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Lake Trout Spawning Site Use In Lake Champlain & The Development Of The Binomial Rolling Residence Test

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LAKE TROUT SPAWNING SITE USE IN LAKE CHAMPLAIN & THE
DEVELOPMENT OF THE BINOMIAL ROLLING RESIDENCE TEST

A Thesis Presented

by

Victoria Pinheiro

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Master of Science
Specializing in Natural Resources

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ABSTRACT

Lake trout populations were extirpated from the lower four Great Lakes by 1960 and from Lake Champlain by 1900. The decline of lake trout populations fueled a wave of restoration-based research that spanned the Great Lakes and filled in many of the gaps in our knowledge of lake trout behavior and ecology. However, remarkably little is known about lake trout spawning behavior, even less about sex-specific differences in spawning site use. Lake trout use specific spawning sites, and may return to the same site year after year. More males are caught on spawning sites than females and are present at spawning sites earlier in the spawning season. The focus of this project is to describe the spawning movements of male and female lake trout within and among spawning seasons and spawning sites. I used acoustic telemetry in Lake Champlain to look at specific questions of spawning site fidelity and whether or not there were differences in male and female movements. I hypothesized that males show site fidelity and remain at a preferred site during the spawning season, whereas females 'sample' multiple spawning reefs to maximize their reproductive success. I established an acoustic telemetry array of ten acoustic receivers placed over eight spawning sites and implanted acoustic transmitters (tags) in 44 male and 48 female lake trout over two years. During two spawning seasons, males spent more time on spawning sites than females. Both male and female lake trout that were active on monitored sites during the spawning season selected a single preferred site. There was no difference in the number of sites visited by males and females. Of the lake trout detected during both spawning seasons, most returned to their capture site in the subsequent spawning season, showing evidence of site fidelity. I also developed a binomial rolling residence test (BRR test) to improve the current method of assessing the duration of a fish’s residence at a single receiver. I measured daily detection probabilities (DP) at a given distance from a receiver site. The BRR test evaluates a tag’s residence every minute by moving a one-hour time window centered on time t across the duration of the data. The daily DPs are incorporated into a binomial test of the null hypothesis that a fish is not within x meters of the receiver at time t. I performed a 48-hour stationary residence test using two onsite tags and two offsite tags and compared the performance of the BRR test to three residence assessment methods found in the literature. The results showed that the BRR test performs better than all of the time-threshold residency evaluations in our 48-hour stationary residence test. We suggest that this method has the potential to advance the field of telemetry by improving the interpretation of telemetry data.
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CHAPTER 1: A LITERATURE REVIEW OF LAKE TROUT SPAWNING BEHAVIOR AND RESIDENCE ASSESSMENTS IN ACOUSTIC TELEMETRY

1.1 History of lake trout in the Great Lakes and Lake Champlain

The lake trout (Salvelinus namaycush) is a freshwater salmonid found throughout the northern portions of the continental US and Canada, where it is one of the more valuable species for commercial and sport fishing (Martin and Olver 1980, Marsden and Langdon 2012). The populations of this cold-water predator were decimated in the Laurentian Great Lakes by invasive sea lamprey (Petromyzon marinus), over-exploitation and poor water quality (i.e., cultural eutrophication, PCB contamination) (Martin and Olver 1980, Berlin et al. 1981, Edsall and Mac 1982, Eshenroder 1992, Noakes and Curry 1995). This decline stimulated restoration-based research that has spanned the Great Lakes and filled in many of the gaps in our knowledge of lake trout behavior and ecology (Elrod et al. 1995, Eschmeyer 1995, Eshenroder et al. 1995, Hansen et al. 1995, Holey et al. 1995, Bronte et al. 2007).

The population of lake trout in Lake Champlain was extirpated by 1900 but there are insufficient data to positively identify the cause of the decline. A relatively small historic commercial lake trout fishery in Lake Champlain was conducted in fall with shoreline seines in the 1800s; it is unlikely that this level of effort could have extirpated the population by 1900. Sea lamprey predation may have contributed to the decline, but there is no historic evidence to support or refute this possibility. Restoration efforts began with the stocking of 68,000 to 90,000 fin-clipped yearlings annually since 1972 (Marsden et al. 2010). Although adult survival is estimated at approximately 50% and fry production is high, an average of only 4% of fish seen in assessments each year since
1982 are unclipped (Chipman 2012). Four percent falls below the accepted cut-off for
fin-clipping error, suggesting that no recruitment of wild fry to the adult population is
occurring (Chipman 2012). Initial research on the causes of poor lake trout recruitment
focused on early life history—determining locations of good spawning habitat, whether
spawning occurred there, and the degree to which eggs were incubating and producing
fry. Spawning substrate has been well described and fry have been collected at multiple
sites lake-wide, but little evidence of recruitment has been found (Ellrott and Marsden

Remarkably little is known about lake trout movements on and between spawning
sites. The details of these movements are of particular interest to researchers because lake
tROUT show many behaviors different from those of most members of the salmonid family.
The study of individual movements on and between spawning sites is in its infancy in the
Great Lakes and is completely new to Lake Champlain. Current lake trout research is
focused on understanding factors that affect their reproductive success, including mate
choice, site choice and courtship behavior (Esteve et al. 2008, Muir et al. 2012, Binder et
al. 2014, Riley et al. 2014). In this study, I have focused on expanding what we know
about lake trout spawning movements on and between sites in a lake-wide study not
feasible in larger systems such as the Great Lakes, with emphasis on differences between
male and female use of spawning sites. Here I review the evolutionary origins of
reproductive strategy and behavior and their application to lake trout spawning behavior.
1.2 Evolutionary context

Natural selection optimizes efficiency: maximizing resources gained while conserving energy and time expended (Darwin 1929, Pianka 1972). This formula applies to the individual organism, where efficient consumption leads to maximum fitness. In addition, this concept applies to the population, where efficient reproductive strategy leads to increased reproductive fitness. The latter application has bearing on the success of a species as a whole; different energetic trade-offs result in a variety of reproductive strategies (Gadgil and Solbrig 1972, Smith and Fretwell 1974, Nussbaum and Schultz 1989, Winemiller and Rose 1992). Trade-offs in the number and size of offspring and the level of parental care provided generally form the starting point for the development of further reproductive behavior models (Smith and Fretwell 1974, Nussbaum and Schultz 1989). A species’ place on the r-K selection spectrum greatly influences their mating strategies (Winemiller and Rose 1992).

Fish, in particular, show a wide array of reproductive strategies. Winemiller defined three broad categories building on the r-K selection framework: opportunistic strategists (r-selected), periodic strategists (r-selected) and equilibrium strategists (K-selected) (Winemiller 1989, Winemiller 1992, Winemiller and Rose 1992). Opportunistic strategists are fast-maturing, short-lived fish that are highly fecund and spawn frequently in environments with unpredictable variation. Periodic strategists are long-lived, late-maturing, highly fecund and spawn periodically in environments with predictable variation. Both periodic and opportunistic strategists have low offspring survivorship. Lake trout fall into the final category: equilibrium strategists. Equilibrium strategists have medium to long generation times, are slow maturing, of medium size, produce smaller

Another way to categorize breeding strategies is by the three broad groups of post-spawning parental care: bearers, including species that gestate and produce live young, guarders, those who lay eggs and provide some measure of parental care, and lastly, non-guarders, who do not protect their eggs or young once spawning is complete (Moyle and Cech 2004). Lake trout fall into the category of non-guarders; they provide no parental care for their offspring after depositing their eggs in clean rocky substrate where they are protected within the interstitial spaces (Gunn 1995, Esteve et al. 2008, Muir et al. 2012, Binder et al. 2014). In many species that do not provide parental care (especially no male parental care), the mating strategy tends to be dependent on the distribution of resources, which will influence the distribution of females (Emlen and Oring 1977). In most species, females produce large, nutrient-rich gametes in limited numbers, while males produce large numbers of small, easily replenished gametes. This difference in energetic cost and availability of sperm and eggs is one of the biggest influences on mating system formation. A female must be selective about her partners to maximize the quality of her offspring and must be selective about access to resources to improve their chances of survival, ensuring that her disproportionate gamete investment is not wasted. Males focus instead on making reproductive investments with the greatest number of mates, because their gametes are more readily available than those of females (Keenleyside 1979, Krebs and Davies 1993, Pitcher 1993). According to this model, if spawning substrate is evenly distributed, females will distribute themselves evenly to gain access to them and the males will follow suit (Krebs and Davies 1993). If resources
are patchy, however, the male’s best strategy is to aggregate on these resource patches in anticipation of the arrival of females (Krebs and Davies 1993). Aggregating over a limited resource increases males’ likelihood of encountering several mates and therefore the likelihood of passing on their genetic material. For lake trout, suitable spawning substrate is the limiting resource that brings males and females together. Like many non-guarding benthic spawners, male lake trout aggregate over spawning sites to await the arrival of females (Muir et al. 2012).

The formation of groups of males to attract females to the spawning sites has been compared to lek behavior (Noakes and Curry 1995). In general terms, lek mating systems involve a large aggregation of males. Males usually fight to defend small territories on which they perform elaborate displays to attract mates. Females observe these events to select the most successful male, which results in a few attractive/dominant males mating with many females (Krebs and Davies 1993). The specifics of lekking behavior are often variable. Four models have been proposed to explain lek behavior. The first is the “hot-spot” model, which states that males select an area frequented by females, often at the center of overlapping female home ranges. In the “female preference” model, females prefer large groups of males because the cost of optimal mate selection is lowered (all the males are lined up for her to choose) or the chance of predation is lowered (safety in numbers). In the “hotshot” model, attractive males entice females to move into the lekking area. In addition, they inadvertently attract other males who hope to benefit from the more appealing male’s attractiveness, leading to a large aggregation. The last model, known as the “black hole” hypothesis, accounts for situations where females show no preference for a particular type of male, or lek size. Females of species that exhibit black-
hole lekking are highly mobile, and mate in whichever lek they encounter (Jiguet and Bretagnolle 2006). The black-hole model is an appealing explanation for the skewed sex ratios often seen on lake trout spawning sites. Female lake trout may seem less abundant because they move widely throughout the system, potentially traveling from site to site. The cornerstone of a lek in its modern definition, however, is that males are not aggregating over a resource; the aggregation itself, and not the resources it is in proximity to, is the factor that is attractive to females (Krebs and Davies 1993). Because lake trout aggregations form over favorable spawning sites, their designation as leks will depend on the definition of lekking that one adopts.

Aggregations over favorable spawning sites often coincide with cyclic spawning migrations. Well-defined annual spawning cycles are common in the majority of fish species in northern latitudes and usually are timed to maximize food availability when larvae hatch (Cushing 1975, Vila-Gispert et al. 2002). This type of “planning” is not necessary in tropical and subtropical areas that experience little variation in climate or production, so spawning often occurs throughout the year (Bye 1984). In regions that experience pronounced seasonal climatic variation, a set spawning period on the same site each year ensures that the larvae coincide in time and space with peak primary production (Cushing 1975). In these settings, site-specific reproductive strategies will be selected for, encouraging the evolution of homing behavior (Leggett and Carscadden 1978). All spawning migrations should end in aggregations over specific spawning sites at predictable times of the year (Leggett and Carscadden 1978, Domeier and Colin 1997).
1.3 Lake trout spawning behavior

Lake trout range throughout northern latitudes, and therefore spawn seasonally. Unlike most salmonids, lake trout spawn in lakes instead of streams. They aggregate in fall over spawning substrates with deep interstitial spaces where eggs and fry will be protected. River-spawning salmonids aggregate in male dominated groups where females establish one or several nests composed of small rocks and pebbles (redds). They have simple courtship rituals, deposit a relatively small clutch of large eggs into substrate interstices and subsequently abandon their offspring (Winemiller 1989, Winemiller and Rose 1992, Moyle and Cech 2004). Males compete with each other for access to females and their nesting territories while females fight with each other and with males to protect their redds (Gunn 1995, Noakes and Curry 1995, Esteve et al. 2008, Muir et al. 2012, Binder et al. 2014). In contrast, lake trout show little apparent agonistic behavior, exhibit no nest-building activity, and spawn exclusively at night or in other low-light conditions (Gunn 1995, Esteve et al. 2008, Muir et al. 2012, Binder et al. 2014).

Stream-spawning salmonids show natal homing behavior, and have a single spawning site/event each year (whether iteroparous or semelparous). The lake-spawning behavior of lake trout is likely a heritage from a population of early salmonids that either colonized or was isolated in a lake system (Esteve et al. 2008). This progenitor population would have spawned on rocky shorelines that had been cleared of silt by wind, wave action and activities of the spawning aggregation (Esteve et al. 2008). Lake trout may have colonized some lake systems due to the presence of glacially-derived bedforms composed of rocky sediment that were cleaned by lake currents (Riley et al. 2014). These tall structures are composed of good spawning substrate and jut up into the
path of prevailing currents, providing well-oxygenated water to eggs incubating in the interstices.

Lake trout spawning activity is triggered by a declining photo-period (Royce 1951, McCrimmon 1958), a sharp autumnal decline in temperature (McCrimmon 1958, Martin and Olver 1980), and the onset of heavy onshore winds (Martin 1957, Deroche 1969), which may help to clear the spawning substrate of silt. The presence of clean substrate may have relaxed selection for nest-building or substrate-clearing females and redirected it towards bet-hedging activities such as traveling extensively to multiple spawning sites (Esteve et al. 2008). The absence of female-female agonistic behavior likely resulted from the lack of nest territories to defend. Male lake trout also show few signs of aggression on spawning sites, possibly because paternity certainty is tightly linked to the proximity of a male to a female at the moment of egg deposition. During the spawning act, several male lake trout sink to the substrate with a female to fertilize her eggs (Esteve et al. 2008, Muir et al. 2012, Binder et al. 2014). Because the likelihood of fertilization is directly correlated with the distance from sperm to egg, abstaining from jostling other sinking males and focusing effort on staying close to the sinking female increases a male’s likelihood of paternity (Hoysak 2001, Liley et al. 2002). However, before lake trout go into the spawning sequence of hover, travel, sink and release, some competition may take place between males for approaching females. Sightings of unexplained splashing, porpoising and breaching behavior could be evidence of aggressive behavior or, alternatively, may merely be courtship displays, especially in Great Bear Lake where the spawning process seems to be more visually driven (Merriman 1935, Esteve et al. 2008, Muir et al. 2012, Binder et al. 2014). Breaching may
also be a method by which females initiate egg-skein rupture, releasing the eggs into the coelomic cavity in preparation for spawning (J.E.M. personal communication). Identifying the sex or sexes responsible for these behaviors is the first step in understanding the evolutionary context of the behaviors.

Relative to other teleosts, lake trout are K-selected, meaning that males should mate with as many females as possible and females should be selective about their mates to increase the number or quality of surviving offspring. The limiting resource responsible for lake trout fry survival is spawning substrate, which occurs in patches (Eshenroder et al. 1995, Muir et al. 2012). Because lake trout do not have to endure an arduous upstream migration, they have the option of spawning in more than one area. A telemetry study in a small lake in the Northwest Territories showed that females traveled to and likely spawned at multiple spawning patches within the lake (Callaghan et al. 2015b). These findings suggest that females are likely to hedge their bets and distribute their eggs amongst several spawning sites to increase egg distribution (increasing survival). An additional benefit would be encountering multiple aggregations of potential mates (increasing offspring quality) (Fitzsimons and Marsden 2014, Callaghan et al. 2015a). Males can maximize their encounters with females by staying at a single, high-quality site and waiting for females to arrive (Krebs and Davies 1993); time spent migrating between sites is lost opportunity to encounter females. In fact, males tend to be captured on spawning sites earlier in the season and in larger numbers than females throughout the season, consistent with these strategies (Martin and Olver 1980, Bronte et al. 2007, Muir et al. 2012). Once males have found and chosen a preferred spawning site that is visited by females, it is in their best interest to keep returning annually to the same
site (Leggett and Carscadden 1978), i.e., we expect them to show spawning site fidelity. Several mark recapture studies have revealed evidence of lake trout spawning site fidelity in other systems; between 40% and 75% of spawning fish were recaptured in the same location the next year (Eschmeyer 1955, Loftus 1958, Rahrer 1968, Schmalz and Hansen 2002, Bronte et al. 2007). However, these studies did not distinguish fidelity between the two sexes.

The purpose of this study is to observe and describe spawning movements of male and female lake trout among spawning sites. We hypothesized that the females would travel to multiple spawning sites and spend less time at each one (Martin and Olver 1980, Bronte et al. 2007, Muir et al. 2012). We hypothesized that fidelity will be shown by males, but not by females, who may split their time amongst several sites.

1.4 Residence assessment using acoustic telemetry

To study large-scale movements, animals must be tracked. We accomplished this in our system using acoustic telemetry. Acoustic telemetry is a relatively new and valuable tool for observing movements of aquatic organisms. Animals are fitted with acoustic transmitters and are monitored either actively, by manually tracking an organism throughout its environment, or passively with strategically placed receivers that record the signals of tagged individuals. Acoustic telemetry gained traction in the fisheries research community in the 1970s when manual tracking of valuable food and sport fish such as Atlantic cod (Gadus morhua), Atlantic sailfish (Istiophorus albicans), Bluefin (Thunnus thynnus) and skipjack tuna (Katsuwonus pelamis) became possible (Yuen 1970, Carey and Lawson 1973, Jolley and Irby 1979). Researchers engineered their own acoustic transmitters and receivers, often publishing equipment designs along with
behavioral results (Mitson and Storeton-West 1971, Carey and Lawson 1973, Kanwisher et al. 1974). Passive telemetry became more popular in the 1980s, allowing researchers to continuously monitor an area without being present (Ralston and Horn 1986, Solomon and Potter 1988, Heupel et al. 2006, Kessel et al. 2014). Since then the technology has expanded rapidly; transmitters have become smaller (expanding the range of species that can be studied), smarter (recording and transmitting data on physiochemical parameters, velocity, depth, feeding habits, predation of a tagged fish, and more), and longer-lived with battery life in larger tags exceeding ten years (Heupel and Webber 2012, Hussey et al. 2015).

There are two major categories of acoustic telemetry research: those using positioning systems to track fine-scale movement and those used for detecting the presence or absence of animals at a particular site (Heupel and Webber 2012). For fine-scale positioning and movement patterns, researchers use regularly spaced receivers deployed at close intervals to triangulate an exact geographic position for each detection (Heupel et al. 2006, Heupel and Webber 2012). In studies that do not require precise animal tracks, a less regular grid with lower receiver density can be used to calculate short-term centers of activity. Weighted mean number of detections at several receivers over set time periods are used to calculate the approximate location of fish during those time periods (Simpfendorfer et al. 2002).

Presence/absence studies using acoustic telemetry can either use gate systems or single receivers. Gate systems employ a string of receivers with overlapping detection ranges to act as a curtain to detect the transmissions of passing animals (Welch et al. 2002, Stark et al. 2005). Gates can be used to monitor travel along a particular path or
migration route (Welch et al. 2002, Finstad et al. 2005) or they can be used to determine an animal’s presence or absence in a larger water body by surveying the entrance to the water body and recording instances where animals passed through (Pecl et al. 2006).

Alternatively, single receivers set throughout a study region can be used to record the presence/absence of tagged animals ((Arendt et al. 2001, Heupel and Hueter 2001, Lowe et al. 2006, Topping et al. 2006, Lindholm et al. 2007, Reynolds et al. 2010).

Some of the many applications for acoustic telemetry technology include assessment of migration patterns, habitat preferences, marine protected areas, survival, spawning behavior, home range, and site fidelity (Heupel et al. 2006, Heupel and Webber 2012). These topics can be investigated using several different receiver arrangements, tag models, and data analysis, but all of them rely on the fact that the acoustic signals emitted by the transmitters must travel through the organism’s environment and, even in perfect conditions, the signals are affected by spreading losses, refraction, and attenuation (Kessel et al. 2014). These factors lead to a decaying probability of detection as distance from the receiver increases. The distance at which the detection probability reaches an unsatisfactory low is often referred to as the receiver’s range. Receiver range can be determined by mooring tags at set distances from a receiver for a designated time period and recording the detection probabilities at the various distances. Mobile range tests, where a transmitter is dragged behind a moving (or intermittently pausing) boat, may also be used (Kessel et al. 2014). Detection probability is affected by noise-producing or -reducing environmental factors, such as surface conditions and meteorological events (Adams et al. 2012, Cooke et al. 2013, Kessel et al. 2014). The variation of these parameters will cause the detection probability at a given distance (and therefore the
receiver’s range) to fluctuate. Testing, understanding, and incorporating fluctuating detection probabilities into acoustic telemetry data analysis are imperative to the accurate interpretation of acoustic telemetry data (Kessel et al. 2014). Any given detection could have been transmitted from a fish 3 km or 3 m from a receiver; a poor understanding of the relationship between distance from the receiver and the effect of environmental conditions on detection probability can lead to significant misinterpretations of one’s results (Payne et al. 2010, Kessel et al. 2014).

I created and tested a probabilistic method that incorporates fluctuating detection probabilities into fish residence duration estimation at a single receiver to improve upon methods found in the literature. My results suggest that this method has the potential to advance the field of telemetry by improving the interpretation of telemetry data.
CHAPTER 2: LAKE TROUT SPAWNING SITE USE IN LAKE CHAMPLAIN

2.1 Abstract

Lake trout populations were extirpated from the lower four Great Lakes by 1960 and from Lake Champlain by 1900. The decline of lake trout populations fueled a wave of restoration-based research that spanned the Great Lakes and filled in many of the gaps in our knowledge of lake trout behavior and ecology. However, remarkably little is known about lake trout spawning behavior, even less about sex-specific differences in spawning site use. Lake trout use specific spawning sites, and may return to the same site year after year. More males are caught on spawning sites than females and are present at spawning sites earlier in the spawning season. The focus of this project is to describe the spawning movements of male and female lake trout within and among spawning seasons and spawning sites. I used acoustic telemetry in Lake Champlain to test several hypotheses related to spawning site fidelity and whether or not there were differences in male and female movements. I hypothesized that males show site fidelity and remain at a preferred site during the spawning season, whereas females should 'sample' multiple spawning reefs to maximize their reproductive success. I established an acoustic telemetry array of ten acoustic receivers placed over eight spawning sites and implanted acoustic transmitters (tags) in 44 male and 48 female lake trout over two years. During two spawning seasons, males spent more time on spawning sites than females. Both male and female lake trout that were active on monitored sites during the spawning season selected a single preferred site. Males and females both traveled to multiple sites between 2 and 56 km apart. Of the lake trout detected during both spawning seasons, most
returned to their capture site in the subsequent spawning season, showing evidence of site fidelity.

### 2.2 Introduction

Lake trout populations in the lower four Great Lakes were extirpated due to a combination of over-fishing and invasive sea lamprey in the mid-1900s. Restoration efforts have failed to bring back viable natural populations. Feral and stocked lake trout locate spawning areas, spawn and produce fry, but the fry are not recruiting into the population (Elrod et al. 1995, Eschmeyer 1995, Eshenroder et al. 1995, Hansen et al. 1995, Holey et al. 1995, Bronte et al. 2007). Research on egg deposition and fry emergence has its roots in restoration; managers need to understand post-zygotic processes in order to protect the stock’s future. A different line of research has focused on understanding basic spawning behavior paradigms of lake trout; detailed courtship rituals have been described based on visual observations and camera work (Esteve et al. 2008, Muir et al. 2012, Binder et al. 2014). However, little research has focused on the broad-scale movement patterns that lead up to courtship.

Lake trout move onto spawning sites shortly after large storms (Fitzsimons and Marsden 2014), following a reduction in photo-period (Royce 1951, McCrimmon 1958), a sharp autumnal decline in temperature (McCrimmon 1958, Martin and Olver 1980), and the onset of heavy onshore winds (Martin 1957, Deroche 1969). Males move onto spawning sites earlier than females and are captured in greater numbers throughout the spawning season (Martin and Olver 1980, Bronte et al. 2007, Muir et al. 2012). Females may travel more widely than males, possibly to maximize the dispersion of their eggs over multiple areas (Callaghan et al. 2015b).
The recent advent of acoustic telemetry methods allows observation of broad-scale lake trout movements. Acoustic receivers are strategically placed to record the signals emitted by acoustic transmitters implanted in fish. These receivers can either stand alone to record the presence of tagged fish, or be arranged in a grid (called a VEMCO positioning system or VPS) to triangulate the geographic position of a fish when a signal is transmitted (Heupel et al. 2006, Heupel and Webber 2012). To date, few published studies have employed this technology to investigate lake trout spawning movements. Riley et al. (2014) used a VPS array covering 18.9 km$^2$ to explore fine-scale lake trout interactions with submerged drumlins at a single spawning area in Drummond Island, Lake Huron. Another 1.5 km$^2$ VPS array at a single spawning site is being used to test the efficacy of natural vs. artificial reefs in Thunder Bay, Lake Huron (J. E. Marsden, personal communication). Marsden’s data have revealed distinct hot-spots of activity within the spawning site monitoring area, which could be construed as distinct spawning “patches” within a more general spawning area.

While the studies in Lake Huron both have the benefit of positional information provided by VPS arrays, their receiver systems cover single spawning areas and do not monitor spawning activity of the tagged lake trout at other, distant spawning sites. In contrast, Callaghan et al. (2015) used a VPS array to cover the entire 4.02 km$^2$ area of Alexie Lake in the Northwest Territories, Canada, to explore the role of wind and physical characteristics in spawning site selection. Their results revealed evidence of lake-wide spawning, possibly as a bet-hedging behavior against environmental stochasticity (Callaghan et al. 2015a, Callaghan et al. 2015b). It is possible that the results of Callaghan et al. are a product of the small size of Alexie Lake; a lake of this size could
be acting as a single spawning area with multiple distinct patches, similar to Marsden’s findings in Thunder Bay, Lake Huron.

Unlike Alexie Lake, Lake Champlain is large enough to have substantial separation between spawning sites (up to 56 km) and, unlike Lake Huron, it is small enough to monitor all known spawning sites with acoustic receivers. Lake Champlain lake trout were extirpated by 1900 but there are insufficient data to pinpoint the cause of the decline (Marsden and Langdon 2012). Lake trout spawning sites, spawning substrate, and egg deposition in Lake Champlain have been well described (Ellrott and Marsden 2004, Marsden et al. 2005). Deploying a lake-wide VPS array throughout the 1,270 km² area of Lake Champlain is not feasible, but by deploying single acoustic receivers at all known spawning sites in Lake Champlain I was able to monitor the movements and locations of tagged fish throughout the year on spawning sites throughout the lake, a feat that is impossible in larger systems like the Great Lakes. I hypothesized that females travel to multiple spawning sites to spread their egg investment across different areas, and therefore will spend less time than males at each site. I collected high-resolution data on lake trout visits to individual spawning sites, how long lake trout remained onsite during the spawning season, whether individuals returned to the same sites year after year, and sex differences in spawning site utilization.

2.3 Methods

Study Site

Lake Champlain is situated between New York and Vermont, with the northernmost portion in Quebec (Fig. 2.1). The lake is relatively long (193 km) and narrow (20 km at its widest point; Marsden and Langdon 2012).
**Receiver Array and Range Testing**

VEMCO VR2W 69 kHz receivers were suspended vertically 2m above the substrate using subsurface buoys and 50kg concrete anchors. Satellite anchors were attached to the mooring anchor with thirty-meter grapple lines to enable retrieval of the receivers. Six VEMCO VR2W acoustic receivers were deployed at four known lake trout spawning sites between October 15-18, 2013. Single receivers were deployed at Arnold Bay, Whallon Bay, and Burlington Bay. Three receivers were deployed at Grand Isle to test for “wandering behavior” at a single site (Fig. 2.1). One receiver was positioned 250 m offshore from the Gordon Landing spawning site (identified by Ellrott and Marsden 2004 as ‘Grand Isle’) and two satellite receivers were positioned at Rockwell Bay, 2.2 km south of Gordon Landing, and Wilco Point, 1.4 km north of Gordon Landing. Limited observations at Rockwell Bay and Wilco Cove indicate potential spawning substrate is present at both sites (Marsden, personal communication). Single receivers were deployed at Saxton Cove, Shelburne Point, Schuyler Point, and Wilsboro Point in May, 2014, for a total of ten receivers (Fig. 2.1). Of the 14 putative spawning sites surveyed by Ellrott and Marsden (2004), I monitored all sites that were actively used by spawners; however, additional undocumented spawning sites may be present in the lake.

 Receivers were in place year-round; data were downloaded from receivers in late November, 2013 and 2014, before weather prohibited access to the lake. A second download in mid-May, 2014 and 2015, retrieved data from the remainder of the spawning season.
I performed a 48-hour range test using transmitters suspended from moorings at 50, 100, 250, and 500 m from a receiver in August, 2014. I defined the receiver range as the distance within which the detection probability was >70%.

*Transmitter Implantation*

Lake trout were anesthetized in a 0.26ml/L solution of AQUI-S 20E (AQUI-S, New Zealand). Individuals remained in the anesthetic bath for a minimum of 5 min before being moved to a surgical cradle for tag implantation (Bowker 2009). Gills were continuously perfused with oxygenated water while a 2-3 cm incision was made approximately 4 cm anterior to the pelvic girdle. A VEMCO V13-1L transmitter (120s nominal ping delay, three-year battery life) was manually inserted and pushed anterior to the incision. Incisions were closed with simple interrupted sutures tied with surgeon’s knots (Wagner et al. 2010).

In 2013, 15 male and 15 female lake trout were captured using trap nets on 5-7 November 2013 at Gordon Landing on Grand Isle, Lake Champlain (Fig. 2.1). Lake trout were held in 1.2 m³ fish pens for a maximum of 12 hours prior to tagging. After the first round of surgeries, lake trout were placed back into the fish pens for 24 hr before being released at the capture site. This extended observation period was implemented as a precautionary measure to monitor for mortality caused by the inexperience of the surgical team. All fish survived; the period was shortened after subsequent surgeries to 20 min (sufficient time to recover from anesthesia).

In 2014, 14 male and 15 female lake trout were captured using trap nets and tagged on 4-5 November 2014 at Gordon Landing. Fifteen male and 18 female lake trout were electroshocked by the U.S. Fish and Wildlife Service on 10 November 2014 in
Whallon Bay, Lake Champlain (Fig. 2.1). These lake trout were held in boat-mounted live-wells for a maximum of two hours prior to tagging. The fish were held for 20 min before release.

*Data Analysis*

Raw detection data were corrected for clock drift and passed through a false-detection filter. When two or more transmissions reach a receiver simultaneously, the receiver can record false detections fabricated from portions of the codes from the original transmissions (Clements et al. 2005, Heupel et al. 2006, Campbell et al. 2012). My filter removed collision-based false detections by using a buffer time of 24 hr before and after each transmission. Any solitary detection from a particular transmitter during this buffer period was rejected; in other words, if no transmissions were received from this transmitter 24 hr before or after the given detection, it was likely a false detection and was excluded from my analysis.

The spawning season was defined as 1 October to 1 December based on egg deposition data from Lake Champlain (Ellrott and Marsden 2004). For fish tagged after 1 October in a given year, analysis began the day after the last fish was tagged and ended on 1 December. To test for a difference in the amount of time each sex spent on any of the eight spawning sites per day, I analyzed the daily detection frequencies (DDF) for each lake trout during each spawning season. DDF (which is actually a proportion of the total expected detections per day) was calculated by tallying the number of detections in a day and dividing that number by 720, which is the expected number of daily transmissions for VEMCO V13 transmitters with a nominal delay of 120 s. Mean daily detection frequencies were calculated for each fish by averaging all DDF values greater
Average male and female DDFs were compared using a t-test to determine which sex spends more time onsite per day.

I used t-tests to evaluate the difference between the number of days males and females were detected at spawning sites, and between the number of sites visited by each sex. A fish was assigned a preferred site if the individual spent 50% or more of their onsite-days (days when a fish was detected at any spawning site) at one site, and was at that site for more than a total of two days.

I tested for a difference in the amount of wandering behavior between males and females that preferred Grand Isle by calculating a “loyalty” value to the main site, relative to time spent at the adjacent sites in Wilcox Cove and Rockwell Bay. For each fish, an average DDF was calculated (see above) for the main receiver and the two satellite receivers. The difference between the average DDFs for each fish was calculated (main DDF minus satellite DDF) and then divided by the sum of the average main DDF and the average satellite DDF to generate a ‘loyalty rating’, a proxy measurement for how much more time a fish spent on one receiver relative to another. A positive value of 0.05, for example, would indicate that a fish spent an average of 5% more time on the main receiver each day, or was 5% more loyal to the main receiver. A negative value of -0.05 would indicate the fish spent 5% more time on the satellite receivers. I tested the difference between male and female loyalty ratings using a t-test.

2.4 Results

Range Test

The receiver range, determined from the 48-hour range test, was 250 m (Fig 2.2). The term “onsite” is will be used hereafter to signify the area with a 250 m radius
around a given receiver.

Telemetry Data

In 2013, data collection started on 8 November and ended on 1 December. All fifteen of the tagged males and 14 of 15 tagged females were detected during the abbreviated spawning season. Males had more onsite days (8.5 ± 1.1 SD) than females (5.0 ± 0.9 SD; p = 0.0221). Males had higher daily detection frequencies (0.20 ± 0.03 SD) than females (0.08 ± 0.02 SD; p = 0.0062). Most males (13 of 14) and females (9 of 15) chose a preferred site. The number of sites visited by males (1.7 ± 0.2 SD) and females (1.4 ± 0.2 SD) was not different (p = 0.2302; Table 2.1). 2013 was the only year with a sufficient number of fish at Gordon Landing to perform the loyalty test. Of fish that preferred Gordon Landing (nine males and nine females), males were more loyal to the main site (0.752 ± 0.062 SD) than females (0.163 ± 0.161 SD; p = 0.0062).

In 2014, eight males and four females tagged at Gordon Landing in 2013 were detected during the spawning season. One of the females remained stationary at one receiver for a period of several months, including the spawning season, and was presumed dead. She was excluded from the analysis. The number of returning males and females was too small to achieve significant power for statistical tests. However, the patterns observed in 2013 persisted. Males had an average of 29.8 ± 4.0 onsite days and females had an average of 20.0 ± 7.2 onsite days. Average daily detection frequency was 0.18 ± 0.04 SD for males and 0.08 ± 0.03 for females. Males visited 2.8 ± 0.5 SD sites and females visited 3.3 ± 1.5 SD sites. All eight males and two of the three females chose a preferred site. Six males and no females preferred the same site in 2013 and 2014. One male and two females only preferred a site in 2014, and one male preferred a different
site each year (Table 2.1; Appendix).

Data for fish tagged in 2014 were collected from 11 November to 1 December. Twenty-nine of the 33 tagged females and 28 of the 29 tagged males were detected during the abbreviated spawning season. Males had more onsite-days (11.5 ± 0.1 SD) than females (8.0 ± 0.9 SD, p = 0.0109). DDF did not differ between males (0.20 ± 0.02 SD) and females (0.14 ± 0.02 SD; p = 0.0637). A total of 23 males and 19 females chose a preferred site. There was no difference in the number of sites visited by males (2.1 ± 0.2 SD) and females (1.9 ± 0.2 SD, p = 0.2804; Table 2.1).

2.5 Discussion

Overall, males spent more time per season and per day on spawning sites than females, and traveled to the same number of sites as females. However, females did move more extensively within a spawning area than males. The difference in male and female residence time on spawning reefs explains in part the skewed sex ratios of fish captured on spawning sites described repeatedly in the literature (Martin and Olver 1980, Bronte et al. 2007, Muir et al. 2012); the number of females on spawning sites may also be reduced because females may not spawn every year (Martin and Olver 1980, Morbey and Shuter 2013, Sitar et al. 2014).

Females spent fewer days than males on a given spawning site, indicating that they are either spawning at multiple sites, or they allocate less time to spawning. I did not find any strong evidence that females visited more sites than males; the number of sites each sex visited did not differ significantly in either year. Once a female has spawned out her eggs she has no reason to remain at a spawning site, thus female residence at a spawning site is likely to be shorter than male residence time. The majority of fish spent
most of the season at one site each year. Visits to other sites were brief in comparison and occurred directly before or after the large time segment spent on the preferred site (Appendix). These visits may simply represent sites encountered during travel to a preferred site, or they may be a behavior in which lake trout sample several sites before selecting one with the best substrate, least competition, best mates, or some other criteria. Spawning sites in larger systems such as Lake Champlain can be widely dispersed; travel to multiple sites during the peak of the spawning season would cost an individual time and energy.

Females also spent less time each day at a spawning site than males, and moved more widely from the spawning site center than males. At the site of the loyalty experiment in 2013, the only year when I had sufficient and equal samples of both sexes at Gordon Landing, females were less loyal to the site center than males; i.e., they were detected more often than males at the satellite receivers 2.2 km and 1.4 km away. Less time spent on-site by females combined with lower “main site loyalty” could be evidence of the “bar vs. bedroom” hypothesis (Pat Bigelow, NPS, personal communication), wherein females may remain just beyond the spawning site for the majority of the day and migrate back when they are ready to engage in courtship behavior, possibly to avoid male harassment at the center of spawning activity. Alternatively, Gordon Landing could be comprised of multiple distinct spawning “patches”, similar to the numerous distinct spawning sites that have been identified in relatively tiny lakes such as Alexie Lake (4.02 km²) in the Northwest Territories in Canada (Callaghan et al. 2015a, Callaghan et al. 2015b). Females may maximize the potential for successful egg incubation by bet-hedging and spreading their egg investment over several potential spawning patches.
within one spawning area. Positional information from a gridded acoustic telemetry array or VEMCO Positioning System would be necessary to determine which, if either, of these two scenarios was occurring. The spawning-patch hypothesis would be supported if female detections were patchily distributed throughout the spawning area. The bar vs. bedroom hypothesis would be supported if female detections were evenly distributed, i.e., they are evenly scattered and distal to the spawning site center, not focused on alternative sites.

I did not account for variable detection probability within my receiver range in this study. Detection probability can vary greatly from day to day, and even hour to hour in a system. The results I obtained provided sufficient evidence to show that males spend more time onsite than females, that there is no difference between number of sites visited by each sex, and that male lake trout show evidence of spawning site fidelity. Because females have a shorter occupation period on spawning sites, future studies should focus on temporally fine-scaled positional data of lake trout on a single spawning site to investigate potential behavioral differences between males and females at the single-site level.
Table 2.1: Summary of 2013 and 2014 spawning season data for cohort 1, tagged in 2013 and cohort 2, tagged in 2014. Metrics include number of fish detected (# fish), average number of days fish were detected by our array (avg. days ± standard deviation), average daily detection frequency (DDF ± standard deviation), average number of sites visited (# Sites ± standard deviation), percentage of fish which showed site preference (site pref.).

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<td>Females 14</td>
<td>-</td>
<td>Males 8</td>
<td>Females 3</td>
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<td>Avg. days</td>
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<td>5.0 ± 0.9</td>
<td>0.0221</td>
<td>29.8 ± 4.0</td>
<td>20.0 ± 7.2</td>
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<td>DDF</td>
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<td>0.08 ± 0.02</td>
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<td>0.0603</td>
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<tr>
<td># Sites</td>
<td>1.7 ± 0.2</td>
<td>1.4 ± 0.2</td>
<td>0.2302</td>
<td>2.8 ± 0.5</td>
<td>3.3 ± 1.5</td>
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<td>100%</td>
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<td>82%</td>
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Figure 2.1. Map of receiver locations in Lake Champlain. Spawning site receivers are indicated by circles. Loyalty experiment satellite receivers are indicated by triangles. Black symbols reflect an October, 2013 deployment, white symbols indicate an August, 2014 deployment.
Figure 2.2. 48-hr acoustic telemetry range test showing detection probabilities at four distances from the receiver.
CHAPTER 3: THE BINOMIAL ROLLING RESIDENCE (BRR) TEST: 
ACCOUNTING FOR FLUCTUATING DETECTION RANGE OF STATIONARY 
ACOUSTIC TELEMETRY RECEIVERS 

3.1 Abstract

Many acoustic telemetry studies measure the duration of an animal’s presence at a single acoustic receiver (i.e., site residence). Current residence assessment methods do not account for fluctuating detection probabilities at a set distance. I developed a binomial rolling residence test (BRR test) to improve on the current method of assessing the duration of a fish’s residence at a single acoustic telemetry receiver. I measured daily detection probabilities (DP) at several distances from a receiver site. The BRR test evaluates a tag’s residence every minute by moving a one-hour time window centered on time t across the duration of the data. The daily DPs are incorporated into a binomial test of the null hypothesis that a fish is not within x meters of the receiver at time t. I performed a 48-hour stationary residence test using two onsite tags and two offsite tags and compared the performance of the BRR test to three residence assessment methods found in the literature. The results showed that the BRR test performed better than all of the time-threshold residency evaluations in my 48-hour stationary residence test. This method has the potential to advance the field of telemetry by improving the interpretation of telemetry data.
3.2 Introduction

Acoustic telemetry tracks animal movements using transmitters that communicate with strategically placed acoustic receivers. Many telemetry studies use single receivers to monitor the presence or absence of animals within the receiver’s range (Arendt et al. 2001, Heupel and Hueter 2001, Lowe et al. 2006, Topping et al. 2006, Lindholm et al. 2007, Reynolds et al. 2010). Studies that use this single receiver system to monitor presence and absence will be called “site residence studies” hereafter. Within the broad category of site residence, a number of topics can be investigated, including site fidelity, site residency, seasonal and diel changes in site use, and, in some cases, definition of home range.

Site residence has been assessed primarily using two methods; the first involves creating time bins and designating a minimum number of detections to determine whether or not a fish is present on the site (usually described as “within range of the receiver”) within that time bin. The residence criteria and duration of each time bin are dependent on the study question. Some examples of binning methods used in previous studies include two detections per day (Reynolds et al. 2010), five detections per day (Topping and Szedlmayer 2011) and one detection per hour (Lindholm et al. 2007). The second method measures residence events (also called “visit events”) as continuous series of detections where a predetermined time interval was not exceeded between sequential detections (Stark et al. 2005, Castro-Santos and Perry 2012). Residence events are bookended by the timestamps of the first and last detections of the series, usually recorded as “time of arrival”, “time of departure” and “duration”. This method allows
compression of the data into residence events rather than the more cumbersome and less informative raw detections.

A range of interval thresholds for the residence events has been used in past studies (Stark et al. 2005, Cabanellas-Reboredo et al. 2012, Castro-Santos and Perry 2012). Because many transmissions go undetected, it is not meaningful to set the threshold interval as the transmission rate of the tags. Instead, a threshold that accounts for missed transmissions due to environmental sound interference must be used (Castro-Santos and Perry 2012). In the past, researchers attempted to address this issue by setting an arbitrary threshold interval for a time interval greater than the transmission rate of the tag (Stark et al. 2005, Cabanellas-Reboredo et al. 2012). Another method is to look at the spread of the durations between sequential detections. The spread can inform threshold selection by using a specific quantile (perhaps the 99th percentile of interval duration) or a visually or statistically distinguishable inflection point or bimodality in the data (Castro-Santos and Perry 2012). These thresholds are basically behaving as error bars.

The above methods for measuring residence events all begin to address the high variability of detection probabilities. If the goal for measuring a residence event is to record an accurate time of arrival and departure of a fish, the calculation should be based on the best estimate of the duration of time the fish was actually within the radius of interest. By using time-threshold intervals that are too long, a fish could come and go and still be counted as present the entire time (a false positive, or type II error, with a null hypothesis that the fish is not on-site). Time-threshold intervals that are too short could indicate that a fish has departed when it has not (a false negative, or type I error). To reduce misinterpretations of behavior due to inaccuracy in the time-threshold method, I
recorded the fluctuations in detection probability at 100 m (a conservative range estimate). I used these recorded detection probabilities to create a binomial rolling residency test (BRR test). I hypothesized that this probabilistic method that incorporates fluctuating detection probabilities would improve the accuracy of single receiver residence evaluation compared to the performance of fixed time-threshold methods. My hypothesis would be supported if the BRR test had a lower occurrence of type I and type II errors than fixed time-threshold methods.

3.3 Methods

Residence test acoustic array

We performed a 48-hour receiver residency test from 0000 hr on 11 August, 2015 to 0000 hr on 13 August, 2015 at Wilcox Point, Lake Champlain, VT, 150 m from shore, at a depth of 6 m, on cobble substrate (Fig. 3.1). I deployed a VEMCO VR2W 69 kHz receiver suspended 2 m off the substrate from a 23 kg concrete anchor. Four VEMCO V13-1L tags (transmitters with a nominal delay = 120s) were suspended 2 m from the bottom from concrete moorings 50, 100, 250, and 500 m from the receiver to simulate stationary fish. I chose these distances based on the results of a 48-hour range test performed in July 2015. Another V13 tag (nominal delay = 120s) was deployed 100 m from the receiver and will be referred to as the sentinel tag (Fig. 3.2). Detection probability (observed detections divided by expected detections within a given time period) was calculated using transmissions from the sentinel tag.

Data Processing

When two or more transmissions reach a receiver simultaneously, the receiver can record false detections fabricated from portions of the codes from the original
transmissions (Clements et al. 2005, Heupel et al. 2006, Campbell et al. 2012). Therefore, raw detection data were corrected for clock drift and passed through a false-detection filter. My filter removed collision-based false detections by using a buffer time of 24 hours before and after each transmission. Any solitary detection in this buffer period was not included in my analysis. I then ran the detection data through the BRR test and the time-threshold method to assess which method assigned residence more accurately. A perfect residence assessment would result in 48 hours of residence for the 50 m and 100 m tags (no type I errors) and 0 hours of residence for the 250 m and 500 m tags (no type II errors). The method that performs better will have lower rates of type I and type II errors than the other method.

**Binomial rolling residence test**

The BRR test evaluates the residence of a tagged fish every minute by moving a one-hour time window centered on time t across the duration of the data. The one-hour window was chosen after running the BRR test on the residence test data using a sequence of window sizes ranging from 12 min to 60 min by 1-min intervals. The type I error rates remained consistently low regardless of window size, while the type II error rates decreased as the window size increased (Fig. 3.3). I chose to cap the window size at 60 min to achieve maximum performance while still operating a timescale that is behaviorally relevant. A four- or five-hr count-window would yield lower type II error rates in this test, but reduce the temporal resolution when used on moving fish. I performed a binomial test of the null hypothesis that the detection probability at the test tag’s location at time t is significantly lower than the detection probability reported by the 100 m sentinel tag, and, by extension, that the test tag was not within 100 m of the
receiver. The inputs for the test are the number of successes (detections), number of trials (expected number of detections based on nominal delay), and the probability of success (detection probability at time t). The result is the probability that the null hypothesis (the tag is within 100 m of the receiver) is true, which I will treat as a p value. When p < 0.05, I reject the null and conclude that the fish was more than 100 m from the receiver at time t. Each minute is then deemed “resident” or “not resident”. Consecutive minutes of residence are grouped into discrete residence events with start- and end-times.

**Time-threshold methods**

The time-threshold residency evaluation measures residence events as continuous series of detections where a predetermined time interval was not exceeded between sequential detections (Stark et al. 2005, Cabanellas-Reboredo et al. 2012, Castro-Santos and Perry 2012). The time interval can be arbitrarily set as a time greater than the transmission rate of the tag. Stark et al. (2005) used 30 minutes, and Cabanellas-Reboredo et al. (2012) cited Stark for the method, but used 60 minutes. Castro-Santos and Perry (2012) recommend using the 99th percentile of interval duration. I ran my data through three iterations of the time-threshold method, using each of the above criteria (30 min, 60 min, and Castro-Santos and Perry’s 99th percentile of interval duration, which for my data was 14 min).

### 3.4 Results

Because I set the criterion distance at 100 m, for the 50 m and 100 m tags any percentage of residence <100% is the rate of type I error. For the 250 m and 500 m tags, any percentage >0% is a rate of type II error. At my criterion distance of 100 m, the 14-min, 30-min and 60-min time thresholds all yielded zero rates of type I errors, but had
considerable type II errors (51-78%) which increased with the length of the time threshold. The BRR test had low rates of type I errors (type I errors occurred 2% of the time at 50 m and 3% of the time at 100 m) and rates of type II errors that were much lower than those of data analyzed with time thresholds (31%) (Table 3.1). However, the 250 m results are not substantially different from those of 50 m and 100 m when using any of the residence analysis methods. Therefore, I decided to make 250 m the new criterion distance, i.e., the BRR test determines whether fish are within 250 m of a receiver.

3.5 Discussion

Overall, the results show that the BRR test performs better than all of the time-threshold residency evaluations in the 48-hr stationary residence test. While the type I error rates for the BBR test were slightly lower than those for the time-threshold residence evaluations, the 2-3% difference is negligible compared to the substantial decline in type II error rates achieved with the BRR-test, 20% lower than the lowest type II error rate achieved with a time-threshold residency evaluation.

The BRR test allows the researcher to make assumptions about a fish’s distance from the receiver during a residence event. My original definition of a residence event was a period during which a fish is within 100 m of a receiver. Because the BRR test does not sufficiently distinguish between residence and non-residence at 100 m and 250 m, I adjusted my definition of residence to be within 250 m of the receiver to reflect these findings. The BRR test uses real-time detection probabilities to determine the duration of a tagged fish’s residence at a specific distance more accurately than time-threshold residence evaluations. This distance is likely environment-specific; researchers using this
method in other systems will need to perform a stationary tag test such as the 48-hour test described here to determine the appropriate range to use in their residence definition. This procedure will allow an accurate interpretation of the results of a BRR test in other aquatic and marine systems. The BRR test allows the researcher to define residence at a specific distance, accounts for fluctuations in the acoustic environment, and performs better than time-threshold residency evaluations. I suggest this method has the potential to advance the field of telemetry by improving the interpretation of telemetry data.
Table 3.1. Percentage of time that tags were observed to be resident using a 14-min time threshold (99th percentile), a 30-min threshold, a 60-min threshold, and the binomial rolling residency test (BRR test) using a 60-min count window. Italicized values show results for off-site tags.

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>14-min. Threshold</th>
<th>30-min. Threshold</th>
<th>60-min. Threshold</th>
<th>BRR test</th>
</tr>
</thead>
<tbody>
<tr>
<td>50</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>98%</td>
</tr>
<tr>
<td>100</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>97%</td>
</tr>
<tr>
<td>250</td>
<td>98%</td>
<td>100%</td>
<td>100%</td>
<td>86%</td>
</tr>
<tr>
<td>500</td>
<td>51%</td>
<td>64%</td>
<td>78%</td>
<td>31%</td>
</tr>
</tbody>
</table>
Figure 3.1. Map of Lake Champlain with residence test site location indicated with black dot.
Figure 3.2. Illustration of residence test layout. Sentinel tag is shown on the far left, 100 m from the receiver. Stationary test tags were placed at 50, 100, 250 and 500 m from the receiver.
Figure 3.3. Effect of time-window size on calculated hours of tag residence using the binomial moving-count residence evaluation.
References


Chipman, B. 2012. Lake Champlain fisheries restoration and management annual report. 103 S. Main St. Waterbury, VT, Vermont State Fish and Wildlife.


APPENDIX

Figure A-1. Raw telemetry data from 11/5/2013-12/1/2013 from fish tagged at Grand Isle in 2013.
Figure A-2. Raw telemetry data from 10/1/2014-12/1/2014 from fish tagged at Grand Isle in 2013.
Figure A-4. Raw telemetry data from 11/11/2014-12/1/2014 from fish tagged at Whallon Bay in 2014.