

Effects of Displacement on the Seasonal Movements and Home Range Characteristics of Smallmouth Bass in Lake Opeongo

MARK S. RIDGWAY AND BRIAN J. SHUTER

Harkness Laboratory of Fisheries Research, Aquatic Ecosystems Research Section
Ontario Ministry of Natural Resources, Box 5000, Maple, Ontario L6A 1S9, Canada

Abstract.—We displaced a subset of adult smallmouth bass *Micropterus dolomieu* implanted with sonic tags to determine if they returned to home ranges held before their displacement. We also compared their home range characteristics and seasonal movements with those of undisturbed smallmouth bass. Fifteen of the 18 displaced fish returned to the home ranges they held before removal. One fish died soon after release, and two fish remained in the area of release. Displaced smallmouth bass remained at the release site for an average of 1 week (range, 0.5–30 d) and returned to their home ranges in approximately 4 d (range, 1–9 d). On average, displaced fish were away from their home ranges for 11 d. Displaced and control smallmouth bass did not significantly differ with respect to home range area, percent overlap between early and late summer shifts in home ranges, or day of the year when fish left their home ranges for overwintering sites. These results indicate that smallmouth bass displaced by tournament anglers will return to their home ranges after spending approximately 1 week at the release site and will use their home range in a manner similar to that of undisturbed fish.

Restricted movements of smallmouth bass *Micropterus dolomieu* have been observed in streams, rivers, and lakes. In streams, smallmouth bass remained in restricted areas and returned if displaced a short distance (Larimore 1952; Gerking 1953; Fajen 1962). In larger river systems, their seasonal movements were more extensive (>50 km); however, they returned to the same 5-km river sections in which they were tagged in previous years (Langhurst and Schoenike 1990). In lakes, smallmouth bass showed strong nest site fidelity in subsequent years (Ridgway et al. 1991). Tag returns from angler surveys (Stone et al. 1954; Webster 1954; Forney 1961; Latta 1963; Pflug and Pauley 1983) and netting programs in lakes (Fraser 1955; Latta 1963) indicated that adult smallmouth bass remain within a few kilometers (range, 3–8 km) of their release site for at least 1 year after tagging. Telemetry data have generally supported the model of restricted movements in this species (e.g., Hubert and Lackey 1980; Langhurst and Schoenike 1990; Kraai et al. 1991; Savitz et al. 1993) but have also indicated that fish shifted their activity to other areas of their home range. Before winter, smallmouth bass leave their home ranges and move to overwintering sites where they remain until the following spring (Webster 1954; Langhurst and Schoenike 1990).

Results from two studies focusing on displacement of externally tagged smallmouth bass suggested some level of fidelity to areas of initial capture. After being displaced 8–24 km from their capture site in Oneida Lake, 54% (27/50 fish) of recaptured small-

mouth bass returned to within 5 km of the site of capture after 1 year (Forney 1961). In Lake Sammamish, Washington, 14 of 240 displaced smallmouth bass were recaptured within 5 d of release in the section of the lakeshore where they were initially captured. Nineteen fish were captured at the release site or between the release site and capture site (Pflug and Pauley 1983).

We monitored use of home range by tracking sonically tagged adult smallmouth bass after the parental care period and by following a subset of fish displaced from their home ranges. Unlike previous researchers, we compared the home ranges of displaced fish with unmanipulated fish to determine if displacement altered the patterns of home range use between these two groups. Our objective was to determine if smallmouth bass returned to old home ranges after displacement. At a fundamental level, the results tested the use of restricted space by smallmouth bass in lakes. At an applied level, the results resolved a fisheries management issue concerning the fate of smallmouth bass displaced by tournament fishing.

Methods

Study site.—Data were collected on the movements of 32 adult smallmouth bass from early July through September in 1990, 1991, and 1992 in Lake Opeongo (45°42'N; 78°22'W), Algonquin Park, Ontario. Lake Opeongo is a large oligotrophic lake (area, 5,860 ha; mean depth, 14.8 m) and the site of long-term field research on the ecology and population dynamics of smallmouth bass.

Smallmouth bass were introduced in the 1920s to supplement the angling fishery for native salmonines. The smallmouth bass population and fishery has been monitored since 1936 with an access point creel survey (Shuter et al. 1987). The main spawning area in Lake Opeongo, Jones Bay, has been monitored since 1955, with continual intensive monitoring since 1976. Further descriptions of the lake and fish community were given by Martin and Fry (1973).

Sonic implants.—Fish were located with sonic tags that were surgically implanted in the body cavity (Winter 1983). Sonic telemetry was selected rather than radio telemetry because of previous reports that smallmouth bass could sometimes live at depths beyond the range of radio telemetry (Winter 1983). All adult males and females that received sonic tags were 36–41 cm in fork length; minimum fish length was determined by the size of our tags (Sonotronics, Inc., CTT-83 tag: 60 mm long \times 16 mm in diameter; weight, 8 g in water). Adult males ($N = 16$) were angled from their nest sites during the hatched embryo stage of offspring development (Ridgway 1988) or captured in trap nets after the parental care period ($N = 3$). Adult females ($N = 10$) were captured in trap nets in spring before spawning or during the parental care period ($N = 3$).

Sonic tags were implanted in fish at the capture site. Fish were anesthetized with MS-222 (tricaine methanesulfonate) until flexure of the gill covers was greatly reduced (approximately 4–5 min). A ventral incision, approximately 2–3 cm long, was made in the body wall between a point anterior to the urogenital opening and a point between the pelvic fins. A sonic tag was then inserted into the body cavity through the incision, and the incision was sutured with either nylon thread or surgical staples. Fish were placed in a large container next to the boat, and their recovery was monitored by observers. Fish were judged to have recovered from surgery when they had properly reoriented in the container. Nesting males were carried in the container back to their nest sites and released. All other fish were released next to the boat. For nesting males, parental fanning and guarding resumed within 30 min as determined by underwater observations. Nests of males that received sonic tags were undisturbed during the capture, surgery, and release procedure.

One week after surgery, a directional hydrophone (range, 0.5–1.5 km) was used to sweep embayments and points of land to search for tagged fish. To locate fish, the boat position was adjusted

by the pass-over technique until the sound of the sonic signal was approximately omnidirectional (Winter 1983). This was recorded as the location of the fish. The combination of using compass triangulation, shoreline features, and close proximity of the boat to locate a fish resulted in an accuracy of ± 20 m. All compass bearings and triangulation data were transferred to maps and stored as UTM (Universal Transverse Mercator) coordinates. All fixes were collected from the end of the reproductive period (early July) until early October of the same year (except for displaced fish 1 and 2 which were located from July to October 1991). Only fixes within the home ranges and not from either the displacement period (capture, release, and return) or the reproductive period (spawning and nesting) were included in home range comparisons of displaced and control fish. In all, 3,153 fixes (mean, 105/fish; range, 19–147) were collected in this study.

Displacement experiment.—A subset ($N = 18$) of the total population of sonically tagged fish were recaptured and displaced from their home range areas to determine if they would return. We found that adult males established home ranges shortly after dispersing from their nest sites, whereas females established home ranges shortly after spawning. After nesting or spawning and before displacement, sonically tagged smallmouth bass were allowed to establish home range areas. A return to within the boundary of this early home range area was used as the criterion for determining if a fish successfully returned to its home range after displacement.

Fish were located with the directional hydrophone and when in close proximity to the shore, a team of swimmers deployed a barrier net (beach seine) and encircled the target fish. When completely enclosed, the smallmouth bass was lifted into a boat and placed in a live well with recirculating water for approximately 2 h. This simulated the practice of many tournament anglers to hold fish in live wells. Fish were released at various sites in the lake (Figure 1; four fish were displaced in a southerly direction; six in a westerly direction, and eight in a northerly direction). Release sites were preselected on the basis of general descriptions of shoreline habitat normally inhabited by smallmouth bass (e.g., areas with rock and cobble shorelines and little vegetation or sandy shorelines; Hubert and Lackey 1980; Kraai et al. 1991). We established a daily routine of searching for and mapping the location of all sonically tagged fish in Lake Opeongo. Fixes taken of fish after displacement and before return to their early home range were not

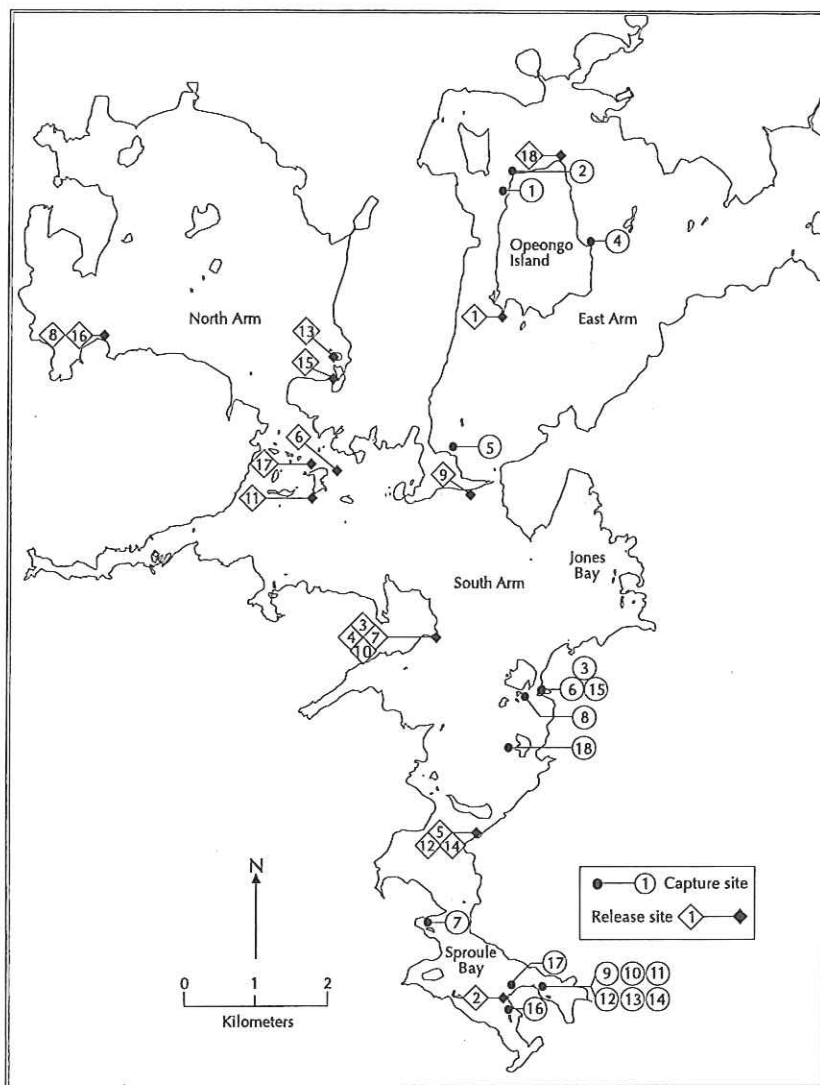


FIGURE 1.—Capture and release sites for displaced smallmouth bass in Lake Opeongo. Numbers identify individual fish. Fish were captured by seine except fish from sites 9–14, which were captured in a trap net.

included in determining home range location or area for displaced fish. However, all other location data collected after the fish nested and before they moved to overwintering sites were used in home range analysis for displaced fish. All location data from control fish collected after nesting and before moving to overwintering sites were used in their home range analysis.

To increase the sample size of displaced fish, six smallmouth bass captured in a trap net on July 10, 1991, were also implanted with sonic tags and displaced. These fish were included with 12 fish captured and displaced as previously described and

were not treated as a separate category of fish for two reasons. First, the home range of these fish was considered to be Sproule Bay because data from all unmanipulated fish indicated that home ranges of smallmouth bass in this part of Lake Opeongo covered most of this bay (Figure 2). Therefore, returning to Sproule Bay was considered a return to an old home range for any of the six fish captured in the trap net and displaced. Second, a comparison of fish captured by the two methods (barrier net versus trap net) versus whether or not they returned to their home range showed no significant pattern (2×2 contingency table;

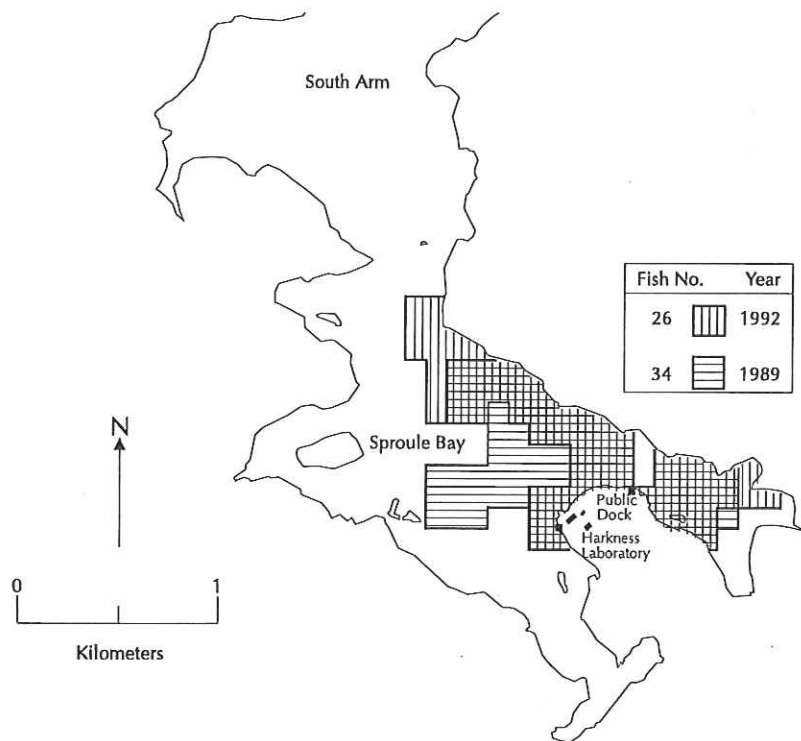


FIGURE 2.—Southern end of Lake Opeongo showing typical home ranges for smallmouth bass.

Fisher exact test; $P = 0.51$; two-tailed). We used Sproule Bay as the early home range area (Figure 2) when comparing seasonal shifts in home range location for three fish captured in the trap net and included in Table 1.

Analysis.—Fixes of fish in the field were positioned on maps by UTM coordinates. The grid cell method ($100 \text{ m} \times 100 \text{ m}$) including “influence cells” (i.e., all eight grid cells surrounding a single cell containing observations) was used to calculate the area of the home range (e.g., Voigt and Tinline 1980; Miller and Menzel 1986; Doncaster and MacDonald 1991; Zoellick and Smith 1992).

Other methods such as the harmonic mean (Dixon and Chapman 1980) were not used because both the home ranges and daily movements of smallmouth bass in Lake Opeongo tended to have a linear aspect, and the data would thus tend to be autocorrelated (based on Schoener's ratio; Swihart and Slade 1985). Also, the harmonic mean method of determining utilization contours regularly included areas that the smallmouth bass did not use (e.g., deep, open-water areas of the lake) or could never use (e.g., land). Similarly, we encountered the problem of incorporating inappropriate areas when using more traditional polygon methods,

such as the minimum convex polygon (Mohr 1947). Fish were generally located one or two times per day between 0900 and 1800 hours.

Smallmouth bass are known to shift their home range locations during the summer (Hubert and Lackey 1980; Savitz et al. 1993). To investigate summer shifts, we used the summer peak in water temperature to divide the summer into an early period (after fish nested and before the peak in temperature) and a late period (after the peak in temperature and before fish moved to overwintering sites). Overlap of the early and late summer home ranges was based on the percentage of the early summer range contained within the late summer range.

The Oneida lake displacement study of smallmouth bass was used to set a prior probability of returning to home ranges in a given year (Forney 1961). This prior probability represented our expectation of the percentage of smallmouth bass returning to old home ranges in Lake Opeongo, and as such, was the basis of comparison in a binomial test of the numbers of fish returning to old home ranges in Lake Opeongo. Data from the Oneida Lake study indicated that 54% of all recaptured smallmouth bass returned to within 4 km of the capture site 1 year after displacement (Forney 1961: Table 6D). An alternative

TABLE 1.—Statistics on smallmouth bass displaced from their home range in 5,860-ha Lake Opeongo.

Statistic	Day of year displaced, $N = 18$	Displacement distance (km), $N = 18$	Days within release site, $N = 17$	Travel days back to home range, $N = 15$	Total days away from home range, $N = 15$	Minimum daily distance traveled back to home range (km), $N = 15$
Mean	200	6.67	7.79	3.97	11.20	2.39
SD	9.30	3.64	7.36	2.55	7.20	2.33
Minimum	191	0.80	0.50	1.00	2.00	0.80
Maximum	220	14.00	30.00	9.00	33.00	9.40

method of determining the probability of returning to a previously held home range would be the use of a random walk model incorporating displacement distances and turning angles. This approach would compare the observed movements of displaced smallmouth bass with those based on the random walk model. We rejected this alternative approach because models of this kind depend critically on assumptions of movements and directional changes per unit time.

Results

Displaced fish were moved an average 6.7 km (range 0.8–14.0 km; Table 1). Fifteen of the 18 (probability, 0.83) displaced fish returned to the home range they held before removal. This frequency of returning fish was significantly greater than expected based on data in the Oneida Lake study (binomial test; $P < 0.002$; prior probability of returning = 0.54; Forney 1961). Of the three fish that did not return, one died soon after release and two remained in the area of their release. Distance from capture site did not appear to be a factor in the absence of home range fidelity for the three fish that did not return. Their release sites were within the displacement distances of the other 15 fish.

Smallmouth bass remained near their release site from less than 1 d to 30 d (mean, 7.79 d; Table 1). Once they left the release site, the fish took 1–9 d to return to their original home range (mean, 3.97 d; Table 1). Displaced smallmouth bass returned to their home range, moving in relative proximity to shore ($N = 9$ for fish located between release site and home range). Half of all fixes of returning fish were within 25 m of shore ($N = 38$ fixes; mean, 34.5 m; range, 10–150 m). Furthermore, returning fish were able to negotiate narrow channels when necessary to return to their home range. The rate of movement toward home ranges was 0.8–9.4 km/d (mean, 2.39 km/d; Table 1).

Home range characteristics of displaced and control smallmouth bass were similar. For both groups of fish, the mean home range area was less than 200 ha and the mean seasonal overlap was less than 50% from early to late summer (Table 2). Home range area and seasonal overlap of early and late summer components of the home range were not significantly different from control fish (Table 2; Wilcoxon–Mann–Whitney test for area: $U = 123$, $P = 0.24$; Wilcoxon–Mann–Whitney test for overlap: $U = 110.5$, $P = 0.70$, two-tailed tests). The observed home range length (i.e., maximum linear distance within a home range) for displaced fish averaged 6.29 km and for control fish 4.24 km, but did not differ significantly (Table 2; Wilcoxon–Mann–Whitney test: $U = 133.5$; $P = 0.16$, two-tailed test). There was no significant difference in the day of the year when displaced and control fish left their home range for their overwintering site (Wilcoxon–Mann–Whitney test; $U = 56.5$; $P = 0.36$; two-tailed test).

Discussion

Our summary of seasonal shifts in home range location contrasts with earlier summaries of the daily movements of smallmouth bass. Previous home range summaries have emphasized frequent changes in location as a means of defining separate

TABLE 2.—Home range characteristics and seasonal movements of displaced versus control smallmouth bass,^a in 5,860-ha Lake Opeongo.

Statistic	Home range area (ha)		Percent overlap of early versus late summer home range		Observed home range length (km)		Day of year fish moved to winter site	
	Displaced ($N = 14$)	Control ($N = 14$)	Displaced ($N = 14$)	Control ($N = 14$)	Displaced ($N = 14$)	Control ($N = 14$)	Displaced ($N = 10$)	Control ($N = 10$)
Mean	152	183	43.84	49.04	6.29	4.24	270	274
SD	66	80	17.20	20.27	3.61	2.35	12.51	9.41
Minimum	71	83	0.00	14.70	2.07	1.24	246	259
Maximum	272	304	65.40	74.40	14.06	9.09	282	289

^a Only 14 fish because of loss of one sonically tagged fish after return to home range.

summer home ranges within a single season (Hubert and Lackey 1980; Savitz et al. 1993). We adopted a more seasonal approach to defining home range as the area occupied after nesting (males) or spawning (females) and before the direct movement to overwintering sites (Webster 1954; Langhurst and Schoenike 1990). We made no attempt to divide the area used by smallmouth bass into separate home ranges based simply on criteria incorporating frequent changes in location (Savitz et al. 1993) or the number of sequential days at a location (Hubert and Lackey 1980). Our seasonal approach to home range analysis used the summer peak in water temperature as a natural boundary to determine if home ranges are stationary or shift in location from early to late summer. In Lake Opeongo, approximately half of the area incorporated into home ranges after the summer temperature peak was not used in early summer. This seasonal shift in summer home range location is in contrast to the traditional image of smallmouth bass moving between multiple home ranges by forays between sites (Larimore 1952; Gerking 1953; Hubert and Lackey 1980; Savitz et al. 1993).

Our study confirmed that the restricted movement patterns observed in earlier studies on large lake systems represent seasonal home range use (Stone et al. 1954; Webster 1954; Fraser 1955; Forney 1961; Latta 1963) or a return to old home ranges after displacement (Forney 1961; Pflug and Pauley 1983). Using netting or angler surveys to map the location of external tags can present problems when one attempts to determine the restricted movements of fish because a large majority of tagged fish are never observed after their initial capture. This in part accounts for the relatively large distances used in some studies to define restricted movements (e.g., recaptured fish within 4 km of initial capture site: Fraser 1955; Forney 1961). However, there is a close match between the observed home range length for control fish in this study (4.24 km in Lake Opeongo; Table 2) and the boundaries for restricted movements used in the earlier tagging studies (approximately 4–5 km: Fraser 1955; Forney 1961).

The return of displaced smallmouth bass to old home ranges extends an earlier observation of nest site fidelity for adult males in Lake Opeongo (Ridgway et al. 1991). These results indicate that the restricted movements observed for smallmouth bass in other large systems may be related to nest site fidelity and restricted movements within seasonal home ranges (e.g., Stone et al. 1954; Fraser 1955; Funk 1957; Forney 1961; Langhurst and

Schoenike 1990). In the case of nest site fidelity, males may be returning to sites of previous reproductive success or perhaps to sites where they were born (Gross et al. 1994). In the case of restricted use of home ranges, smallmouth bass may be using foraging profitability to determine the location of adult home ranges.

Whatever mechanism is used to determine the location of adult home ranges, the area occupied by adult smallmouth bass in Lake Opeongo is clearly greater than previously recorded for this species. Estimates of home range area in other studies are <1–43 ha (Kraai et al. 1991; Savitz et al. 1993), whereas in Lake Opeongo, estimates are 71–304 ha (Table 2). This is perhaps the result of differences in the functional definition of home range from the area occupied over a few days (Savitz et al. 1993) to the area occupied over the summer and early fall (our study). However, it is conceivable that in oligotrophic northern lakes like Opeongo, a larger home range may be required by smallmouth bass to meet daily foraging needs.

Management Implications

There are several implications from this study for fisheries managers concerned with the effects of angling tournaments on smallmouth bass populations. First, fisheries managers should consider adopting a cautious policy in the temporal spacing of tournaments because our results indicate that smallmouth bass displaced by tournaments may be away from their home range for up to a month. Also, our results indicate that most displaced fish will return to previously held home ranges, even if this movement includes negotiating narrow channels between adjacent areas of lakes. Second, fisheries managers should encourage, or consider policies that encourage release of tournament-caught fish at various locations around lakes or reservoirs because displaced smallmouth bass remain at the release site for approximately 1 week. Such policies would perhaps prevent additional fishing mortality resulting from increased fishing effort concentrated at release sites in the immediate posttournament period. Third, the fidelity to summer home ranges shown in this study and suggested in earlier external-tagging studies (Fraser 1955; Forney 1961), the fidelity to nest sites (Ridgway et al. 1991), and the fidelity to overwintering sites (Webster 1954) indicate that conservation of smallmouth bass populations requires consideration of all three of these habitats as well as the habitat used by smallmouth bass while traveling between these locations.

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