant reduction in predator numbers. Certain populations of animals such as snowshoe hares (Lepus americanus)(Keith and Windberg 1978), white-tailed deer (Odocoileus virginianus)(Stout 1982), and ruffed grouse (Umbellus bonasa)(Rusch et al. 1972) are thought to be stabilized in this manner.

Although pike are reported to be preyed upon by a variety of animals, for example wolves (Kuyt 1972), bald eagles (Dunstan and Harper 1975), ospreys and black bears (Scott and Crossman 1973), there are few studies which quantify the effect of this predation. In the present study, I determined which animals were preying upon pike and estimated the effect of one predator species, bald eagles, on the pike population of Neagle Lake.

5.2 METHODS AND MATERIALS

The study was conducted during 1981 and 1982 at Neagle Lake. During all seasons I made irregular (at least twice per month) searches of the lakeshore and the shoreline of the inlet and outlet streams near Neagle Lake. All evidence of predation on pike was recorded. The identity of the predator was determined by examination of scats, nearby tracks and location of the remains.

Since bald eagles were by far the most important predator of pike, the pike requirement of the eagle population at Neagle Lake was determined. A modification of the method of Craighead and Craighead (1956) for determining the prey requirement of a raptor population was followed (Figure 8).

The remains of prey consumed by eagles were collected at feeding perches located on rocky reefs and points, near low snags along the lakeshore and on bare knolls overlooking the lake. All of the pike remains included either cleithra or dentaries. A reference collection of 37 dentaries and 65 cleithra was made in 1982 from pike of known length. The relationship between dentary length (measured in millimeters with a flexible ruler from the anterior symphysis to the posterior extremity, along the outside curve) and pike standard length (in centimeters) was determined. A similar relationship was obtained from cleithrum length (measured in millimeters from the origin along the anterior surface to the ventral extremity) and pike standard length. Based on these relationships, the standard length of pike represented in the prey remains was calculated from the dentary and cleithrum measurements. The weight of these pike was then calculated from a sample of 29 pike of known weight and length. I calculated an energy content for whole pike

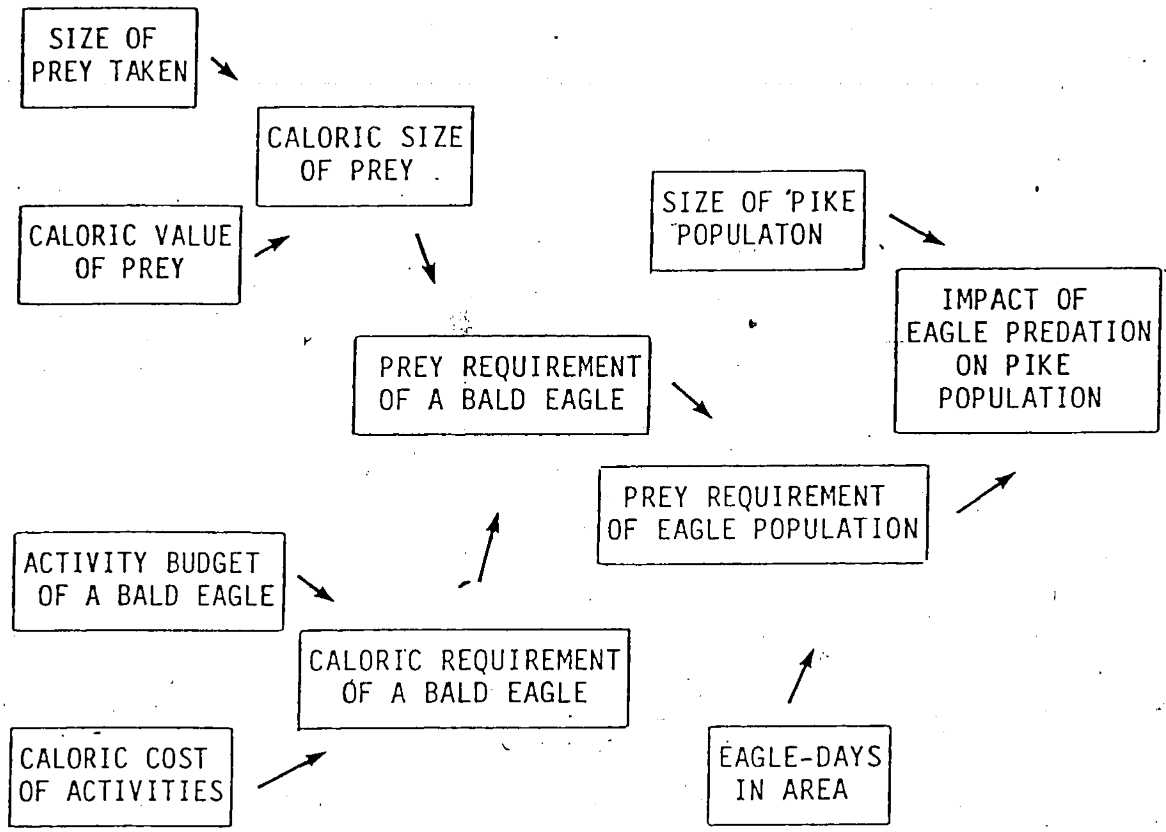


Figure 8. Method of determining impact of predation by bald eagles on population of pike. After Craighead and Craighead 1956.

of 1.2 kcal/g wet weight during the ice-free season using the caloric values of pike given by Diana and Mackay (1979).

The activity budget of eagles was estimated by direct observations made from 0.2 to 1.0 km away using 9x36 binoculars. Relative proportions of the time spent perching and flying were determined. The ratio of powered:gliding flight of 41:59 reported by Gerrard et al. (1980) was applied to the total flight time to derive time spent in powered and gliding flight. Observations were made throughout daylight hours and values thus obtained were converted to a 24 hour activity budget (assuming no nocturnal flight).

I was at Neagle Lake year-round and usually observed the arrival and departure of the eagles and could calculate their length of stay to within a few days. Their period of residency was compared to the period when pike were available in open water. The number of days when eagles were at the lake and pike were available in open water was multiplied by the number of eagles at the lake and expressed as eagle-days.

An estimate of the size of the pike population was made based on published estimates of densities compared to the area of suitable habitat in Neagle Lake. The estimate included only adult pike (>30 cm standard length). The prey requirement of the eagle population was then compared to the pike population and the impact of predation by eagles was determined.

5.3 RESULTS

Eagles were identified as the predators of pike in 95% of the cases identified (Table 2). Pike comprised 87% of the diet of the eagles (Table 3). The size of the pike taken by eagles was determined from the dentary length - standard length relationship (Appendix 3), and the cleithrum length - standard length relationship (Appendix 4) . The mean standard length of pike taken by eagles was 43.3 cm, SE=1.04, n=74 (Figure 9). The mean weight would have been 623 g (based on a sample of 29 pike with standard lengths between 40 and 45 cm, mean weight =623 g, SE=21.4). The average pike taken by eagles would therefore have a caloric content of 748 kcal (623 g x 1.2 kcal/g).

Adult eagles were observed for 1018 minutes in daylight hours during August and September 1982. The eagles spent 940 minutes (92%) perching and 78 minutes (8%) in flight. Assuming that the eagles remained perched at night (approximately 10 h), the 24 hour activity budget would be 96% perching and 4% flight. Using the powered flight:gliding flight ratio reported by Gerrard et al. (1980) results in a 24 hour activity budget of 96% perching, 1.6% powered flight and 2.4% gliding flight.

The caloric cost of perching was determined from Stalmaster and Gessaman (1982). The existence metabolism (considered equivalent to perching metabolism) of a 4.5 kg bald eagle at 15° C (mean summer air temperature at Neagle Lake) was calculated as 316 kcal/day. Stalmaster (personal communication) estimates a value based on Gessaman (1980) of 12.5 x B.M.R. for powered flight in bald eagles, with B.M.R. at 299.25 kcal/day. Powered flight would therefore cost 3741 kcal/day. The energy cost of gliding flight has been estimated at 2 to 4 x B.M.R. (Pennycuick

Table 2. Frequency of identified predator feeding on remains of northern pike. Neagle Lake, Sask. March 1981 to December 1982

PREDATOR	NO. OF IDENTIFIED CASES	%
Bald eagles	74	95
Mink	2	3
Fox	1	1
Wolf	1	1
TOTALS	78	100

Table 3. Diet of bald eagles as determined from remains of prey. Neagle Lake, Sask. Summers 1981,1982

PREY SPECIES	N	%
Northern pike	74	87
White suckers	6	7
Unident. ducks	4	5
Snowshoe hare	1	1
TOTALS	85	100

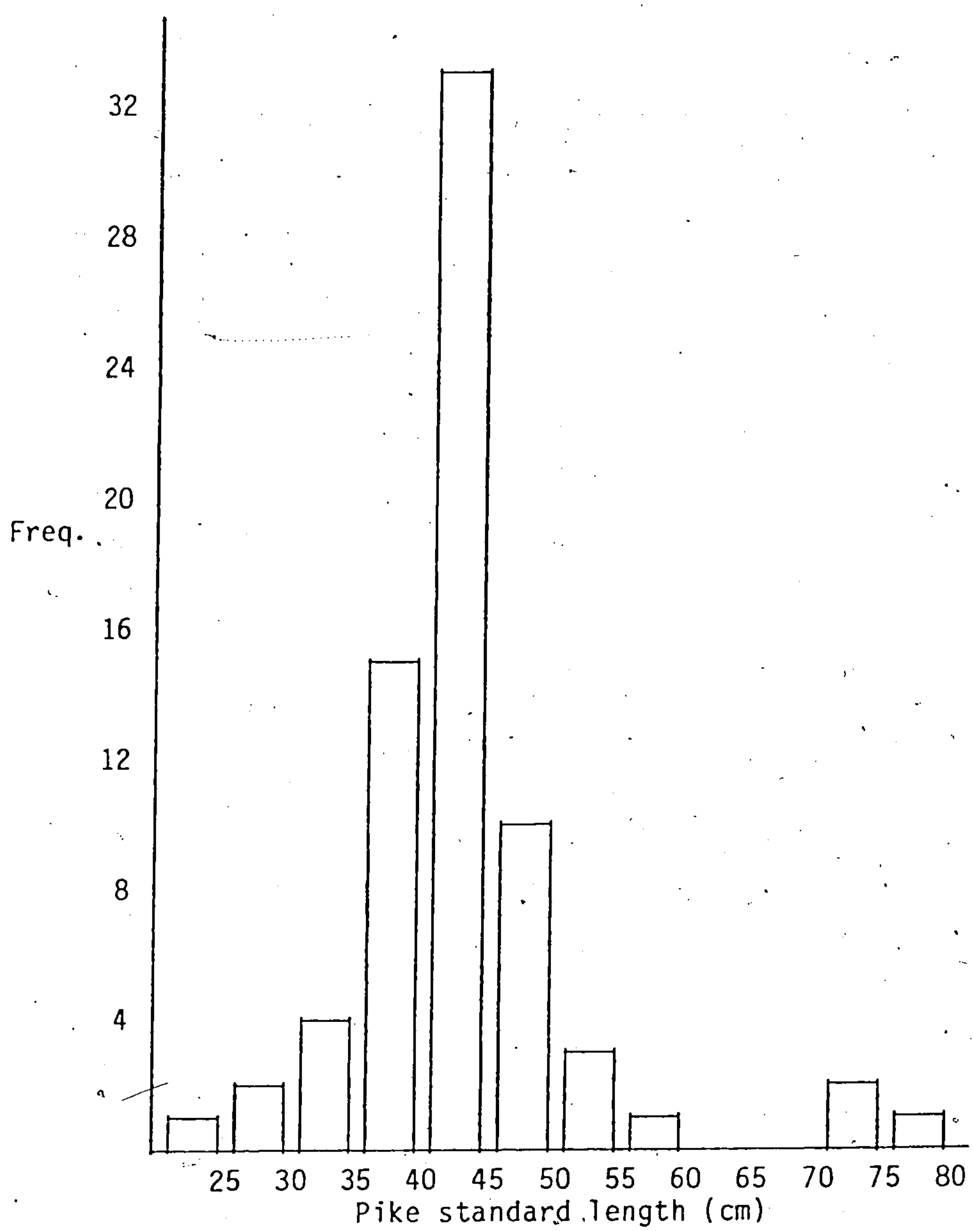


Figure 9. Size of pike taken by bald eagles as determined from collection of prey remains. Neagle Lake, Sask. 1982

1972, Baudinette and Schmidt-Nielsen 1974.) Using 3.5 x B.M.R. (Stalmaster, personal communication) resulted in a gliding metabolic rate of 1047 kcal/day.

The energy metabolized per day was calculated from the caloric cost of these activities and their relative proportions in the activity budget. The result was that 418 kcal/eagle-day is the energy metabolized by a free-ranging, non-breeding, adult bald eagle during summer.

The average pike taken by eagles would have a caloric content of 748 kcal (623 g x 1.2 kcal/g). Assuming a 73% assimilation efficiency (Kirkwood 1979, Stalmaster and Gessaman 1982) an eagle should retain 539 kcal as metabolizable energy. With 418 kcal metabolized per day and a pike size of 539 kcal of metabolizable energy, a bald eagle would require 0.78 pike/day or one pike every 1.29 days.

Total eagle-days at Neagle Lake during 1981 was 735 and was 550 during 1982 (Figure 10).

In 1981, 735 eagle-days requiring 0.78 pike/day would have resulted in 429 pike being taken. As shown in Table 3 however, pike represented 87% of the eagles' diet. As the preceding calculations assume a total diet of pike, the calculated number of pike taken should be reduced by 13%, to 467 pike in 1981 and 349 pike in 1982.

Based on a habitat size of 700 ha and published estimates of pike densities (Moyle et al. 1948, Munro 1957, Kipling and Frost 1970), I estimated there were between 8,000 and 12,000 adult pike in Neagle Lake. The number of pike taken by eagles in 1981 (467) divided by the two extremes of population size results in a range of 4% to 6% of the population being taken by eagles. The 1982 harvest, with 350 pike taken, represents 3% and 4% of the population.

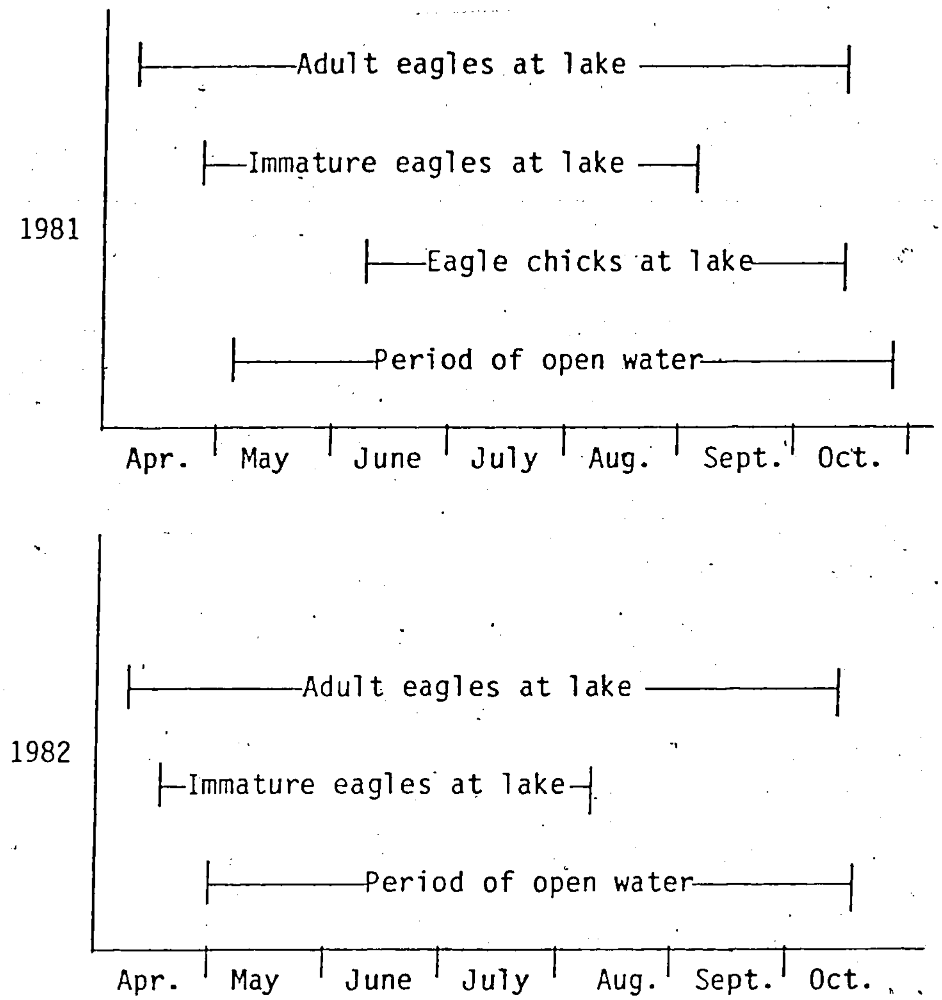


Figure 10. Residency periods of eagles at Neagle Lake.

5.4 DISCUSSION

The major predators of fish in Neagle Lake appeared to be bald eagles, which fed almost exclusively on pike. Bald eagles are opportunistic predators (Brooks 1922, Murie 1940, Hancock 1964, Retfalvi 1970), feeding on the most abundant prey species in the area. Many researchers (Brooks 1922, Wright 1953, Southern 1963, Dunstan and Harper 1975, Todd et al. 1982) have found that fish are the most common prey of bald eagles, especially in inland areas, with pike often being one of the predominant species.

The pike consumed by eagles may have been scavenged. However, in 8 cases when I observed eagles feeding and collected the remains immediately afterward, the prey remains appeared fresh (no fungal growth or putrid odor, gill and skin fragments brightly colored, fresh blood smears). In 2 cases when I observed eagles capturing prey, the prey appeared to be alive. Eagles at Neagle Lake preyed on live pike, although some pike (particularly those larger than 70 cm) were likely scavenged.

The calculations of the daily caloric requirement are based on a 4.5 kg, non-breeding adult bald eagle at 15° C. The results were applied equally to all eagles on the study area: chicks, juveniles, breeding adults and non-breeding adults. The limited scope of the study precluded detailed studies on the activity budgets and metabolic requirements of each class of eagles. However, the caloric requirements of a non-breeding adult gives a usable index which probably approaches a mid-point in the range of caloric requirements for the eagle population, considering differences in body size, requirements for growth and social activities (territory defence, mating and parental care).

The prey requirements I calculated for wild eagles (0.73 pike/eagle-day, based on a pike weight of 623 g) is about 65% higher than the food requirement of captive bald eagles (Chura and Stewart 1967, Stewart 1970). Both of these studies on captive, unexercised eagles used ground fish as the major component of the diet and found daily food intake per eagle to be 250-300 g (caloric values were not given). On a weight basis, my calculations showed the daily food intake for wild eagles to be 455 g. Stalmaster and Gessaman (1982) estimated the minimum prey requirement for a wild bald eagle during a 90 day winter period at 13 salmon, 20 rabbits or 32 ducks. For a 90 day summer period, my calculations indicated that 66 pike would be taken. On a caloric basis, this is approximately 89% higher than Stalmaster and Gessaman's estimate

Gerrard et al. (1980) observed an immature bald eagle in northern Saskatchewan feeding on fish, likely tullibee, (C. artedii) (Gerrard, personal communication), once every 16 hours during the summer. My calculations indicate a similar feeding frequency of once every 19 daylight hours (0.73 pike/day; 14 h daylight/day).

An annual mortality rate of 3% to 6% because of eagle predation likely has little influence on pike populations. Total annual mortality rates (those other than man-induced) are around 20% to 30% for adult pike (Kipling and Frost 1970). Additionally, pike populations can withstand exploitation up to 60% per annum (Kipling and Frost 1970, Snow 1974). Eagle predation as well as predation from other interspecific predators is therefore unlikely to influence pike numbers.

6. Space Use of Northern Pike

6.1 INTRODUCTION

Regulation of animal populations can occur through spacing behaviour. Evidence from a variety of studies (Orians 1961, Chapman 1962, Le Cren 1965, Van den Assem 1967, Watson 1967, Clark 1970, Krebs 1971) supports this hypothesis, although Watson and Moss (1970) and Davies (1978) caution that when spacing behaviour occurs, it can, but does not necessarily regulate populations. Spacing behaviour which regulates a population is usually some form of territorial behaviour. For my purposes, I will use Pitelka's (1959) definition of territory as "an exclusive area", without reference to the mechanism by which other animals are excluded, since it is this exclusive nature of territoriality which provides the mechanism of regulation.

Previous studies on northern pike have resulted in a wide variety of descriptions of their use of space. Malinin (1970, 1971) and Makowecki (1973) suggested that pike were sedentary and likely territorial. Christiansen (1976) suggested that pike were non-territorial, but with restricted home ranges within which a locally exclusive area is maintained. Diana _et al_. (1977) described pike space use as non-territorial, being composed of random movements within suitable habitat. The reasons for this diverse range of observations likely include biases due to short-term observation periods and restricted sampling areas. In the case of Malinin (1970, 1971) and Diana _et al_. (1977) the maximum tracking periods were 70 h and 47 days respectively. Descriptions of the habitat use of pike (Makowecki 1973, Diana et al. 1977, Chapman and Mackay 1983) are generally similar in stating that pike prefer shallow, vegetated areas, but differ in describing the strength of this preference and generally describe habit preference only during summer.

I conducted a long-term radio-location study where the pike could move and be located throughout the lake over periods of several months. This allowed me to make observations and describe the general space use of male and female pike during different seasons, and specifically, to determine if territoriality was exhibited and was a possible regulatory mechanism for the pike population.

6.2 METHODS

The telemetry procedure as described in Chapter 1 was used to observe the movements and space use of pike. At each radio-location, depth, density of vegetation and distance to shore were recorded. Depth was recorded as the water depth to the nearest meter. This was measured initially using a sounding line, and later in the study, using a bathymetric map (Appendix 7). Depth at each location is therefore water column depth and not the actual depth of the radio-tagged pike. Underwater observations (Chapman and Mackay 1983, Turner 1984) indicate that pike are almost always within 50 cm of the bottom. Vegetation density was recorded in categories of percent cover during the period of peak vegetation growth (early August). The most common types of vegetation which provided cover were Potamogeton spp., Nuphar sp. and Sagittaria sp. Vegetation density was not recorded during the winter because of the difficulty in observing vegetation through up to 1.2 meters of ice. The distribution of radio-tagged pike with regard to depth, vegetation density and distance to shore, was compared to the distribution of each of these parameters in the lake and tested for significance using the Chi-square test. In order to present a brief description of the use of space by pike, the selection of each habitat parameter was compared by season and by sex of pike. The central tendency of each distribution was compared using the Mann-Whitney U-test or the Kruskal-Wallis test. More detailed analysis of this data will be presented elsewhere. Results were considered significant if $P<0.05$. Since the pike were tagged in the south-west bay and 94% (1524 out of 1614) of all locations were in the south-west bay, only this area was used to calculate the distributions of depth, vegetation density, and distance to shore. The radio-location procedure was also used to determine whether pike maintain a territory (exclusive area). If so, overlap between areas of use would not be expected to occur, nor would other pike be present within the area of use. Ten-day minimum polygon areas of use were plotted on 1:10,000 maps of Neagle Lake (as described previously). Areas were considered to overlap (and therefore violate the assumption of exclusive use) if the boundaries crossed during the same ten-day period and included an area of overlap of more than 2 ha (10% of mean size of minimum polygon area of use). Angling was also conducted as close as possible to radio-tagged pike to determine whether other pike were nearby, although this was kept at an anecdotal level due to the risk of injuring the tagged fish.

6.3 RESULTS

A total of 1614 radio-locations were made on 21 different pike during the spring, summer and autumn of 1981 and the winter and autumn of 1982. The radio-tagged pike selected depths significantly different from random (Chi-square=37.7, df=8, P=0.00001). Most locations (n=1013, 63%) were in 2 and 3 m of water (Figure 11). Female pike were found in slightly deeper water than male pike (female mean depth=2.7 ±0.05 m, n=920, mean ± S.E., number of locations; male mean depth = 2.4 ± 0.05 m, n=694, U=293379, P=0.0038, Figure 12). Although this is statistically significant, the small actual difference in mean depths suggests that this difference has indefinite biological significance. Pike selected different depths with respect to season (H=192.4, df=4, P<0.001). Pairwise contrasts based on ranks indicated that pike were found in shallowest water during summer and autumn (1981) (summer 2.1 ± 0.05 m, n=321; autumn 1981, 2.1 ± 0.03 m, n=477) and in deepest water during winter (3.9 ± 0.13 m, n=213) (Figure 13).

The pike also selected their locations with respect to vegetation density significantly different from random (Chi-square =13.5, df=4, P=0.009). Pike tended to avoid areas of dense vegetation and were associated with open water most of the time (75% during summer to 92% during autumn 1982) and as often as would be expected from random selection (Table 4). Although the distribution of pike with respect to vegetation differed between the seasons (H=-11.616, df=3, P<0.001), this likely results from vegetation growing and dying in areas in which the pike were already residing. Male and female pike did not differ in selection of vegetation cover (U=314541.5, df=inf., P=0.3737), both being associated with open water nearly 90% of the time (Table 5).

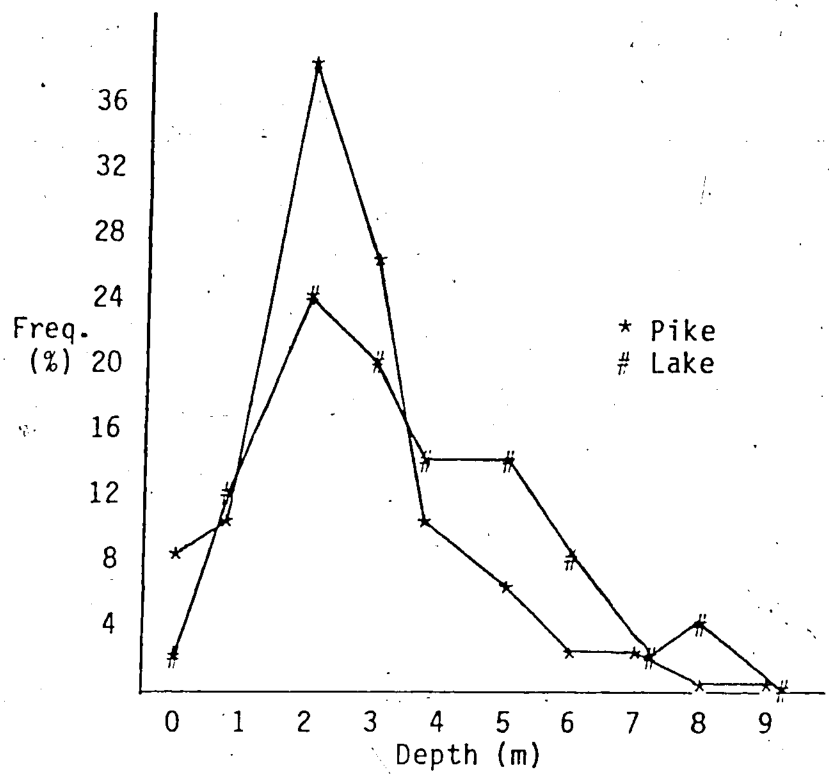


Figure 11. Distribution of lake depths and depths chosen by radio-tagged pike. Neagle Lake, Sask.

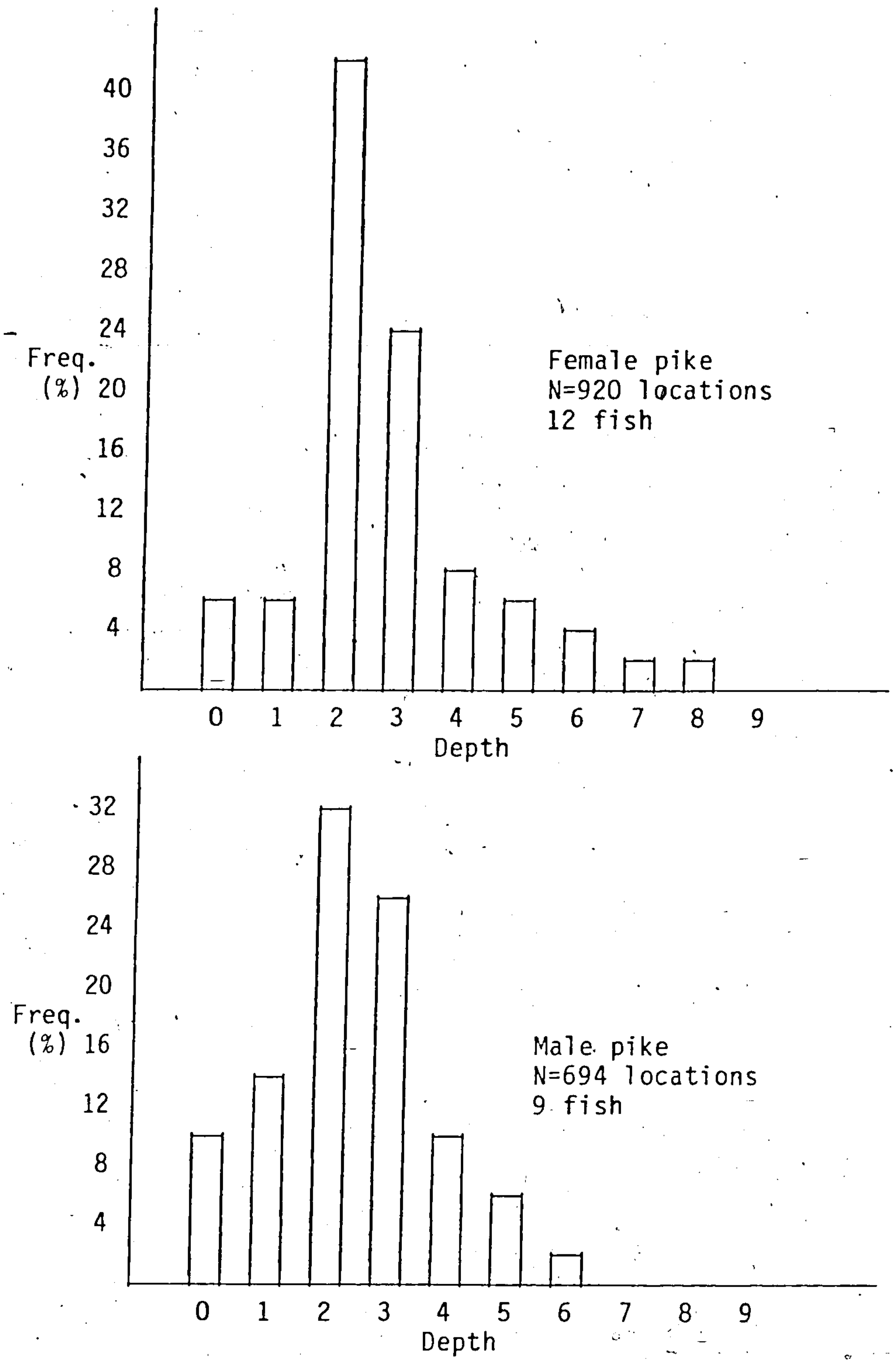


Figure 12. Distribution of depths chosen by male and female pike. Neagle Lake, Sask.

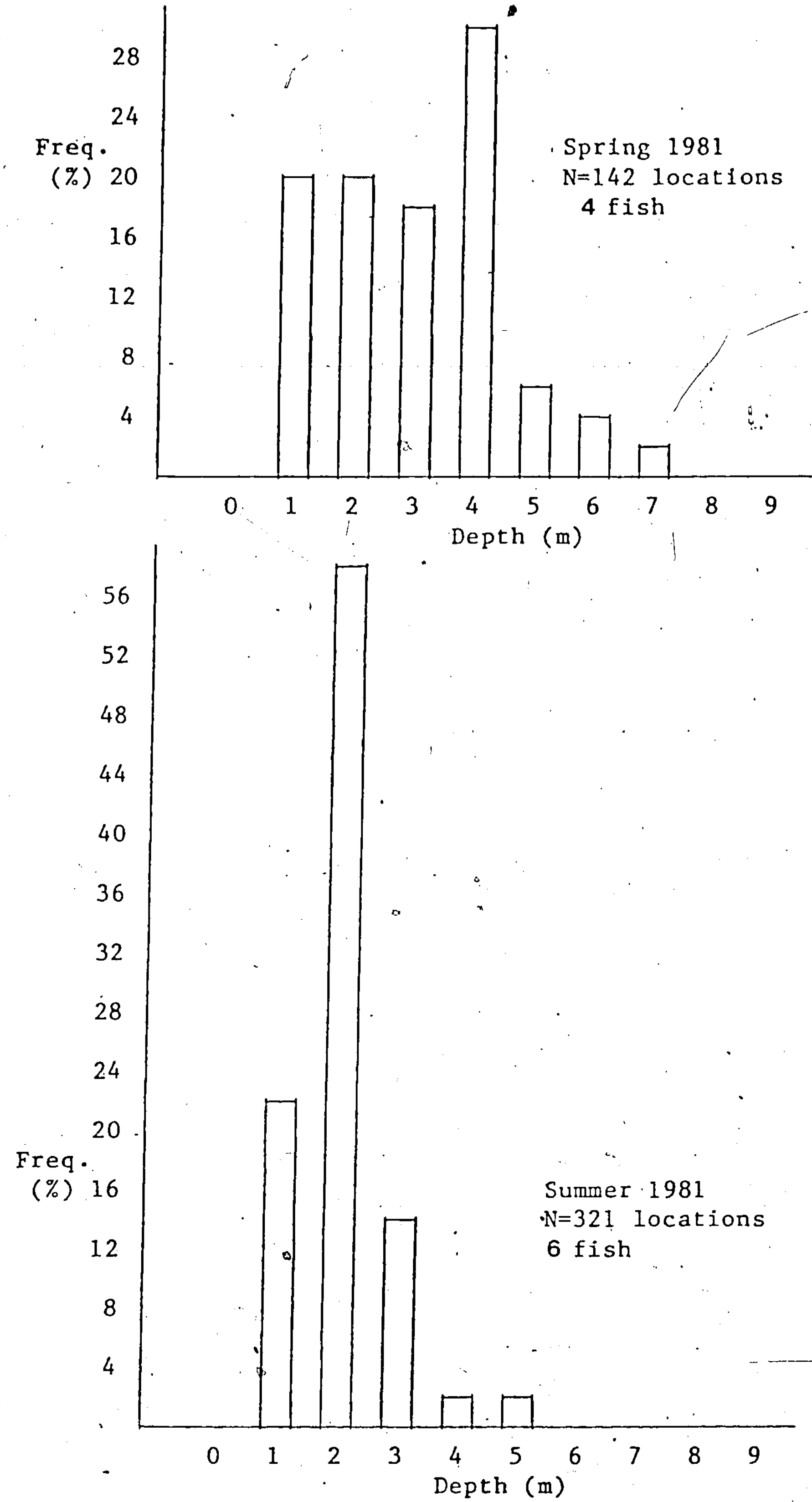


Figure 13. Distribution of depths chosen by radio-tagged pike during each season. Neagle Lake, Sask.

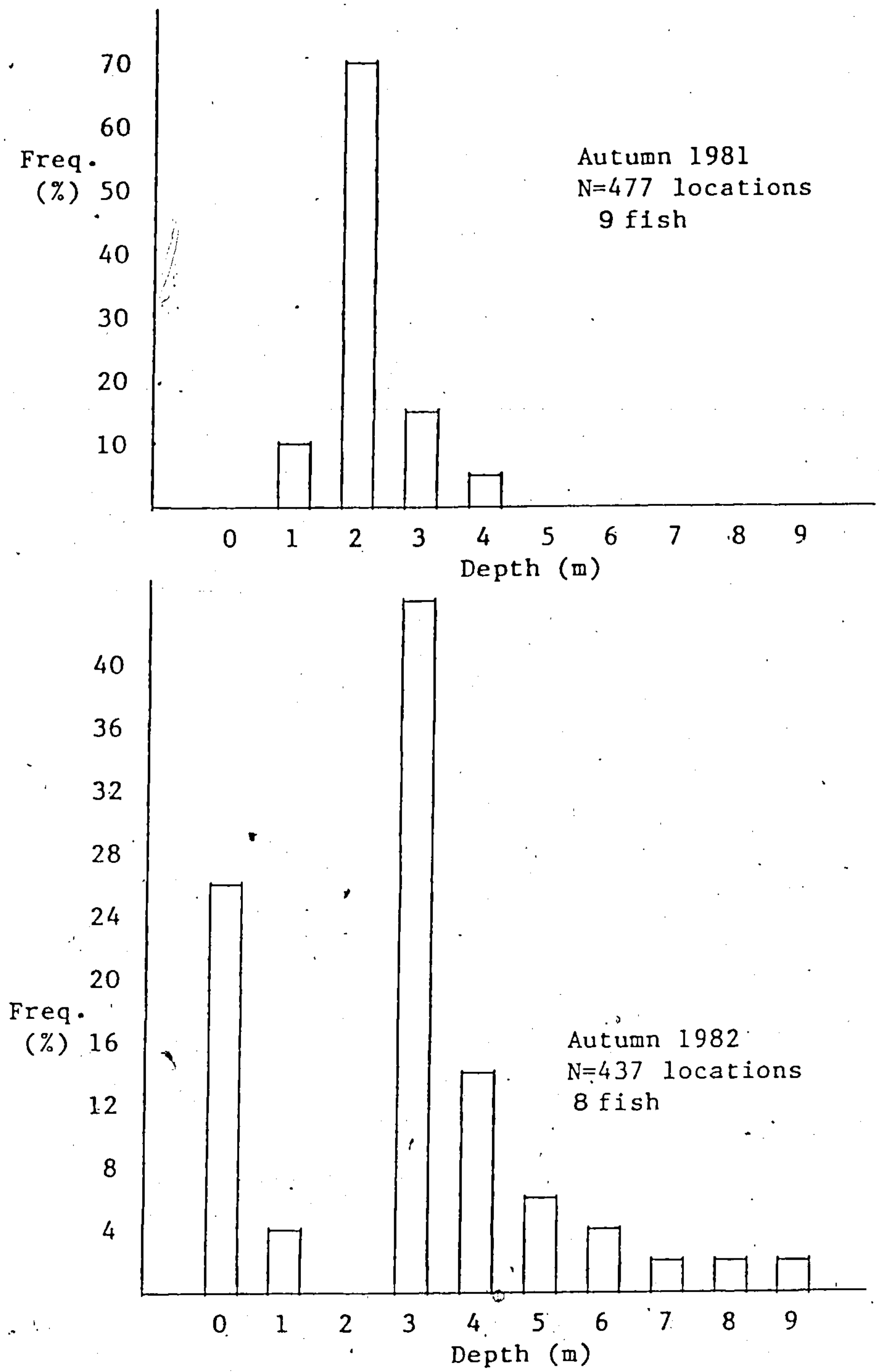


Figure 13. (CONTINUED)

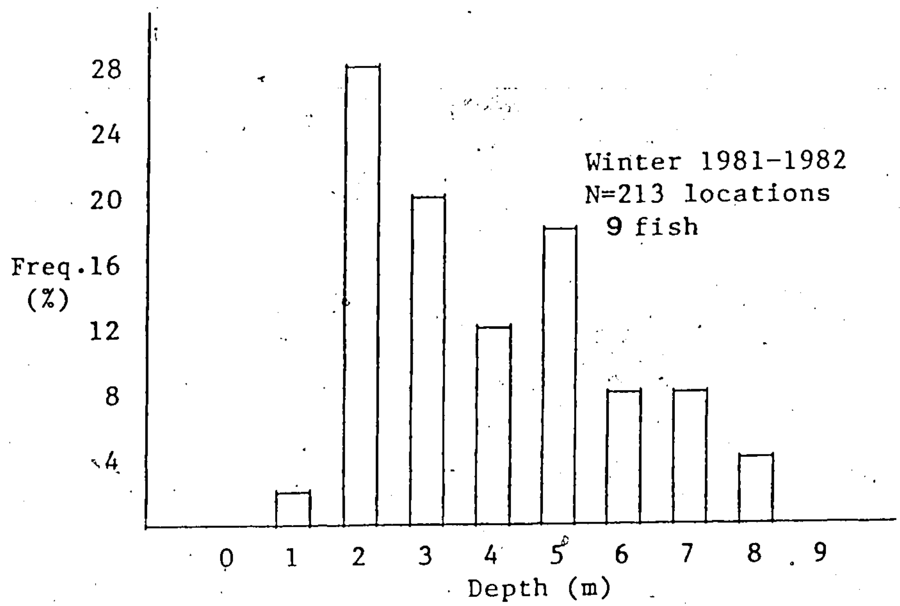


Figure 13. (CONTINUED)

Table 4. Distribution of radio-tagged pike with respect to season and to density of vegetation in Neagle Lake.

Vegetation Density (% cover)	Locations of Tagged Pike				Veg. Density in Lake (S.W. bay)
	Spring	Summer	Autumn 1981	Autumn 1982	
0%	125(88%)	239(75%)	415(87%)	400(92%)	76% (137 ha)
25%	7(5%)	24(8%)	29(6%)	34(8%)	4% (7 ha)
50%	6(4%)	29(9%)	14(3%)	0(0%)	4% (7 ha)
75%	4(3%)	11(3%)	14(3%)	2(1%)	4% (7 ha)
100%	0(0%)	18(6%)	5(1%)	1(0%)	12% (22 ha)

Table 5. Distribution of radio-tagged pike with respect to sex and density of vegetation in Neagle Lake.

Vegetation Density (% cover)	Locations of Tagged Pike: Female	Locations of Tagged Pike: Male	Veg. Density in Lake (S.W. bay)
0%	801(87%)	615(89%)	76% (137 ha)
25%	54(6%)	40(6%)	4% (7 ha)
50%	37(4%)	12(2%)	4% (7 ha)
75%	22(2%)	9(1%)	4% (7 ha)
100%	6(1%)	18(3%)	12% (22 ha)

Pike appeared to select their locations with respect to distance from shore (Chi-square =8.7, df=2, P=0.0127), being found closer to shore than would be expected from random selection. The distribution of pike with respect to distance from shore differed between the seasons (H=16.59, df=4, P=0.002, Table 6). Pairwise contrasts based on ranks indicated that the only difference was that locations during spring were closer to shore than during autumn (1982) (P<0.05). Male and female pike did not differ in their selection of locations with respect to distance from shore (U=4469, df=inf., P=0.114, Table 7).

No evidence of territorial behaviour was observed, either with radiotelemetry or with visual observations during the spawning period. Overlap in areas of use between radio-tagged pike was observed in all seasons except spring (Table 8). However, pike were angled near (<5 m) radio-tagged pike in each season. Overlap occurred between males, males and females, and females. Instances of one area of use being entirely within another also occurred (Figure 14). Overlap was to be expected based simply on the size of the areas of use, the size of the lake (700 ha) and the probable size of the pike population. If the smallest mean area of use (11.9 ha, summer) was an exclusive area, only 59 pike would be in the lake instead of 8,000-12,000 pike (estimated population size).

Many aspects of pike space use cannot be quantitatively measured; therefore a qualitative description is also warranted. Generally, the radio-tagged pike were restricted to the area of the lake where they were initially captured. Neagle Lake is roughly Y-shaped, with each of the three arms being approximately equal in size (200-250 ha). Out of 21 radio-tagged pike, only 4 moved out of the arm where they were tagged (during approximately 8 months of tracking). During the open water

Table 6. Distribution of radio-tagged pike with respect to season and distance to shore in Neagle Lake.

Distance from Shore	Locations of Tagged Pike					Distribution in Lake (S.W. bay)
	Spring	Summer	Autumn 1981	Autumn 1982	Winter	
0-50 m	112(78%)	192(59%)	331(73%)	168(57%)	133(73%)	54% (97 ha)
51-100 m	16(11%)	114(35%)	99(22%)	82(28%)	50(27%)	30% (54 ha)
101+ m	15(10%)	17(5%)	21(5%)	44(15%)	0(0%)	16% (29 ha)

Table 7. Distribution of radio-tagged pike with respect to sex and distance to shore in Neagle Lake.

Distance from Shore	Locations of Tagged Pike			Distribution in Lake (S.W. bay)
	Female	Male	Total	
0-50 m	468(62%)	468(73%)	936(67%)	54% (97 ha)
51-100 m	233(31%)	128(20%)	361(26%)	30% (54 ha)
101+ m	55(7%)	42(7%)	97(7%)	16% (29 ha)

Table 8. Instances of overlap in areas of use of pike by seasons.

Season	Instances of Overlap	Total Number of Areas of Use
Spring	0	5
Summer	7	11
Autumn	48	34
Winter	4	17

Figure 14. Instance of one area of use contained entirely within a larger area of use. Pike #23 located within area occupied by pike #21, September, 1982

season (late May to mid-October), all the pike remained within the arm where they were tagged. The movements to other arms occurred during break-up (one movement) and freeze-up (three movements). During most of the year, I was able to locate the tagged pike by going to its previous location and usually found the fish within 200 m of this location. This method was not effective just before freeze-up. I was able to continuously track pike during the period when most of the smaller bays were frozen and up to one day before the entire lake was frozen. During this time (approximately 5 days), I was unable to locate pike on numerous occasions and believed it was because they were moving extensively. During break-up (mid-May), I was unable to track pike because of dangerous ice conditions, but the relatively few times I located pike suggested that they were moving extensively.

Except for freeze-up and break-up, the pike seemed either to move slowly at random (Figure 15) or reside in a small area for several days, then move to another area (Figure 16). These two behaviours represent the two ends of a continuous scale of pike behaviour and many examples of movements were of an intermediate type. For example, pike #12 stayed near a small bay for 6 days, then moved over a large area, apparently at random, for 4 days (Figure 17). Several interesting modifications of this behaviour were observed. One male pike was located almost every day for about 30 days near (<5 m) a submerged jackpine. During this time, a strong gale felled another jackpine into the water about 10 m from the first tree. The pike moved and spent much of the remainder of the time (about 20 days) near the new tree. During the 30 days, the pike made several excursions of up to 700 m from the trees but returned to the trees within a day or two. On another occasion (mid-June 1981), a pike

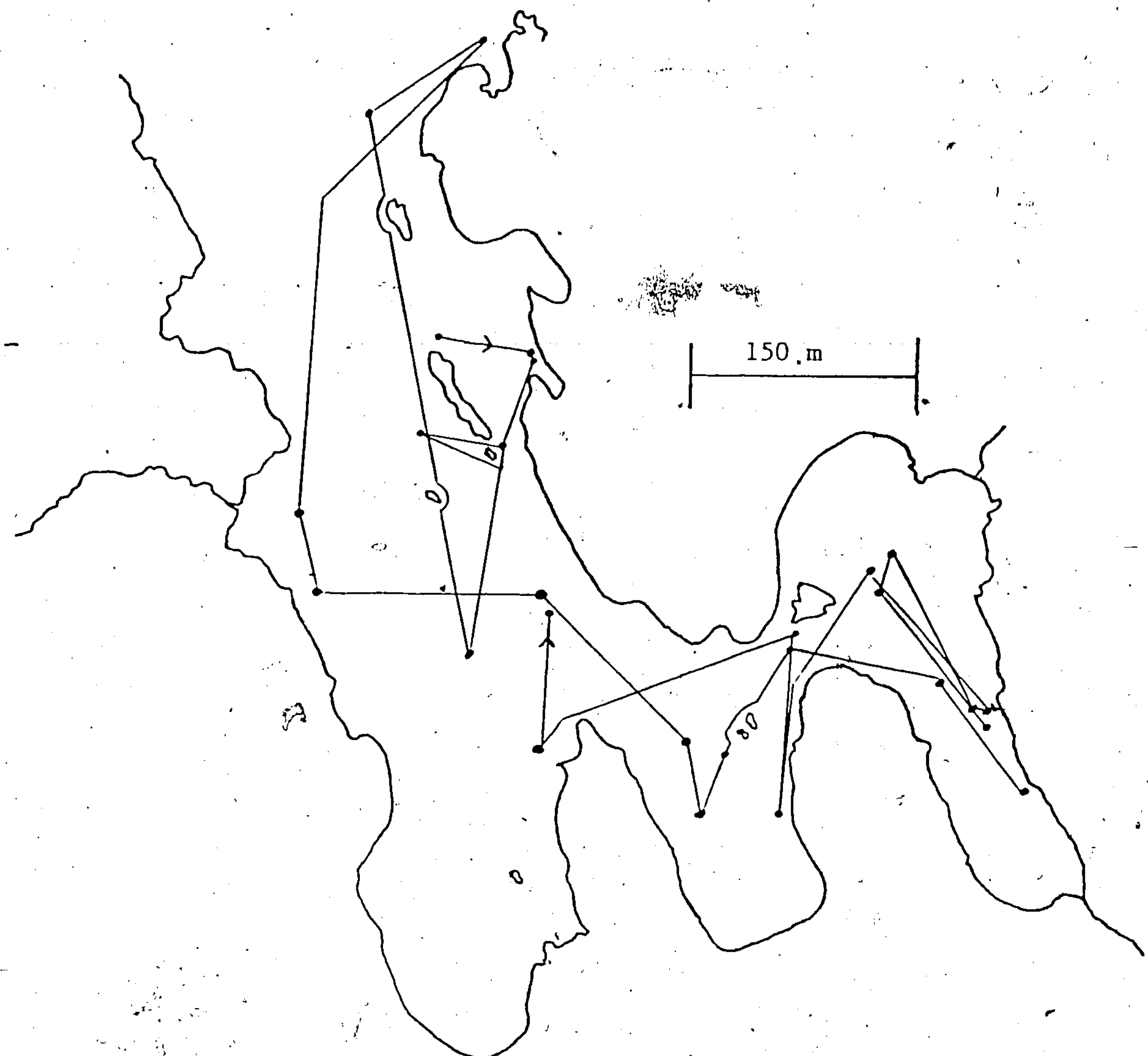


Figure 15. Movement of radio-tagged pike (#07) during 22 Sept.- 1 Oct. 1981. Located twice each day at 5 hr intervals. South-west bay, Neagle Lake, Sask.

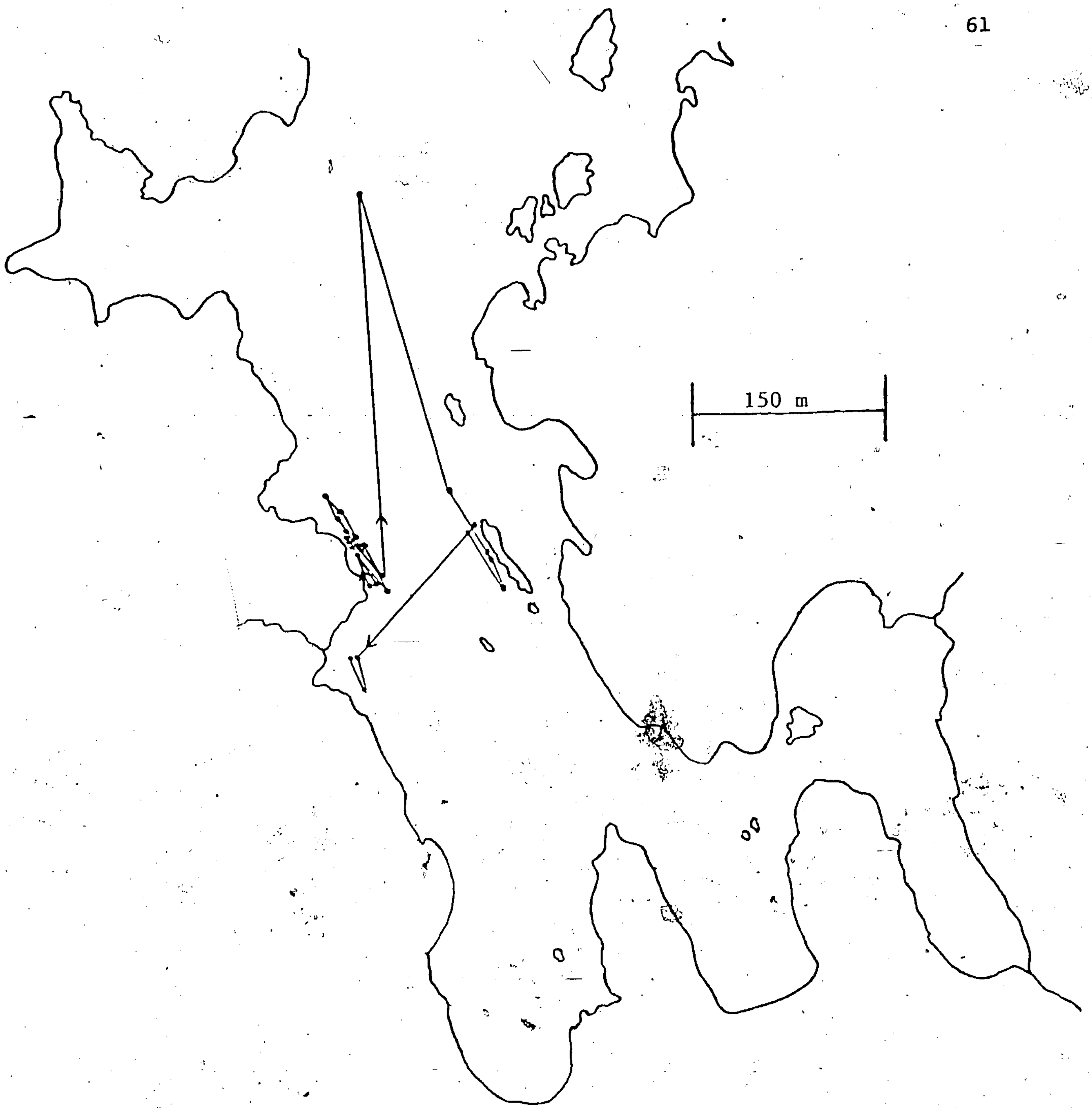


Figure 16. Movement of radio-tagged pike (#12) during 22 Sept.- 1 Oct. 1981. Located twice each day at 5 hr intervals. South-west bay, Neagle Lake, Sask.

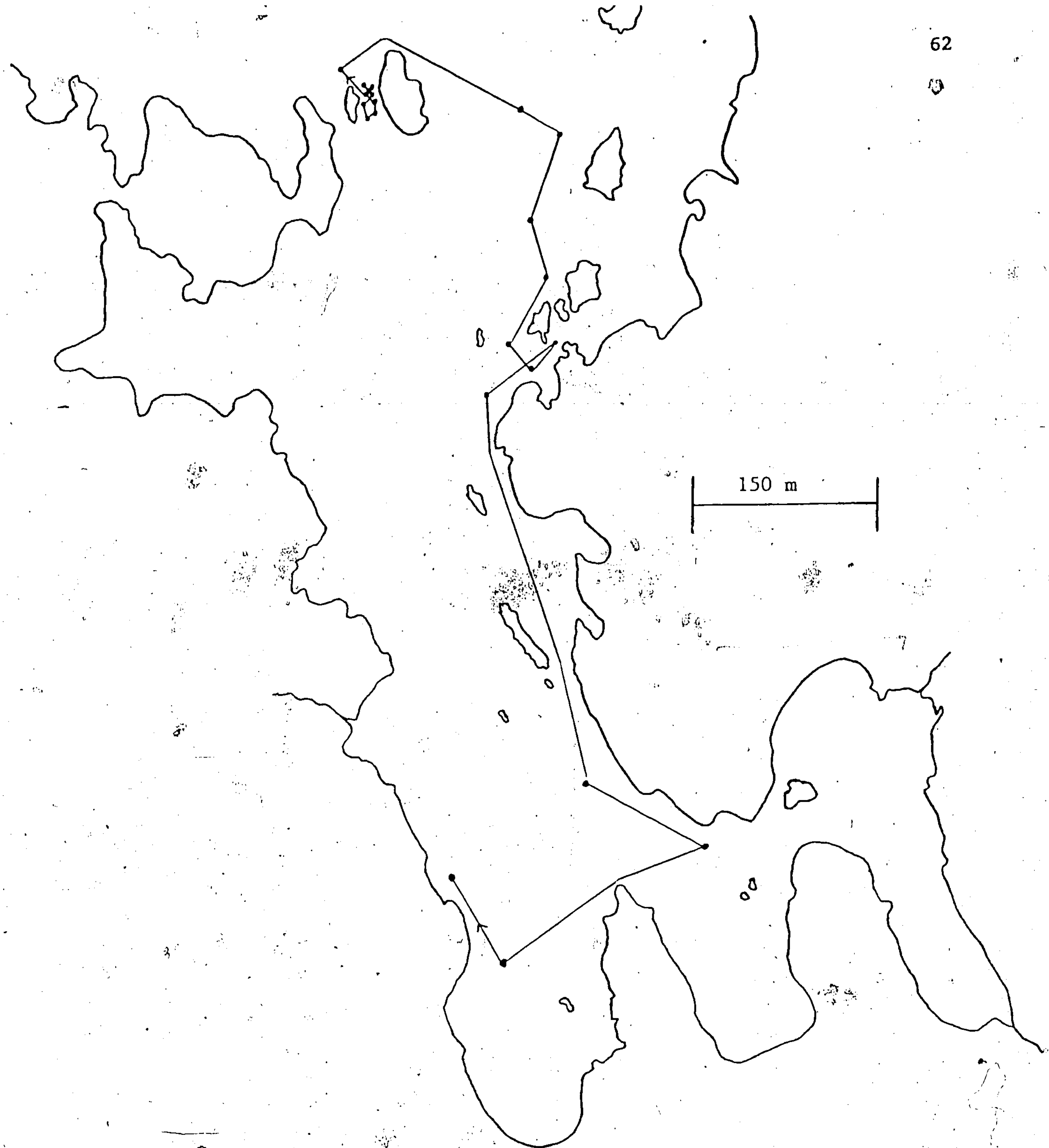


Figure 17. Movements of radio-tagged pike (#17) during 1 Sept.- 10 Sept. 1981. Located twice e^ch day at 5 hr inter^als. South-west bay, Neagle Lake, Sask.

spent 10 days within a 2 ha area except for one mid-day excursion of 2300 m (Figure 18). This excursion is especially interesting because the pike was in the small bay in the morning, travelled over 1 km along three separate shorelines and returned via the same route by evening. The Sechi disc reading on this occasion was 2.5 m, there was a light breeze and it was raining lightly. A person assisting me with the study lost her direction attempting to follow the same route.

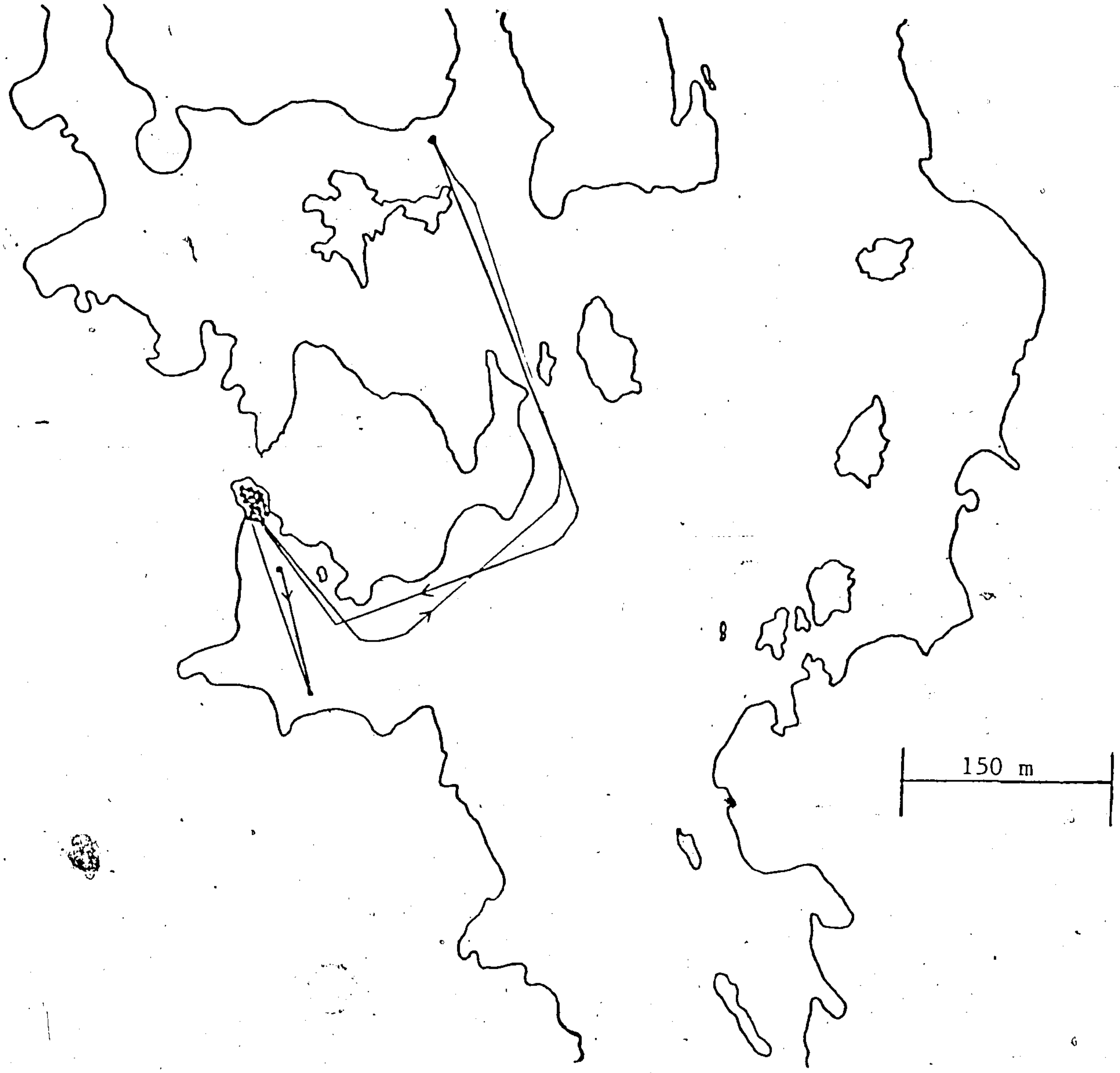


Figure 18. Movements of radio-tagged pike (#13) during 8 Oct.- 21 Oct. 1981. Located twice each day at 5 hr intervals. South-west bay, Neagle Lake, Sask.

6.4 DISCUSSION

My observations suggest the following description of pike movements. During the open water season, pike wander through a somewhat restricted area of the lake, often exhibiting short-term site fidelity. They prefer depths of 2 to 3 m and avoid dense vegetation but do not show a distinct preference for unvegetated areas. The vast majority of time they are found within 100 m of the shore. During winter, they prefer slightly deeper water, but remain in areas fairly close to shore. There may be extensive movements throughout the lake during ice break-up and freeze-up. The movements during break-up are likely related to finding a spawning site and the freeze-up movements may be related to finding a deep area which is close to shore. At no time during the year did the pike show a type of territorial behaviour or exhibit exclusive use of space. No major differences in behaviour between male and female pike were noted.

This model of space use by pike is in general agreement with Diana _et al_.(1977) who found that pike tend to move at random throughout a narrow zone around the edge of the lake. Christiansen (1976), Diana _et al_.(1977) and Chapman and Mackay (1984) also noted the tendency of pike to remain in a small area for several days. These conclusions contradict those of Malinin (1970, 1971) and Makowecki (1973) who felt that pike are largely sedentary, although my results indicate that pike are somewhat restricted in their movements, but on a much larger scale than was previously thought.

I was able to track pike for only one complete cycle of seasons, and therefore cannot present strong evidence for seasonal changes in space use. However, my results are supported by those of Diana _et_ al. (1977) who also found that pike were in deeper water during winter than during summer, although in the lake they studied, the pike were required to move further from shore to find deep water. At Neagle Lake, deep water could be found near shore at many locations. Miller (1948) and Makowecki (1973) suggested that pike move extensively during early spring. My observations tend to support this and further suggest a late autumn movement.

It is a dogma in pike biology, substantiated by many authors (Makowecki 1973, Scott and Crossman 1973, Paetz and Nelson 1970, Diana et al. 1977), that pike prefer vegetated areas. My findings show that pike in Neagle Lake are found associated with open water and avoid dense vegetation. This supports the hypothesis of Chapman and Mackay (1984) who suggest that pike are highly versatile in their selection of habitats and broad generalizations should be viewed with caution.

Although I present evidence that pike show no form of territorial or exclusive space use behaviour, it must be realized that this conclusion refers to behaviour over a fairly large scale in time and space. Christiansen (1976) suggested that pike may maintain an individual elastic sphere of territory. Effectively, this would be a personal distance that pike would remain away from other pike in spite of random, large-scale wanderings. A system such as this could theoretically result in population regulation. Both Christiansen's (1976) and my results indicate that this personal space, if it exists, is likely smaller than 5 m in diameter. A territory of this size (20 m^2) would only have a regulatory effect on pike densities approaching 500 pike/ha. Reported densities of pike range as high as 66 pike/ha, with 10-15 pike/ha being most common (review by Toner and Lawler 1966). High densities where space use could be a regulating factor may occur in spawning areas. However, my own observations, as well as other reports (Toner and Lawler 1966, Koshinsky 1979), indicate that pike show no form of territorial behaviour during spawning.

Due to the lack of large-scale territorial behaviour or exclusive use of space, I conclude that spacing behaviour has no function in the regulation of pike populations.

7. Is cannibalism a possible mechanism for regulation of a pike population?

7.1 INTRODUCTION

Cannibalism or intraspecific predation may be the mechanism by which the size of a pike population is regulated. This could have a direct effect, if adult pike consume enough young pike to reduce their numbers and limit recruitment to the adult population. It may also have an indirect effect, if adult pike prey on young pike and cause them to frequent very shallow, sub-optimal habitat as an anti-predation strategy. This strategy could result in an increased mortality due to other factors, such as avian predation (Johnson 1976).

Beyerle (1971) and Fago (1977) have suggested that these mechanisms have the potential to regulate pike populations, but they considered it to be a minor effect or only applicable in special cases because of the low incidence of cannibalism in most pike populations. Frost (1954), Lawler (1965), Wagner (1972), Mann (1976) and Diana ~~(1979)~~ noted that pike generally composed less than 2% of the prey items taken by pike.

Grimm (1981a, 1981b) felt that this low incidence of cannibalism was enough to regulate pike populations. He studied pike populations in small, heavily exploited artificial ponds and found that the numbers of small pike were negatively correlated with the numbers of older, large pike.

I conducted stomach analyses on pike from Neagle Lake in order to determine the incidence of cannibalism in this natural, unexploited population. I further determined that this incidence was theoretically sufficient to regulate the recruitment of young pike into the adult population.

7.2 METHODS

Pike were captured during each season from March 1981 to December 1982. Late May and June were considered to be the spring months, July and August were the summer months, September and October were the autumn months and December to April were the winter months. Samples were generally not taken in early May and November because of unsafe ice conditions. Only pike between 45 cm and 55 cm (std. length) were included in this analysis. This was done in order to [illegible] s few fish as possible yet still collect data which could indicate [illegible] position of the diet of the radio-tagged pike. Pike were captured mainly by angling, although gill-nets (140 mm mesh) were also used to a lesser extent.

The stomach contents of the pike were removed and analyzed in the field. The contents were identified, when possible, as to species and number of individuals present. The identifications were made based on visual examination of whole or incomplete specimens or on distinctive bones and scales. The incidence of cannibalism was calculated as the number of stomachs containing pike divided by the number of stomachs containing identifiable prey items.

7.3 RESULTS

The incidence of young pike in the stomachs of adult pike was approximately 20% during the entire year (Table 1). The high incidence of cannibalism (52%) during the winter is mainly the result of a sample of 31 pike taken soon after the lake froze in November. In this sample, 16 pike had identifiable food in their stomachs, 14 of which contained young pike. The number of pike per stomach ranged from 1 to 7 (mean =1.9). If this one sample is not included, the overall incidence of cannibalism is reduced to 6.5% (5 stomachs containing pike in a sample of 77 stomachs containing identifiable remains).

7.4 DISCUSSION

The incidence of cannibalism at Neagle Lake (20%) is considerably higher than the 1% to 2% reported for other pike populations (Frost, 1954, Lawler 1965, Wagner 1972, Mann 1976, Diana 1979). However, these studies were conducted on pike populations receiving heavy exploitation pressure from man. In isolated northern (and presumably unexploited) waters, the incidence of cannibalism appears to be higher, approximately 5% to 10% (Alt 1968, Jessop et al. 1973, Dryden and Jessop 1974, Craig and Wells 1975, Tripp et al. 1980). In my study, if the one early winter sample where cannibalism was high is not included, the overall incidence is reduced to 6.5%.

The existence of higher levels of cannibalism in unexploited populations compared to exploited populations has not been objectively tested. This difference may simply be an artifact of sampling since many of the studies of unexploited populations involved low sample sizes (for example, 1 or 2 stomachs containing pike from a sample of 20 would result in a reported incidence of cannibalism of 5% or 10%). If these differences are real, it could be the result of exploitation drastically drastically numbers of adult pike, which in turn could result in few young being produced. This may cause a concomitant decrease in the incidence of cannibalism because of reduced availability of young pike as prey items.

The high levels of cannibalism during the early winter sample may have important significance. Young pike may become highly vulnerable to predation by older pike if the vegetative cover in the shallows is removed (Snow 1974, Forney 1977, Grimm 1981a). This may occur during early winter, when ice formation and die-off of vegetative cover force young of the ye pike out of shallow, protected areas and into open water. Adult , being opportunistic predators (Frost 1954), may take large number of young pike at this time, reducing the size of the population to a level where small pike are no longer a highly available prey. This would result in a reduction of the incidence of cannibalism during the remainder of the year. The investigators who report low incidences of cannibalism may simply have not sampled during this period of vulnerability (sampling would be difficult because of dangerous ice or inclement weather conditions).

An incidence of cannibalism of about 10% may be sufficient to limit the number of young pike surviving to enter the breeding population. Based on calculations of Kipling and Frost (1970) for the pike of Lake Windermere, I estimated that approximately 130,000 young of the year pike may be in Neagle Lake at the end of the summer, with an adult population of 10,000. Each adult would therefore need only to consume 13 young pike to eliminate the entire year class. An adult pike may take approximately 80 meals per year (Diana 1979, W.C. Mackay personal communication). An incidence of cannibalism of 10% (consisting of 2 pike per meal) would mean that 16 young pike may be taken each year. This is more than the amount which would eliminate the year class of young pike. An incidence as low as 5% would result in 60% of the young being cannibalized. This system would have a feedback effect on the population since increased adult numbers would cause lowered survival of the young and eventually result in reduced levels of recruitment, thereby decreasing the size of the adult population. Clearly, the potential exists for cannibalism to reduce the popu ion.

8. SUMMARY AND CONCLUSIONS

Populations of northern pike in unexploited lakes exhibit characteristics such as stable year-class strengths, stable size distributions and relatively unfluctuating population sizes. This suggests that a density-dependent mechanism of regulation exists in these populations. In order to determine what this may be, I investigated four mechanisms of population regulation: food limitations, predation, spacing behaviour and cannibalism.

If pike were food limited, they would be expected to optimize their activity with respect to their energy requirements. The energy requirements of pike are highest during spring and decline to low values during winter. Using radio-location telemetry, I found that the activity patterns of pike remained relatively constant throughout the year. In addition, the energy requirements of female pike are nearly double that of male pike, yet I found that the activity patterns of both sexes were similar. From these results, I conclude that populations of pike are not limited by the constraints of their prey requirements.

I studied the effects of interspecific predation on the pike of Neagle Lake to determine if this was regulating the population. Bald eagles were found to be the most important predator on these pike. By determining the energetic requirement of the bald eagle population at Neagle Lake and calculating the number of pike necessary to meet this requirement, I was able to estimate that bald eagles killed fewer than 6% of the adult pike population each year. This is far below the level necessary to regulate the size of the pike population.

To determine if pike were regulating their numbers through spacing behaviour, I monitored the sizes of the areas or home ranges occuppied by 25 individuals. These areas did not appear to be used exclusively and were too large to have a function in the regulation of the population. At no time during the year was territorial behaviour observed.

The incidence of cannibalism by adult pike on young of the year pike was measured throughout the study. I extrapolated the effects of the observed level of cannibalism and concluded that it was of sufficient magnitude to limit recruitment of young pike into the breeding population.

Based on the evidence presented herein, a tentative model of regulation of unexploited pike populations can be proposed. The numbers of adult pike are not directly controlled by proximate factors such as food, predation or space limitations, but are controlled indirectly through regulation of recruitment of young into the breeding population. A feedback system involving adults preying on young pike (perhaps for a short period of time in the autumn) would result in recruitment levels being inversely proportional to the size of the adult population. This would damp fluctuations in year-class strengths, producing a stable adult population size. A breakdown of this system in exploited populations would result from a reduction in the number of adults, especially in the larger size classes. Fewer (and smaller) adults would take fewer young pike, reducing the juvenile mortality rate and increasing the recruitment rate. Fluctuations in year-class strength caused by density-independent factors such as spring water levels and temperatures would not be damped since food is apparently in abundance, predation pressure is low and space restrictions are absent. The overall incidence of cannibalism (in addition to total number of young eaten) may be lowered as reduction of adult numbers (through exploitation) may result in a super-abundance of prey items. This may decrease the relative availability of pike as prey, lowering the incidence of cannibalism and further inhibiting the stabilization of population fluctuations.

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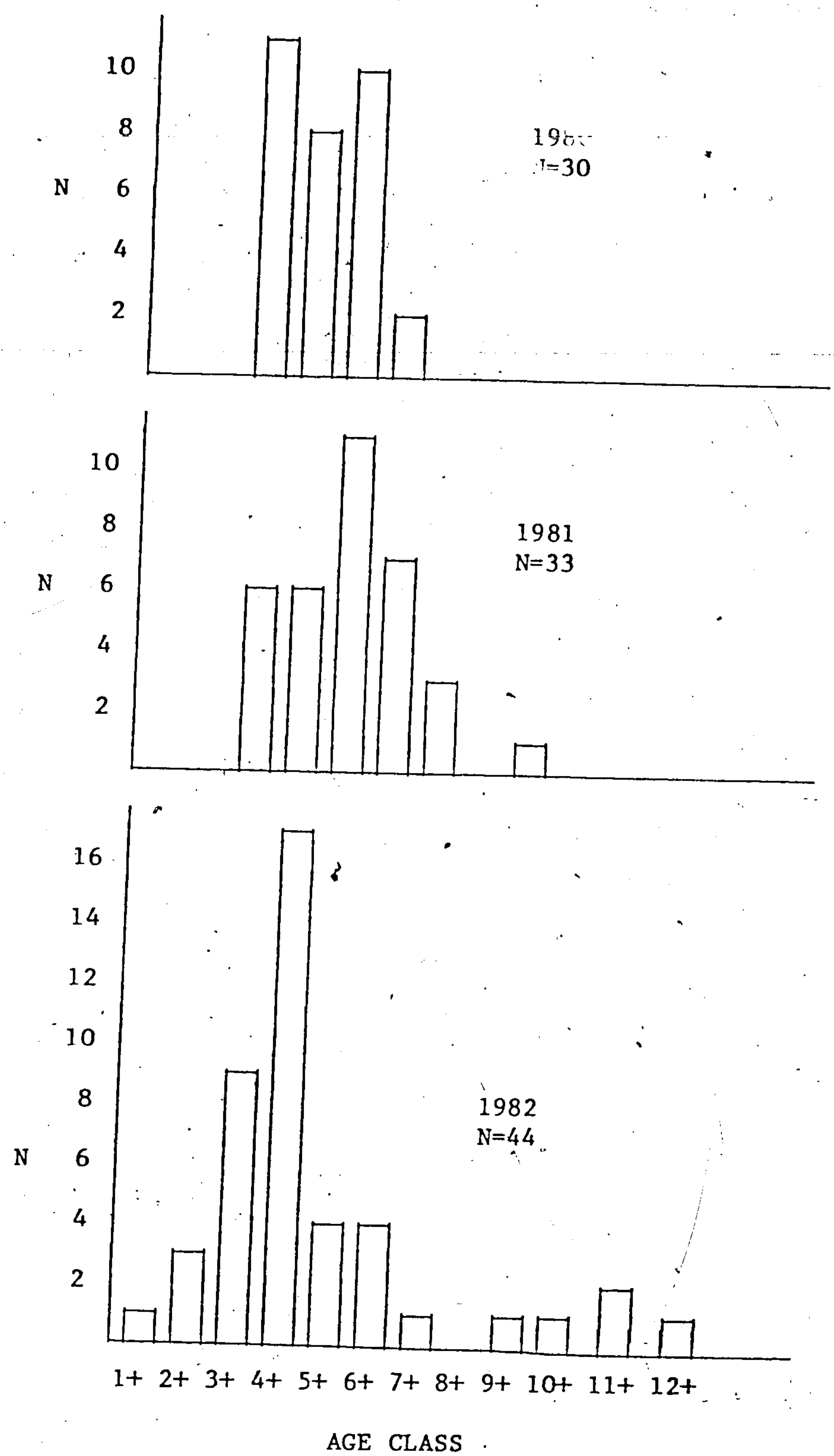
APPENDICES

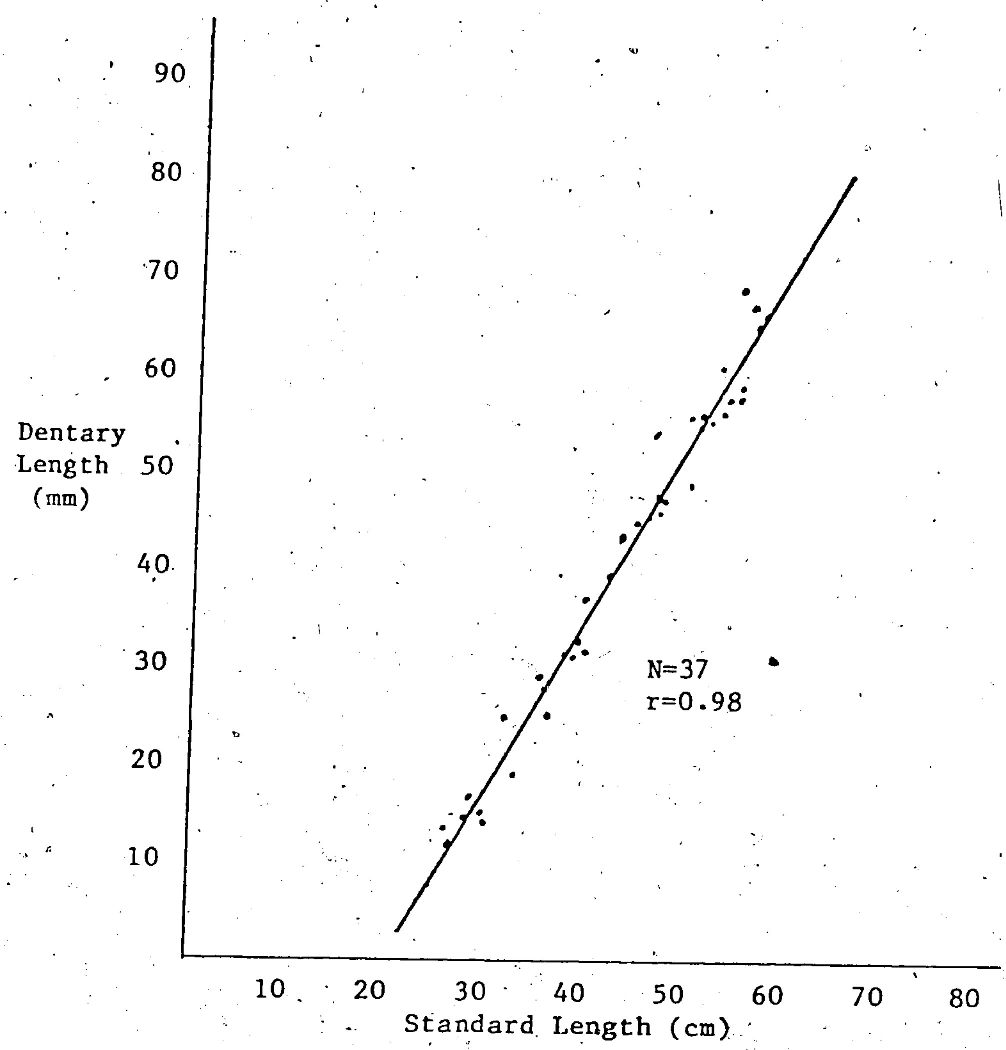
APPENDIX 1. Age class composition of pike from Neagle Lake, Sask.



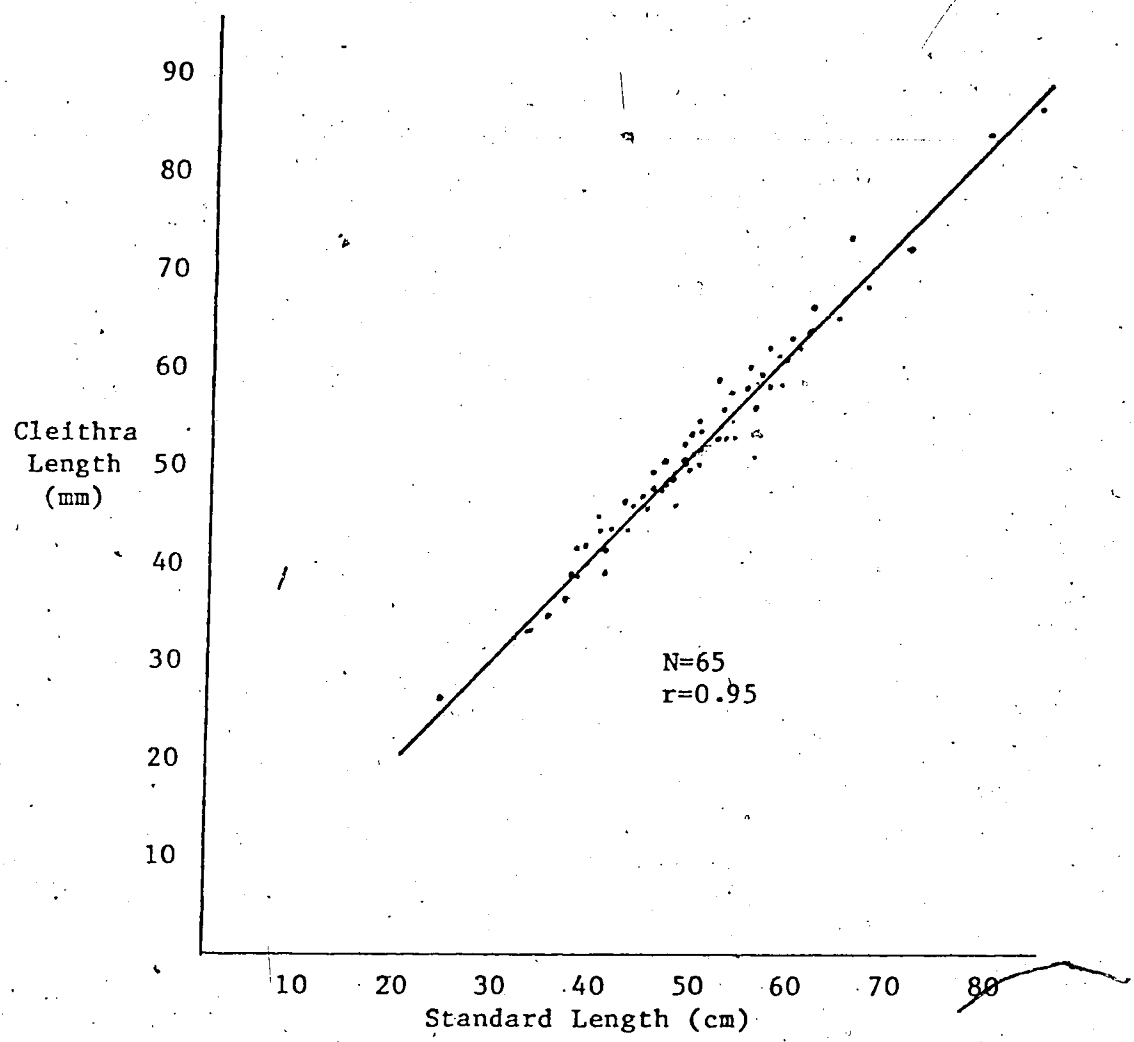
APPENDIX 2. Identification, sex and size of radio-tagged northern pike. Neagle Lake, Sask. 1981, 1982

FISH IDENTIFICATION	SEX	STANDARD LENGTH
02	F	55.0
03	F	59.0
04	F	52.0
06	F	50.0
07	F	52.0
08	F	55.0
09	F	50.0
01	F	49.0
10	M	50.0
11	M	50.0
12	M	49.0
13	M	45.0
14	M	45.0
15	M	53.0
16	M	48.5
17	M	49.5
18	M	47.5
20	F	54.0
21	F	53.5
22	F	55.5
23	F	49.0

Appendix 3. Relationship between standard length of pike and dentary length of pike from Neagle Lake, Sask. (X = ¯5.15 + 1.81 Y)



Appendix 4. Relationship between standard length of pike and cleithra length of pike from Neagle Lake, Sask. (X = 0.85 + 1.03 Y)



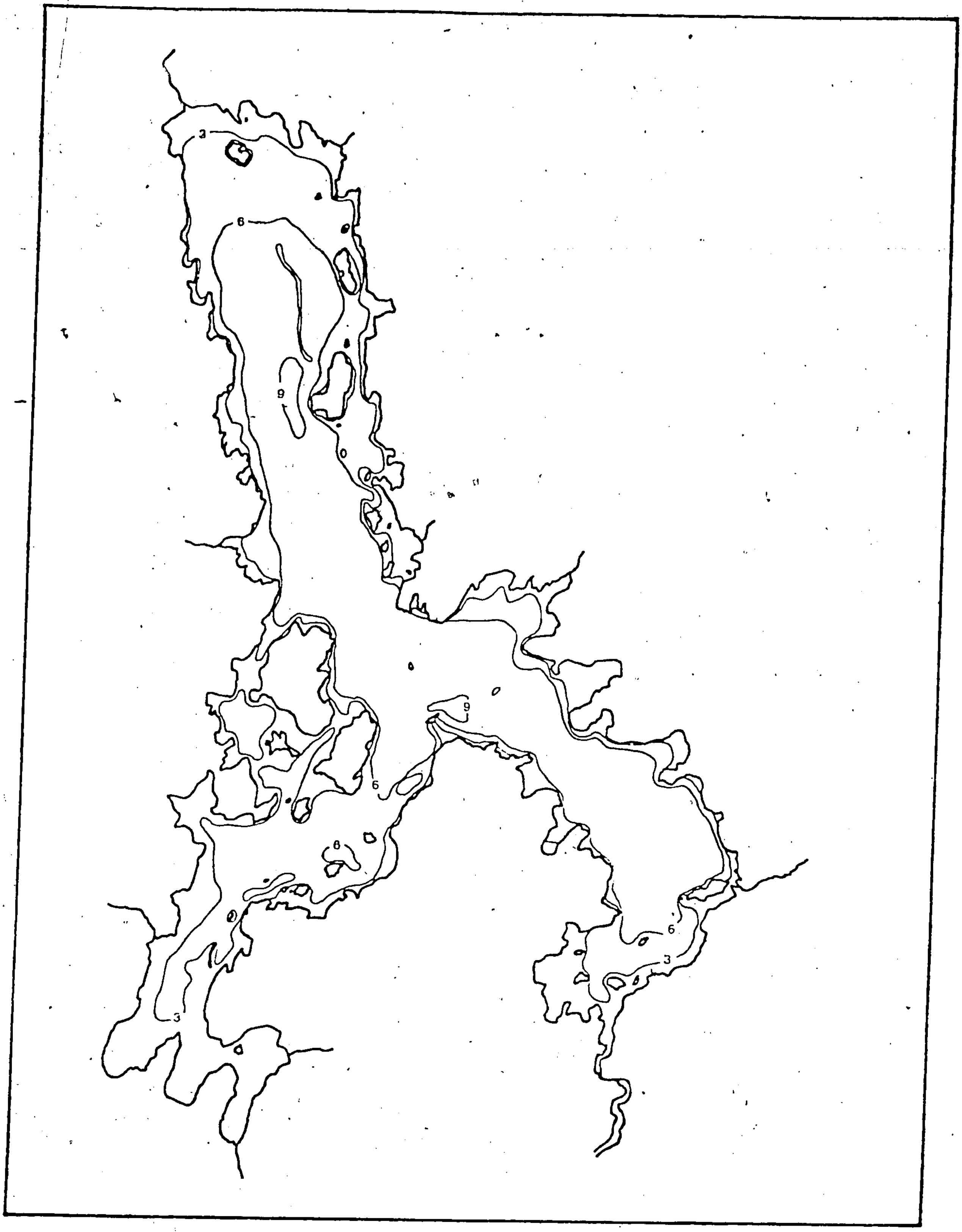
APPENDIX 5. Areas of use of radio-tagged pike, calculated using the grid square method. Areas are hectares occupied during 10 day tracking periods. The identification number of each pike is given in parentheses following the area of use. Areas of use of males and females are given separately.

SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
M	F	M	F	M	F	M	F
4(10)	5(02)	2(10)	11(04)	6(12)	8(07)	17(16)	28(20)
12(11)	4(03)	7(11)	2(04)	6(12)	4(04)	14(16)	16(20)
	4(03)	6(12)	8(06)	4(13)	6(06)	17(15)	23(21)
		2(10)	4(07)	5(12)	5(04)	14(15)	22(21)
		4(11)		8(14)	11(07)	19(18)	9(23)
		7(12)			11(06)	17(18)	8(23)
		12(12)			3(06)		10(22)
					10(07)		13(22)
					11(04)		
					23(01)		
					21(09)		
					9(08)		

WINTER (DEC.-APR.)	
M	F
5(12)	2(01)
4(13)	2(06)
4(12)	3(07)
5(13)	6(07)
2(10)	3(08)
6(12)	3(09)
	2(06)
	2(01)
	4(08)
	3(09)
	7(04)

APPENDIX 6. Areas of use of radio-tagged pike, calculated using the minimum polygon method. Areas are hectares occupied during 10 day tracking periods. The identification number of each pike is given in parentheses following the area of use. Areas of use of males and females are given separately.

SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
M	F	M	F	M	F	M	F
2(10)	31(02)	2(10)	16(04)	11(12)	17(07)	1(17)	41(20)
18(11)	9(03)	20(11)	7(04)	11(12)	3(04)	44(17)	18(20)
	7(03)	9(12)	11(06)	1(13)	2(06)	13(16)	27(21)
		1(10)	8(07)	8(12)	8(04)	38(16)	30(21)
		3(11)		17(14)	27(07)	8(15)	7(23)
		13(12)			17(06)	19(15)	9(23)
		43(12)			34(06)	23(18)	69(22)
					30(07)	24(18)	
					26(04)		
					34(01)		
					41(09)		
					25(08)		



APPENDIX 7. Bathymetric map of Neagle Lake. 3 m contour intervals. Sounded July, 1984.

APPENDIX 8. Displacement of radio-tagged pike measured in meters moved during 5 hour observation periods. Frequency of displacements for each category of displacement distance is given for each season and sex.

DISPLACEMENT DISTANCE(m)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
0	0	3	10	10	12	14	3	2
1-9	1	2	16	6	12	20	4	3
10-19	1	1	17	3	7	9	5	3
20-29	4	9	24	9	11	27	7	6
30-39	0	4	13	11	14	23	16	8
40-49	2	3	14	9	8	20	12	5
50-59	3	2	9	6	6	16	5	6
60-69	2	4	4	4	4	10	10	2
70-79	5	3	2	3	7	11	16	7
80-89	0	1	9	9	3	20	8	3
90-99	2	5	5	1	2	4	5	4
100-109	3	3	4	0	8	6	11	11
110-119	0	3	4	2	1	12	4	6
120-129	2	1	3	2	3	6	4	3
130-139	1	0	5	3	1	8	7	4
140-149	1	2	2	1	3	8	5	3
150-159	0	3	5	3	1	6	8	4
160-169	1	1	3	2	2	6	4	6
170-179	1	2	2	1	1	4	4	4
180-189	0	1	3	1	3	7	2	7
190-199	4	2	2	1	0	6	4	4
200-209	0	0	2	2	2	5	5	9
210-219	2	2	3	0	3	4	2	9
220-229	0	1	2	1	1	3	5	2
230-239	2	1	1	3	0	4	2	5

APPENDIX 8. (CONTINUED)

DISPLACEMENT DISTANCE(m)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
240-249	0	1	1	1	1	10	0	4
250-259	0	1	2	1	1	0	5	6
261-269	0	2	0	1	1	6	1	4
270-279	0	0	0	1	0	5	3	1
280-289	1	0	2	1	3	6	0	4
290-299	1	0	0	0	1	2	1	0
300-309	1	0	0	1	0	3	3	1
310-319	0	3	2	0	1	3	2	3
320-329	1	0	0	1	0	0	3	2
330-339	0	2	0	0	0	5	1	3
340-349	0	0	0	1	0	2	1	2
350-359	0	0	0	0	1	3	2	3
360-369	1	0	0	0	1	2	0	0
370-379	0	1	1	1	0	2	0	3
380-389	0	0	1	0	0	1	0	1
390-399	0	0	1	1	1	1	1	0
400-409	0	0	0	0	0	1	3	1
410-419	0	1	2	0	0	4	1	1
420-429	0	0	0	2	1	0	1	1
430-439	1	0	1	0	1	2	0	2
440-449	1	0	1	0	1	1	2	2
450-459	0	0	0	2	0	0	1	1
460-469	0	0	0	0	0	2	1	1
470-479	0	0	1	0	0	0	0	1

APPENDIX 8. (CONTINUED)

DISPLACEMENT DISTANCE(m)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
480-489	0	1	1	0	0	0	1	1
490-499	0	1	0	0	0	0	1	2
500-509	0	1	0	0	0	1	1	1
510-519	0	1	1	0	0	0	0	0
520-529	1	0	0	0	1	1	0	1
530-539	0	0	0	0	0	0	2	1
540-549	0	0	1	0	1	0	0	2
550-559	0	1	0	0	0	1	0	1
560-569	0	0	1	0	0	0	1	0
570-579	0	0	0	0	0	0	0	1
580-589	0	0	0	1	1	1	0	1
590-599	0	1	0	0	0	0	0	0
600-609	0	0	0	0	0	0	1	0
610-619	0	0	0	0	2	2	0	0
620-629	0	0	1	0	0	1	0	0
630-639	0	0	0	0	0	0	1	1
640-649	0	0	0	1	0	0	1	1
650-659	0	0	0	0	1	0	0	0
660-669	0	0	0	0	0	0	0	0
670-679	0	0	0	0	0	0	1	0
680-689	0	0	0	0	0	1	0	0
690-699	0	0	0	0	0	1	0	0
700-709	0	0	0	0	0	0	0	0
710-719	0	0	1	0	0	1	0	0

APPENDIX 8. (CONTINUED)

DISPLACEMENT DISTANCE(m)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
720-729	0	0	0	0	0	0	0	0
730-739	0	0	0	0	0	0	0	1
740-749	1	0	1	0	0	1	1	0
750-759	0	0	0	0	0	0	0	1
760-769	0	0	0	0	0	1	1	0
770-779	0	0	0	0	0	1	1	0
780-789	0	0	1	0	0	0	1	1
790-799	0	0	1	0	0	0	0	0
800-809	1	0	0	0	0	1	0	2
810-819	0	0	0	1	0	0	0	0
820-829	0	0	0	0	0	0	0	0
830-839	0	0	0	0	0	0	1	1
840-849	1	0	0	0	0	1	0	0
850-859	0	0	0	0	0	0	0	0
860-869	0	0	0	0	0	0	0	0
870-879	0	0	0	0	0	0	0	0
880-889	0	0	0	0	0	0	0	1
890-899	0	0	0	0	0	0	1	0
900-909	0	0	0	0	0	0	0	1
910-919	0	0	0	0	0	0	1	0
920-929	0	0	0	0	0	0	0	1
930-939	0	0	0	0	0	0	0	1
940-949	1	0	0	0	0	1	0	0
950-959	0	0	0	0	0	0	0	1

APPENDIX 8. (CONTINUED)

DISPLACEMENT DISTANCE(m)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
960-969	0	0	0	0	0	0	0	1
970-979	0	0	0	0	0	0	0	0
980-989	0	0	0	0	0	0	1	1
990-999	0	0	0	0	0	0	0	0
1000-1009	0	0	0	0	0	0	1	0
1010-1019	0	0	0	0	0	0	1	1
1020-1029	0	1	0	0	0	0	1	1
1030-1039	0	0	0	0	0	1	0	0
1040-1049	0	0	0	0	0	0	0	0
1050-1059	0	0	0	0	0	0	0	0
1060-1069	0	0	0	0	0	0	0	0
1070-1079	0	0	0	0	0	0	1	0
1080-1089	0	0	0	0	0	0	0	0
1090-1099	0	0	0	0	0	0	0	0
1100-1109	0	0	0	0	0	0	0	0
1110-1119	0	0	0	0	0	0	0	0
1120-1129	0	0	0	0	0	0	0	0
1130-1139	0	0	0	0	0	0	1	1
1140-1149	0	0	0	0	0	0	0	0
1150-1159	0	0	0	0	0	0	1	0
1160-1169	0	0	0	0	0	0	0	0
1170-1179	0	0	0	0	0	0	0	0
1180-1189	0	0	0	0	0	0	0	0
1190-1199	0	0	0	0	0	0	0	0
1200+	0	0	1	0	0	0	0	1

APPENDIX 9. Displacement of radio-tagged pike measured in body lengths moved during 5 hour observation periods. Frequency of each category of displacement distance is given for each season and sex.

DISPLACEMENT DISTANCE(B.L.)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
0	0	5	12	5	12	14	4	3
1-25	1	2	18	11	12	17	3	5
26-50	3	9	28	10	18	19	12	6
51-75	2	5	18	10	14	25	9	9
76-100	2	3	19	11	14	38	15	8
101-125	3	6	10	6	4	19	10	5
126-150	5	3	2	4	10	18	24	7
151-175	2	7	9	10	2	20	3	4
176-200	2	2	7	1	9	5	12	13
201-225	3	4	6	2	4	11	12	6
226-250	0	0	4	2	3	12	6	6
251-275	3	4	5	4	3	9	7	5
276-300	1	2	4	2	1	8	5	4
301-325		3	5	2	3	9	9	6
326-350	0	1	4	2	2	6	4	10
351-375	1	1	4	0	3	8	5	6
376-400	4	2	2	3	1	6	2	10
401-425	2	2	2	0	0	8	6	6
426-450	0	1	5	2	2	3	4	11
451-475	2	2	0	2	1	6	3	4
476-500	0	1	1	2	0	8	2	3
501-525	0	1	2	0	3	6	4	4
526-550	0	0	0	3	1	5	3	4
551-575	1	2	1	0	1	7	2	3
576-600	1	0	0	1	0	4	1	4

APPENDIX 9. (CONTINUED)

DISPLACEMENT DISTANCE(B.L.)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
601-625	1	2	0	1	0	3	1	3
626-650	1	0	2	0	1	1	3	2
651-675	0	1	0	2	0	4	3	2
676-700	0	1	0	0	1	5	1	4
701-725	0	0	0	1	1	4	3	1
726-750	1	1	1	0	0	1	1	1
751-775	0	0	1	0	1	0	0	1
776-800	0	0	1	1	0	2	1	1
801-825	0	1	1	2	0	4	1	1
826-850	0	0	0	0	1	2	3	1
851-875	1	0	1	1	2	1	0	1
876-900	1	0	1	0	1	0	1	2
901-925	0	2	1	0	0	2	1	2
926-950	0	1	1	0	0	0	2	2
951-975	0	0	1	0	0	0	1	1
976-1000	0	1	0	0	0	1	1	3
1001-1025	0	1	0	0	0	0	0	0
1026-1050	1	1	1	0	1	1	1	2
1051-1075	0	1	0	0	1	0	2	1
1076-1100	0	1	1	0	0	1	2	0
1101-1125	0	0	0	1	0	0	0	1
1126-1150	0	2	1	0	0	1	0	1
1151-1175	0	0	0	0	0	0	0	0
1176-1200	0	0	0	0	0	2	1	0

APPENDIX 9. (CONTINUED)

DISPLACEMENT DISTANCE(B.L.)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
1201-1225	1	2	0	0	0	2	0	1
1226-1250	1	0	0	1	0	0	0	0
1251-1275	0	1	1	0	0	0	2	0
1276-1300	0	1	0	0	0	0	0	0
1301-1325	0	0	0	0	1	0	1	0
1326-1350	1	1	0	0	1	2	3	0
1351-1375	0	0	0	0	0	0	0	1
1376-1400	0	0	0	0	0	1	1	0
1401-1425	0	1	0	0	1	0	0	0
1426-1450	0	0	0	0	0	1	0	0
1451-1475	1	0	1	0	0	0	0	1
1476-1500	1	0	1	0	0	1	0	1
1501-1525	0	2	0	0	0	1	0	1
1526-1550	0	1	0	0	0	0	0	1
1551-1575	0	0	0	1	0	1	2	0
1576-1600	0	0	1	0	0	0	2	0
1601-1625	0	0	1	0	0	0	0	0
1626-1650	1	0	0	0	0	1	0	2
1651-1675	0	0	0	0	0	0	0	1
1676-1700	0	0	0	0	0	0	2	0
1701-1725	0	0	0	0	0	0	0	0
1726-1750	0	0	0	0	0	0	0	1
1751-1775	0	0	0	0	0	0	0	0
1776-1800	0	0	0	0	0	0	0	2

APPENDIX 9. (CONTINUED)

DISPLACEMENT DISTANCE(B.L.)	SPRING (MAY-JUNE)		SUMMER (JULY-AUG.)		AUTUMN 1981 (SEPT.-OCT.)		AUTUMN 1982 (SEPT.-OCT.)	
	M	F	M	F	M	F	M	F
1801-1825	0	0	0	0	0	0	0	1
1826-1850	0	1	0	0	0	1	0	2
1851-1875	0	0	0	0	0	0	0	1
1876-1900	1	0	0	0	0	0	0	0
1901-1925	0	1	0	0	0	0	0	0
1926-1950	0	0	0	0	0	0	1	0
1951-1975	0	1	0	0	0	0	0	0
1976-2000	0	0	0	0	0	0	1	0
2001-2025	0	0	0	0	0	1	0	0
2026-2050	0	0	0	0	0	0	0	0
2051-2075	0	0	0	0	0	0	0	0
2076-2100	0	0	0	0	0	0	0	0
2101-2125	0	0	0	0	0	0	0	0
2126-2150	0	0	0	0	0	0	0	0
2151-2175	0	0	0	0	0	0	0	0
2176-2200	0	0	0	0	0	0	0	0
2201-2225	0	0	0	0	0	0	0	0
2226-2250	0	0	0	0	0	0	0	0
2251-2275	0	0	0	0	0	0	0	0
2276-2300	0	0	0	0	0	0	0	0
2301-2325	0	0	0	0	0	0	0	0
2326-2350	0	0	0	0	0	0	0	0
2351-2375	0	0	0	0	0	0	0	0
2376-2400	0	0	0	0	0	0	0	0

APPENDIX 10. Comparison of variation within fish to variation between fish. Values are grid-square areas of use (ha) for individual fish. Standard deviation is used for comparison of variation. Between fish variation calculated from mean value of individual areas within each season.

FISH IDENTITY	SPRING	SUMMER	AREAS OF USE (ha) AUTUMN(1981)	AUTUMN(1982)	WINTER	STD.DEV. WITHIN FISH
01			23		2,2	8.12
02	5					–
03	4,4					–
04		11,2	11,5,4		7	3.72
05						
06		8	6,11,3		2,2	5.33
07		4	8,11,10		3,6	3.22
08			9		3,4	3.21
09			21		3,3	10.40
10	4	2,2			2	1.00
11	12	7,4				4.04
12		6,7,12	6,6,5		5,4,6	2.29
13			4		4,5	0.58
14			8			–
15				17,14		–
16				14,17		–
17						
18				19,17		–
19						
20				28,16		–
21				23,22		–
22				10,13		–
23				9,8		–
STD.DEV BETWEEN FISH	3.86	2.42	6.80	5.15	1.70	

Mean standard deviation within fish = 4.30

Mean standard deviation between fish = 3.99

APPENDIX 11. Comparison of variation within fish to variation between fish. Values are mean log-displacement (m / 5 hr) for individual fish. Standard deviation is used for comparison of variation. Between fish variation calculated from mean value of individual areas within each season.

FISH ID.	LOG DISPLACEMENT (m / 5 hr) SPRING	SUMMER	AUTUMN(1981)	AUTUMN(1982)	STD.DEV. WITHIN FISH
01			1.97		-
02	1.68				-
03	1.95,2.06				-
04		2.06,1.66	1.52,1.97,1.85		0.22
05					
06		1.64	1.61,1.90,1.78		0.13
07		1.65	1.62,2.09,2.05		0.25
08			1.80		-
09			2.12		-
10	1.99	1.39,1.61			0.30
11	2.13	2.00,1.27			0.46
12		1.53,1.94,1.89	1.61,1.64,1.73		0.16
13			1.40		-
14			1.91		-
15				1.94,1.90,2.08	0.09
16				1.86,2.47,2.06	0.31
17				1.91,1.75,2.32	0.29
18				2.15,2.24,2.13	0.06
19					
20				2.36,1.92,2.28	0.23
21				2.08,2.41,2.29	0.17
22					
23				2.17,1.75,2.36	0.31
STD.DEV BETWEEN FISH	0.19	0.13	0.21	0.11	

Mean standard deviation within fish = 0.23
Mean standard deviation between fish = 0.16

APPENDIX 12. Sample record of pike caught at Neagle Lake, Sask.

SAMPLE RECORD CAR

♀		♂
1	Immature	6
2	Maturing	7
3	Mature	8
4	Ripe	9
5	Spent	10

Lake or Stream Neagle Lake, Sask. Date Mar./1981-Oct./1

Species Esox lucius Time

Mesh Size Depth of Set

Location of Set

Sample Recorder

NUMBER	SAMPLE NUMBER	LENGTH Inch. ☐ cm. ☑	WEIGHT Oz. ☐ Gms. ☑	AGE	MATURITY	CYST COUNT	REMARKS
	81-1	58.0		6+			
	81-2	42.0		3+			
	81-3	47.5		4+			
	81-4	55.0		5+			
	81-5	48.0	1100	5+			
	81-6	47.5	1300	3+			
	81-7	60.0	1800	6+			
	81-8	45.0		4+			
	81-9	49.0		4+			
	81-10	57.0		5+			
	81-11	50.5		5+			
	81-12	47.0		4+			
	81-13	48.5	800	3+			
	81-14	45.5	800	3+			
	81-15	4[illegible]	500	4+			
	81-16	48.[illegible]	900	4+			
	81-17	55.0	1200	5+			
	81-18	36.0	500	3+			
	81-19	53.0	[illegible]00	5+			
	81-20	55.0	[illegible]	[illegible]			
	81-21	48.0	10[illegible]	5+			
	81-22	49.0	1000	3+			
	81-23	43.0	600	3+			
	81-24	45.0	700	5+			
	81-25	46.0	800	3+			
	81-26	51.0	1200	5+			
	81-27	43.5	600	3+			
	81-28	43.0	500	3+			
	81-29	44.5	700	4+			

SAMPLE RECORD CA

♀			♂
1	Immature	6	
2	Maturing	7	
3	Mature	8	
4	Ripe	9	
5	Spent	10	

Lake or Stream ______ Date ______
Species ______ Time ______
Mesh Size ______ Depth of Set ______
Location of Set ______
Sample ______ Recorder ______

NUMBER	SAMPLE NUMBER	LENGTH Inch. ☐ cm. ☑	WEIGHT Oz. ☐ Gms. ☑	AGE	MATURITY	CYST COUNT	REMARKS
	81-30	47.5	1000	4+			
	81-31	54.0	1300	5+			
	81-35	46.0		6+			
	81-36	45.0		6+			
	81-37	54.0		5+			
	81-39	42.0		3+			
	81-40	79.0	4000	9+			
	82-1	40.0	600	3+			
	82-2	48.0	900	4+			
	82-3	43.0	700	4+			
	82-4	43.0	700	3+			
	82-5	44.0	700	3+			
	82-6	42.0	700	3+			
	82-7	56.0	1300	5+			
	82-8	52.0	1200	4+			
	82-9	51.0	1400	7+			
	82-10	55.0	1400	5+			
	82-11	54.0	1150	5+			
	82-12	44.0	850	5+			
	82-13	55.0	1400	6+			
	82-14	55.0	1500	5+			
	82-15	53.5	1500	6+			
	82-16	51.0	1150	5+			
	82-17	59.0	1700	6+			
	82-18	52.0	1250	6+			
	82-19	50.0	1200	4+			
	82-20	51.5	800	5+			
	82-21	49.0	1200	5+			

SAMPLE RECORD CARD

♀			♂
1	Immature	6	
2	Maturing	7	
3	Mature	8	
4	Ripe	9	
5	Spent	10	

Lake or Stream ____ Date ____

Species ____ Time ____

Mesh Size ____ Depth of Set ____

Location of Set ____

Sample ____ Recorder ____

NUMBER	SAMPLE NUMBER	LENGTH Inch. ☐ cm. ☑	WEIGHT Oz. ☐ Gms. ☑	AGE	MATURITY	CYST COUNT	REMARKS
	82-22	54.0	1400	5+			
	82-23	49.0	1000	4+			
	82-24	55.0	1400	4+			
	82-25	49.0	850	4+			
	82-26	49.5	900	6+			
	82-27	43.0	500	4+			
	82-28	39.0	500	4+			
	82-29	39.5	500	4+			
	82-30	44.5	675	4+			
	82-31	58.0	1475	5+			
	82-32	41.5	600	4+			
	82-33	39.0	500	2+			
	82-34	41.5	550	3+			
	82-35	82.0	3750	10+			
	82-36	47.5	800	5+			
	82-37	54.0	2000	9+			
	82-38	60.0	1600	6+			
	82-39	56.0	1100	7+			
	82-40	45.5	650	4+			
	82-41	44.0	600	4+			
	82-42	34.0	300	3+			
	82-43	37.0	400	3+			
	82-44	43.5	550	4+			
	82-45	41.5	500	4+			
	82-46	53.0	1000	6+			
	82-47	45.0	700	5+			
	82-48	43.0	600	4+			
	82-49	46.5	900	4+			

SAMPLE RECORD CARD

♀		♂
1	Immature	6
2	Maturing	7
3	Mature	8
4	Ripe	9
5	Spent	10

Lake or Stream ____________ Date ____________

Species ____________ Time ____________

Mesh Size ____________ Depth of Set ____________

Location of Set ____________

Sample ____________ Recorder ____________

NUMBER	SAMPLE NUMBER	LENGTH Inch. ☐ cm. ☑	WEIGHT Oz. ☐ Gms. ☑	AGE	MATURITY	CYST COUNT	REMARKS
	82-50	56.0	1200	5+			
	82-51	44.0	850	3+			
	82-52	44.0	800	3+			
	82-53	45.0	900	3+			
	82-54	41.5	700	3+			
	82-55	49.0	1000	4+			
	82-56	38.0	600	3+			
	82-57	48.0	900	4+			
	82-58	39.5	600	3+			
	82-59	47.5	700	4+			
	82-60	44.5	850	4+			
	82-61	39.0	650	2+			
	82-62	36.0	550	2+			
	82-63	48.0	900	4+			
	82-64	52.5	1000	6+			
	82-65	24.0	115	1+			
	82-66	87.0	5000	11+			
	82-67	86.0	5000+	12+			