Hydrobiologia **483:** 137–146, 2002.
E.B. Thorstad, I.A. Fleming & T.F. Næsje (eds), Aquatic Telemetry.

Integration of acoustic telemetry and GIS to identify potential spawning areas for lake trout (*Salvelinus namaycush*)

L.S. Flavelle[1,2,*], M.S. Ridgway[2], T.A. Middel[2] & R.S. McKinley[3]
[1]*Department of Biology, University of Waterloo, 200 University Ave. W., Waterloo, Ontario N2L 3G1, Canada*
[2]*Harkness Laboratory of Fisheries Research, Aquatic Research and Development Section, Ontario Ministry of Natural Resources, 300 Water St., Peterborough, Ontario K9J 8M5, Canada*
[3]*Faculty of Agricultural Sciences, The University of British Columbia, #270, 2357 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada*
[*]*Present address: Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2NT, Canada*

Key words: lake trout, reproductive ecology, spawning, GIS, habitat, biotelemetry

Abstract

Locations of potential spawning areas for lake trout (*Salvelinus namaycush*) were predicted in Lake Opeongo, Ontario, Canada using information gained via acoustic telemetry and geographic information system (GIS) technologies. From 1998 to 2000, 18 adult lake trout (mean fork length 553 mm) implanted with acoustic transmitters (battery life 2 years) were manually tracked. For evening fall locations within the erosive zone of the lake (determined using an existing sedimentation model), habitat variables (slope, depth, and effective fetch) were summarised using GIS. Sites selected by lake trout during the spawning window were in areas of mean fetch equal to 1.5 km and mean slope of 10.6% ($n = 50$ fixes). We used GIS to identify areas that matched the mean habitat criteria and thus locate potential spawning areas. This model correctly identified 19 of 21 known spawning sites, as well as additional sites used by spawning females in an earlier telemetry study. Depths of traditional fall netting sites are shallow compared to areas in which telemetered lake trout were found during evenings of the spawning period (means 3.1 vs. 5.1 m, respectively). Through the use of information on spawning habitat selection gained through telemetry and knowledge of the physical characteristics of the lake, we provide an alternative means of identifying potential spawning habitat for lake trout.

Introduction

Lake trout (*Salvelinus namaycush*) have a mating system unlike most salmonines. Females do not prepare redd sites; instead they release negatively buoyant eggs over substrates composed mainly of cobble and rock on shoals ranging in depth from 1 to 50 m (Martin, 1955; Martin & Olver, 1980; Gunn, 1995). Spawning occurs in the early evening hours under windy conditions, and spawning fish are active on the shoals for approximately four hours each night, beginning at dusk (Martin, 1957). Males appear to compete for proximal position to spawning females but do not appear to establish nor defend territories on the spawning grounds (MacLean et al., 1990). As a consequence, males do not develop any clear sexually dimorphic traits (Martin & Olver, 1980), such as the pronounced kype common to males in competitive salmonine mating systems (Gross, 1984).

Most reports of the location of lake trout spawning shoals are based on traditional netting records in areas known for the capture of gravid females and ripe males (Fitzsimmons & Williston, 2000). Direct observations of spawning (Liimatainen et al., 1987), and observations of egg deposition derived from substrate collectors or nets (Sly, 1988; Fitzsimmons, 1995; Schreiner et al., 1995) also provide evidence of spawning locations. These observations and anecdotal reports indicate that lake trout select shorelines with considerable fetch (McCrimmon, 1958). Presumably, the windswept nature of spawning shoals provides a mechanism to move eggs into interstitial spaces, provide oxygenation, and prevent accumulation of fine sediments (Martin, 1957; Sly, 1988).

Wind-driven wave energy is a strong determinant of the distribution of fine-grained sediments in lakes (Rowan et al., 1992). In areas characterised by low fetch, high rates of particulate accumulation could increase the risk of egg suffocation, and also lead to increased incidence of infestation by fungus (e.g. *Saprolegnia*) (Martin, 1957). Gunn (1995) suggests that lake trout may selectively choose spawning sites that have low rates of particulate accumulation. Fetch (or wind exposure) may not be the only important factor in this selection, and the choice of windswept shorelines may point to more fundamental limnological processes driving lake trout spawning habitat selection.

Rowan et al. (1992) suggest that slope effects can result in distribution of coarse-grained sediments at depths greater than would be expected from waves alone. Their model predicts a boundary depth between high-energy erosive environments (characterised by coarse-grained, non-cohesive sediments) and low-energy depositional zones (characterised by the accumulation of fine-grained, cohesive sediments) in lakes based on an interaction of slope and fetch (Rowan et al., 1992). This boundary, termed the mud deposition boundary depth (mud DBD), predicts a depth limit to the distribution of fine-grained sediments in lakes, and therefore provides a preliminary means of rejecting certain habitats as suitable lake trout spawning areas.

The main objective of this study was to use telemetry in combination with GIS to determine potential locations for lake trout spawning in a large inland lake system. Given that lake trout will spawn only on clean substrates, the sedimentation process model of Rowan et al. (1992) was employed to identify the subset of telemetry locations that were most likely representative of the spawning activities of lake trout.

Methods

Study area

Lake Opeongo is in central Ontario, Canada within the borders of Algonquin Provincial Park (45° 42′ N, 78° 22′ W) (Fig. 1). The lake is made up of four distinct basins, the North, South and East Arms and Annie Bay (Fig. 1). This large (58.6 km^2) oligotrophic lake has a littoral area of 17.2 km^2 and mean and maximum depths of 14.8 and 51.8 m, respectively. In the early summer, a stable thermocline is established in all of the basins at an approximate depth of 10 m. The start of the fall period in this study was defined as the onset of destratification, determined for each year based on data from temperature recorders set at various depths throughout the water column (Shuter, unpubl. data).

Depth (m), slope (%), and maximum fetch (km) were determined from bathymetric maps of the lake using GIS software; ARCVIEW Version 3.2 and Spatial Analyst (ESRI, Redlands, California). The mud DBD was calculated using the empirical equation,

$$\log \mathrm{DBD} = -0.107 + 0.742 \log F + 0.0653S, \quad (1)$$

where F is fetch (km), and S is slope (%) (Rowan et al., 1992). Wind data for Lake Opeongo (Middel, unpubl. data) show the most predominant and strongest annual winds from a W-SW direction. We used this effective maximum fetch in lieu of geometric maximum fetch to model the erosive zone, in order to account for the effect of strong winds on erosive processes (Rowan et al., 1992). Locations at which actual depth was equal to the predicted mud DBD defined the boundary of the erosive zone. Areas within 1 m depth of the DBD were considered as a transition zone between the erosive and depositional zones of the lake.

Transmitter implantation

Adult lake trout (mean fork length 553 mm, range 449–620 mm) were equipped with acoustic transmitters in the spring seasons of 1998, 1999 and 2000. The transmitters were 65 mm in length, 16 mm in diameter and weighed 21.2 g in air and 17.0 g in water (Model CTT-83-2, Sonotronics Inc.). The transmitters never constituted more than 1% of the body weight of the fish. All transmitters contained temperature sensors, and had an expected battery life of 2 years.

We captured fish in the South and North Arms of Lake Opeongo at various depths during daylight hours, using short gillnet sets (15 min per set) to minimize mortality. We anaesthetised fish in an aerated bath of ethanol and clove oil (in a ratio of 9:1) and 20 L of fresh water (60 ppm anaesthetic concentration). We followed the surgical implantation procedures outlined by Wagner & Stevens (2000), with the exception that our transmitters did not have antennae, and therefore no puncture of the lateral body wall was required. Incisions were made on the midline and closed with three interrupted sutures using 2-0 gauge black braided

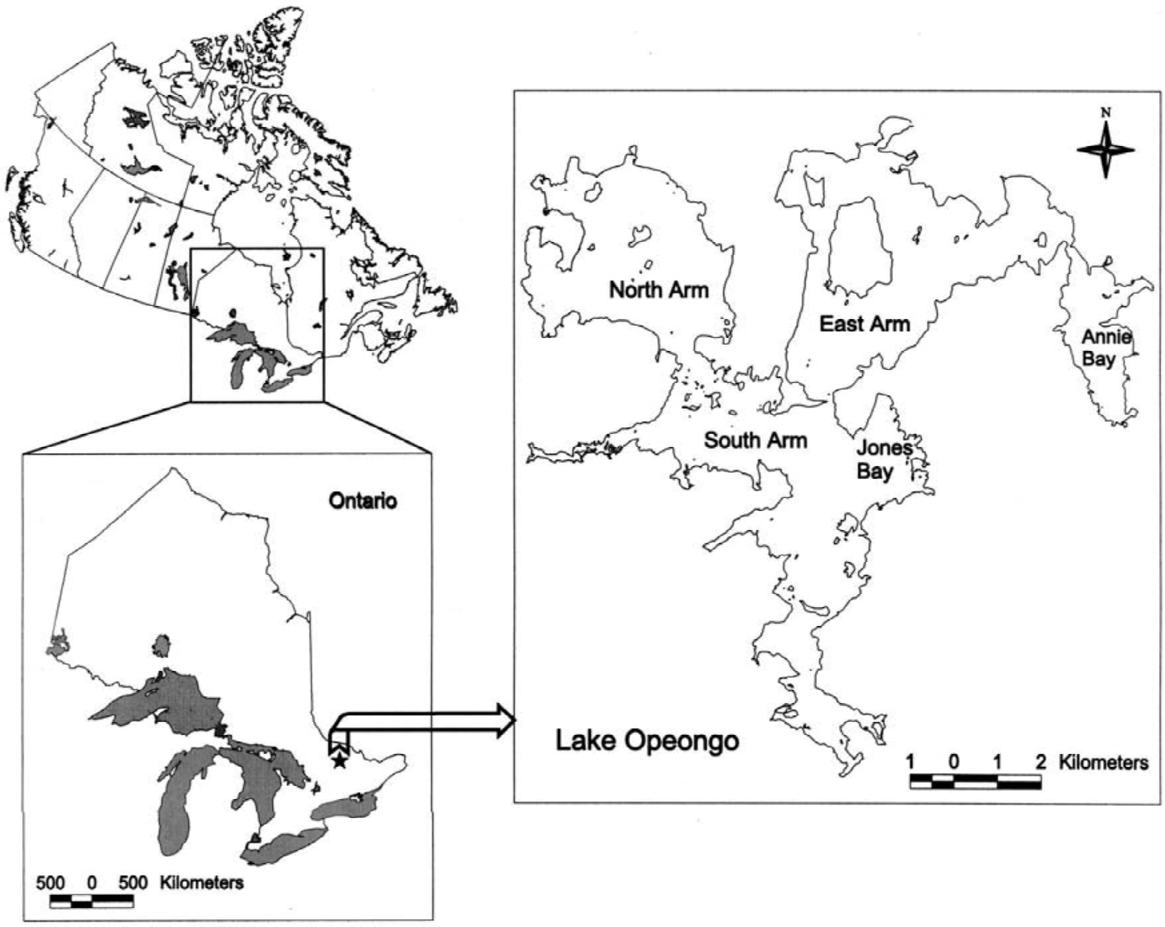

Figure 1. Location of study site in Canada and outline of Lake Opeongo.

surgical silk (Ethicon Inc.). Fork length and weight were recorded, however sex determinations were not possible since implantation occurred in spring, and the small size of the incision precluded internal observation. Fish were revived in a fresh water bath until they were upright and actively swimming, and were then released at the location of capture.

Manual tracking

Manual mobile tracking was conducted using a DH-4 directional hydrophone and Model USR-5W receiving unit (Sonotronics Inc.). We defined a fix as an event where date, time, fish identification code, pulse interval (later translated to temperature), and fish location (UTM coordinates), determined using a geographic positioning system (GPS), were recorded. Accuracy in acoustic manual tracking varies depending on several factors in lakes. The depth of transmitter and presence or absence of thermocline (which acts as a thermal barrier to sound) both affect accuracy of location fixing. Blind testing of manual tracking staff in the summer of 2000 indicated a mean error of 8.5 m in fix position when a transmitter was set at 15 m depth. Errors in location generally decrease when transmitters are closer to the surface of the water. In order to account for this error in the analysis of positional data, an error buffer of 15 m was incorporated when fish locations were plotted using GIS.

Autocorrelation of location estimates made on the same night was examined for each individual using Schoener's ratio, t^2/r^2 (1981). When more than one location estimate per evening per individual was performed, successive observations were separated by a time lag of at least 1.5 h.

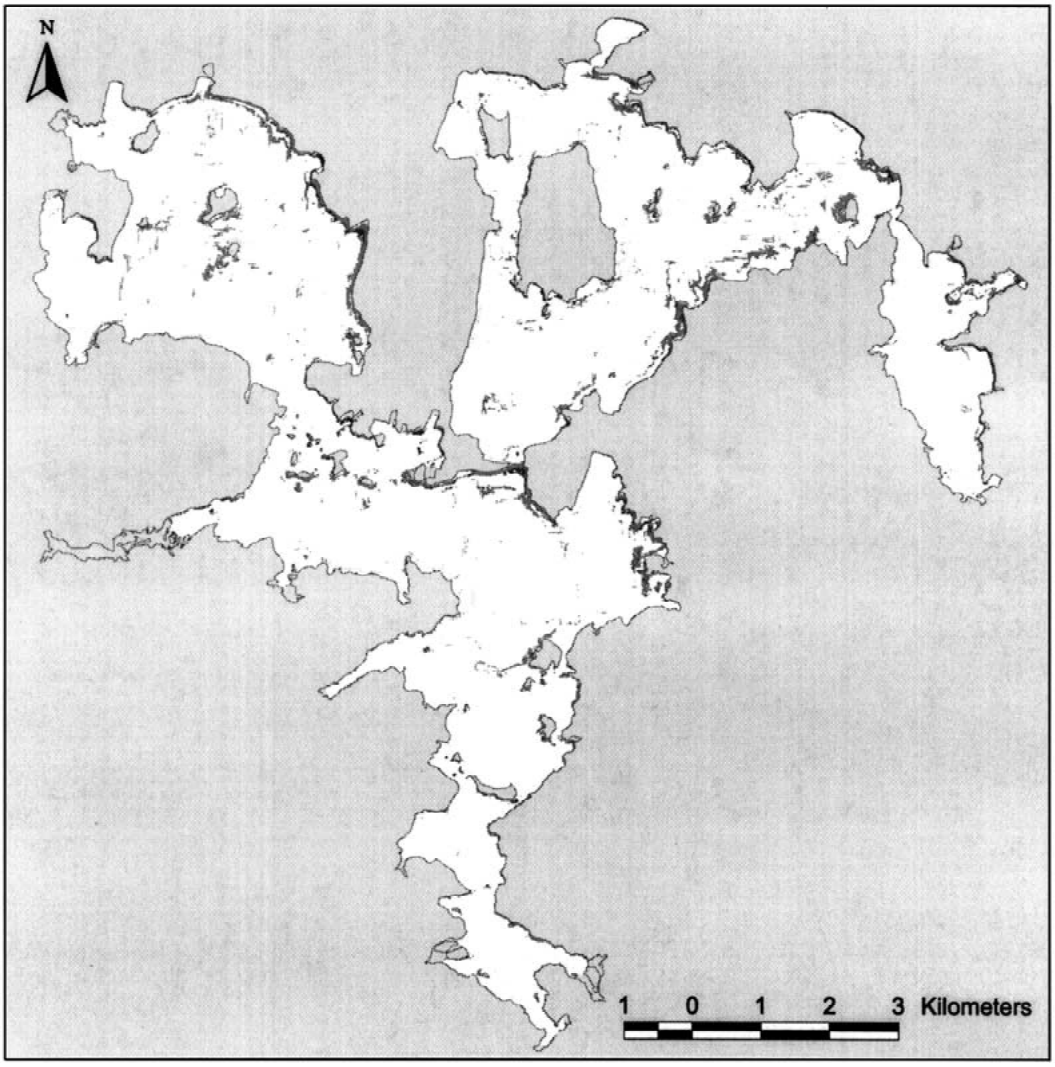

Figure 2. Sedimentation zones determined by mud DBD model. Dark grey areas signify either erosive or transition zones, and white areas of the lake represent the depositional zone.

Determination of spawning habitat features

We defined the spawning period for all years based on the peak spawning date (determined through the number of ripe females captured on known shoals), as well as air and surface water temperatures in each year. On average, lake trout spawning periods last approximately 10 days (Martin, 1957), so we defined the spawning period as 5 days on either side of the peak spawning date for each year. Evening fish locations were defined as those that were observed at or later than dusk on each day (Martin, 1957). We determined the percentage of evening fish locations during the spawning windows that fell within the erosive or transition zone, and since lake trout spawn only on clean substrates (Martin & Olver, 1980), only the information from these fixes was used to predict potential spawning sites. For the remaining fixes, we measured the distance to the nearest erosive zone to assess non-erosive habitat selection. We calculated effective fetch during the spawning period using the predominant wind directions for the month of October (W and N). Habitat characteristics (slope, effective fetch and depth) were summarised for the areas under the 15 m buffer polygons of the fish locations. The mean (± 1 SD) habitat characteristics of locations that fell within the erosive/transition zone were then used to build a GIS query to identify potential spawning sites.

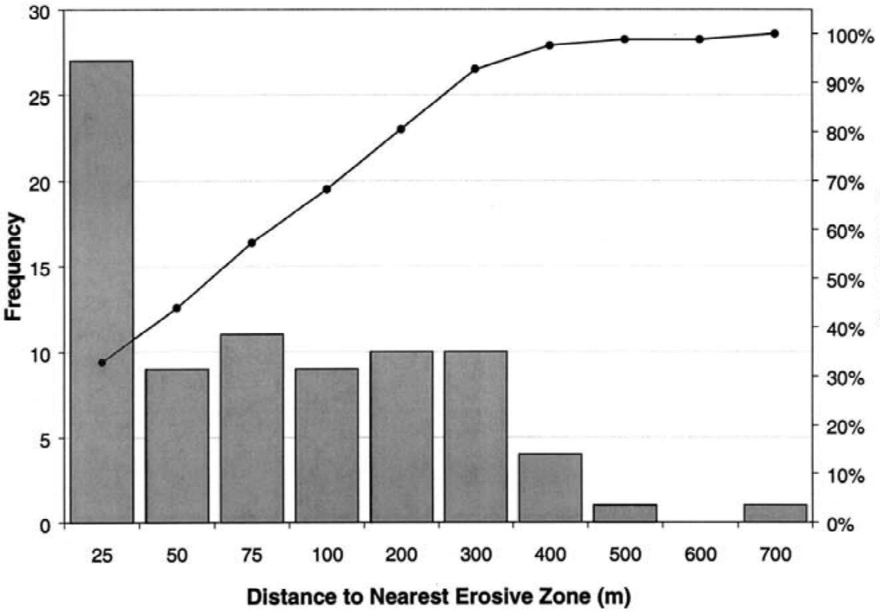

Figure 3. Cumulative frequency histogram for distance to nearest erosive zone for fish locations in the deposition zone during evenings of the spawning period.

Results

Sediment process model

The extent of the erosive zone of Lake Opeongo was predicted by Equation (1) (Fig. 2). The transition zone encompasses both the actual boundary between the high-energy erosive and low-energy depositional zones described by Rowan et al. (1992) (i.e. where actual depth is equal to the mud DBD) and 1 m depth below that boundary. Based on the incorporation of the predominant annual wind direction into the model, the areas of erosive and transition zones were 2.86 and 1.28 km^2, respectively. The use of the predominant fetch direction creates a physical shadow effect (Fig. 2); areas of deposition are more prevalent on the western shores and protected areas of the lake.

Identification of potential spawning areas

A total of 23 adult lake trout were implanted with acoustic transmitters over the three-year study. However, only 18 fish were tracked during the fall seasons, as 5 fish were lost to angling during summer seasons, or batteries may have failed in their second year (Table 1). An analysis of the independence of successive (within evening) fixes using Schoener's ratio (1981) suggests positive autocorrelation ($t^2/r^2 < 2$) in 71% of cases ($n = 14$ pairs of successive observations). Despite positive autocorrelation of some positions, all evening erosive/transition zones fixes were included in the model predicting potential spawning areas.

Table 1. Number of evening spawning period fix positions (by fish) used in habitat selection model (erosive/transition observations) and outside of erosive habitat during the study years

Fish ID	Erosive Transition n_{obs}				Depositional n_{obs}			
	1998	1999	2000	Total	1998	1999	2000	Total
1	5	1	2	8	7	–	1	8
2	4	3	–	7	7	2	–	9
3	–	1	–	1	10	–	–	10
4	–	–	1	1	–	1	–	1
5	3	–	–	3	7	–	–	7
6	6	–	–	6	6	–	–	6
7	2	–	–	2	11	–	–	11
8	8	–	–	8	3	1	–	4
9	5	–	–	5	9	–	–	9
10	2	–	–	2	7	–	–	7
11	–	–	2	2		–	1	1
12	–	–	1	1	–	–	1	1
13	–	–	2	2	–	–	–	0
14	–	–	–	0	–	–	2	2
15	–	1	–	1	–	–	–	0
16	–	1	–	1	–	3	–	3
17	–	–	–	0	–	2	–	2
18	–	–	–	0	–	1	–	1
		Grand total		50		Grand total		82

Table 2. Summary of habitat characteristics for traditional netting sites and fish positions as revealed through telemetry. Values in parentheses are the 1SD range of values that were input as a GIS query to identify potential spawning areas

	n_{obs}	Mean slope (%)	Mean effective fetch (km)	Mean depth (m)
Netting sites	21	8.3 (3.6–13.0)	1.7 (1.2–2.1)	3.1 (0.3–5.9)
Evening fixes in erosive Zone during spawning period	50	10.6 (4.1–17.0)	1.5 (0.8–2.3)	5.1 (1.7–8.4)

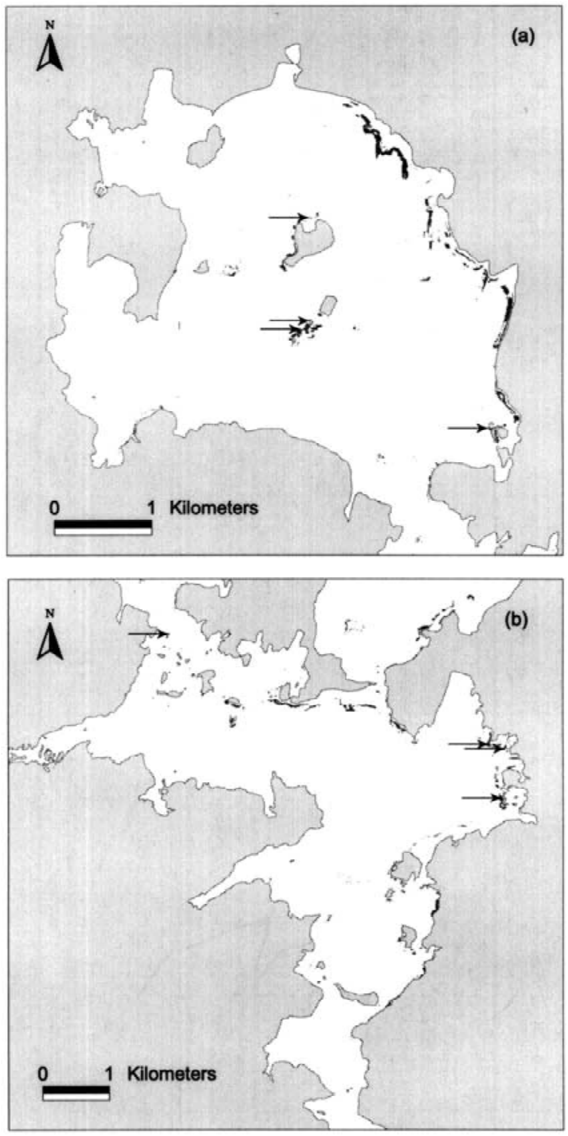

Figure 4. Predicted potential spawning areas (dark grey) in (a) North Arm and (b) South Arm. Arrows denote known spawning (traditional netting) sites.

Of a total 132 evening fixes for fish tracked in the fall, only 38% (50 fixes) were within the erosive or transition zone. The remaining fixes (62%), although outside of the erosive or transition zones, were often found near to the erosive zone (75% within 100 m of erosive habitat; Fig. 3). Potential spawning areas were mapped using a GIS query to identify erosive areas that matched the means (±1 SD) of the habitat characteristics (slope, fetch, and depth) inferred from telemetry (Table 2). This model accurately predicted 19 of the 21 known spawning areas in this system, including those in the East Arm, where no tracking of individual fish was conducted (Figs 4 and 5). The two netting sites that did not correspond to predicted netting sites were in the same area of the East Arm (Lucky Strike), and were only 6 m and 27 m from the nearest predicted spawning area. In total, an area of 0.6 km^2 was predicted as potential spawning area. This represents 15% of the total erosive/transition zone of the lake.

A comparison of the spawning habitat features drawn from telemetry fixes and those of historical netting sites (known spawning areas) reveal some differences (Table 2). On average, lake trout were found on slightly steeper slopes compared to the slopes of known spawning areas. Fetch in known spawning areas was similar to areas occupied by telemetered lake trout. Known spawning areas in this system were slightly shallower than the depths of telemetered fish. Of 21 traditional netting sites, 7 (33%) were located at depths between 1 and 2 m. Telemetry results (n = 50 fixes) show higher frequencies of fish locations at depths between 2 and 6 m (Fig. 6).

Locations of two telemetered female lake trout from an earlier telemetry study in the East Arm (MacLean et al., 1981: 1694, Fig. 5) were overlaid on the predicted spawning area map (Fig. 5). Half of the fixes in the erosive or transition zones (7 of 14) were found within spawning areas predicted by our model.

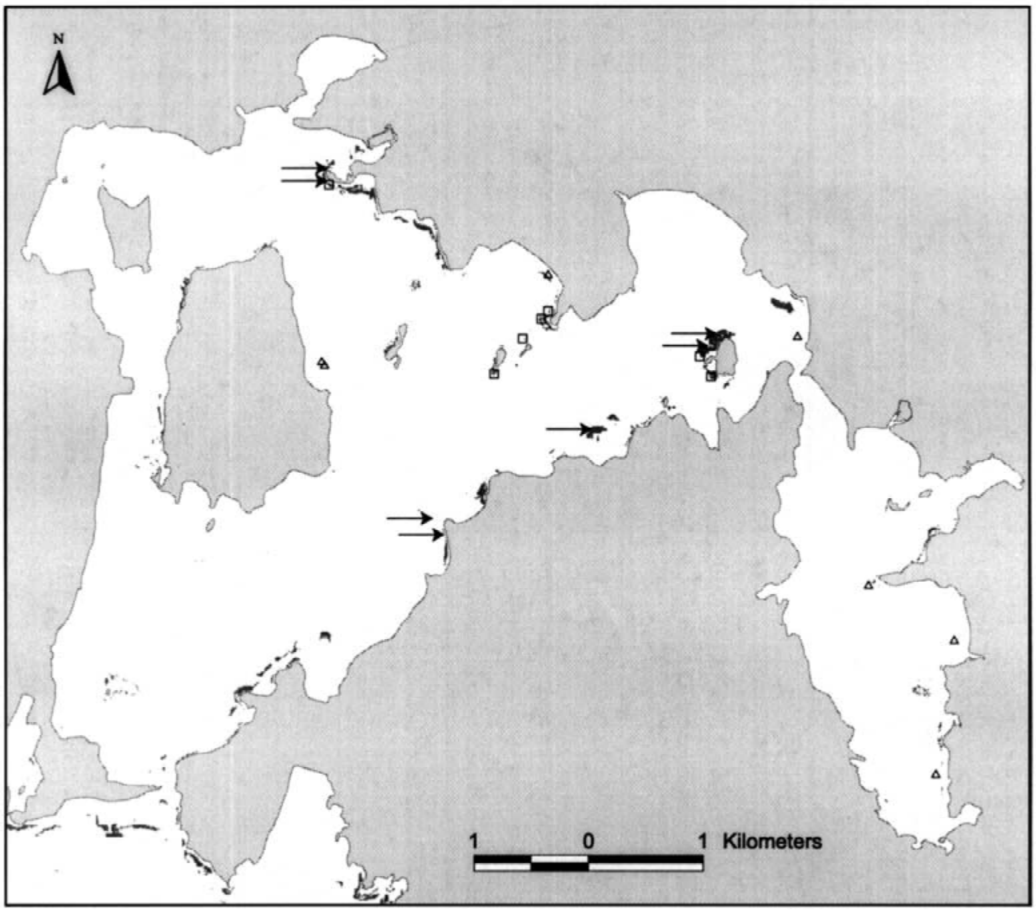

Figure 5. East Arm outline showing potential spawning areas (dark grey) predicted by model. Arrows denote known spawning (traditional netting) sites. Open symbols mark the erosive zone positions of two telemetered females from the MacLean et al. (1981) study; squares (□) are those within the predicted spawning areas, triangles (△) are those outside of the predicted spawning areas.

Those fixes that did not correspond to predicted areas were often found near to these areas (Fig. 5).

Discussion

The combination of telemetry and GIS technologies proved to be an effective tool in identifying potential lake trout spawning habitat in this large inland lake system. Telemetry allows for insights into fish behaviour and has been applied in many areas of behavioural ecology, including estimation of home ranges and habitat selection. Assessment of independence of successive telemetry observations is an important aspect of any telemetry study. Especially in studies of circular home ranges, positive autocorrelation of observations can be problematic, leading to biased estimates (Swihart & Slade, 1985). However, in some cases, autocorrelation of location estimates can reveal important biological information. Strong autocorrelation is often seen in animals with non-random movement patterns (Swihart & Slade, 1985) which we may expect in spawning fish. In a study of a coastal otter species, Blundell et al. (2001) concluded that highly positively autocorrelated data did not negatively influence estimates of linear home ranges, and in fact were critical in the identification of reproductive strategies. For lake trout, we believe that similar, non-random patterns of movement occur in relation to spawning activities, and therefore we considered all evening fixes in the erosive zone during the spawning window as potential spawning-related observations, regardless of autocorrelation.

The importance of substrate in spawning site selection is well-documented (Sly, 1988; Marsden et al., 1995). Lake trout generally spawn only on windswept shorelines (Martin, 1957; DeRoche, 1969). This is generally thought to be a behavioural adaptation, since the incidence of active cleaning of the substrate has rarely been observed (but see Martin & Olver, 1980 for a review). Consequently, substrates already swept clean by wave action are likely preferred. Since lake trout broadcast negatively buoyant eggs over substrate (Gunn, 1995), the successful incubation of eggs and subsequent survival of emergent fry is directly dependent on the size of interstitial spaces of the spawning sites selected (Sly, 1988). Thus, the size of spawning substrates is a key factor in spawning habitat selection. The range of suitable sediment sizes and shapes reported in the literature is great (2–91 cm; DeRoche, 1969; McAughey & Gunn, 1995; Sly & Evans, 1996; Fitzsimmons & Williston, 2000). Other than the standard 'clean cobble/rock' characterisation of substrates for lake trout spawning, there is little agreement in the literature as to what size of substrate is preferred. Lake trout in a small inland lake near Sudbury, Ontario selected smaller spawning substrates (2–10 cm) than predicted (McAughey & Gunn, 1995). Results for a series of lakes studied by Sly & Evans (1996) suggest optimal particle sizes of 4–10 cm. The discrimination of substrate sizes and types in lakes with large littoral areas is a daunting task, and detailed substrate information is rarely available. If substrate surveys are conducted, they are usually depth-limited. If, as our results suggest, lake trout choose spawning sites deeper than areas where visual observations can be made, then standard littoral substrate surveys may not detect all potential spawning areas. The use of a sedimentation model such as the one provided by Rowan et al. (1992) to estimate the distribution of different types of sediments proves very useful in the analysis of spawning habitat selection by lake trout.

Directly related to substrate size, but of perhaps greater importance, are the characteristics of fetch and slope. When measures of these two variables, as well as depth, were derived from telemetry results and subsequently applied in a habitat selection model, the majority (90%) of known spawning areas in this system were accurately predicted. Spawning areas predicted by the model that do not correspond to known spawning areas have not been assessed in the past, since the objective of the netting program in this system has not been identification of new spawning areas, but rather the marking of adults for mark-recapture estimates. Fitzsimmons (1996) discusses the difficulty in using randomly set gill netting observations as indicators of spawning locations, particularly in larger systems where distances between shoals may be greater and

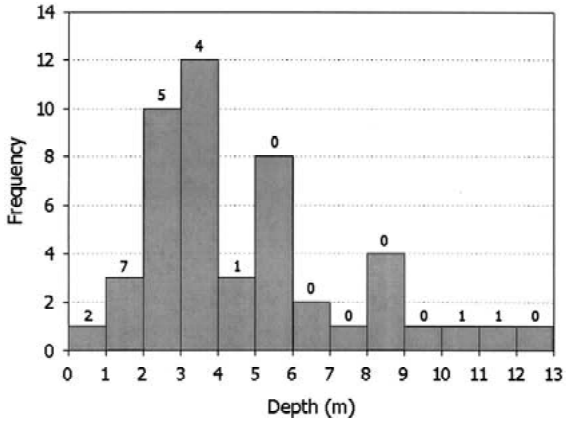

Figure 6. Frequencies of depths recorded at evening fish locations during the spawning periods of 1998, 1999 and 2000. Numbers above bars represent the number of traditional nets set (of 21 total) at the corresponding depths.

movements of spawning fish are potentially more extensive. This increases the probability of catches to represent movements en route to spawning areas. The traditional netting sites in our study have been utilized over several years, and substantial numbers of ripe adults are consistently found in these areas.

Marsden et al. (1995) defined the quality of spawning habitat based on intensity of use by spawners and the degree of success in incubation of eggs and subsequent survival of fry to emergence. Some authors contend that the only accepted direct evidence of spawning habitat use by lake trout is the collection of eggs, fry or YOY (Marsden et al., 1995). Although collection of embryos should indeed be considered irrefutable proof of spawning, the collection of this type of information, particularly in systems where there is a lack of traditional knowledge of spawning areas, can be difficult. Also, Fitzsimmons (1996) expressed concerns regarding the spatial variation in egg trap or tray collections, even within a single small spawning reef. This, combined with the labour of searching for sites suitable for deployment of egg collection gear in larger lakes (Gunn et al., 1996), makes this type of spawning habitat verification method problematic. The use of fetch and slope as deterministic variables in spawning habitat selection emerges as a viable alternative to methodologies that require detailed knowledge of substrate characteristics. Rowan et al. (1992) determined that slope effects in lakes could result in coarse-grained sediments at depths greater than expected from wave energy alone. The identification of several potential spawning shoals located offshore in deeper water is an interesting feature of this study. A model put forth by Fitzsimmons (1994) predicts that lake trout spawning depths are a function of lake size (or surface area). The expected depth of spawning for Lake Opeongo lake trout as determined by this model is 1.68 m. Our telemetry data suggest that this prediction is an underestimate of the depths that spawning adults select in this system. Deeper offshore areas (4 – 6 m), while potentially too deep to receive any wind generated currents, may have sufficient slope and appreciable exposure to internal currents to qualify as potential spawning areas in a lake of this size.

In general, traditional fall netting practices tend to target nearshore areas for spawning lake trout collection. Information from our telemetry results suggests that netting could be concentrated in deeper waters (1 – 5 m). In contrast to smaller inland lake systems, the depth distribution of spawning shoals can be much deeper than the lake size-spawning depth relationship (Fitzsimmons, 1994) predicts; longer fetches result in the occurrence of deeper distribution of clean substrates through wave action. MacLean et al. (1990) maintain that potential reproductive habitat based on fetch occurs in areas of lakes with fetches greater than 0.5 km. These authors felt this standard was liberal, given that the mean fetch of spawning sites in their study was 2.96 km ($n = 151$ lake trout lakes in Ontario). The mean fetch of spawning areas determined through our telemetry agrees with this general rule.

In addition to the accurate prediction of known spawning sites, we identified other nearshore potential spawning areas. Some positions of two females in a 1979 telemetry study of spawning adults in the East Arm (MacLean et al., 1981) coincided with areas predicted by our model. Those positions that were not found within the predicted spawning areas were often nearby. Since full accounts of tracking details were not provided in the MacLean et al. (1981) study, full agreement between their telemetry data and the spawning areas predicted by our model was not expected. However, the conformity of any observations from a historical study has important implications for the predictive value of our model.

Confirmation of natural spawning events is considered of great evidentiary importance in the Great Lakes, where recovery of lake trout stocks is thought to be hampered by low rates of natural reproduction (Fitzsimmons & Williston, 2000). The identification of potential spawning areas is an important first step in description of critical spawning habitats. In addition, our ability to extend information gained from telemetry to areas where no tracking occurred has important implications for the future application of this method for delineation of lake trout spawning habitat.

Acknowledgements

Staff and students of the Harkness Laboratory of Fisheries Research provided limitless assistance throughout the study. Special thanks to G. Ridout for essential support and information on lake trout spawning in Lake Opeongo and to N. Lester for providing comments on the manuscript. Thanks to the Ontario Ministry of Natural Resources for financial and logistical support. Funding was also provided by an NSERC grant to RSM.

References

Blundell, G. M., J. A. K. Maier & E. M. Debevec, 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecol. Monogr. 71: 469–489.

DeRoche, S. E., 1969. Observations on the spawning habits and early life of lake trout. Prog. Fish-Cult. 31: 109–113.

Fitzsimmons, J. D., 1994. An evaluation of lake trout spawning habitat characteristics and methods for their detection. Can. Tech. Rep. Fish. aquat. Sci. No.1962: 1–26.

Fitzsimmons, J. D., 1995. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. J. Great Lakes Res. 21: 337–347.

Fitzsimmons, J. D., 1996. The significance of man-made structures for lake trout spawning in the Great Lakes: are they a viable alternative to natural reefs? Can. J. Fish. aquat. Sci. 53: 142–151.

Fitzsimmons, J. D. & T. B. Williston, 2000. Evidence of lake trout spawning in Lake Erie. J. Great Lakes Res. 26: 489–494.

Gross, M. R., 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In Potts, G. W. & R. J. Wootton (eds), Fish Reproduction: Strategies and Tactics. Academic Press Inc., London: 55–76.

Gunn, J. M., 1995. Spawning behaviour of lake trout: effects on colonization ability. J. Great Lakes Res. 21: 323–329.

Gunn, J. M., M. Conlon, R. J. Kirk & S. C. McAughey, 1996. Can trained observers accurately identify lake trout spawning habitat? Can. J. Fish. aquat. Sci. 53: 327–331.

Liimatainen, V. A., E. J. Snucins & J. M. Gunn, 1987. Observations of lake trout (*Salvelinus namaycush*) spawning behaviour in low pH lakes near Sudbury, Ontario. Ontario Fisheries Acidification Report Series No. 87–10: 1–71.

MacLean, J. A., D. O. Evans, N. V. Martin & R. L. DesJardine, 1981. Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario lakes. Can. J. Fish. aquat. Sci. 38: 1685–1700.

MacLean, N. G., J. M. Gunn, F. J. Hicks, P. E. Ihssen, M. Malhiot, T. E. Mosindy & W. Wilson, 1990. Environmental and genetic factors affecting the physiology and ecology of lake trout. In: Physiology and Ecology Working Group, Lake Trout Synthesis. Ontario Ministry of Natural Resources, Toronto, Ontario: 1–84.

Marsden, J. E., D. L. Perkins & C. C. Krueger, 1995. Recognition of spawning areas by lake trout: deposition and survival of eggs on small, man-made rock piles. J. Great Lakes Res. 21: 330–336.

Martin, N. V., 1955. The effect of drawdowns on lake trout reproduction and the use of artificial spawning beds. Trans. N. am. Wildl. Conf. 20: 263–271.

Martin, N. V., 1957. Reproduction of lake trout in Algonquin Park, Ontario. Trans. am. Fish. Soc. 86: 231–244.

Martin, N. V. & C. H. Olver, 1980. The lake charr, *Salvelinus namaycush*. In Balon, E. K. (ed.), Charrs: Salmonid Fishes of the Genus *Salvelinus*. Dr W. Junk Publishers, The Hague, Netherlands: 205–277.

McAughey, S. C. & J. M. Gunn, 1995. The behavioral response of lake trout to a loss of traditional spawning sites. J. Great Lakes Res. 21 (Suppl. 1): 375–383.

McCrimmon, H. R., 1958. Observations on the spawning of lake trout, *Salvelinus namaycush*, and the post-spawning movement of adult trout in Lake Simcoe. Can. Fish Cult. 23: 3–11.

Rowan, D. J., J. Kalff & J. B. Rasmussen, 1992. Estimating the mud deposition boundary depth in lakes from wave theory. Can. J. Fish. aquat. Sci. 49: 2490–2497.

Schoener, T. W., 1981. An empirically based estimate of home range. Theor. Pop. Biol. 20: 281–325.

Schreiner, D. R., C. R. Bronte, N. R. Payne, J. D. Fitzsimons & J. M. Casselman, 1995. Use of egg traps to investigate lake trout spawning in the Great Lakes. J. Great Lakes Res. 21: 433–444.

Sly, P. G., 1988. Interstitial water quality of lake trout spawning habitat. J. Great Lakes Res. 14: 301–315.

Sly, P. G. & D. O. Evans, 1996. Suitability of habitat for spawning lake trout. J. Aquat. Ecosyst. Health 5: 153–175.

Swihart, R. K. & N. A. Slade, 1985. Testing for independence of observations in animal movements. Ecology 66: 1176–1184.

Wagner, G. N. & E. D. Stevens, 2000. Effects of different surgical techniques: suture material and location of incision site on the behaviour of rainbow trout (*Oncorhynchus mykiss*). Mar. Fresh. Behav. Physiol. 33: 103–114.