Movement patterns and spatial segregation of two populations of lake trout Salvelinus namaycush in Lake Huron

Thomas R. Binder a,*, J. Ellen Marsden b, Stephen C. Riley c, James E. Johnson d, Nicholas S. Johnson e, Ji He d, Mark Ebener f, Christopher M. Holbrook e, Roger A. Bergstedt e, Charles R. Bronte b, Todd A. Hayden a, Charles C. Krueger h

a Department of Fisheries and Wildlife, Michigan State University, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, MI 48759, USA
b Rubenstein Ecosystem Science Laboratory, University of Vermont, 3 College St., Burlington, VT 05401, USA
c U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA
d U.S. Geological Survey, Great Lakes Science Center, Hammond Bay Biological Station, 11188 Ray Rd., Millersburg, MI 49775, USA
e Chippewa Ottawa Resource Authority, 179 West Three Mile, Sault Ste. Marie, MI 49783, USA
f U.S. Fish and Wildlife Service, Green Bay Fish and Wildlife Conservation Office, 2661 Scott Tower Dr., New Franken, WI 54229, USA
g Department of Fisheries and Wildlife, Center for Systems Integration and Sustainability, 115 Manly Miles Building, Michigan State University, East Lansing, MI 48824, USA

Article history:
Received 10 June 2016
Accepted 29 March 2017
Available online 4 April 2017

Abstract
Movement ecology is an important component of life history and population dynamics, and consequently its understanding can inform successful fishery management decision-making. While lake trout populations in Lake Huron have shown signs of recovery from near extinction in recent years, knowledge of their movement behavior remains incomplete. We used acoustic telemetry to describe and compare movement patterns of two Lake Huron lake trout populations: Drummond Island and Thunder Bay. Both populations showed high spawning site fidelity, with no evidence of co-mingling during non-spawning season. Detections between spawning periods were mainly limited to receivers within 100 km of spawning locations, and suggested that the two populations likely remained segregated throughout the year. Drummond Island fish, which spawn inside the Drummond Island Refuge, primarily dispersed east into Canadian waters of Lake Huron, with 79–92% of fish being detected annually on receivers outside the refuge. In contrast, Thunder Bay fish tended to disperse south towards Saginaw Bay. Large proportions (i.e., >80%) of both populations were available to fisheries outside the management zone containing their spawning location. Thunder Bay fish moved relatively quickly to overwinter habitat after spawning, and tended to repeat the same post-spawning movement behavior each year. The consistent, predictable movement of both populations across management zones highlights the importance of understanding population dynamics to effective management of Lake Huron lake trout.

© 2017 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

Introduction
An understanding of the movement ecology of fish populations can benefit fishery management because movement is a primary component of life history, diversity, and population dynamics (Nathan et al., 2008), and is critical to understanding and controlling fishery mortality. For example, knowledge of population-specific movement patterns can contribute to management decisions by informing the appropriate location for management boundaries (Hourston, 1982), identifying potential sources of mortality (Cooke et al., 2004; Keefer et al., 2008), defining appropriate spatial requirements and layout of sanctuaries constructed for population/community conservation (Halpern and Warner, 2003; Quesne and Codling, 2009), and identifying the composition of mixed stock fisheries (Rooker et al., 2014; Veinott et al., 2012). This knowledge is especially valuable for highly mobile species like lake trout, Salvelinus namaycush, which have high social and economic value, and which have been the subject of extensive restoration efforts in the Laurentian Great Lakes since the 1950s, following a basin-wide crash due to over-harvest and predation by invasive sea lampreys, Petromyzon marinus (Hansen, 1999; Muir et al., 2012).

Restoring self-sustaining lake trout populations in the Great Lakes has been slow, with most populations outside of Lake Superior still dependent on juvenile stocking programs. In Lake Huron, however, lake trout have seen a substantial increase in wild recruitment since the early 2000s which has been attributed to improved sea lamprey control in the St. Marys River, a reduction in fishing mortality due to the 2000 Consent Decree, and the lake-wide crash of alewife, Alosa

* Corresponding author.
E-mail address: bindert@msu.edu (T.R. Binder).

http://dx.doi.org/10.1016/j.jglr.2017.03.023
0380-1330/© 2017 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.
psuedoharengus (He et al., 2012; Johnson et al., 2015b; Madenjian et al., 2008; Riley et al., 2007). Additionally, two lake trout refuges (Drummond Island Refuge in northern Lake Huron, and Six Fathom Bank Refuge in central Lake Huron) were established on historic spawning areas on the Michigan side of Lake Huron in the 1980s to protect populations from fishing mortality (Stanley et al., 1987). However, because we do not know to what extent lake trout remain within these sanctuaries, our understanding of the degree to which they serve to improve recruitment in Lake Huron remains limited.

Currently, lake trout fisheries in Lake Huron are regulated based on 18 statistical grids (inset in Fig. 1) established in the 1960s (Smith et al., 1961), which make up a total of 15 management units; the four southernmost statistical grids on the Michigan side (i.e., MH-3, MH-4, MH-5, and MH-6) were merged to form a single management unit. The biological significance of the management zone boundaries is unclear because little information exists on movement patterns of lake trout in Lake Huron. Most of what is known about lake trout movements in the Great Lakes comes from conventional mark-recapture studies on lakes Superior (Eschmeyer et al., 1953; Kapuscinski et al., 2005; Rahrer, 1968), Michigan (Bronte et al., 2007; Eck and Wells, 1986; Schmalz et al., 2002; Smith and Van Oosten, 1940), and Ontario (Elrod, 1987; Elrod et al., 1996). The majority of studies have suggested that adult lake trout show relatively high fidelity to spawning locations, which for hatchery-reared fish is often near stocking locations (Binder et al., 2016; Bronte et al., 2002, 2007; Eschmeyer, 1955; Rahrer, 1968; Swanson, 1973).

Between spawning seasons, adult lake trout can disperse widely. Adult movements in western Lake Superior were cyclical, with lake trout remaining close to spawning sites during October and November, dispersing between December and July, and then moving back towards spawning locations in August and September (Kapuscinski et al., 2005; Rahrer, 1968). Movements > 200 km have been observed in lakes Superior (Eschmeyer et al., 1953; Kapuscinski et al., 2005; Rahrer, 1968) and Michigan (Schmalz et al., 2002), but these long-distance movements appear to be rare. The majority of studies have suggested that lake trout tend to remain within about 100 km of their respective spawning grounds (Eschmeyer et al., 1953; Rahrer, 1968; Schmalz et al., 2002). However, these studies have relied on fishery recaptures and reporting, so it is possible that movements are more extensive than the spatial extent of fishery operations.

As far as we are aware, no published observations of population-specific lake trout movement patterns exist for Lake Huron. Therefore, our objective was to describe the movement patterns of two Lake Huron lake trout populations and determine if these two populations...
segregate spatially during spawning and non-spawning periods. Acoustic transmitter detections collected over ~2.5 years were used to compare movement patterns of lake trout populations spawning in the Drummond Island Refuge (DI array; Fig. 1), in northern Lake Huron, and in Thunder Bay (TB array; Fig. 1), approximately 100 km south and slightly east of Drummond Island (Fig. 1). These two populations were originally tagged for purposes other than the current study. However, these tagged fish presented a serendipitous opportunity to use existing data and resources (the Great Lakes Acoustic Telemetry Observation System (GLATOS) receiver network) to learn more about lake trout movements in Lake Huron. To achieve our objective, we: 1) compared general year-round movement patterns of Drummond Island and Thunder Bay lake trout; 2) quantified the degree to which Drummond Island and Thunder Bay lake trout overlapped in their spatial distribution during the spawning season; and 3) quantified overlap of Drummond Island and Thunder Bay lake trout in their spatial distribution outside of the spawning season. Based on the results of previous movement studies in other Great Lakes (cited above), we predicted that the two populations would show high fidelity to their respective spawning locations during the spawning season. We also expected lake trout to disperse after spawning, but predicted that few fish from each population would be detected on receivers ~100 km from their spawning location. Lastly, given that these two spawning locations were about 100 km apart, we predicted that the spatial distribution of Drummond Island and Thunder Bay lake trout would overlap little during the non-spawning season.

Methods

Study animals

Adult lake trout of wild and hatchery origin from the Drummond Island and Thunder Bay spawning populations were tagged with acoustic transmitters for telemetry studies at both spawning locations. The Drummond Island population spawns in the Drummond Island Refuge, a no-harvest lake trout sanctuary established in 1985 to alleviate fishing pressure on the Drummond Island spawning stock (Fig. 1; Stanley et al., 1987). Adult lake trout (n = 390), representative of the adult spawning population, were captured with trap nets and gill nets at several sites within 5 km of the Drummond Island array (DI) and tagged internally with V16-6H transmitters (VEMCO; Halifax NS, Canada) in mid-August to early October 2010, and late September to early October 2011 (see Binder et al., 2016 for complete handling and tagging details). Of the 390 lake trout tagged, 263 (median length = 680 mm, range = 566–890 mm) were determined to be part of the Drummond Island spawning population because they were detected in the array during spawning in at least one year of the 5-year study. Transmitters transmitted at random intervals between 50 and 130 s, had a battery life of about 8 years, and were divided among hatchery-reared (identified based on fin-clips; N = 213) and wild-reared (N = 177) males and females (Binder et al., 2016). Hatchery-reared fish were on average 35 mm larger than wild-reared fish (t-test; df = 261, t = 5.462, p < 0.001), but 72% of all tagged fish had length within 10% of the median length for the group. Each tagged fish from both populations also received a pair of Floy Tags (Floy Tag & Mfg. Inc.; Seattle, Washington, USA) inserted through the dorsal musculature that indicated a $100 reward for return of any tag recovered by fishers.

Great Lakes Acoustic Telemetry Observation System (GLATOS)

This study took advantage of the GLATOS acoustic telemetry array (http://data.glos.us/glatos), a network of acoustic telemetry receivers (VEMCO; Halifax NS, Canada) deployed and maintained through cooperation among Great Lakes researchers using acoustic telemetry in their studies. The GLATOS network was established in 2010 to facilitate sharing of detections among telemetry researchers across the Great Lakes basin. Detection sharing is done through a centralized database where researchers submit their raw detection data, and in return, have access to all detections in the database for their transmitters (i.e., principal investigators are considered the owner of all detection data for tags they purchased).

Receiver coverage changed over time as projects ended and new projects began (Fig. 2). In addition, some receiver lines and arrays were in place year-round, while others covered only specific periods (e.g., spawning periods, ice-free period). For the purpose of this study, individual receiver lines are identified by a 3-letter code (e.g., SBI, OSC; Fig. 1) and the two positional arrays that encompassed the spawning grounds of the two study populations are represented by a
two-letter code (DI and TB; Fig. 1). In Lake Huron, consistent year-round receiver coverage has occurred along most of the US shore and in the channels to the east and west of Drummond Island since autumn 2010 (Figs. 1 and 2). Six lines of receivers along the Canadian side (southern and eastern shore) of Lake Huron were added more recently. The two southernmost lines (BFW & HBB; Figs. 1 and 2) were added in summer 2012, with two more lines (GBD & GDR; Figs. 1 and 2) added in summer 2013. The remaining Canadian lines (PTC, SHN, BTM, & MIS; Figs. 1 and 2) were added in spring and summer 2014. Receivers on either side of Drummond Island (DTR & FDT; Fig. 1), and receivers in the channel between Cockburn Island and Manitoulin Island (MIS), which were added in 2014, monitored passages between northern Lake Huron and the North Channel. Additional lines of receivers monitored passage between Lake Huron and Georgian Bay (BTM; Fig. 1), the entrance into Thunder Bay (THB; Fig. 1), and the entrance into Saginaw Bay (SBI & SBO; Fig. 1). Positional telemetry arrays (2D receiver configurations that provide positions accurate to 10 m) were deployed seasonally at Drummond Island (DI; Fig. 1) and Thunder Bay (TB: Fig. 1). The DI array was deployed during late summer and autumn each year (August–September to late November) between 2010 and 2014 and the TB array was deployed during the same period between 2012 and 2014. Most receivers were deployed in water depths of 40 m or less, and had detection ranges up to several kilometers depending on local lake conditions (e.g., wave height) and weather (Hayden et al., 2016).

To eliminate the potential for bias due to varying distribution of receivers over time, we limited our analysis to the period that tagged fish from both populations were at large and available for detection (i.e., we excluded detections for Drummond Island fish prior to October 2012). All fish had equal opportunity to be detected on deployed receivers at a given location and time, so differences in the distribution of detections over time and space were considered representative. Possible false detections, which can occur when transmitted codes from two or more transmitters overlap in time to produce another existing transmitter code (Simpfendorfer et al., 2015), were filtered from the dataset prior to analysis using the short-interval procedure (Pincock, 2012). Specifically, individual transmitter detections not accompanied by a second detection for the same transmitter on the same receiver within 1 h were filtered from the dataset (Thunder Bay: 1.2% of 4,597,654 detections were filtered out; Drummond Island: 3.6% of 16,017,632 detections were filtered out).

To account for differences in sample size between the two populations and annual losses due to mortality, the distributions of fish detections among receiver lines for the two lake trout spawning populations were normalized for each population and year by calculating the percentage of individuals detected anywhere in Lake Huron that same year. Detections were partitioned based on whether they occurred during the spawning period (October and November) or non-spawning periods, at least 92% (95% in 2014) of Drummond Island fish were detected on GLATOS receivers after 01 October 2012 (the start date for this comparative study). The number of tagged Drummond Island fish detected during spawning (October and November) each year decreased from 176 in 2012 to 119 fish in 2014. Three Drummond Island fish that were detected nearly continuously throughout the study on receivers in the False Detour Channel (FDT; n = 2) or Detour Channel (DTR; n = 1) likely died within detection range of those receivers. Twenty-four Drummond Island fish were caught and reported by commercial or recreational fisheries between 01 October 2012 and 31 May 2015. The number of Thunder Bay tags detected during spawning also decreased, from 40 fish in 2012 (tagging year) to 18 fish in 2014. Eleven of the 40 fish (27.5%) tagged in October 2012 were not detected on any receiver in the GLATOS network after 31 December 2012. All but one of these 11 fish left Thunder Bay (i.e., they were detected at the line of receivers at the entrance to the bay) and half of the remaining ten fish migrated south at least 70 km before disappearing from the detection record. The ten Thunder Bay fish that left Thunder Bay but were not detected again after 31 December 2012 either died sometime during the first winter, or remained outside the range of any GLATOS receivers. Eleven additional Thunder Bay fish ceased being detected on GLATOS receivers prior to the end of the study period, including six that were caught in commercial or recreational fisheries.

Fish from both populations were detected most often during the spawning period, when they aggregated on spawning reefs within the positional telemetry receiver arrays (Fig. 3). However, during 2013 and 2014, when detection data were available during both spawning and non-spawning periods, at least 92% (92% in 2013 and 95% in 2014) of Drummond Island fish and 91% (96% in 2013 and 91% in 2014) of Thunder Bay fish detected each year were detected before or after the spawning period that same calendar year. Monthly detection rates outside the spawning period ranged from 7% to 72% of individuals detected each year for Drummond Island fish and from 30% to 80% of individuals detected each year for Thunder Bay fish (Fig. 3).

The spatial distribution of detections for each population was consistent in all three years of the study, with little spatial overlap between Drummond Island and Thunder Bay fish. Detections of Drummond Island fish were generally limited to receiver lines in the north section of the lake (Figs. 4 and 5), defined by an imaginary line between the PRS and BTM receiver arrays (Fig. 1), with only six fish (3.3%) over the duration of the study detected south of this line. Only 11% (20 of 176) of Drummond Island fish detected in 2012 and 10% (15 of 156) of Drummond Island fish detected in 2013 were detected on receivers outside of DI, DTR, and FDT (the three sites around Drummond Island; Fig. 1). That proportion increased to 67% (84 of 125) in 2014 after the addition of the Mississagi Strait (MIS; Fig. 1: ~30 km from the DI site) and Georgian Bay (BTM; Fig. 1: ~150 km from the DI site) receiver lines on either side of Manitoulin Island, and was 48% (30 of 63) in 2015, a partial year (01 January 2015 to 31 May 2015). Approximately 41% of Drummond Island fish detected in a given year (70 of 156 fish in 2013, 46 of 125 fish in 2014, and 32 of 77 fish in 2015) were detected in the two channels (DTR & FDT; Fig. 1) immediately adjacent to Drummond Island from May through July, which suggests that those fish may have remained close to Drummond Island during late spring and summer. Nevertheless, between 79% and 92% of all Drummond Island fish detected each year between 2013 and 2015 (123 of 156 fish in 2013, 115 of 125 fish in 2014, and 70 of 77 fish between 01 January and 31 May 2015) were
detected on receivers outside the Drummond Island Refuge, which spans only the south shore of the island (Fig. 1). Post-spawning dispersal from the DI spawning site was rapid, with >50% of first detections on receivers outside the Drummond Island Refuge (closest receiver outside the refuge was ~10 km from the DI site) occurring during the first week after a fish was last detected at the DI spawning site (Fig. 6). None of the Drummond Island fish were detected on Thunder Bay receivers during the study (Figs. 4 and 5).

Receivers to the east of Drummond Island detected more Drummond Island fish than receivers to the west of the island (Figs. 4 and 5), which indicates that a large portion of Drummond Island fish moved east into Canadian waters along the northern shore of the main basin and in the North Channel. During 2014 and part of 2015, when receivers were present in the Mississaga Strait (MIS) and at the entrance of Georgian Bay (BTM), 57% (2014) and 33% (partial-year 2015) of Drummond Island fish were detected on MIS receivers, and 5.8% (2014) and 4.7% (2015) were detected on BTM receivers (Fig. 5). The high detection rates in the passages connecting the North Channel to the northern main basin of Lake Huron suggested that fish moved between the main basin and North Channel. Moreover, one-third (14 of 42 fish) of Drummond Island fish caught and reported from commercial or recreational fisheries (based on reward-based transmitter recoveries) since the start of the Drummond Island study in 2010 came from the North Channel.

In contrast to Drummond Island fish, which were largely confined to the north end of Lake Huron, detections of Thunder Bay lake trout were limited primarily to the western side of the central main basin of Lake Huron, on receivers located between Thunder Bay and Saginaw Bay (Figs. 4 and 5). Throughout the study, only four Thunder Bay fish (10%) were detected north of the PRS receiver line (i.e., northern Lake Huron), and only three fish (7.5%) were detected south of the Saginaw Bay receiver lines (i.e., southern Lake Huron). Like Drummond Island fish, spatial detection patterns of Thunder Bay fish were consistent among years between the spawning and non-spawning periods (Figs. 4 and 5). While Drummond Island fish tended to move east from their spawning location, most Thunder Bay fish dispersed south soon after spawning, towards Saginaw Bay. The abundance of receiver lines along the southern shore of Lake Huron provided a better opportunity to explore post-spawning movements of Thunder Bay trout than was available for Drummond Island trout. Similar to Drummond Island fish, Thunder Bay fish dispersed rapidly from the Thunder Bay spawning site immediately after the spawning season. Among fish that were detected in multiple years, 78% (18 of 23) displayed highly consistent post-spawning detection patterns (i.e., dispersal direction and distance) among years (Fig. 7). Of the 29 fish known to have survived the first winter, 12 fish (41%) appeared to overwinter relatively close to Thunder Bay and 16 fish (56%) overwintered at least 70 km south of the Thunder Bay spawning site. Six of 29 fish (21%) consistently overwintered within Saginaw Bay (Fig. 7). ~100 km from the TB spawning site. One fish (3%) moved north after spawning in 2012 and overwintered at the north end of the lake near the Mackinac Straits (~170 km from the Thunder Bay spawning site). Most detections during spring and summer were on receiver lines between Saginaw Bay and Thunder Bay. No Thunder Bay fish were detected on receivers along the Canadian shore of Lake Huron.

Most lake trout returned annually to their respective tagging site during spawning season. The annual probability that a confirmed surviving Thunder Bay fish returned to the TB spawning site during spawning was 0.91. Ninety percent (26 of 29) of fish tagged in Thunder Bay returned to the TB site during each spawning season they were confirmed alive. Only three of 29 Thunder Bay fish (10%) that were detected after the first winter post-tagging did not return to the TB spawning site during each spawning season in which they were

![Graph](image-url)
confirmed to be alive. Two of the three fish either skipped spawning or spawned at another site in 2013, but returned to the TB site in 2014 during the spawning season. The third fish (a hatchery-reared male) abandoned the TB site after tagging and was detected on the DI array 18 d later (10 November to 13 November), when spawning was believed to have been completed (Fig. 7: tag 29517). The fish remained in the vicinity of Drummond Island (i.e., detected on DRM, DTR, or FDT; Fig. 1) for only 7 d before swimming back south past Thunder Bay to
The fish overwintered in Saginaw Bay during both subsequent years of the study, but was never again detected at either spawning site (Fig. 7: tag 29517).

**Discussion**

Drummond Island and Thunder Bay lake trout populations showed high fidelity to their respective spawning sites and low overlap between
their apparent ranges during non-spawning months (December through September) over the multi-year study. Consistent with our prediction that the two populations would segregate spatially during spawning, no co-mingling was evident between the two groups of tagged lake trout during the spawning season. Among Thunder Bay fish that we could confirm were still alive, the annual probability of returning to the TB spawning site was 0.91, and was comparable to mortality-independent annual site fidelity estimates of 0.78–0.94 previously presented for the same group of tagged Drummond Island fish that were used in this study (Binder et al., 2016). However, the value of 0.91 for Thunder Bay fish should be interpreted as a maximum estimate of annual spawning site fidelity because we cannot confirm that fish not detected on any of the GLATOS receivers in Lake Huron after the first year, which we assumed died, did not spawn elsewhere, and thus avoided detection. Among the three Thunder Bay fish that did not return to the TB spawning site every year they were known to be alive, two fish returned to the TB site in 2014, which suggested they either spawned elsewhere or skipped spawning (Sitar et al., 2014) in 2013. One hatchery male Thunder Bay fish did swim north to Drummond Island within days of being tagged in 2012; however, given that the fish was tagged on the TB spawning grounds during the peak of spawning, and it arrived late in the spawning season at the DI site, it is unlikely that the fish intended to spawn with the Drummond Island population that year. While we did not detect any evidence of interbreeding between the two populations, we acknowledge that our sample sizes were small relative to the total number of fish in each of the spawning populations; therefore, interbreeding could occur at levels that are below the resolution of our data.

Dispersal distances of these two Lake Huron lake trout populations outside the spawning season were consistent with post-spawning dispersal distances noted in lakes Michigan and Superior and supported our prediction that most fish would not be detected on receivers farther than 100 km from their respective spawning site. For example, 90% of recaptured fish tagged in the Apostle Islands area of Lake Superior were caught within 80 km of the tagging site (only 9.3% were captured farther than 160 km from the site; Eschmeyer et al., 1953). Similarly, 90% of adult lake trout tagged during spawning in the Clay Banks area of northwestern Lake Michigan were recaptured <69 km from the tagging location (Schmalz et al., 2002), and 90% of coded-wire tagged yearling lake trout stocked into Lake Michigan were caught as spawning adults within 109 km of the stocking site (Bronte et al., 2007). Moreover, consistent with our prediction that the two populations would overlap little during the non-spawning season, the two populations appeared to remain spatially segregated throughout the year. We cannot confirm that the two populations did not mix in the middle of Lake Huron where there was no receiver coverage; however, the pattern of detections on receivers suggests that this is unlikely. Both populations in our study displayed directional bias in their post-spawning dispersal, with Drummond Island fish dispersing primarily eastward and into the North Channel, and Thunder Bay fish dispersing primarily southward towards Saginaw Bay. If unobserved mixing between these two populations did occur, it would most likely have occurred during winter months when reduced detection rates suggested that both populations moved into deep water. Similarly, we predict based on the pattern of detections that, if unobserved mixing did occur, it likely would have occurred in deepwater areas between Thunder Bay and Georgian Bay.

Detection records for Drummond Island lake trout outside the spawning period were sometimes sparse, due largely to their propensity to move eastward into Canadian waters where receiver coverage was limited. Nonetheless, results from Thunder Bay fish suggested that lake
trout dispersed quickly from the spawning site to overwinter habitat soon after spawning, and that most individuals may consistently choose the same overwinter locations year-after-year (see Fig. 7 for examples). Martin and Oliver (1980) described lake trout adults as nomadic, and concluded that most of their movements appeared to occur in response to variables such as spawning, feeding, and changes in environmental variables. Swanson (1973) suggested that lake trout post-spawning migration patterns might be related to current patterns in the lake, with lake trout tending to disperse with prevailing currents (i.e., downcurrent). Circulation patterns in Lake Huron show a prevailing southward current outside Thunder Bay (Beletsky et al., 1999; Saylor and Miller, 1979) and, consistent with Swanson (1973), suggest a downcurrent trend for Thunder Bay fish. Dispersal patterns of Drummond Island fish are difficult to compare to prevailing currents because modeled circulation patterns in the northern part of Lake Huron are complex, due in part to interactions with the St. Marys River; and direct circulation observations, particularly in the area near Drummond Island, are unavailable (Beletsky et al., 1999). Nonetheless, Lake Superior empties into Lake Huron via the North Channel, so Drummond Island fish that moved from the main basin into the North Channel probably swam against the current (i.e., upcurrent), rather than downcurrent.

Another possibility is that lake trout migrate in response to thermal gradients in the lake. Behavioral thermoregulation has been noted in numerous fishes, particularly in systems where temperatures exceed the maximum temperature tolerance for a species (Baird and Krueger, 2003; Matern et al., 2000; Moss, 1985; Snucins and Gunn, 1995). However, given that post-spawning dispersal of lake trout occurs during a period when the lake is well-mixed, cool, and largely isothermal and that, during summer months, the fish would have access to most temperatures simply by changing their vertical swimming depth, it seems unlikely that temperature would be the primary driver of horizontal movements in the lake in November. This assertion is supported by previous research showing that lake trout in northern Lake Huron showed a significant reduction in temperatures occupied between 1998 and 2001 and 2002–2005 (Bergstedt et al., 2012). The change in thermal occupancy could not be explained by changes in the temperature of the lake itself, but did coincide with substantial changes in the food web of Lake Huron (Riley et al., 2010). This suggests that the trout may have altered their behavior in response to changes in prey abundance and distribution (Bergstedt et al., 2012).

Given the rapid, long-distance migrations observed, particularly for Thunder Bay fish, we similarly hypothesize that post-spawning dispersal from spawning sites most likely reflects a need to replenish energy resources expended during spawning. Thus, post-spawning migration patterns may reflect the distribution of prey species in the lake, a hypothesis in need of testing. Prey distribution could explain the observation that many Drummond Island lake trout moved into the North Channel during the non-spawning season. The North Channel contains significantly higher pelagic prey fish densities than either Georgian Bay or the main basin of Lake Huron (O’Brien et al., 2015) and could be an important foraging area for Drummond Island lake trout. Detectability of both populations was lowest during winter, which suggests that the fish became less active, or moved into deep water where receiver coverage was absent. Indeed, lake trout have been shown to occupy deeper water during winter than during spring or fall in Lake Huron, based on archival depth-temperature tags (Bergstedt et al., 2012). Nonetheless, the high degree of individual variation and annual repeatability of individual post-spawning migratory behavior suggests that
post-spawning migratory patterns are likely based on previous experience. Thus, individual lake trout likely have the flexibility to alter migratory patterns to compensate for changing ecological and environmental conditions in the lake.

Management implications

While the Drummond Island Refuge provides protection to the Drummond Island population during the spawning period, most Drummond Island fish were detected on receivers outside the refuge between spawning periods, where they are unprotected from fisheries during much of the year. Spill-over from the refuge is necessary if the purpose of the refuge is not only to protect fish during the spawning season but to also to increase overall fishery yield and buffer adjacent populations against overfishing (Akins et al., 2015; Crowder et al., 2000; West et al., 2009). However, the migration rate (i.e., % that leave the refuge) must be balanced with the exploitation rate outside the refuge (i.e., a high migration rate can be supported if exploitation rates are low outside the refuge). A recent investigation of the effectiveness of the Gull Island Shoal Refuge in western Lake Superior concluded that the Gull Island Shoal Refuge was of adequate size to protect the stock, in light of a maximum observed migration rate of 11% (Akins et al., 2015). The Drummond Island Refuge (380 km²; Stanley et al., 1987) is similar in size to the Gull Island Shoal Refuge (336 km²; Akins et al., 2015), but our results indicated that fish migrated from the Drummond Island Refuge at a much higher rate than occurred at Gull Island Shoal. In fact, the high proportion of fish detected >30 km from Drummond Island in 2014 and 2015 (after the MIS and BTM lines were deployed) suggests that at least 60% of Drummond Island fish were vulnerable to the fishery for several months each year. Nonetheless, a comprehensive analysis that incorporates both movement ecology and population dynamics (e.g., Akins et al., 2015; Johnson et al., 2015a) is necessary before any conclusions can be made about the effectiveness of the Drummond Island Refuge and what contribution, if any, the refuge has made to improving the status of lake trout in Lake Huron.

Spawning groups at Drummond Island and Thunder Bay acted as source populations for fisheries outside the management units that contained these two spawning locations. Lake Huron is divided into 18 statistical districts (6 in Michigan waters and 12 in Ontario waters; Fig. 1) for regulating lake trout fisheries. On the Ontario side, each statistical district is treated as a management zone, but on the US side, the six statistical districts have been reduced to three management zones; MH-1, MH-2, and a combination of MH-3, MH-4, MH-5, and MH-6. Thunder Bay fish that spawned in MH-2 contributed to populations in MH-3 and MH-4, with 80% of Thunder Bay fish detected on receivers in MH-3, and 35% of Thunder Bay fish detected on receivers in MH-4. Similarly, 72% of Drummond Island fish that spawned in MH-1 were detected on receivers in Canadian waters of Lake Huron, where they were subjected to Ontario fishing regulations. Our finding that lake trout in these two study populations displayed frequent and repeatable non-random transboundary movements suggests that lake trout movement in Lake Huron may benefit from additional population-specific studies on movement ecology and population mixing, which could lead to more biologically-relevant management zone boundaries. Moreover, the observation that a large portion of the Drummond Island population is subjected to Ontario fisheries and their fishing regulations emphasizes the importance of the existing international cooperation in managing the lake trout fishery. State, tribal, and provincial management agencies on Lake Huron have long been aware of the need to quantify the exchange of lake trout among statistical districts to refine management of harvest on recovering lake trout populations (Aderlein et al., 2007). Since 2010, as part of a larger interagency, coordinated program (Bronze et al., 2012), all lake trout stocked into U.S. waters of Lake Huron (and Lake Michigan) have received coded-wire tags and recoveries of these fish in future years will inform on source-sink population dynamics among zones.

Conclusions

Seasonal migratory movements and dispersal distances were similar between the two lake trout populations. However, our analysis suggests that the two populations most likely remained spatially segregated throughout the year. Over time, spatial segregation and differential habitat use among recovering lake trout populations, which due to the near extirpation of native Lake Huron stocks trace to hatchery introductions, could lead to local phenotypic adaptations and an accumulation of adaptations within discrete spawning populations (Conover et al., 2006). Unfortunately, due to the serendipitous nature of this analysis (i.e., the groups were not originally tagged to test for differences in movement patterns), the spawning locations of the two populations compared in this study were located far apart relative to the scale of movements shown by the fish. Therefore, an important question remains as to whether seasonal movement patterns exhibited by lake trout are truly population-specific, or if they occur on a more regional scale, with adjacent populations displaying similar migratory behavior and habitat use. Future studies could address this question by comparing the movement patterns of more geographically close populations than was done in the present study. This approach would also contribute to an improved understanding of population-level movement patterns, which could be used to identify important patches of critical habitat in the lake, and may help further inform the delineation of management zones and size required for sanctuary areas to ensure that they are biologically-relevant.

Analysis of acoustic telemetry detections shared through the GLATOS network provided valuable information about the ecology of two recovering lake trout populations in Lake Huron. Two important challenges we faced in our analyses are that likely to be common in studies that use shared data from large acoustic telemetry networks included: 1) sub-optimal receiver placement to address the question of interest, owing primarily to the fact that individual receivers in the network are typically deployed to address focused species- or population-specific study objectives; and 2) seasonal and annual variability in receiver coverage. Nonetheless, even with sub-optimal receiver coverage, we have shown that long-term continuous sampling by receivers in telemetry networks can reveal important movement information that would not be practical within the resources available to conduct a single research project. The present study, which was almost entirely dependent on detections collected and shared by other researchers through the GLATOS database, is an excellent example of how participation in telemetry networks can provide researchers with opportunities to address important management questions that are beyond the scope of their original projects. At a minimum, observations based on detections shared through telemetry networks have the potential to serve as a foundation on which to pose novel research questions and develop testable hypotheses.

Acknowledgements

Thanks to E. Larson, H. Thompson, C. Wright, T. Buchinger, S. Fisset, L. Lesmeister, D. Operhall, B. Lamoreux, S. Farha, Z. Wickert, J. Osza, Z. Holmes, J. Hinderer, R. Darmon, K. Smith, and P. Wigren for their assistance with the acoustic telemetry field work. Lake trout for the Drummond Island telemetry were provided by P. Barbeaux, and the Chippewa Ottawa Resource Authority (many thanks to R. Reinig, A. Handziak, and D. Pine). Lake trout for the Thunder Bay telemetry were provided by Michigan DNR, and we thank J. Diemond, B. Wellenkamp, and K. Glomski among others for essential field assistance. We also thank researchers that contributed data to the GLATOS database, and N. Nate, who facilitated the transfer of detection data to us from the GLATOS database. M. Hansen and C. VanderGoot provided helpful comments on an early draft of the manuscript, and Stuart Ludsin and two anonymous reviewers provided helpful comments during the peer-review process. This work was funded by the Great Lakes
Fishery Commission by way of Great Lakes Restoration Initiative appropriations (GL-00E23010-3). This paper is contribution 25 of the Great Lakes Acoustic Telemetry Observation System (GLATOS). The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References


