

ADIRONDACK FISH COMMUNITY DYNAMICS AND MANAGEMENT IN RESPONSE
TO ANTHROPOGENIC STRESSORS

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Fish communities in New York's Adirondack mountain region face numerous threats including the continued impacts of acidification, introduction of non-native species, and loss of connectivity. Effective management relies upon the strength of assessment techniques, which are necessary both to detect impacts and to evaluate the success of any mitigation efforts. To address this need, I began by evaluating the methodology behind boat electrofishing, a widely-used tool for fish community assessment. Results from this study indicate that the predominant metric for "effort", time fished, has the potential to be biased by gear saturation when catches are high, leading to inaccurate catch indices. Two alternate effort methods, shoreline length and a novel "area fished" metric, were not biased by gear saturation. Next, I validated a new population estimation technique known as close-kin mark-recapture, which allows for genotype-based estimates of absolute abundance and survival. A side-by-side comparison suggests that the method produces contemporary population estimates for brook trout (*Salvelinus fontinalis*) comparable to those obtained using traditional techniques. Close-kin mark-recapture is more flexible than traditional techniques and can also provide accurate historical estimates of abundance. I built upon this work to provide context for the ecological changes that these techniques can help to detect and assess. First, I investigated changes to the trophic dynamics of Honnedaga Lake following the colonization of two zooplanktivores: the native invertebrate

Chaoborus punctipennis and introduced rainbow smelt (*Osmerus mordax*). Analyses of the zooplankton community composition indicated that both colonization events rapidly changed trophic dynamics. Zooplankton community response to colonization by *Chaoborus* also suggested that cryptic changes in their abundance may explain regional zooplankton trends, especially in relation to increased lake browning. Finally, I addressed connectivity issues by using PIT-based telemetry and mark-recapture modeling to investigate movement of white sucker (*Catostomus commersoni*) in the Bisby chain of lakes and the resulting implications for connectivity. Results revealed extensive and previously unrecognized diel movement between lakes, underscoring the need to consider connectivity in systems often regarded as isolated units. Ultimately this work highlights the need to consider complex interactions between stressors when managing aquatic ecosystems and provides tools to accomplish that goal.

BIOGRAPHICAL SKETCH

Born in Ann Arbor, Michigan in 1988 to Sherry Marcy and Nancy Quay, Ben spent the majority of his childhood exploring the woods, streams, and lakes around his home and abroad. While on family vacations that ranged from treks in Canada's Northwest Territories to houseboat trips down the Mississippi River, he cultivated a keen interest in the natural world around him. Ben's high school years were spent at the Leelanau School, a small boarding school on the shore of Lake Michigan. In 2010, Ben earned his Bachelor's of Science in Environmental Science from Allegheny College.

Following graduation from college, Ben worked with at-risk youth in Colorado and Utah before taking a job conducting biodiversity surveys with the New York State Department of Environmental Conservation. His experience there and encouragement from his supervisor and mentor, Suzanne Beyeler, motivated him to pursue a graduate degree. Ben joined the Department of Natural Resources at Cornell University in 2012 where he is jointly advised by Drs. Clifford Kraft and Patrick Sullivan. He earned his M.S. in 2015 and transitioned to Ph.D. research. During his time at Cornell Ben thoroughly enjoyed the opportunity to conduct field sampling as part of the Adirondack Fishery Research Program and surprised himself by discovering a passion for modeling and quantitative methods.

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This work could not have been possible without the advice, assistance, and support of a great many people. I would especially like to thank my parents, Nancy Quay and Sherry Marcy, for introducing me to the outdoors and supporting me since then in far too many ways to list. I owe my education in part to a number of excellent teachers and mentors. Robert Karner, Joseph Blondia, and Bruce Hood of the Leelanau School science department fueled my passion for ecology and environmental science. My graduate career is due in part to Suzanne Beyeler, who inspired me to be a diligent, conscientious scientist and pushed me to continue my education.

While at Cornell I have had the privilege to be advised by a fantastic special committee. I especially want to recognize my Dr. Clifford Kraft who gave me the freedom to explore my scientific interests while providing thoughtful and incisive feedback. He has been a wonderful advisor and I deeply respect his curiosity-driven approach to studying the natural world. I am also grateful to my other co-chair, Dr. Patrick Sullivan who introduced me to the world of quantitative fisheries research and provided support and encouragement throughout my graduate studies. I would like to similarly thank the other members of my special committee, Drs. Suresh Sethi and Nina Therkildsen. This work would not have been possible without their valuable insights and feedback.

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Finally, learning and research are inherently community endeavors and I appreciate the years of support and friendship from my fellow DNR graduate students. I have had the opportunity to bond, discuss, and commiserate with many fantastic humans during my time at Cornell and I am deeply grateful to all of you. This has been a wonderful journey and I could not have done it without your help. Thank you all.

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CHAPTER 1 – TIME VERSUS SPACE: CHOICE OF EFFORT METRIC CAN AVOID BIAS IN BOAT ELECTROFISHING CPUE

ABSTRACT

While catch per unit effort (CPUE) is the most widely used metric for expressing and comparing boat electrofishing catch data, "effort" has been inconsistently defined. Boat electrofishing guidelines refer to both time- and distance-based metrics with little consensus about the appropriateness of one over the other. Catch rate metrics that use time-based effort may potentially be biased by gear saturation due to handling time. We evaluated the potential for bias resulting from effort metric choice by comparing catch rates based on one temporal and two spatial effort metrics – time, shoreline length, and a GPS-based areal measure – using three years of data from 288 sampling occasions when all three metrics were recorded simultaneously. We used pairwise comparisons to isolate the effect of effort metric choice and fit six candidate models to each potential pair of CPUE metrics: a simple linear model, four models with separate slopes for survey variables (lake, season, night/day, and habitat), and an asymptotic model. The best-fit model was asymptotic when the time-based CPUE metric was compared to both space-based metrics, and the linear model accounting for habitat was the best-fit model for the comparison between both spatial methods. These results indicate that using a time-based measure of effort resulted in hyperstable CPUE when fish densities were high due to gear saturation. By comparison, spatial measures of effort were robust to changes in fish density. Observed habitat-based variation in the relationship between the two spatial metrics suggests that a CPUE measure based on shoreline distance is adequate for assessing trends in abundance within waters or areas with homogenous habitat, but not locations with contrasting conditions.

We recommend the use of an areal-based effort metric due to its robustness to gear saturation, comparability between waters, and potential for incorporating other variables that influence the performance of CPUE.

INTRODUCTION

Catch per unit effort (CPUE) is the most widely used metric for expressing and comparing boat electrofishing catch data. Despite its ubiquity, however, the standard definition of effort has been inconsistently applied. In *Standard Methods for Sampling North American Freshwater Fishes* (2009), the chapter on sampling small standing waters (Pope et. al 2009) recommends that for electrofishing, "Effort should be transformed to a per-hour basis... ..as measured by the electrofisher timer." However, these authors then state that, "Recording distance sampled (actual distance the boat moves) for each segment is encouraged for future computation of effort based on segment length." Other guidelines for both large standing waters (Miranda and Boxrucker 2009) and rivers (Guy et al. 2009), however, discuss only various methods for computing effort based on time and make no reference to spatial metrics. This contrasts with a more comprehensive section on electrofishing in *Fisheries Techniques 3rd Edition* (Reynolds and Koltz 2012) that states, "At the beginning of a sampling program, both distance and time for each sample should be measured" and adds, "The variable most predictive of catch, both in terms of linearity and confidence limits, is the one to use as an effort index." Bayley and Austen (2002) note simply in the discussion of their extensive investigation of boat electrofishing capture efficiency, "If fish retrieval or navigation around snags reduces mean boat speed, CPUE with effort measured as time fished is inherently biased" and, "in all cases effort should be measured as the length of shoreline fished."

The utility of CPUE as an index of abundance stems from recognizing that catch can be related to overall population abundance through the relationship between overall fishing effort and a coefficient known as catchability (Arreguin-Sanchez 1996). Stated simply, catchability is the proportion of a population that is captured by one unit of sampling effort. This relationship takes the form:

$$C = qEN \quad (1)$$

Where C refers to the total catch, E is the fishing effort, N is the true population abundance, and q denotes the catchability coefficient (Quinn and Deriso 1999). This relationship and accompanying assumptions provide a foundation for all uses of C/E (i.e., CPUE) to index population abundance. When effort is measured directly and true abundance is the unknown parameter of interest, the dynamics of catchability must be understood in order to draw conclusions about population status. It is important to recognize that this does not mean the true value of catchability must be known; for a relative index of abundance, it is sufficient to know that catchability is constant between samples or – if that information is not available – to understand how it changes. Numerous studies challenging the assumption of constant catchability have concluded that q can be affected by many variables including fish size (Donlan and Miranda 2003), conductivity (Hansen 2004), water temperature (Borkholder and Parsons 2001), and season (Schoenebeck and Hansen 2005). A recent study of Rainbow Trout (*Oncorhynchus mykiss*) in the Colorado River examined direct estimates of capture probability, or qE , from mark-recapture and found that q varied widely between surveys, reaches, fish densities, and fish size classes (Korman and Yard 2017). The authors concluded that q often varied in response to the proportion of the population present in the volume available to the netter, which was determined by physical habitat (e.g. bank angle and turbidity). An inverse

relationship was specifically observed between q and density, which was attributed to handling time and aggregation effects. Both of those effects can lead to a phenomenon known as hyperstability, where CPUE is not linearly related to density (Paloheimo and Dickie 1964). The inverse relationship between catch and gear efficiency that leads to this form of hyperstability has been denoted “gear saturation” (Peterman and Steer 1981).

Handling time leads to gear saturation when the survey method and definition of E require that a proportion of E be devoted solely to the capture of each individual. Given that q is defined as the proportion of N caught per E , increased handling time reduces the maximum number of individuals caught per unit of E , causing q to vary inversely with N . In boat electrofishing gear saturation can take two forms: 1) fish are missed due to forward progress by the boat, or 2) the boat is slowed as necessary in order to net all fish. In the former case, full-saturation is characterized by a C and E that remain constant while q varies inversely with N . This results in stable C/E and a capture probability, or qE , for each individual that varies inversely with N . Missed fish due to this form of saturation may be noticed by the netter but cannot be accounted for when analyzing the resultant data without additional information necessary to estimate qE . Tag returns from a marked population provide this information, and mark-recapture studies may therefore be the best way to evaluate gear saturation in constant-speed surveys (Hansen et al. 2004; Korman and Yard 2017). In the second case, slowing the boat to net as many fish as possible adds to both E and N . Under ideal circumstances (e.g. the boat is slowed only as much as is necessary to net all fish present) the increase in E and N is proportional and qE is constant. The probability of catching an individual fish during a survey will therefore be constant regardless of population size. However, as both C and E are positive functions of N , the observed C/E will remain stable regardless of any increase in N . In either case

the overall result is a CPUE that does not reflect trends in N (i.e., becomes hyperstable) at high fish densities.

We implemented a study comparing time-based CPUE to two alternative CPUE metrics incorporating spatial measures of E (shoreline length and a measure of area surveyed). We computed CPUE using three simultaneously collected measures of effort (time, shoreline length, and a GPS-based areal measure) and conducted pairwise comparisons using each survey as a replicate sample to calculate the relationships between the different CPUE metrics. Boat speed varied in our surveys as required to net as many detected fish as possible. As a result, the time-based measure of effort represented the time required to survey the site at low densities (a function of speed and true survey area), plus additional time proportional to the number of fish that would have been missed at a constant speed.

We compared catch rates from all three metrics within each sampling occasion to isolate their influence from other variables that might affect q . Although q cannot be estimated directly using our approach, pairwise comparisons of C/E using different effort metrics isolate their influence on q from other factors such as conductivity and turbidity that are constant for the same sampling occasion. A nonlinear relationship between two catch rates (each calculated for the same set of occasions) indicates that one or both of the effort metrics are not independent of N and C , in which case q is also not independent of N and C .

We chose two separate measures of spatial effort for comparison with time-based effort: length of shoreline fished and area fished. Shoreline distance has historically been suggested as an alternative to time (Reynolds 1983) and continues to be used in recent studies (Tyszko et al. 2017, Kiraly et al. 2014). In contrast, area fished is a relatively novel metric made possible by

advances in GPS technology and embedded systems. Our objectives of this study were to 1) determine whether the use of a time-based effort metric led to hyperstable CPUE estimates in our system relative to spatial metrics and 2) evaluate the performance of an area-based effort metric relative to shoreline distance. To accomplish this, we fit a candidate model set consisting of a series of linear models based on physical and temporal survey characteristics as well as a nonlinear, asymptotic model. We hypothesized the asymptotic model would provide the best fit for the relationship between the time-based catch rate and both space-based catch rates, while the comparison between the two space-based rates would be best fit by a linear model that incorporated site habitat.

METHODS

Sampling.—Electrofishing surveys were conducted between 2016 and 2018 on two lakes in the Adirondack region of New York State, First Bisby Lake (63 ha) and Little Moose Lake (290 ha). Typical of the region, conductivity of both lakes was low and clarity was high (Table 1). Surveys occurred between sunset and sunrise in mid-May and mid-September each year. Additional sampling was conducted during daytime hours in late-May and early June as part of an ongoing Smallmouth Bass (*Micropterus dolomieu*) removal program (Weidel et al. 2007). Nighttime surveys targeted all species present (Table 2), whereas daytime surveys specifically targeted Smallmouth Bass. For the purposes of this study species-specific capture numbers were then pooled, thus "catch" represents the total number of fish captured during a survey-site combination. Aggregate numbers (C) were used because saturation is dependent upon the total number of fish a netter must capture during a given effort unit, rather than the abundance of an individual species. Surveys targeting a single species may still be affected by overall density, as greater numbers of stunned non-target fishes may increase the time required to locate target

individuals. As described by Weidel et al. (2007), the shoreline of each lake was divided into segments of contiguous habitat based on substrate type (defined as either rock or fine sediment) and whether submerged woody cover was present. Thus each site was classified as one of four potential substrate-cover combinations: sediment, sediment/wood, rock, and rock/wood. Surveys encompassed the entire perimeter of each lake, with catch and effort metrics recorded for each continuous-habitat segment (site). This classification resulted in 15 sampling sites in First Bisby Lake and 32 sampling sites in Little Moose Lake. GPS coordinates were recorded at the beginning and end of each site to ensure consistent sampling and aid in later shoreline measurement. The electrofishing boat had a double-boom cable dropper electrode arrangement approximating that described and recommended by Miranda and Kratochvil (2008), and two individuals netted fish from the bow. A Smith-Root (Vancouver, Washington) Type VI-A electrofishing unit was used to energize the electrodes. Low water conductivity ranging between 18-30 $\mu\text{S}/\text{cm}$ necessitated the use of high voltage; electrofisher settings were standardized to 60 Hz pulsed DC at 1016V and a 25% duty cycle. These settings were chosen because they were consistent with current sampling guidelines (Reynolds and Koltz 2012) and performed well in the field. We note that while this method does not employ power standardization, which can reduce between-survey variation in catch (Burkhardt and Gutreuter 1995; Miranda et. al. 2009), it is appropriate for a study such as ours that focuses solely on potential differences between simultaneously measured metrics.

TABLE 1. Study lake characteristics

Lake	Area (ha)	Perimeter (km)	Conductivity ($\mu\text{S}/\text{cm}$)	Secchi Depth (m)
			Mean (SD)	Mean (SD)
First Bisby	63	5.1	21.6 (2.1)	6.5 (2.1)
Little Moose	290	11.5	26.8 (2.3)	7.8 (1.64)

TABLE 2. Fish species documented in Little Moose and First Bisby lakes during the 2000-2018 sampling period. Introduced (i.e., non-native) species are denoted with an asterisk (*) and periodically stocked species with a dagger (†) (George 1980). Species denoted with a double dagger (‡) are considered extirpated as of 2018 (defined as no detection by any capture method for 5+ years).

Little Moose Lake

Atlantic Salmon <i>Salmo salar</i> *†	Lake Whitefish <i>Coregonus clupeaformis</i>
Brook Trout <i>Salvelinus fontinalis</i>	Pumpkinseed Sunfish <i>Lepomis gibbosus</i>
Brown Bullhead <i>Ameiurus nebulosus</i>	Rainbow Smelt <i>Osmerus mordax</i> *
Blacknose Dace <i>Rhinichthys atratulus</i> ‡	Rainbow Trout <i>Oncorhynchus mykiss</i> *†‡
Central Mudminnow <i>Umbra limi</i> *	Round Whitefish <i>Prosopium cylindraceum</i>
Common Shiner <i>Luxilus cornutus</i>	Slimy Sculpin <i>Cottus cognatus</i>
Creek Chub <i>Semotilus atromaculatus</i>	Smallmouth Bass <i>Micropterus dolomieu</i>
Lake Trout <i>Salvelinus namaycush</i>	White Sucker <i>Catostomus commersonii</i>

First Bisby Lake

Atlantic Salmon <i>Salmo salar</i> *†	Lake Trout <i>Salvelinus namaycush</i>
Brook Trout <i>Salvelinus fontinalis</i> *	Rainbow Trout <i>Oncorhynchus mykiss</i> *†‡
Central Mudminnow <i>Umbra limi</i> *	Smallmouth Bass <i>Micropterus dolomieu</i> *
Creek Chub <i>Semotilus atromaculatus</i>	White Sucker <i>Catostomus commersonii</i>

Effort metrics.—Three different effort metrics were calculated: time fished, length of shoreline fished, and area fished (Figure 1). Time fished was recorded from the Type VI-A's built-in counter upon completion of each site survey, consistent with standard practice (Pope et al. 2009).

Shoreline distance was calculated in GIS using the start/end coordinates for each site and lake perimeter data from the National Hydrography Dataset (U.S. Geological Survey 2018). The perimeter for each study lake was divided into segments corresponding to each site, and the lengths of the resulting segments were used as the site shoreline distances in subsequent analyses. We chose this method as it uses publicly available information and allows sampling distances to be approximated for nearly any waterbody in the US. While real-time measurements of true distance (i.e., a boat track) are always preferable, high-accuracy civilian GPS is a recent development and many historical surveys lack this information. Thus NHD shoreline distance provides a way to back-calculate spatial effort for whole-lake surveys and those with known start and stop locations.

Area fished was calculated using a device constructed by the lead author that continually recorded GPS coordinates while the electrofisher was energized. This device consisted of a custom circuit board containing a microcontroller, a GPS module, and a flash memory interface. An external current sensor was placed on the electrofisher control circuit and continuously polled by the microcontroller to detect electrofisher operation. The microcontroller recorded GPS coordinates and times for each activation, deactivation, and at 2-second intervals while the electrofisher was operating. A pushbutton enabled the operator to increment an internal counter variable, allowing separate sites to be distinguished. Coordinates recorded by this unit were used to generate "tracks", lines made up of points representing continuous electrofisher operation. Each track was then buffered by a set distance to create a rounded polygon. A buffer value of

two meters was chosen to represent the maximum distance from the center point between the boat's anodes at which fish were likely to be immobilized, observed, and netted (thus a total field width of four meters). This value was derived from experiments conducted by Miranda and Kratochvil (2008) using a double-boom electrode arrangement similar to our own. Individual tracks were then merged for each site, removing any overlapping regions, and the area of the resulting polygon size was used as the estimate of total area fished.

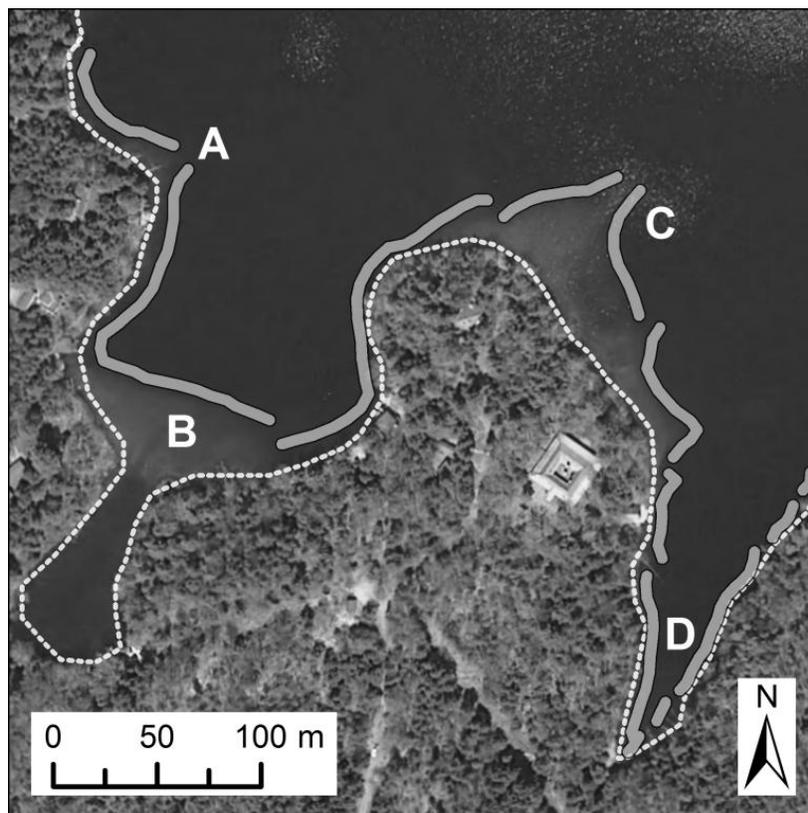


FIGURE 1. Hypothetical example of how measures of spatial effort based on shoreline length (finely dotted line) from the National Hydrography Dataset and actual area fished (gray polygons) may differ. Potential reasons for discrepancies between the two measures include maneuvering irregularities and discontinuous operation due to downed wood (A), underwater features (B and C), and complex shorelines (D).

We chose to buffer our boat tracks and create an areal metric because we consider this method more robust to differences in boat operation. For example, small boat position adjustments may result in a "stacked" boat track if the operator pauses to net large aggregations of fish and leaves the power on (or uses a tracking method that does not register electrofisher operation). This will add to survey length but does not actually represent a greater area surveyed. In a similar manner, tight turns to avoid submerged trees or boulders may cause the field to pass over an area that was surveyed only moments before. We eliminated this potential for "double-counting" by merging overlapping areas.

Pairwise comparisons.—Performance of the three metrics was assessed by fitting a set of six regression models to each of the three potential pairings of CPUE metrics (Table 4). These consisted of a simple linear regression (Eq. 2), four linear regressions with slopes that differed by site or survey characteristics (Eq. 3), and an asymptotic model similar to that used by Halls et. al. (2005) and Lae (1997) to describe overfishing (Eq. 4):

$$\frac{C}{E_1} = a \frac{C}{E_2} \quad (2)$$

$$\frac{C}{E_1} = a_{character} \frac{C}{E_2} \quad (3)$$

$$\frac{C}{E_1} = a(1 - e^{-b \frac{C}{E_2}}) \quad (4)$$

For the simple linear model (Eq. 2), a represents a single slope term estimated for all sampling occasions. The characteristic-specific models (Eq. 3) included models with separate slopes for each lake, each season (i.e., a_{spring} , a_{fall}), each survey type (i.e., a_{day} , a_{night}), and each of the four substrate habitats (e.g., $a_{sediment}$, $a_{sediment/wood}$, etc.). In the asymptotic model described by Eq. 4, parameter a represents the maximum catch rate and b dictates the rate at which a is reached. Regressions for all model comparisons were through the origin, as both the dependent and independent variables shared a numerator with a minimum value of zero.

Goodness of fit for each model was assessed using two metrics, the root-mean-square-error (RMSE) and Akaike's Information Criterion (AIC). The RMSE, also known as the standard error of the regression, is the standard error of the residual values and therefore provides a measure of accuracy in dependent variable units that can reveal model performance differences (Chai and Draxler 2014). Akaike's Information Criterion provides a relative ranking of model precision that inherently penalizes overfitting (Burnham and Anderson 2004). We followed Burnham and Anderson's recommendation and used the second-order criterion, AIC_C , which prevents overfitting with small sample sizes while converging to AIC for large samples. Together the metrics allowed us to rank relative model performance while also evaluating the real-world impact of differences in fit.

We did not use the coefficient of determination (R^2) for two reasons. First, R^2 is a relative measure that compares the amount of variation described by a model to that described by a null model. For simple linear regression with a slope and intercept, the null model is the intercept term, i.e., the mean of the response variable. When fitting a regression through the origin, however, the null model is simply zero. Therefore R^2 values for such models will generally be much larger than those for models incorporating an intercept term, and relative differences

between models will be correspondingly smaller, making any improvement in fit difficult to discern. Second, despite its continued widespread use, R^2 has long been recognized to be inappropriate for nonlinear models (Kvalseth 1985; Spiess and Neumeyer 2010).

For spatial analyses, we used ArcGIS version 10.2.2. Statistical calculations were completed using Program R version 3.5.1 (R Core Team 2018). Linear models were fit using the *lm()* function, while the nonlinear models were fit using *nls()* (both available in the base libraries). Confidence intervals for nonlinear models were calculated using the first-/second-order Taylor expansion method available in the "propagate" package. This method uses a second-order polynomial around $f(x)$ and therefore produces more realistic confidence intervals than the first-order Taylor expansion-based "Delta Method" used in many other approaches that assume linearity around $f(x)$ (Spiess 2014).

RESULTS

A total of 288 survey-site combinations were included in the analysis, 90 in First Bisby Lake and 198 in Little Moose Lake. Average CPUE values for both lakes were high regardless of effort metric, with considerable variation between individual sites. In general, CPUE values were higher within lakes for nighttime surveys than those conducted during the day. Night survey CPUE values were higher in Little Moose than in First Bisby, but the magnitude of this difference depended on the choice of effort metric. For example, mean nighttime catch/min was 1.6X higher in Little Moose than First Bisby (9.06 vs. 5.70), while mean nighttime catch/m was 3.9X higher (0.47 vs. 0.12). Average daytime catch/min and catch/m² were higher for First Bisby than for Little Moose, but daytime catch/m was slightly lower (0.08 vs. 0.09) (Table 3).

TABLE 3. Summarized effort metrics for electrofishing sites on study lakes.

Lake	Survey Type	N	Mean catch/min (SD)	Mean catch/m (SD)	Mean catch/m² (SD)
First Bisby	Day	30	3.61 (2.55)	0.08 (0.09)	0.04 (0.04)
First Bisby	Night	60	5.7 (2.41)	0.12 (0.07)	0.06 (0.03)
Little Moose	Day	59	2.23 (1.41)	0.09 (0.11)	0.02 (0.02)
Little Moose	Night	139	9.06 (3.23)	0.47 (0.36)	0.14 (0.08)

Regression estimates for all models and parameters were highly significant ($P < 0.05$). We found that AIC strongly supported the hypothesis that the best model for the relationship between time fished and both spatial effort factors was asymptotic, rather than linear. Using RMSE as a measure of fit, the asymptotic model provided a much better fit than any linear model (Table 4).

TABLE 4. Model fits for all pairwise comparisons and candidate models

Model	AIC	k	Δ AIC	AIC Weight	RMSE
Time Fished vs. Shoreline Distance					
Asymptotic	1210.53	2	0.00	1	1.96
Linear - by habitat	1390.91	4	180.38	0	2.66
Linear - by lake	1569.28	2	358.75	0	3.65
Linear - by survey type	1639.99	2	429.46	0	4.13
Linear - by season	1640.44	2	429.91	0	4.13
Linear - simple	1641.25	1	430.72	0	4.15
Time Fished vs. Area Fished					
Asymptotic	875.72	2	0.00	1	1.10
Linear - by lake	1124.86	3	249.13	0	1.69
Linear - by habitat	1132.47	5	256.75	0	1.70
Linear - by survey type	1195.04	3	319.31	0	1.91
Linear - simple	1211.21	1	335.48	0	1.97
Linear - by season	1211.31	3	335.59	0	1.96
Shoreline Distance vs. Area Fished					
Linear - by habitat	1113.69	5	0.00	1	1.64
Linear - by lake	1257.77	3	144.08	0	2.13
Asymptotic	1262.47	2	148.78	0	2.14
Linear - by season	1263.61	3	149.91	0	2.15
Linear - simple	1266.03	1	152.33	0	2.16
Linear - by survey type	1268.03	3	154.33	0	2.16

Similar patterns were observed for the comparison between catch/min and catch/m², although the magnitude of the difference between the best and worst models was reduced. In the comparison between shoreline length and area fished, AIC strongly indicated that a linear, habitat-dependent relationship was the best model, and RMSE showed smaller differences in fit between models relative to the other pairs (Table 4). AIC values for the top models in nearly all cases were far better than the next best model ($\Delta\text{AIC} > 100$) while values for lower ranked models were closely clustered with each other. The exception to this was the comparison between catch/min and catch/m; the linear model including habitat performed better than the next best model ($\Delta\text{AIC} 178$), but still much worse than the asymptotic model ($\Delta\text{AIC} 180$) (Table 4). Poor performance of models for survey type and season relative to the top models for each pairwise comparison suggested that handling time dynamics did not differ strongly between spring and fall or between night all-species surveys and day bass-only surveys. Visual inspection confirmed that the asymptotic model fit both time-space comparisons better than a linear relationship, and the asymptotic fit for the area fished-shoreline comparison approximated a linear relationship for the range of the data (Figure 2). Plots of fit for all models are included in the supplementary information (Appendix Figure S.1).

The best model for the comparison between the two measures of spatial effort incorporated a separate slope for each habitat type. Rocky sites had the highest slope (4.28), indicating that more area was fished per meter of shoreline. Fine sediment sites had an intermediate slope (2.63), and both habitat types with submerged wood had the smallest shoreline-area fished slope estimates (rock/wood: 1.64, sediment/wood: 2.01) (Figure 3). In general, catch rates for the two spatial effort metrics were highly correlated within habitats, though greater variation was observed in sites categorized as rock.

Estimates of the asymptote a , a measure of catch per unit effort, were similar in both time-space comparisons (Table 5; also Figure 2A & 2B). For the comparison of time fished versus area fished (Figure 2B & 2C), the asymptote value indicates the fish density at which gear saturation occurs. The implications of this estimate can be evaluated by considering that a one-meter forward boat movement in our study surveyed four square meters, therefore an areal CPUE of 0.38 fish/m² (e.g. at the high end of our observed range) indicates that 1.52 fish would be caught per meter of forward movement. Given our asymptote estimate of 15.07 fish/min (SE: 0.43) for the time fished versus area fished comparison (Table 5, Figure 2B), a boat traveling 9.9 m/min, or 0.59 km/h, would experience full gear saturation. A lower catch rate of 5 fish/min would experience minimal saturation, but require a much reduced constant forward speed of 0.13 km/h.

TABLE 5. Asymptotic model parameter estimates for both time-space pairwise comparisons

Parameter	Estimate	SE	<i>P</i>
Time Fished vs. Shoreline Distance			
<i>a</i>	11.32	0.31	<0.001
<i>b</i>	5.04	0.34	<0.001
Time Fished vs. Area Fished			
<i>a</i>	15.07	0.43	<0.001
<i>b</i>	7.43	0.38	<0.001

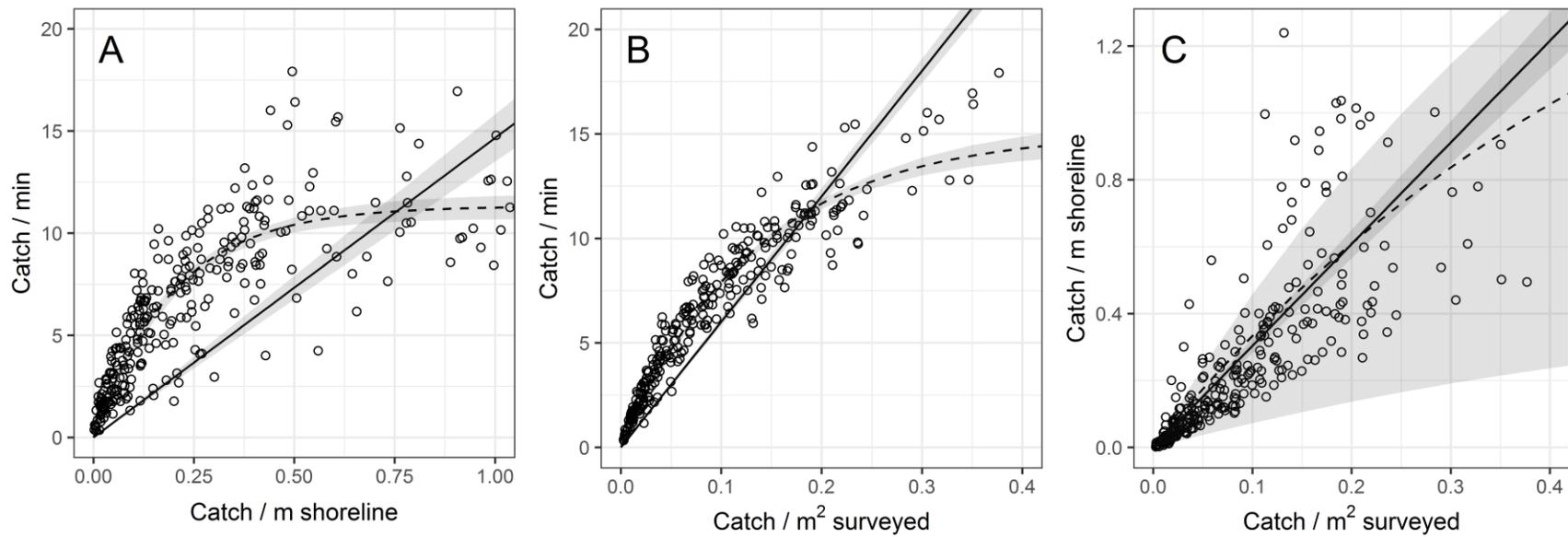


FIGURE 2. Simple linear (solid line) and asymptotic (dashed line) regression estimates versus actual data (points) for each of the three effort metric comparisons. Shaded areas represent 95% confidence intervals.

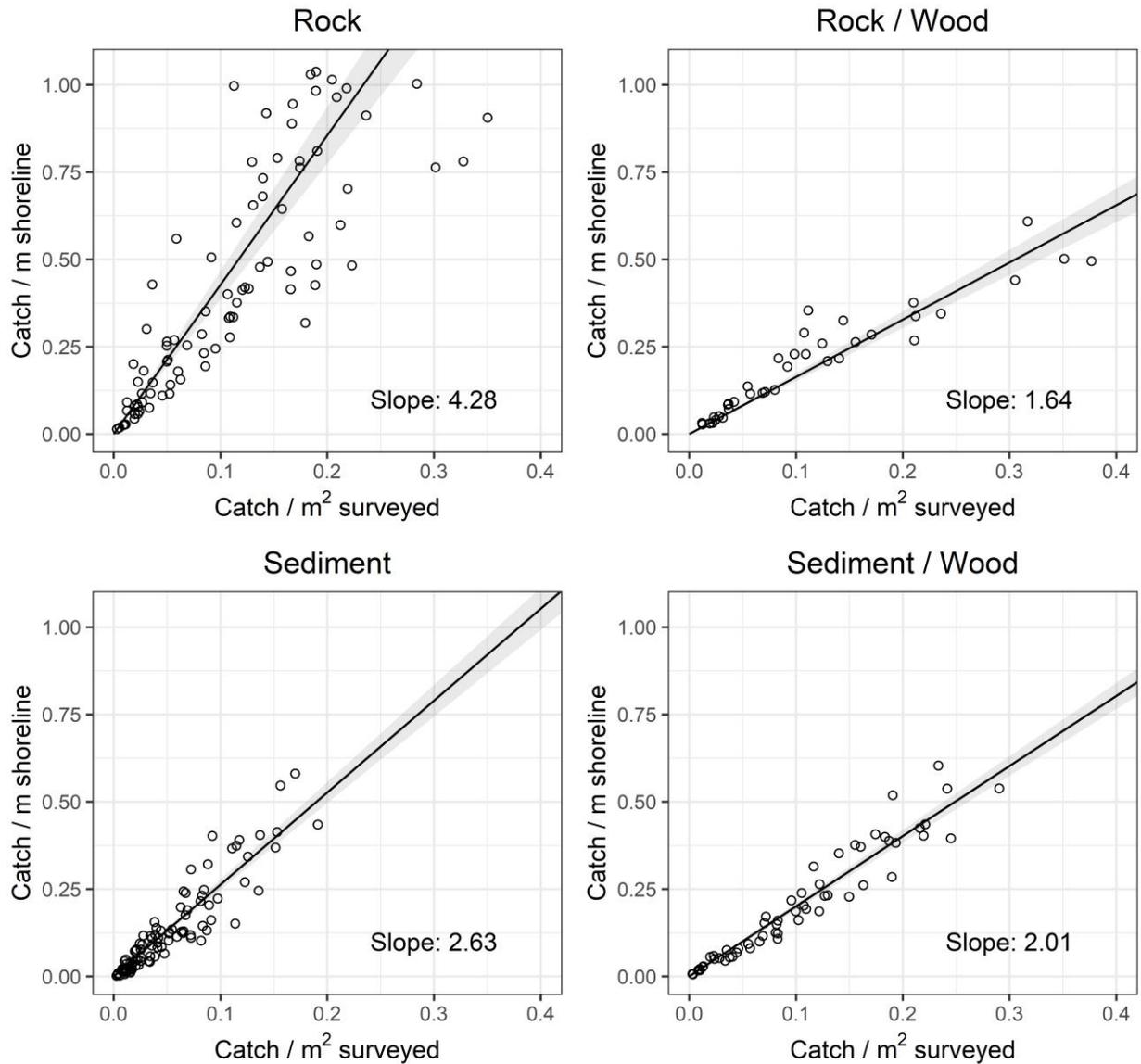


FIGURE 3. Habitat-specific regression slope fits for the comparison between the two spatial measures of electrofishing effort. Figure shows actual values (points), slope estimate (solid line), and 95% confidence interval (gray polygon) for each habitat type.

DISCUSSION

We found a nonlinear relationship between a CPUE metric based on time and two alternative metrics based on space, indicating that time-based boat-electrofishing CPUE may not serve as a representative index of abundance. An asymptotic model provided the best fit, suggesting that gear saturation can bias CPUE estimates when densities of fish are high. Compared to each other, the two spatial CPUE metrics were found to be linearly related. The slope of this relationship varied between habitats, likely due to boat operation differences in the presence of obstacles such as boulders and large submerged wood. Greater variability in this relationship was observed when surveying "rock" habitat, which likely reflects greater variation in this type of habitat in our study lakes. The shoreline of some study sites categorized as "rock" were relatively steep, therefore the area fished was effectively represented by shoreline length; other "rock" sites were wide, boulder-strewn flats that necessitated complex maneuvering. Overall, habitat-based differences in this relationship suggests that a CPUE measure based on shoreline distance is adequate for assessing trends in abundance within lakes similar to our study lakes, yet may not be suitable for comparing relative abundance between waters with contrasting littoral habitats.

A similar comparison between effort metrics was recently published by Tyszko et al. (2017). As in our study, these authors found a significant, positive linear relationship when fitting a simple linear model in their comparison of time fished and shoreline distance fished. Those authors used that finding to conclude that no gear saturation had occurred and time-based CPUE was therefore an appropriate index of abundance. However, visual inspection of their comparison between the two metrics (Figure 5 in their article) suggests that an asymptotic model might provide a better fit to their data, similar to our analysis. Tyszko et al. (2017) supported

their conclusion by referencing a study by McIrney and Cross (2000), which also compared time fished to shoreline distance and found no evidence for a non-linear relationship. Yet McIrney and Cross (2000) reported that the maximum encounter rate in their study was ~80 fish/hr. Their encounter rate was much lower than that in either our study or that of Tyszko et al. (2017) and was well below our estimated saturation levels.

In multispecies assemblages, saturation due to handling time may lead to single-species CPUE estimates that are biased unpredictably, both in direction and magnitude. This occurs because – while the numerator of the CPUE equation (i.e., catch) is a function of a focal species' abundance – saturation causes the denominator to be a function of the total catch of all species surveyed. Large differences in the catch of relatively abundant species, or those that are difficult to net, could therefore disproportionately influence total effort. This can produce time-based single-species CPUE estimates that are not proportional to the abundance of that species. This concept is well-established in hook-and-line fisheries where handling time has long been recognized as influencing CPUE (Sinoda 1981, Deriso and Parma 1987).

For our study lakes, we calculated that a forward speed of no more than 0.13 km/h in a constant-speed survey would be necessary to avoid saturation effects. This speed is far slower than the 1-3 km/h that Miranda and Boxrucker (2009) recommended for electrofishing surveys in lakes larger than 200 ha. Our smallest lake, First Bisby, had a total shoreline length of 5.1 km and would require approximately 39 hours of fishing time to fully survey at 0.13 km/h. As others have noted, constant speed is required in time-based surveys in order to ensure that sampling distances are constant (Miranda et al. 2009). However, one of the important outcomes of our analysis is that constant speed is not required for surveys using spatial metrics of effort. As a result, spatial measures of effort provide more flexibility, allowing boat operators to modulate

boat speed (and overall survey time) in order to net dense assemblages of fish or navigate complex habitats without adding to effort and therefore hindering comparability between surveys.

We found that area is a more robust measure of effort when comparing measures of spatial fishing effort in terms of area and shoreline length. We calculated the area surveyed using an assumed field width, drawn from literature values (Miranda and Kratochvil 2008). For the purpose of calculating catch density, our areal metric is therefore equivalent to a linear metric, with the exception of some slight variation due to turns or where shoreline geometry caused overlapping surveys of the same location. Measures of effort based on shoreline length assume that the path of the boat and the amount of time the electrofisher is activated are comparable from occasion to occasion. Our area-based metric provides a better measure of the true area fished during each survey and more effectively accommodates between-site variation in fishable habitat due to variables other than shoreline length.

An areal metric may also have advantages for future improvements to electrofishing standardization. We used an assumed static field width for our study, but other studies have shown that field size and power transfer are highly dependent on a number of factors including conductivity (Reynolds 1996), substrate composition and distance (Bohlin 1989), electrode geometry (Miranda and Kratochvil 2008; Reynolds 2016), and duty cycle (Miranda and Dolan 2004). Current approaches typically standardize boat configuration and adjust electrofisher settings to achieve a predetermined peak power output because variations in field size produce differences in catchability (Miranda 2009). Yet other variables that influence field size, such as depth and substrate, have largely been ignored when standardizing between surveys. Use of an areal metric introduces the potential for differences in field size to be directly incorporated when

measuring effort. This could be used to standardize CPUE between boats with different geometries and in situations where prescribed peak power outputs cannot be met.

It is important to note that gear saturation is but one of many potential sources of instability in catchability. As mentioned previously, studies such as those by Korman and Yard (2017), Schoenebeck and Hansen (2005), and others have shown that characteristics of the environment and fish community in question can substantially affect q . At low fish densities these effects probably have a far greater impact on CPUE estimates than any effect of gear saturation. However, at high densities the effects of gear saturation may strongly influence CPUE. For example, our asymptotic model fit indicates that a 100% increase in catch/m shoreline (0.5 fish/m to 1.0 fish/m) would, on average, only result in a 10% increase in fish/min (10 fish/min to 11 fish/min). In all circumstances, boat operators should attempt to control for variables that may influence q ; the choice of effort metric represents one way to do so.

In conclusion, we reflect upon the statement by Reynolds (1983) in the first edition of *Fisheries Techniques*: "Distance of shoreline sampled is also a good effort index, but this requires shoreline measurements for each sample unless permanent stations are repeatedly used". That advice occurred when mapping sites was laborious and likely imprecise, yet time fished provided a simple and seemingly accurate index of sampling effort. Thus, for most purposes, time was the best measure of effort by virtue of being the only feasible option. In the 35 years since Reynolds' publication, technological advances have increased the availability and accuracy of spatial data. With the implementation of the Global Positioning System in 1993, precise measurements of position have become readily available. Despite these improvements, guidelines for measuring electrofishing effort published in the third edition of *Fisheries Techniques* (Reynolds and Koltz 2012) are almost identical to those published nearly 30 years

before – with the exception of a single new line stating that "Global Positioning System equipment may be useful for locating critical habitat or developing a repetitive electrofishing track." Although this is accurate as stated, the utility of GPS technology to electrofishing extends well beyond its use as a navigational aid. We encourage those implementing future electrofishing surveys to re-examine the use of time as the default measure of electrofishing effort and give consideration to methods utilizing area that were not available when early guides for electrofishing were published.

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APPENDIX

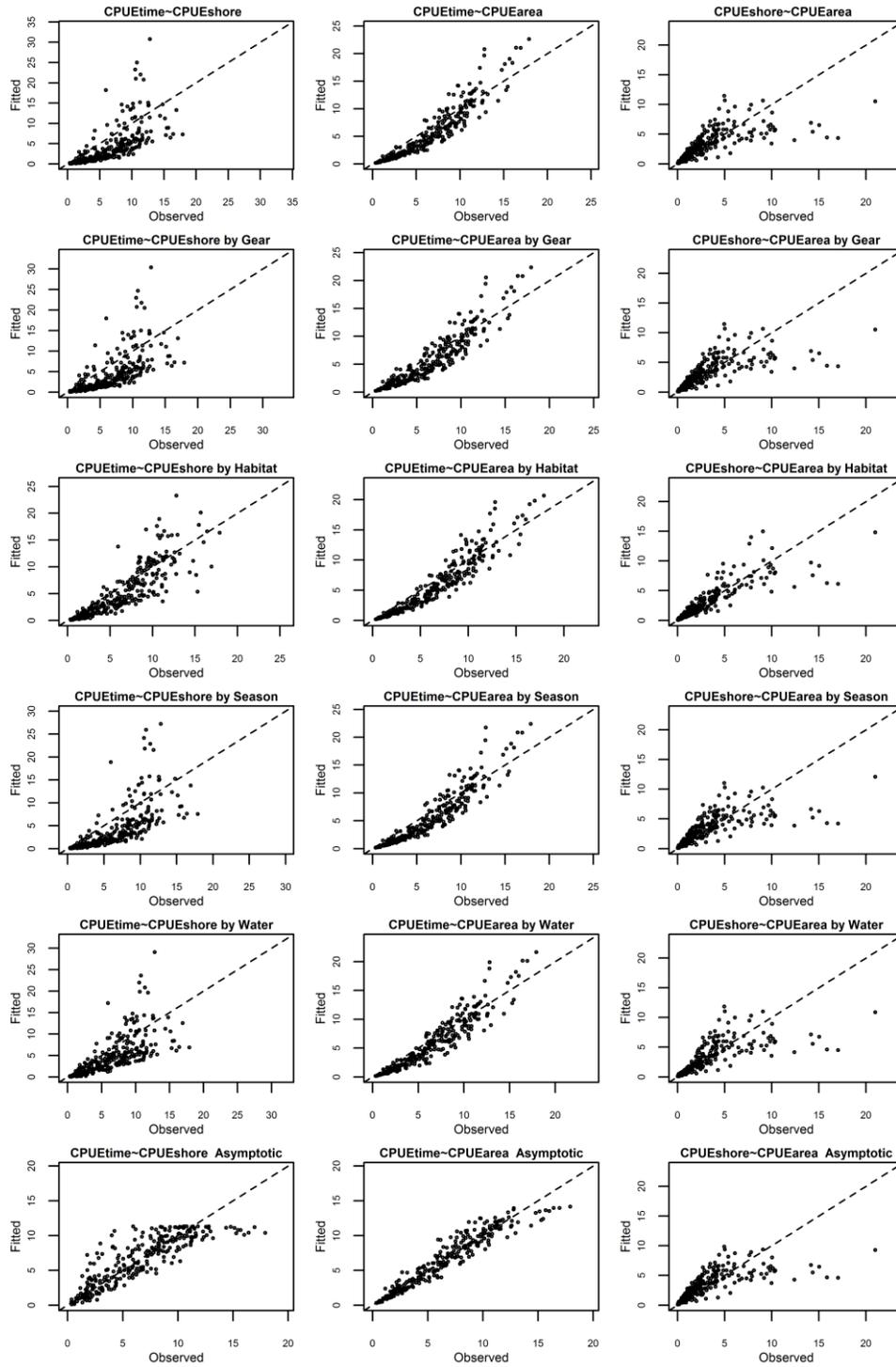


FIGURE S1. Plots of fit for all models. Figure shows values for each sampling occasion (points) versus a 1-to-1 relationship (dashed line)

CHAPTER 2 – EXPANDING THE FEASIBILITY OF FISH AND WILDLIFE ASSESSMENTS WITH CLOSE-KIN MARK-RECAPTURE

ABSTRACT

Close-kin mark-recapture is a powerful new method for the assessment of fish and wildlife populations. Unlike traditional mark-recapture techniques, the use of kinship as an identifying “mark” is robust to many forms of capture heterogeneity including variation in gear efficiency and tagging-based effects such as loss and differential mortality. In addition, close-kin methods can be applied to a wider range of sampling designs than traditional methods including single-occasion surveys, can provide retrospective historical abundance estimates, and can produce survival estimates from as few as two sampling occasions. We evaluated the ability of close-kin mark-recapture to provide estimates of abundance and adult survival, and then compared results to those from traditional mark-recapture. This analysis incorporated data from a three year study of lake resident brook trout (*Salvelinus fontinalis*) where individuals were both physically (PIT) tagged and genotyped for 44 *de novo* developed microsatellites with high throughput sequencing. Traditional mark-recapture estimates were derived using Pollock’s Robust Design, relying upon three primary “open” sampling occasions and four secondary “closed” occasions. We found that close-kin methods produced contemporary estimates of adult abundance and survival that were similar to those produced by traditional mark-recapture in both magnitude and precision. Furthermore, close-kin mark-recapture provided abundance estimates for multiple years prior to sampling and, when restricted to data from a single year, could still produce reliable abundance estimates for at least one and as many as three years. Retrospective abundance estimates corresponded with those from a separate historical two-sample mark-recapture dataset. This study provides support for the use of close-kin mark-recapture as a robust

and sampling-efficient alternative to traditional mark-recapture methods of assessing population parameters.

INTRODUCTION

The recovery of marked individuals has provided a foundation for estimating animal abundance and survival, providing tools to assess fish and wildlife populations that would be infeasible to census directly. Closed population estimation approaches, such as the two-sample Chapman estimator (Chapman 1951) and a wide-variety of multiple-recapture models (e.g. Burnham and Overton, Schnable, etc.) (Sutherland 2006) utilize short sampling intervals to estimate abundance with the assumption that no loss or gain of individuals has occurred. Open estimators like the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965) use longer intervals to estimate additional parameters such as survival. Pollock (1982) combined these approaches using a "robust" design that estimates abundance from a set of closed-population surveys and survival from open periods between these surveys. Many subsequent modifications and applications continue to extend mark-recapture models (Lebreton et al. 1999; Williams et al. 2002; Cooch 2008; Amstrup et al. 2010), with some recent advances leading to integrated population models that combine mark-recapture analysis with other forms of demographic modeling and data (Zipkin and Saunders 2018).

Although widely used, mark-recapture models rely upon assumptions that inevitably bias population estimates when they cannot be met (Pollock 1980; Kendall 1999). At the heart of mark-recapture techniques is the idea of capture probability i.e. the probability of an individual being detected (captured) in a single unit of sampling effort. Indeed, one of the most challenging assumptions for any field survey to meet is to avoid "unmodeled" capture heterogeneity during survey efforts; that is, capture probability cannot vary within or between data collection periods

in any way that is both systematic and not included within the underlying model (Link 2003). Yet, capture probability is almost always influenced by size-selectivity (Anderson 1995), gear efficiency (Seber 1970), or capture location (e.g. habitat type), violating this key assumption (Royle et al. 2013). In addition, model estimates ultimately rely on recapture events, requiring that previously handled individuals are catchable and distinguished from previously uncaptured individuals, which introduces bias due to mortality from tag implantation, increased predation after handling, and tag loss (Pine et al. 2012). Similarly, behavioral responses to capture can also bias parameter estimates, as individuals may become more or less likely to be recaptured on subsequent occasions, referred to as “trap-happiness” or “trap shyness” (Geis 1955).

Molecular techniques offer a promising approach to minimize many of the factors that confound mark-recapture models. Genetic markers can provide individual identification while avoiding the negative impacts common to physical tags (Taberlet et al. 1999). Some techniques, such as hair snares, have been used for two decades to collect genetic samples for individual identification without any direct handling of animals by researchers (Woods et al. 1999). However, until recently these genetic techniques have largely been applied as a direct replacement for physical tags. Close-kin mark-recapture (CKMR) builds on this framework by using genotype-derived estimates of kinship (i.e. not just individual identification) to extend mark-recapture methods to circumstances where sparse sampling or lethal capture makes direct-recapture unlikely or impossible (Bravington et al. 2016b, 2016a).

CKMR compares the number of kinship pairs observed in a sample or set of samples to the total number of potential pairs (based on observed age structure), making possible an estimate of the total number of potential parents (i.e. mature adults) present during one or more mating-years. By relying upon an individual's genotype as the initial "mark" and capture of

closely-related individuals the “recapture” events, CKMR obviates many challenges inherent to traditional mark-recapture modeling. For example, capture heterogeneity due to individual size is accounted for in CKMR by the overall number of potential kinship pair comparisons; a capture method that selects for larger individuals will result in a sample with fewer potential offspring, thereby decreasing both the total number of comparisons examined and the expected number of kin-pairs. Another confounding influence on traditional mark-recapture is alleviated with CKMR because individuals in a set of samples are only considered once for the purposes of comparison, therefore effects that occur after initial capture, such as trap-shyness, do not influence the overall number of comparisons or the probability of identifying a kin-pair. As unique individuals are only considered once, it becomes possible with CKMR to obtain abundance estimates from sampling designs that would traditionally be difficult or impossible to model with traditional MR including single capture occasions and from any combination of 'dead recovery' events (i.e. lethal sampling).

The ability of CKMR to obtain estimates under challenging capture conditions and robustness to many variables that impact traditional MR studies has led this approach to be applied to wide-ranging and difficult to capture marine species such as southern bluefin tuna (*Thunnus maccoyii*) (Bravington et al. 2014a) and Antarctic blue whale (*Balaenoptera musculus*) (Bravington et al. 2014b). Ruzzante et al. (2019) recently provided the first in situ validation in a freshwater system by comparing CKMR to contemporary Chapman abundance estimates from double-pass electrofishing for a set of stream-dwelling brook trout (*Salvelinus fontinalis*) populations and concluded that estimates from the two techniques were statistically indistinguishable. Their approach implemented an alternative parameterization of the CKMR statistical model, using it to estimate population abundance for a set of discrete populations.

While that work represents an important validation of CKMR, in this study we explore a suite of additional features useful for fish and wildlife assessments that are available through CKMR.

Population estimation techniques that make efficient use of small sample sizes and flexible study designs can be usefully applied to a wide range of animal populations. Coupled with the rapid decrease in genotyping cost, CKMR represents a technique that may be both efficient and cost-effective for biologists and managers seeking to better understand population demographics. To further assess the potential of this technique we conducted a side-by-side comparison of estimates obtained by parent-offspring-pair-based CKMR and traditional mark-recapture (Robust Design and Chapman models) using data from three sampling efforts on brook trout in an isolated Adirondack lake. The availability of a multi-year dataset from a long-lived population allowed us to evaluate the accuracy of estimates of adult survival and abundance from a CKMR analysis. We show that CKMR can achieve single-sampling occasion abundance estimates, survival estimates with only two sampling occasions, and depending on the ages of sampled specimens, can reconstruct abundances for previous years not directly sampled. These results demonstrate that CKMR is a promising technique for a wide range of systems that include small, spatially discrete populations as well as large, wide-ranging ones.

METHODS

Overview

Our study involved three main efforts. First, we sampled and tagged brook trout in order to obtain the tissue samples needed for CKMR, as well as the recapture data used in the traditional mark-recapture side of our comparison study. Next, we used the genotypes to identify parent-offspring pairs (POPs) within our dataset. This involved three substeps: marker discovery, genotyping, and kinship analysis. Marker discovery is necessary when there are no pre-existing

marker sets with sufficient power for parentage analysis. Although both microsatellites and RAD-seq derived single nucleotide polymorphisms (SNPs) have previously been developed for our target species (Perry et al. 2005; Lamaze et al. 2012), the possibility that a bottleneck caused by acid precipitation might have reduced allelic diversity within the population led us to develop a new set of 44 microsatellite markers that were highly polymorphic in our target population to increase our parentage assignment power. Each individual was genotyped for the new marker set through efficient and cost-effective amplicon sequencing. The genotype data were then combined with ancillary information (e.g. age) to determine whether each individual's parents are included in the dataset. Inclusion of age information allowed impossible parent-offspring combinations to be removed from consideration. Finally, the resulting information (recaptures and POPs) was used to estimate survival and abundance within the traditional mark-recapture and CKMR model frameworks.

Study area and sampling

Honedaga Lake is located in the southwestern Adirondack Mountain region of New York State and has a surface area of 312 ha and a maximum depth of 55.8 m (Map 1). This lake was highly susceptible to acid deposition due to its location and small, poorly buffered watershed (Schofield 1965), which led to the near-extirpation the native brook trout population until regulation of air pollution spurred recovery in the early 2000's (Kraft 2019).

From 2015-2017, we surveyed brook trout during the first two weeks of May each year using ten Oneida-style trap nets (car 1.2 x 1.2m, lead 30 m, wings 1.6m, mesh 12 mm) and four hoop nets (4 hoops, diameter 1.5 m, mesh 6 mm) deployed at standardized sites throughout the lake (Figure 1). Nets were allowed to soak for 48-72 hours prior to each capture event and were

reset immediately after tending until a total of four sequential capture occasions had been conducted during each May sampling period.

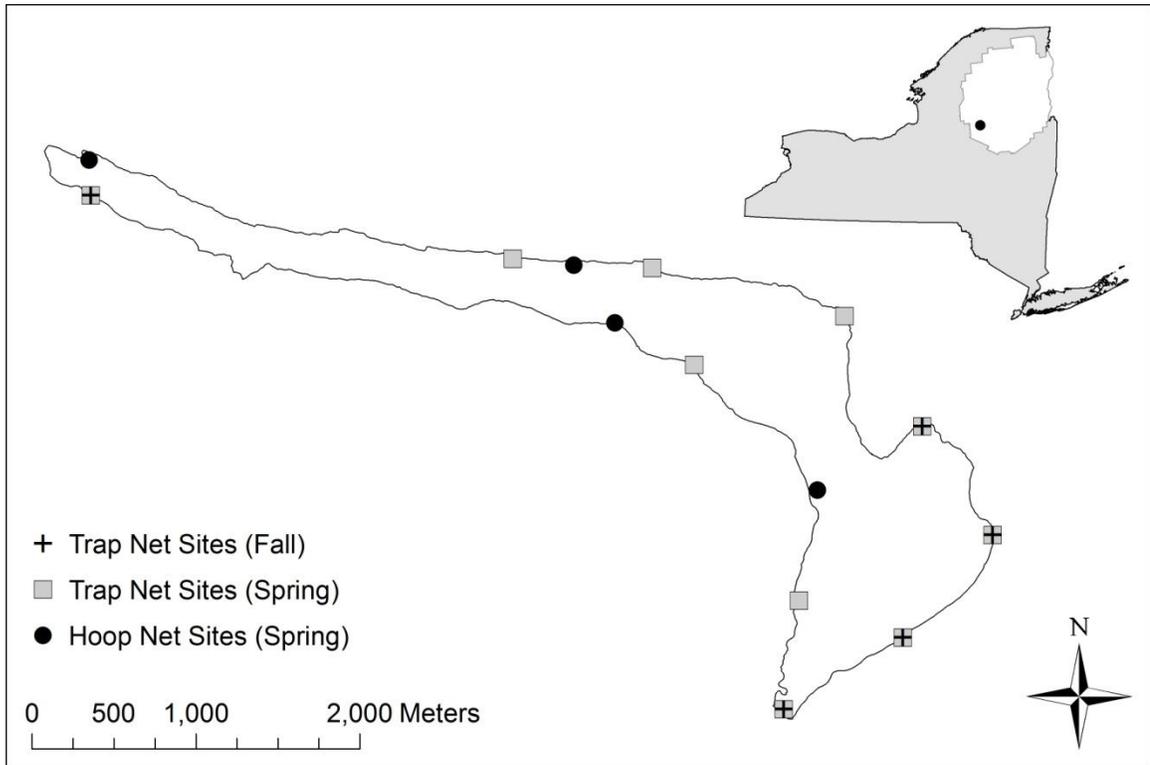


FIGURE 1. Honnedaga lake with fall trap net sites (crosses), spring trap net sites (gray squares), and spring hoop net sites (black circles).

Captured fish were measured, weighed, and scanned for previously deployed tags. Fish 150mm or larger that had not previously been captured were tagged with a 23mm HDX PIT tag (OregonRFID) and given a partial-adipose fin clip to allow tag loss to be detected. From 2016-2017 we preserved these clips in 95% EtOH and froze them for genetic analysis. Although genetic samples were not taken for 2015, we were able to use tag data to identify individuals that were recaptured and genotyped during subsequent years. For example, a fish that was tagged in 2015, recaptured in 2016, and genotyped from a tissue sample taken during that second occasion would be considered a genotyped fish for both years. Following recovery, we released fish in an

offshore location within the general area of the lake where they were originally captured. Sampling events for the historical (pre-study) traditional mark-recapture estimates were similar and consisted of single-occasion fall (October) surveys from 2012-2018 using the same gear and sites. Fish captured during these surveys were either tagged with Hallprint (2012-2014), or PIT (2015-2018) tags. We assigned a probable age to each fish based on observed length distributions and length-age information from a set of 831 previously aged fish (Appendix S3: Figure S1).

Samples were aggregated differently for each of the three estimation models (Figure 2). For the Robust Design traditional mark-recapture model, each spring sample occasion and year were treated separately. Samples were compared within each year to estimate abundance for that year, while comparison between years was used to estimate survival. In the CKMR model, samples from all occasions within a year were pooled together. Estimated age and capture year were then used to estimate each individual's year of conception. This allowed us to identify potential POPs based on relative conception years. For example, in a population that matures at age one, an individual from the 2010 cohort and one from the 2012 cohort would constitute a viable potential POP regardless of the capture year for either individual. Finally, the historical Chapman estimates were based on the pre-study dataset of single-occasion fall captures.

Molecular Analysis

Genomic DNA was extracted from all tissue samples using the Truett et al. (2000) HotSHOT protocol, which combines a 30-minute hot (95°C) incubation with sodium hydroxide followed by treatment with a neutralizing agent (Tris-HCL). We amplified 74 newly identified microsatellites in two multiplex polymerase chain reactions (PCRs) per individual, built a dual-indexed library

with all the amplicons for each individual, and sequenced the libraries on an Illumina HiSeq 2500 instrument. The resulting sequence data were processed with a custom bioinformatic pipeline for automated quality filtering and genotyping. In total, 44 loci passed our filtering criteria and were used for kinship analysis. Detailed information about our microsatellite discovery, library preparation, and genotyping procedure is provided in Appendix S1.

Genetic Kinship Analysis

Kinship analysis.— We used the software CERVUS 3.0 to analyze kinship and assign parent-offspring pairs because A) the program allows for the assignment of parent pairs (i.e. parent-offspring trios), B) it accommodates parents of unknown sex, and C) it allows for genotyping error (Marshall et al. 1998; Kalinowski et al. 2007). As CERVUS can accommodate some missing data, all well-performing loci typed for more than half (n=215) individuals were included in the parentage analysis (n = 44) (Appendix S1: Table S1; Table S2). We used likelihood ratio scores to assign likely trios and determined 99% confidence critical values using a simulation of 10,000 offspring, 2200 parents (the maximum allowed by the software given our dataset), and an error rate of 0.05 (chosen based on observed error rates, see Appendix S1). We chose to use a 99% confidence threshold as false-positives are far more likely to negatively affect CKMR estimates than false-negatives (Anderson 2019). Simulations suggested broad separation between likelihood ratio scores for true parent-offspring combinations and unrelated individuals (Appendix S2: Figure S1), indicating that our genotype data has high power to correctly infer POPs. Offspring not assigned to a trio were re-evaluated for a single-parent analysis using the same simulation settings and acceptance standards.

Population Estimation Modeling

Close-kin mark-recapture.— Close-kin mark-recapture is based on the idea that, given two individuals with sufficiently different ages to potentially constitute a POP the probability of the pair actually being a POP is the number of potential parents roles (e.g. one if the potential parent's sex is known, two if not) divided by the total number of potential parents that were alive when the younger individual was spawned. Thus for non-lethal sampling with unknown sexes, the probability of potential parent i and offspring j with birth years y_i and y_j being a kin-pair K (i.e. a parent-offspring pair in this case) can be expressed as:

$$\mathbb{P}[K_{ij} = \text{POP}] = \frac{2 \mathbb{I}[y_i + \alpha \leq y_j]}{N_{adult\ y_j}}$$

where the indicator function \mathbb{I} determines whether i was old enough at y_j given the age-at-maturity α . This indicator is multiplied by two for unknown sexes because each potential offspring has two parents i.e. two chances for a given adult to be their parent. Because identity is based on the potential offspring's genotype, the true parents can be considered "marked" regardless of whether they are actually observed. As the probability is conditioned on the fact that both compared individuals are alive at the time of capture (and therefore alive during the potential offspring's conception year), adult mortality does not affect the estimate. The exception to this is when the potential parent was sampled prior to the potential offspring's conception year, in which case the numerator must be discounted by the adult survival rate φ (i.e. by the chance that the potential parent died post-sampling and pre- the potential offspring's conception). This takes the form:

$$\mathbb{P}[K_{ij} = \text{POP}] = \frac{2 \mathbb{I}[y_i + \alpha \leq y_j]}{N_{adult\ y_j}} \times \begin{cases} 1 & t_i > y_j \\ \varphi^{(y_j - t_i)} & t_i < y_j \end{cases}$$

Studies that include samples from more than one year can therefore be used to estimate adult survival as long as least one observed POP includes a parent that was captured before its offspring's birth. Extended to all potential POPs, this probability function follows a binomial distribution (Hillary et al. 2018). Close-kin mark-recapture can also accommodate the inclusion of covariates that may influence an adult's reproductive potential. For example, size is often closely related to fecundity and larger individuals may therefore be more likely to be potential parents (Ruzzante et al. 2019). This approach is particularly useful when the gear used to capture parents may be highly size selective (Bravington et al. 2016b; Skaug 2017). Here we expect the gear to produce a catch with minimal size selectivity within adult year classes, as selectivity of trap nets a function of mesh size (Millar and Fryer 1999), and therefore model fecundity as constant for simplicity.

In our study we used length-based estimated age and year of capture to determine the year class (i.e. spawning year) of each individual. Because potential POPs are determined by year class, fish can be compared between any number of sampling events within and between years. Thus for the analysis we pooled fish from all surveys and years. Our offspring dataset was restricted to fish age-3 and younger at the time of capture, as we were less confident in our ability to assign length-based ages beyond age-4 (i.e. we could not confidently discriminate between an age-4 individual and an age-5 individual) (Appendix S3: Figure S1). This restriction reduced both the number of potential parent-offspring combinations and the expected number of identified POPs for earlier year classes, reducing the precision of estimates for those years but leaving them unbiased. This choice also allowed us to use the parent-centric formulation described by Bravington et al. (2016b) that is simpler but relies on predetermined ages rather than the offspring-centric approach described by Skaug (2017) and used by Ruzzante (2019).

Based on gonad development of previously captured and aged fish from fall samples, we set $\alpha = 1$ because 93% of the age-1 fish caught during the spawning season were reproductively mature. We compared each individual in this restricted dataset (potential-offspring) to each individual in the full dataset (potential-parent) to obtain our total number of combinations for the model.

Robust design mark-recapture.— We used Pollock's closed robust design which uses datasets consisting of multiple closed-capture occasions separated by larger open intervals to estimate both yearly abundance and survival from traditional tagging data (Pollock 1982; Kendall et al. 1995). Beyond abundance and survival, the model has been extended to accommodate generic capture heterogeneity among individuals through a ‘temporary emigration’ process i.e. the probability that an individual leaves and re-enters the capturable population during the study period (Kendall et al. 1997), and to include various divisions of capture probability parameters to accommodate systematic capture heterogeneity such as trap shyness. For our model we assumed that no effect of capture on capture probabilities and estimated a separate capture probability for each sampling occasion.

Chapman estimator.— To estimate historical annual abundance estimates for comparison to CKMR estimates for years preceding those for which robust design mark-recapture estimates could be generated (2012-2014), we used a separate dataset of yearly single-occasion fall trap net surveys, as described previously, in conjunction with the standard Chapman modification of the Lincoln-Petersen estimator (Lincoln 1930; Chapman 1951). The Chapman estimator carries an assumption of population closure, which may not be satisfied in our present study due to mortality and the potential for recruitment between years. However, under the assumption that mortality is equal across the tagged and untagged population, and that immigration or emigration

does not occur, the estimator can provide valid abundance estimates under specific population closure violations, providing a census at the time of the first sampling occasion for any pair of sampling occasions (Seber 1982). Long term continued capture and tagging efforts on the Honnedaga Lake brook trout population indicate fish are robust to capture effects, with specimens being caught multiple times over sampling years. Thus we believe there is little to no additional mortality associated with fish sampling and that the assumption of equal mortality among tagged and un-tagged fish is plausible. Similarly, as Honnedaga Lake is isolated, migration of fish into the lake is not feasible. Recruitment of fish from the Honnedaga Lake population between any two specific years would be a form of ‘immigration’, however, to eliminate the potential for recruitment between any pair of yearly sampling occasions that could bias estimates, we limited our secondary sample to fish that were at least 50 mm longer than the minimum tagging size for the primary sample (150 mm). Thus, consistent with our robust design estimates, abundance estimates were developed specifically for the portion of the Honnedaga Lake brook trout population > 150mm in size.

Model Implementation.— We used Bayesian implementation for all three models. Close-kin mark-recapture and Chapman models were run using using rjags (Plummer et al. 2018), a Program R-based interface for the JAGS library (Plummer 2003), with the jagsUI wrapper (Kellner 2018) to allow for parallel processing which greatly increased analysis speed. Three MCMC chains were used and each run for 10,000 iterations. Our Bayesian robust design model used the code provided by Rankin et al. (2016) adapted for our data and, as with our CKMR model, was estimated in Program R using JAGS (Plummer 2003) through the rjags interface (Plummer et al. 2018) with dclone used for parallel processing (Solymos 2019). Three MCMC chains were run for 100,000 iterations each.

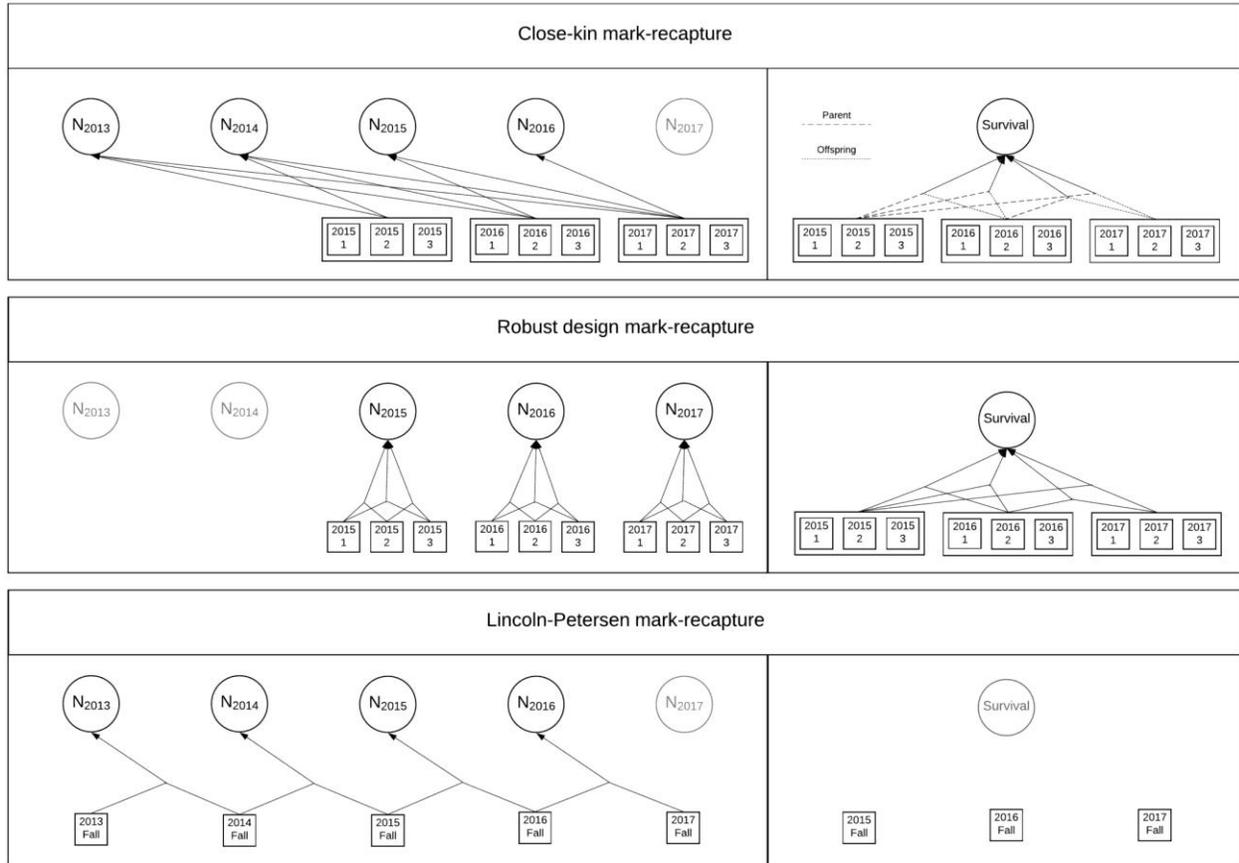


FIGURE 2. Contribution of sampling occasions (rectangles) to yearly Honnedaga lake Brook trout parameter estimates (circles), including abundance (left boxes) and survival (right boxes) for three different model types. Single lines represent the potential for estimates based solely upon that sampling occasion while joined lines denote the requirement for information from both occasions (e.g. mark and recapture). Joined lines with differing broken line types indicate the requirement for information from two separate individuals where the relation and order of individuals matters. I.e. close-kin mark-recapture survival estimates can only be obtained when a parent is sampled prior to its offspring's conception while robust design mark recapture can provide survival estimates when any individual is captured and recaptured across an open sampling occasion. Consecutive closed spring sampling occasions are denoted by year and sequential numerals. Pooled sampling occasions, i.e. those combined without regard to timing, are enclosed within a second rectangle. Years for which the given model and sampling occasions cannot provide parameter estimates are shaded grey

RESULTS

Sampling during the spring 2015-2017 field seasons resulted in capture and tagging of 716 unique fish (Table 1). In total 44 of our newly developed microsatellites passed our data filtering criteria and were genotyped in the 384 individuals caught during the 2016-17 spring sampling occasions. The mean number of successfully genotyped loci per individual was 36.2 loci (82.3%). The number of alleles per locus ranged from 2-11 (average of 7.07 alleles) with heterozygosity between 0.29 and 0.95 (average of 0.72). Mean observed genotyping error rates were 0.02 for known parent-offspring trios and 0.04 for replicate samples. More details of genotyping procedures and performance are available in Appendix S1.

TABLE 1. Summary of spring sampling returns for 2015-2017 including the number of taggable-sized individuals caught during each occasion as well as the number of recaptures for both the closed period and the larger open dataset. Also included is the number of individuals caught during each occasion that were later genotyped.

Occasion	Individuals captured*	Recaptures (within year)	Recaptures (total)	Individuals genotyped
May 6, 2015	90	N/A	N/A	16 [†]
May 8, 2015	86	7	7	19 [†]
May 11, 2015	192	8	15	44 [†]
May 13, 2015	168	12	21	28 [†]
May 4, 2016	78	N/A	3	68
May 6, 2016	35	2	3	33
May 9, 2016	84	1	11	69
May 11, 2016	27	4	5	25
April 28, 2017	32	N/A	4	28
May 1, 2017	38	0	1	36
May 3, 2017	29	1	2	25
May 5, 2017	20	1	1	20

* Number of individuals captured reflects only those that were large enough to tag (≥ 150 mm).

[†] No tissue samples were taken during 2015. Number reflects tagged individuals that were recaptured and genotyped during subsequent years.

Of the 384 genotyped individuals, 257 were young enough (age ≤ 3) for consideration as potential offspring. This yielded 98,431 potential combinations of which 67,840 had an age difference large enough for consideration as a POP. Fall surveys captured a total of 2987 fish over the 11-year 2012-2018 period (Table 2). Parentage assignment identified 72 parent-offspring pairs from among the 384 specimens collected during 2016-2017 spring sampling, including two parent-offspring trios (offspring, mother and father) that met the critical value for 99% confidence.

TABLE2. Summary of fall sampling returns for 2012-2018 including the number of individuals caught during each occasion as well as the number of recaptures from the previous year.

Year	Individuals captured*	Individuals recaptured
2012	312	25
2013	217	32
2014	314	36
2015	526	71
2016	384	79
2017	330	35
2018	246	24

* Number of individuals captured reflects only those that were large enough to tag (≥ 150 mm).

Presence of at least two POPs for each potential-offspring cohort year allowed CKMR estimates of fall adult abundance for 2011-2015. All parameters for the CKMR model converged successfully with Gelman-Rubin \hat{R} statistics < 1.1 (Table 3) (Gelman and Rubin 1992). Estimates for abundance during the study period displayed an upward trend from 2011-2014 with tight 95% confidence intervals. Chapman estimates paralleled those for CKMR, displaying a similar upward trend (Figure 3). The robust design traditional mark-recapture model also

successfully converged for all parameters and provided similar estimates of abundance for 2015-16 (Table 4). Although convergence was successful for the 2017 abundance estimate, the 95% confidence interval was extremely wide (2889 – 14258) due to the low number of closed recaptures during the 2017 sampling occasions (Figure 3).

TABLE 3. Parameter estimates for the Close-Kin Mark-Recapture model including adult abundance for all estimable years ("N-[year]") and annual survival. Also provided are the number of potential parent-offspring comparisons and number of identified parent-offspring pairs (POPs) for each parameter. R-hat refers to the Gelman-Rubin diagnostic which indicates poor MCMC convergence when values are above 1.1 (Gelman and Rubin 1992).

Parameter	# Comparisons	# POPs	Estimate	R-hat
N-2011	1066	2	602 (136 - 1733)	1.00
N-2012	6370	16	1016 (479 - 1978)	1.00
N-2013	14490	19	1788 (1013- 2875)	1.00
N-2014	26606	25	2126 (1410 -3039)	1.03
N-2015	17850	10	2093 (1321 - 3119)	1.00
Survival	5200	7	0.811 (0.46 – 0.99)	1.00

TABLE 4. Parameter estimates for the Robust Design model with number of potential parent-offspring comparisons and number of identified parent-offspring pairs for each parameter

Parameter	Estimate	R-hat
N-2015	1729(1042 - 3268)	1.01
N-2016	2979 (2289 - 3907)	1.00
N-2017	6141 (2889 - 14742)	1.00
Survival	0.74 (0.49 - 0.97)	1.00

An additional nine POPs were identified where the parent was sampled one year prior to their offspring's spawning, allowing survival of mature fish (age-2 or greater) to be estimated

using CKMR from these two year's data. The resulting estimate of annual adult survival was 0.80 (95% CI: 0.44-0.99). Traditional robust design estimates of adult survival were similar with a mean of 0.75 (95% CI: 0.49-0.99).

In addition to the analysis using the full dataset, CKMR estimates were successfully obtained for each of the single-year sampling datasets in isolation. Samples from 2015 were able to provide fall abundance estimates for 2011 and 2012 while samples from 2016 provided estimates for falls 2011, 2013, and 2014. Samples from the spring 2017 surveys could only provide an abundance estimate for fall 2015. Single year abundance estimates were comparable to those obtained from the full dataset in both mean and 95% CI. However, survival estimates require at least one POP where the parent was sampled prior to the offspring's conception, therefore estimates of survival cannot be obtained from any single-year CKMR

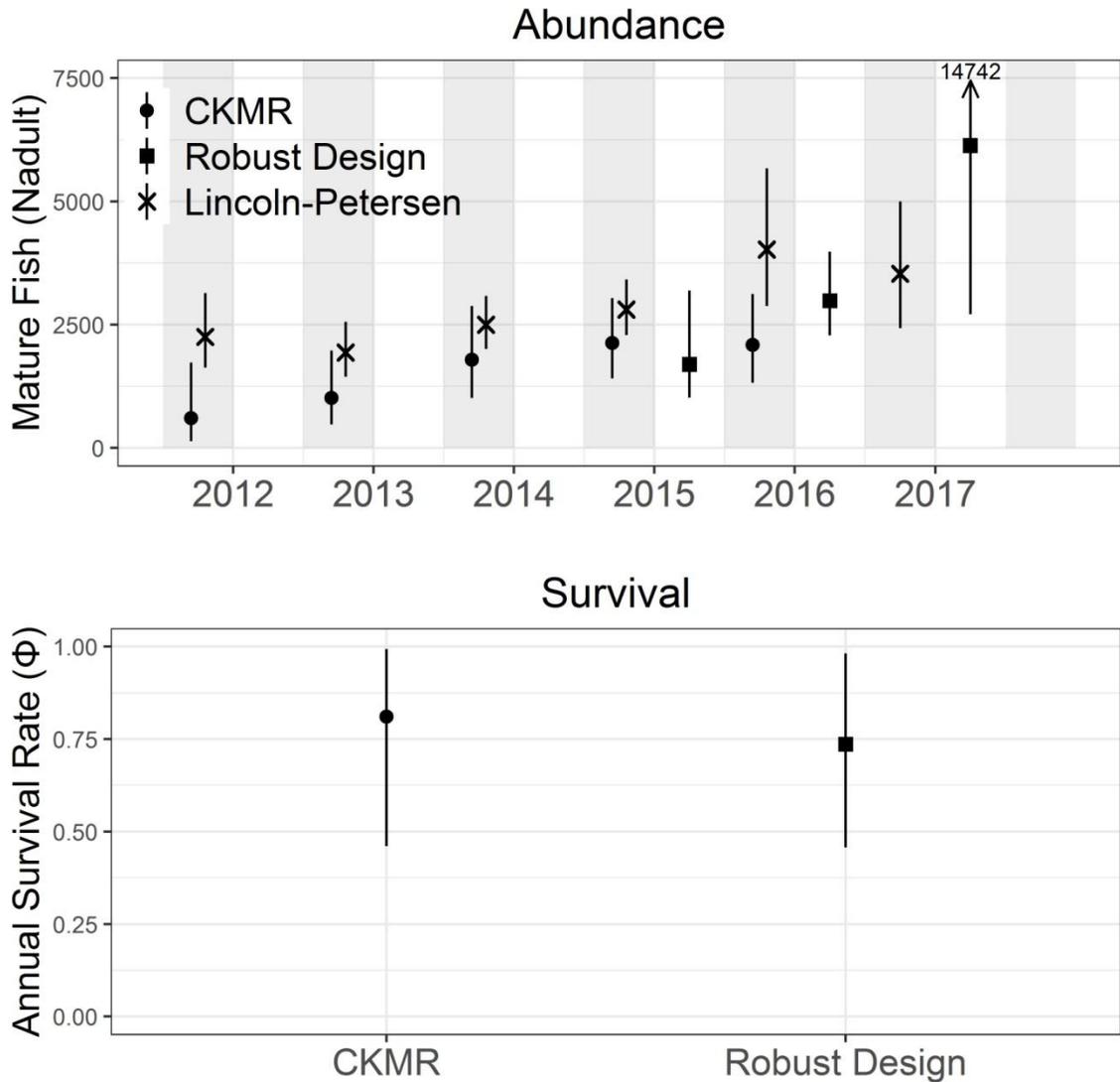


FIGURE 3. Estimates of abundance and annual survival from the full-sample Close-Kin Mark-Recapture (circles) and Pollock's Closed Robust Design (squares) models for spring survey data as well as estimates of abundance from the fall survey-based between-year Lincoln-Petersen estimators (triangles).

DISCUSSION

Our estimates of abundance for fall 2014-15 and annual survival from the CKMR model were comparable to those for spring 2015-2016 obtained from the robust design traditional mark-recapture model despite relying upon almost entirely different sets of data. While correspondence between the models does not necessarily mean that either is free from bias, this broad agreement suggests that differences in bias between the two models are minimal. For example, 95% confidence intervals from the robust design model overlapped the CKMR estimates for the both one-year periods for which estimates were available from the two models. In both cases, models suggested that approximately 2500 adult brook trout inhabit the study lake. The two models also provided median posterior estimates of adult survival with very similar (albeit low) precision. The estimated mean annual survival rates were approximately 0.80, consistent with a population inhabiting a lake without other piscine predators, few avian predators and ample thermal refuge. We consider it notable that the CKMR and robust design estimates had similar precision, though the CKMR model used a much lower sample size (Table 1). Tissue samples were not collected during spring 2015, which if available could have provided information about parents of younger age classes caught in 2016 and 2017.

Historical estimates of abundance from CKMR compared favorably with those obtained from between-year Chapman estimators using individuals collected during fall sampling occasions (Figure 3). In both cases, an upward trend in abundance from 2012 to 2015 was evident and – while Chapman estimates were higher than those given by the CKMR model – the 95% confidence intervals of each overlapped. It is important to note that since fall surveys captured many more fish than did spring surveys (Table 1, Table 2), the Chapman estimates are based on a much larger number of fish than are the CKMR estimates. Additionally, between-year

Chapman estimates required several key assumptions: no migration, no difference in survival between tagged and untagged individuals, no negative effect of capture (i.e. "trap shyness"), and a 50 mm cutoff for the second capture occasion fish to eliminate incorporating new recruits in the data evaluated. Although decades of collective experience surveying this population lead us to consider these assumptions valid, we recognize that some degree of systemic violation may persist and that these assumptions are difficult to evaluate.

The ability of CKMR models to provide abundance estimates for years prior to sampling and thereby detect trends is a key advantage over traditional models, especially when applied to long-lived species. This contrasts with traditional mark-recapture models relying upon closed capture occasions that only provide estimates of abundance during the closed period. By contrast, CKMR models are able to estimate abundance for all breeding years when at least one POP was detected. Although this restricts CKMR estimates to the most recent breeding season, it also provides the ability to retrospectively assess changes in abundance. We were able to obtain historical abundance estimates from both our multi-year CKMR analysis and for analyses restricted to data from each of our sampling years in isolation. While the multi-year analysis provided the most comprehensive set of historical estimates (five years), our single-year analyses were able to estimate abundance for at least one and as many as three previous years (Appendix S2: Figure S2). In this study of a relatively short-lived species, we restricted our use of offspring data to age-3 and younger fish due to low confidence in length-age assignment beyond age-4. This restricted our earliest estimate of abundance to 2012 (e.g. from age-3 fish caught in 2015). However, use of accurate aging techniques coupled with a longer-lived species could provide much longer-term estimates of historical abundance, making it possible to study the impact of historical drivers of population abundance based solely upon contemporary sampling. Potential

also exists for the development of hybrid models that integrate data from both kinship and true recapture, boosting the precision of contemporary estimates while still providing information about historical abundances.

Close-kin mark-recapture requires genotyping, which introduces additional time, labor, and financial costs relative to mark-recapture methods that rely upon physical tags. We estimate that our genotyping using the microsatellite sequencing technique cost approximately US\$8 per sample (~\$6.50 excluding microsatellite discovery). However, genotyping techniques are widely recognized to be advancing rapidly (Meek and Larson 2019) and techniques such as GT-seq can currently be performed for as low as \$4 per sample (Campbell et al. 2015). This approaches the cost of physical tags per fish evaluated, especially PIT tags that currently retail for \$1-2 per unit. Nevertheless, studies using CKMR in the near-future will likely be more expensive than those employing traditional mark-recapture on a per-captured-individual basis. However, we expect that CKMR may still be cheaper than traditional mark-recapture studies in many instances due to its flexibility. Samples for genetic analysis can be preserved almost indefinitely with proper storage, then analyzed when interest or resources allow. CKMR sampling can also “piggyback” on other work (or use previously-collected samples) and, without a requirement for true recapture, study designs employing as little as one capture occasion become feasible.

Close-kin mark-recapture's efficient use of sampling effort and robustness to many problems associated with capture heterogeneity offer the potential to estimate abundance and survival from populations and datasets for which this was previously infeasible. While the individuals included in our CKMR model were collected using consistent gear, effort, and timing, this was only necessary for accurate estimation using the traditional mark-recapture model. Because CKMR does not rely upon (and in fact ignores) true recapture, effects such as

size-selectivity are only important insofar as they affect the overall age-structure of the dataset. This provides a great deal of flexibility to accommodate opportunistic sampling with poorly standardized capture effort or even deliberate sampling with different gear types to target coverage over a broader age structure or to adapt to changing personnel or survey conditions.

For example, we present three potentially desirable and pragmatic study assessment scenarios that are poorly suited for traditional mark-recapture but are feasible with CKMR methods, opening up opportunities to study a diverse range of animal populations:

- 1) Assessments employing a single, high-effort survey. This design is suited for evaluating populations where access is difficult or in situations where factors such as seasonality, personnel constraints, and expense limit the ability to repeatedly survey a population over time. In order for this type of study to be effective, survey gear must be capable of capturing a variety of ages of the target animal in order to yield a suitable number of POP comparisons. Unlike the other two examples listed below, this approach necessarily restricts the dataset to a single year and therefore can provide only abundance estimates, rather than both abundance and survival.
- 2) Assessments employing a large number of low-effort surveys. CKMR's robustness to variation in effort and size-selectivity make it ideal for situations that rely upon genetic samples collected from volunteers and therefore include extensive between-survey variation in effort. Examples include samples collected by recreational hunters and anglers for which effort and gear efficiency are unknown or poorly controlled.
- 3) Assessments using a combination of highly size-selective gears. As an example, genetic data collected from a coverboard or pitfall trap survey targeting adult amphibians could be combined with aquatic surveys of larval individuals. Traditional mark-recapture

methods would be of little use in this scenario as one could not expect recaptures between the two gears; by contrast CKMR methods using POPs would be highly effective. This approach may also be usefully combined with design #2, e.g. samples from an adult-selective recreational fishery could be combined with those from a gear type optimized for juvenile individuals such as a larval fish survey.

Effective application of CKMR hinges upon the ability to accurately estimate relative ages and kinship status within a population. Techniques for the former are well established for many species, particularly a fast-growing, pulse-breeding species such as brook trout. However, most aging methods rely on whole organism measurements (e.g. length) or analysis of specific structures (e.g. otoliths, teeth), both of which require additional data or samples. Recently developed epigenetic aging techniques offer potential improvements that could allow determination of both age and kinship based solely upon tissue samples (Polanowski et al. 2014). This method has been successfully used for CKMR modeling of Antarctic blue whales (Bravington et al. 2014b), but additional work is required before these tools can be applied to other species. Simulation-based studies of how imprecise or biased age estimates effect the performance of CKMR could also be useful, especially for researchers seeking to apply the technique to new systems. While methods for genotyping and kinship analysis are well established, further advances would enable wider application of CKMR. Perhaps the greatest potential benefit from advances in genotyping would be further cost reduction, which could reduce the cost of evaluating each individual to the same or less than physical tagging. But even using current aging and genotyping techniques, this study provides empirical demonstration of the potential widespread utility of CKMR as a useful alternative to traditional mark-recapture

methods and for extending abundance and survival estimation to populations for which traditional mark-recapture assessment is untenable.

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APPENDIX S1: Genotyping methods

Marker Development — We created a genomic library enriched for simple repeats following the procedure of Nali et al. (2014) using DNA extracted from a single, randomly chosen individual from our Honnedaga lake collection. This enriched library was sequenced on an Illumina MiSeq (250 bp paired-end reads) to identify tetra-repeats throughout the genome. We used the msatcommander 1.0.3 software (Faircloth 2008) with the "design primers" function to select microsatellites with a product size range of 330-350 bp. From these, we chose a total of 100 candidate loci with intermediate values of repeat count and sequencing coverage and synthesized forward and reverse primers for each with Nextera XT compatible 5' and 3' tails ('TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG' added to the 5' end of each forward primer and 'GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG' added to the 5' end of each reverse primer (locus-specific primer sequences in Appendix S1: Table S1). We tested each primer pair in separate polymerase chain reactions (PCRs) with DNA from seven randomly chosen individuals using the Qiagen Multiplex PCR *Plus* kit. Reaction volumes of 10 μ L were used with 1.5 μ L template DNA (0.1-10 ng), 5 μ L 2X master mix, 2.5 μ L H₂O, and 1 μ L of 2 μ M primer stock. PCR conditions followed the manufacturer recommendations with a 5 minute activation at 95°C followed by 35 cycles of 30 seconds at 95°C, 90 seconds at 60°C, and 90 seconds at 72°C and ending with a 10 minute extension at 68°C. PCR amplification results were assessed using gel-electrophoresis. Primers that produced a single, strong band in the expected size range for all test samples were included in our multiplexed amplicon sequencing (n = 74).

PCR and Barcoding —The 74 validated primer pairs were combined into two equal multiplex groups (n = 37) using output from the ThermoFisher Multiple Primer Analyzer (Breslauer et al. 1986; Thermo Fischer 2019) to minimize the number of interactions. We then performed a

separate PCR for each sample and multiplex group using the same reaction and cycling conditions as described for the individual locus testing above, including a 10 μ L reaction volume and 2 μ M total primer concentration. The PCR products from the two multiplex reactions for each individual were combined and custom-synthesized dual index (barcoded) adapters (Illumina Nextera-style i5 and i7) were added in a second PCR-step following the protocol from D'Aloia et al. (2017), resulting in a uniquely indexed library for each individual. The indexed libraries were pooled in equal parts by volume (2 μ L of each library), diluted with 4 μ L of H₂O, and then purified using two rounds of cleanup with Ampure XP beads using a ratio of 0.7:1 Ampure beads to library. The cleaned library pool was sequenced using 18% of both lanes on an Illumina HiSeq 2500 rapid run (paired-end 250 bp reads) which yielded 79,597,647 reads.

Filtering and Haplotyping — The sequencing data were processed using a custom Perl script that 1) assigned reads to the correct locus and individual, 2) merged the overlapping ends of each read pair into contigs, 3) created a catalogue of unique haplotypes observed for each locus across all individuals (D'Aloia et al. 2017), and 4) identified the top two haplotypes for each individual. More specifically, reads were assigned to individuals using their unique barcode sequence and then filtered using Trimmomatic (Bolger et al. 2014) to remove reads that had a phred +64 quality score below 20 or were shorter than 150 bp. Read pairs were merged using FLASH (Magoč and Salzberg 2011) with a minimum overlap of 20 bp, a maximum overlap of 250 bp, and a mismatch rate of 0.05. Sequences that did not form a contig were discarded and remaining sequences were matched to loci using the set of known forward primers with two mismatches allowed. The identified sequences were then collapsed to create A) a list of unique sequences for each individual and locus and B) a count of reads for each individual, locus, and unique sequence. The mean number of qualifying reads per individual was 26,491 (SD: 34,626; Min:

21; Max: 350,055) while the mean number of qualifying reads per locus was 885,923 (SD: 1,161,463; Min: 5345; Max: 5,187,503).

We next identified the top two haplotypes (i.e. the diploid genotypes) for each individual at each locus after completing the following four-step filtering of the unique sequence read counts in R:

- 1) We converted unique sequences to repeat counts using regular expressions and the known motif for each locus. Only repeats that were adjacent or had a gap of no more than the motif length between them and the next match were counted. Unique sequences with the same number of repeats for a locus and individual were then combined. This step helped to eliminate false alleles caused by genotyping errors and allowed us to use allele size-based metrics such as Garza and Williamson's (2001) M-ratio. It should be noted that collapsing sequences by repeat number may eliminate useful information provided by SNP differences in the flanking sequence, however this information is also eliminated in traditional size-based scoring of microsatellites and we felt that the benefits (e.g. a reduced error rate in our known trios and replicates) outweighed the potential loss of information.
- 2) We discarded alleles represented by less than 1% of the total number of reads or that appeared in only one individual. We reasoned that these low-count and ultra-rare alleles were most likely to represent errors.
- 3) For each individual we discarded alleles represented by only a single read as these were more likely to represent an error than a true allele.
- 4) We assigned two haplotypes to each individual (i.e. a diploid genotype) based on the ratio of read counts for an individual's top two alleles. If the top allele had more than

60% of the top two read counts summed (i.e. a 6:4 ratio or greater) we considered the individual a homozygote. If the ratio was less than 6:4 we considered the individual a heterozygote for the top two alleles. We chose this ratio because it produced the lowest observed error rates (from known trios and replicates). However overall sensitivity was low with higher ratios producing relatively similar results. Individuals without any valid alleles after filtering were recorded as missing genotypes.

After genotypes had been assigned to each individual we conducted a final filtering step to remove poorly-performing loci. First, loci that could be typed for less than half of the individuals (<192) were removed from consideration, resulting in 47 remaining loci. Genotyping error rate was then assessed by A) comparing genotypes for a set of three “known” trios i.e. parent-offspring pairs where the offspring were the result of hand-fertilized eggs and B) 12 replicate samples where tissue from the same individual was used for separate extraction, PCR, and sequencing steps. This allowed us to eliminate loci that performed especially poorly which we defined as loci that caused mismatches (i.e. impossible genotypes) for more than one trio or replicate individual. This left a set of 44 loci detailed in Tables S1 and S2 which were used for subsequent kinship analyses.

TABLE S1. Names, motifs, and primer sequences for all loci used for kinship analysis.

Locus	Motif	Forward Primer	Reverse Primer
locus75	ACAG	TCTCAATCCTAACCTAGCCAC	AGGTCTGTATGCATATCTAGCCC
locus111	ACAG	GGCCTCTGACAGATGTTCTCC	CCTTACCCTGAGTACTGAGACC
locus126	ACAG	ACTATATAGGGAACAGGCTGCC	CCCACCTCCTATCTGAAATTCAC
locus140	ACAG	TGGTCAGATCTTCCCATAGTACTG	AGAGAGCTGGAATGTGGCAC
locus175	ACAG	ACTGATTAACCTAACAGCACCC	GTTTAGGGCCAGATAGCATTGG
locus432	ACAG	TAGAACGTTTCATTCACACACC	TCTCAATGCATGCCTCTCAATG
locus480	ACAG	TGCTGGCTCTCCTTCAGG	CCCAGCCCTCTATAGTTCTCTAG
locus488	ACAG	ACAATGGAGTTCTACTGATTCAC	CTTCTTGTTCTGTGCTGCTCTC
locus749	ACAG	ACCACCACAGCTACCTTAGTC	GACCTGTAGCCCTTGACGAC
locus788	ACAG	TACACAGCTCAGGACTGGAATG	CGTCTCATGTGTGTTCTCCAG

locus821	ACAG	AACACTGGGCTAGCGTTAG	GAACTGCCGCATCAATAAGGAG
locus847	ACAG	TTACAAGGATAAGGAGGCCAGG	TGAAATGACATTGCTGACGGAG
locus1190	ACAG	CCCGCTAGATACATTTGGAGTG	CGAAGCCATCATGCAAACAAAG
locus1194	ACTC	GCTACTTGACTGAATTCTGCAGG	CTACGTGTCTACAGTATGCAGAG
locus1300	ACAG	GGCAACCAGTGAAGAACAAC	CTGTCCTGTATTTGTGCTAGCC
locus1440	AGAT	TGCTGTACTTTATGCCTCATATTG	TATTCAGAGAGGGGAGGAAGCAC
locus1563	ACAG	GGACTGAGATCACTGGGACTAC	GTCAAGCCTCATCTCTCTCCAG
locus1712	ACTC	AGACTGTTCTGCTGTGGTCTAC	TCTCTCTCCTTGTTCCTTTGTG
locus1935	ACTG	ATAGTAATGGAGAGGGCTGGAG	CTTCGTCACTCCTAGCTCAGAG
locus2083	ACTC	CTGAATCAAACGCTCCTCTGTG	CCTAGGAAGACGATGGATCAGG
locus2135	ACAT	GGTGAGAGAAGCGCCGAG	CTGACTCTGCTTACACTGAACG
locus2136	ACTC	AGTCACCTTGTTTATAAGTCAGGC	CACACTGACTACACCTAGCATTG
locus2288	AGAT	CACCAGTCAAACGCTTCAGTG	GGAGCAGTGCATATACGGTTTG
locus2342	ACAG	TCTGCTTTCCACTTATTCACCC	TGAGTGGTCACATTATGCAATTC
locus2481	ACAG	TGCAAACTATCTTGTACATGGAC	GAGAGTAGAGCAGGTCCAGC
locus2770	ACAG	CCATGAGCAGCCACAAGTTG	ATCATCAAACCTCCAGGAACAGC
locus3042	ACAG	ATCCCAGCAGTTATTCCAATGG	AGAGTTATCAGGAGTCCTCTAGC
locus3161	ACTC	GGGTGTGTCTCGCTTCTCC	TGAGCAATATGGTGGATATCTGAC
locus3226	ACAG	TTTGCTCTGTACCCAAAGTGC	GTTGCGGTCTGACAGAAGTTC
locus3540	ACAG	CACTGTTTGAACGCCACC	GCGATTGGAAGCAATAGATAGAGG
locus3819	ACAG	CTCTCTAAGGTCAGGGCGTG	CTCCCTAGGCCCTTCTCTC
locus4123	ACTC	CCAGATGGCTTGGTACCAGATG	TGAATCCAACAACCTCCTGCC
locus4190	ACAG	CCCTCACCTGAATATTGTGAC	TACTCTCACAGCCCTCAGG
locus4258	AAAG	TGACAAAGCAGACAGAAACCC	TCTCTACCTCAGCCTCAATCAC
locus4432	ACAG	TGTCTGTTTGTCTCTATGTCCAG	GTGACATAACTGCTTGATGTTGG
locus4453	ACTC	GGGAACACAAACCTATCGCAG	GAGAGGTTAGCTGAAATCACGG
locus4745	ACTC	TGAGAATGGTAAATGCTTTCCTG	TTGTGCCAAGGAAATGAATGG
locus5023	ACAG	AACTCAACTCGCCGTGTTTG	ACACACAAATGACCATACCAGC
locus5336	ACTC	GTTGAACGTTTCTCATTACCAGC	GCAAAGGGTGGCTACTTTCAAG
locus5427	AAAG	CACTTGCCATCTCCTCATTTG	CTGAGTGGCTAGGGTTGGAG
locus6988	ACAG	TGTTTCCAAGCCAATAAAGCC	ACCTTGCTGCCTTTAAACG
locus7107	ACAG	CACCACAGAGAAACCCAATCAG	CACACATATGGAAGTGCTCAGG
locus8932	ACAG	TGAGAAGCACATGATCACACAG	GTGAAGAGAAGCATGACAACCG
locus9168	ACAG	TTTCCTTGTTATCGATGTTGCG	AGGCTGGCAAGTCTCAGAG
locus17305	ACAG	CACCAGGGATTTATAGACATACTG	TTCATTTACGCACCCCACTTG

TABLE S2. Performance details for each locus including percent of individuals successfully genotyped (out of n=385 total), number of alleles, heterozygosity, and haplotype length range

Locus	Percent of individuals genotyped	Number of alleles	Heterozygosity	Haplotype range (repeat units)
locus75	93.0	9	0.80	15 - 23
locus111	72.2	8	0.71	14 - 21
locus126	54.3	9	0.79	12 - 22
locus140	100.0	10	0.91	18 - 29
locus175	71.9	6	0.68	17 - 24
locus432	100.0	8	0.78	12 - 20
locus480	100.0	7	0.88	19 - 27
locus488	100.0	5	0.71	15 - 20
locus749	80.0	2	0.29	13 - 24
locus788	96.1	10	0.80	12 - 24
locus821	100.0	9	0.95	11 - 22
locus847	99.7	9	0.79	14 - 22
locus1190	99.0	7	0.85	23 - 31
locus1194	51.7	7	0.65	14 - 26
locus1300	100.0	7	0.88	16 - 24
locus1440	100.0	9	0.92	10 - 20
locus1563	100.0	5	0.76	16 - 27
locus1712	100.0	8	0.91	13 - 21
locus1935	100.0	7	0.76	19 - 26
locus2083	100.0	8	0.87	13 - 23
locus2135	98.4	7	0.82	11 - 21
locus2136	100.0	7	0.50	19 - 31
locus2288	99.5	4	0.60	14 - 17
locus2342	98.2	4	0.33	19 - 26
locus2481	97.1	7	0.73	11 - 18
locus2770	53.0	5	0.61	24 - 28
locus3042	70.9	5	0.70	19 - 23
locus3161	66.0	9	0.63	16 - 27
locus3226	98.2	7	0.84	14 - 20
locus3540	74.3	9	0.74	14 - 23
locus3819	69.9	4	0.38	18 - 21
locus4123	65.5	8	0.69	12 - 21
locus4190	55.3	11	0.89	11 - 22
locus4258	100.0	6	0.69	10 - 27

locus4432	53.8	11	0.82	10 -36
locus4453	94.5	8	0.82	14 - 23
locus4745	100.0	5	0.64	25 - 29
locus5023	81.0	5	0.58	16 - 23
locus5336	77.7	7	0.60	10 - 25
locus5427	80.5	8	0.83	10 - 29
locus6988	100.0	8	0.63	10 - 19
locus7107	95.8	5	0.59	14 - 18
locus9168	99.2	5	0.66	17 - 26
locus17305	100.0	6	0.79	12 - 16

APPENDIX S2: Supplemental kinship and model performance figures

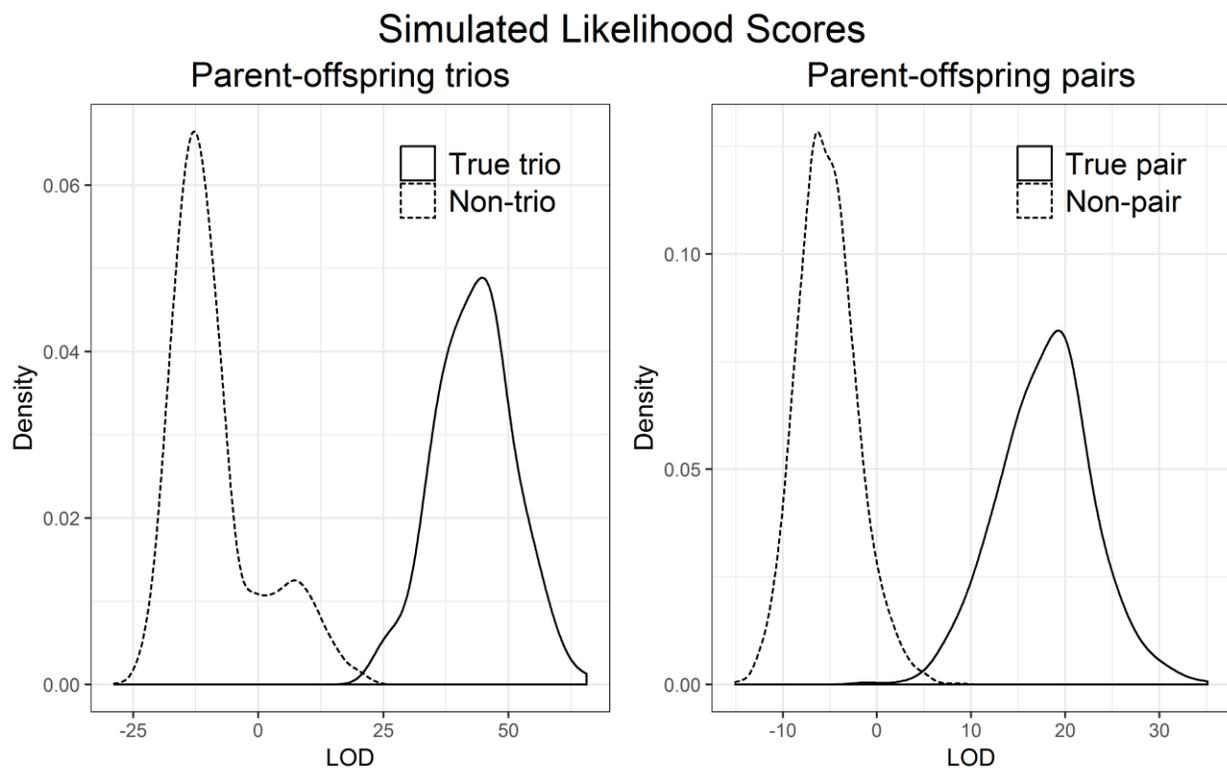


FIGURE S1. Likelihood ratio density distributions for simulated parent-offspring pairs and trios versus non-parent-offspring combinations.

TABLE S1. Parameter estimates for single-year Close-Kin Mark-Recapture analyses with number of potential parent-offspring comparisons and number of identified parent-offspring pairs for each parameter.

Sample Year	Parameter	# Comparisons	# POPs	Estimate	R-hat
2015	N-2011	986	2	1010 (300 - 2172)	1.00
2015	N-2012	5244	14	556 (299 - 987)	1.00
2016	N-2011	986	3	649 (102 - 1809)	1.00
2016	N-2013	6688	7	1260 (641 - 2182)	1.00
2016	N-2014	18000	11	1360 (838 - 2129)	1.00
2017	N-2015	5900	2	1635 (814 - 2779)	1.00

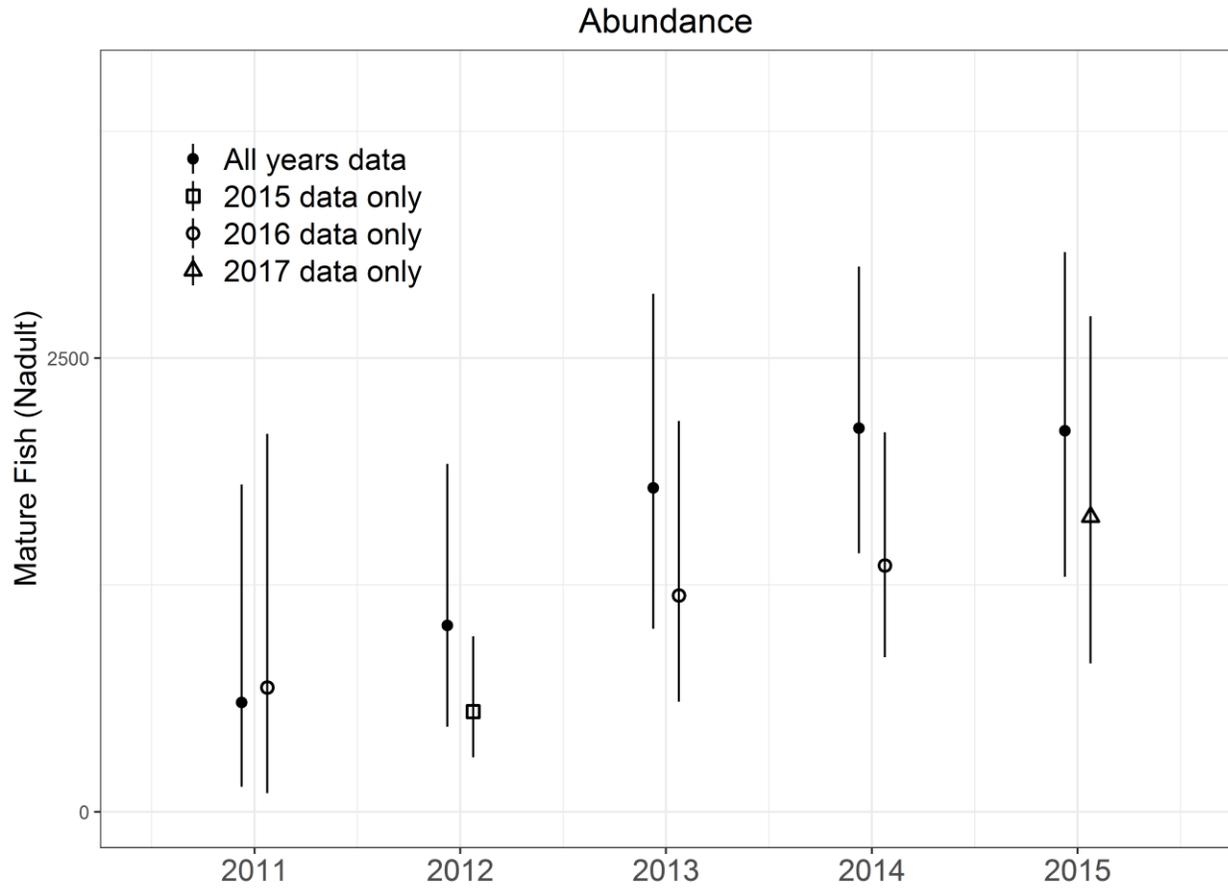


FIGURE S2. Close-kin mark-recapture estimates of abundance from the full sample (closed circles) and each of the three sampling years in isolation (open shapes).

APPENDIX S3: Supplemental population information

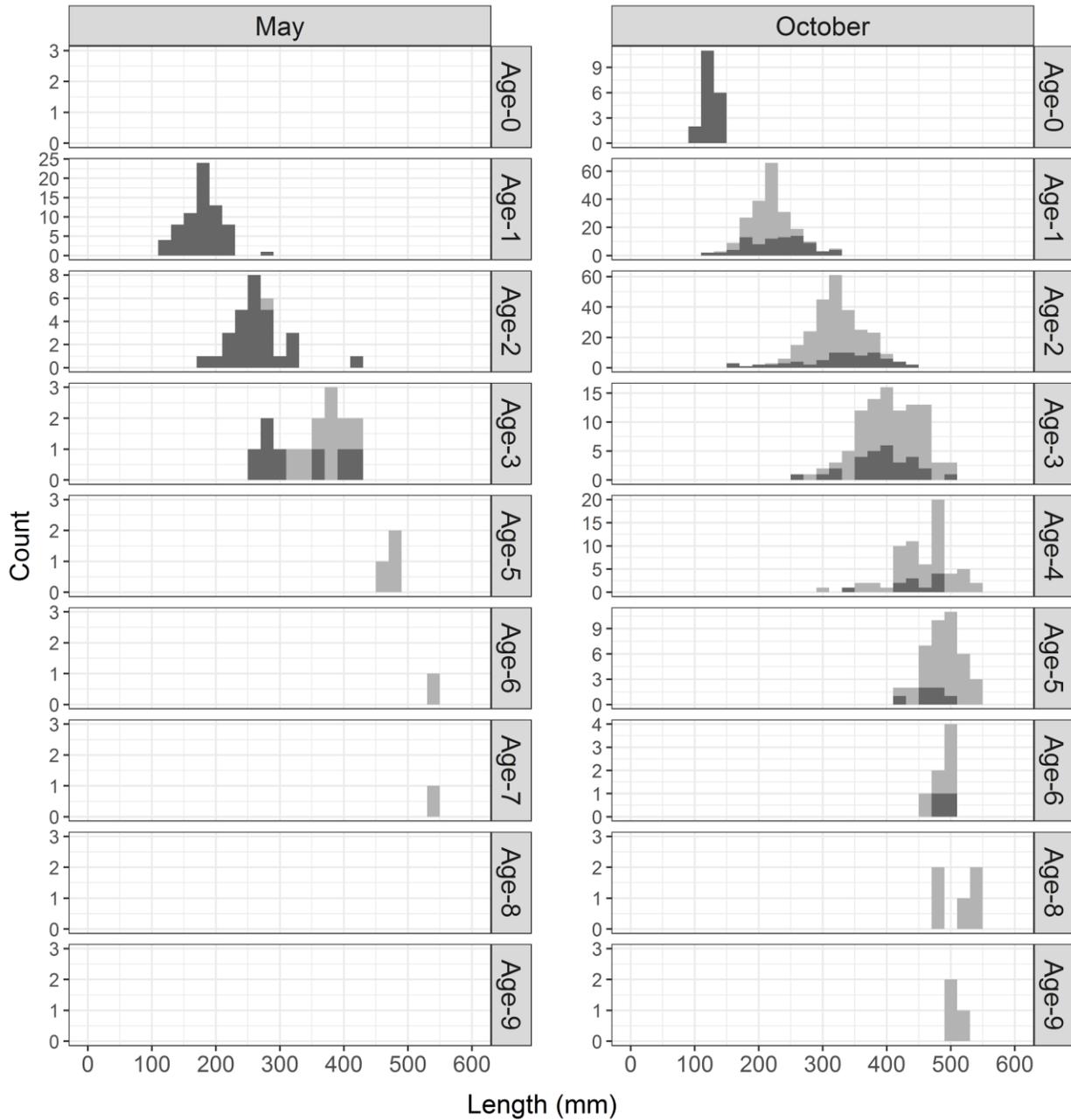


FIGURE S1. Length-age histograms for fish captured in May and October from 1998-2018. Ages are based upon either sagittal otolith sections scored by two separate readers (dark gray bars, May N=104, Oct. N=223) or recovery of fish clipped during annual summer YOY surveys (light gray bars, May N=14, Oct. N=490).

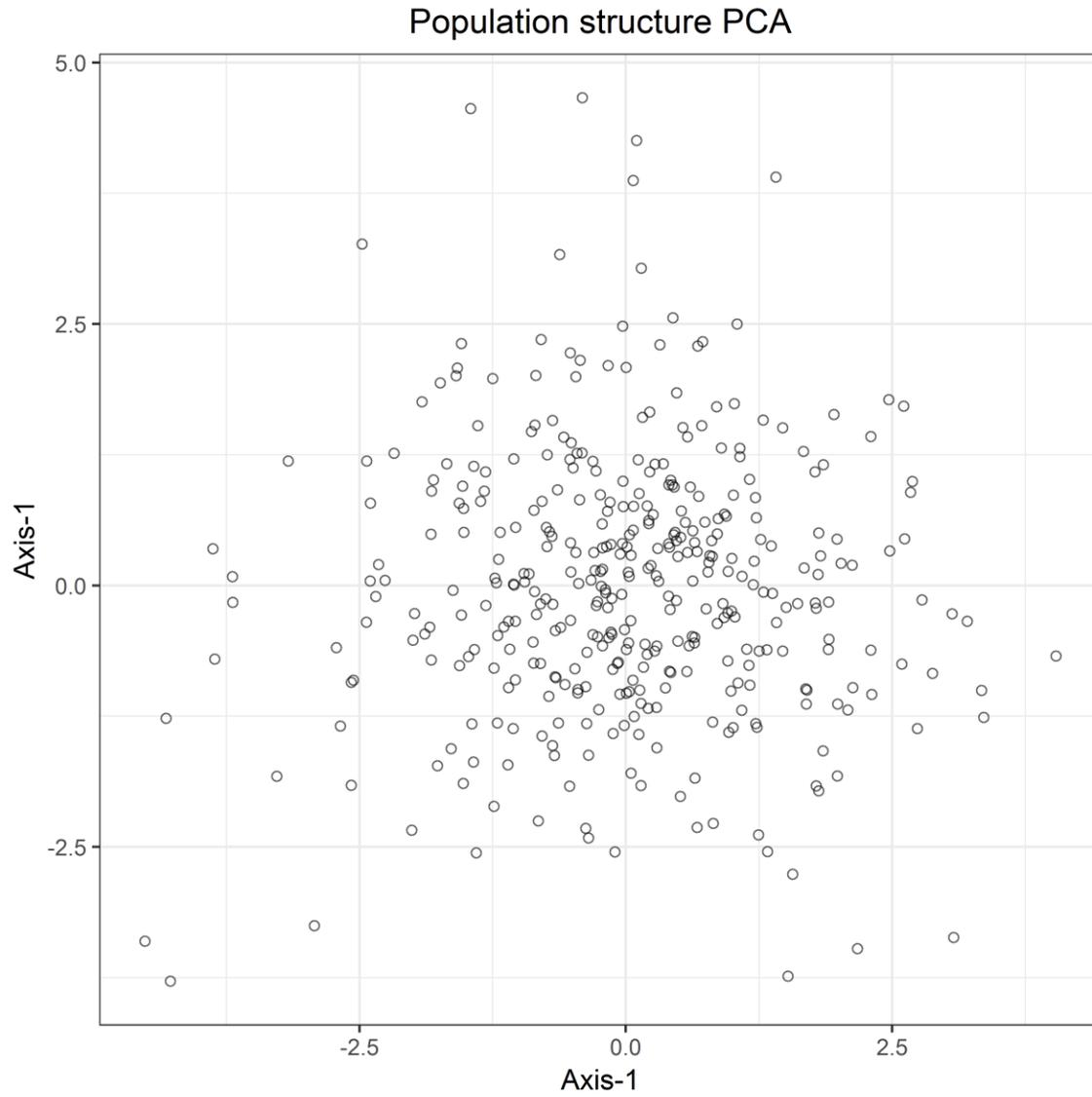


FIGURE S2. Principle components analysis of all individual genotypes included in the close-kin mark-recapture analysis.

CHAPTER 3 – RESPONSE OF ZOOPLANKTON COMMUNITY AND LAKE TROPHIC DYNAMICS TO THE SUCCESSIVE COLONIZATION OF *CHAOBORUS PUNCTIPENNIS* AND RAINBOW SMELT (*OSMERUS MORDAX*)

ABSTRACT

Due to their intermediate and central role in lake food webs, zooplankton communities reflect broader influences within these aquatic ecosystems. Understanding the biotic and abiotic drivers of zooplankton community dynamics is therefore important for understanding the effects of anthropogenic stressors. One example of this is acidification, where zooplankton community composition can indicate chemical recovery. However, many long-term and landscape-scale studies of recovery from acidification have shown mixed responses, with some waters shifting towards a diverse, large-bodied community typical of recovery while others have remained unchanged. Correlation studies point to DOC and species invasions as additional drivers of zooplankton community composition. We evaluated the combined impacts of acidification recovery, increasing DOC, and species invasion on zooplankton community dynamics using long-term data from an Adirondack (NY, USA) lake. Results indicated strong shifts in zooplankton biomass and species composition coincident with colonization by the invertebrate predator *Chaoborus*, resulting in a community similar to that associated with recovery from acidification. This was reversed by the introduction of rainbow smelt (*Osmerus mordax*), returning zooplankton community composition to a state similar to when the lake was acidified. Previous studies have found that *Chaoborus* abundance may be influenced by DOC, suggesting why other studies have found a correlation between apparent biotic recovery and DOC. Overall, we highlight intersections between browning and biotic recovery from acidification, the threat that invasive species pose to this process, and trophic dynamics associated with these shifts.

INTRODUCTION

The structure of lake zooplankton communities depends on a complex combination of complementary physical and biotic factors, including nutrient availability and predation (Carpenter and Kitchell 1996). Due to their intermediate and central role in lake food webs, zooplankton communities reflect broader influences within these aquatic ecosystems (Xu et al. 2001; Jeppesen et al. 2011). Factors affecting community composition are often complementary, with nutrient availability influencing food web structure (Mills and Forney 1988) but also in turn being influenced by higher trophic levels, e.g. through size selective predation changing zooplankton structure (Carpenter et al. 1985). Understanding the drivers of community dynamics is therefore a complex endeavor fundamental to limnology (Carpenter and Kitchell 1996) and important for understanding aquatic systems increasingly affected by anthropogenic activities (Zanden et al. 2016).

Acidification resulting from increased sulfate deposition strongly impacted northern aquatic systems during the 20th century, resulting in the complete extirpation of fish in many waters (Schofield 1976; Kraft 2019). Following the Clean Air Act Amendment of 1990, gradual chemical recovery has been noted in many waters within the United States including the heavily impacted Adirondack Mountain region of New York State (Driscoll et al. 2003). However, indicators of biotic recovery in Adirondack lakes, such as increases in crustacean zooplankton community richness and average size, have remained incomplete or delayed. For example, Leach et al. (2019) observed zooplankton community shifts due to a reduction in the biomass of small acid-tolerant species rather than an increase in large-bodied cladoceran abundance (Leach et al. 2019). A similar decline in acid-tolerant calanoid copepods – without an accompanying increase in acid-sensitive species – was also observed following an experimental lime addition

manipulation of an Adirondack lake (Bukaveckas and Shaw 1997). In that study the authors attributed the absence of a biomass increase in acid-sensitive species to increased predation by the simultaneously recovering fish community; however, they could not explain the reduction in calanoid biomass. Studies of Canadian lakes recovering from acidification have reported similarly mixed zooplankton community responses: some waters showing a shift towards larger bodied zooplankton communities, others remaining unchanged (Yan et al. 2008). In a temporal comparison of recovery, Yan et al. (2008) point to DOC as a potential driver behind difference in observed responses. This finding is echoed by Gray et al.'s (2012) observation that DOC was strongly correlated with differences in zooplankton community metrics in a between-waters comparison of acidified and chemically recovered Canadian lakes. Both Yan et al. (2008) and Gray et al. (2012) postulate several mechanisms for the influence of rising DOC on zooplankton communities, including reduction in UV irradiance, changes to stratification, and reduction in predator efficiency.

Predation can strongly influence zooplankton community composition, both directly and indirectly (Hall et al. 1976; Strecker et al. 2011; Vanderploeg et al. 2012). While predation by vertebrates such as planktivorous fish has often been considered to be the main driver of zooplankton community size structure in lakes inhabited by fish, studies have shown that predation by larger invertebrates such as larvae of the dipteran midge *Chaoborus* can also exert strong influences on zooplankton (Lane 1979). Unlike vertebrate predation which tends to eliminate large-bodied zooplankton (Brooks and Dodson 1965; Chang et al. 2004), invertebrate predation disproportionately affects the smaller-bodied zooplankton (Fedorenko 1975; Sutor et al. 2001; Vogt et al. 2013). Case studies also suggest that shifts towards invertebrate predation can increase diversity in zooplankton communities (Black and Hairston 1988; McNaught et al.

2004). However, predator communities are themselves subject to change due to a variety of factors. While many invertebrate predators, such as *Chaoborus*, are not limited by transport due their aerially-dispersing adult stages, their distribution may be determined by environmental factors such as susceptibility to UV exposure in clear lakes (Williamson et al. 1999; Persaud and Yan 2003). Non-native fish predators and the invasive predatory cladoceran *Bythotrephes* (Yan et al. 2002) disperse more slowly, but rising human access to remote waters have accelerated these potential impacts on lake zooplankton communities.

Honnedaga Lake in the Adirondack Mountain region of New York is well-placed to study response to anthropogenic stressors such as invasion as it has been central to studies of Adirondack lake acidification since the 1960's (Webster 1961), culminating in the first documented natural recovery of native brook trout (*Salvelinus fontinalis*) in the early 2000's (Kraft 2019). While surveys of this lake through 2007 indicated gradual chemical recovery with surface pH values ranging from 5.0-5.6 and inorganic monomeric aluminum levels below the 2.0 $\mu\text{mol/L}$ threshold associated with mortality of brook trout (Baldigo et al. 2007), the lake's zooplankton community remained dominated by small calanoid copepods rather than larger, less acid-tolerant cladocerans (Josephson et al. 2014). However, continued growth of the brook trout population since 2007 suggest that further shifts might be occurring in the Honnedaga food web. Colonization by invertebrate zooplankton predators such as *Chaoborus*, which are prevalent in nearby waters, was one likely explanation for the observed increase in fish condition. The potential for additional system-wide shifts was further accelerated by the accidental introduction of a vertebrate zooplanktivore rainbow smelt (*Osmerus mordax*) into the lake in 2015 (personal observation).

We studied the effects of these combined impacts on zooplankton community dynamics and overall food web structure using existing long-term data on water chemistry, fish abundance, fish isotopic composition, and zooplankton biomass in Honnedaga Lake. We augmented this data set by extending analyses to the present day, re-analyzing zooplankton samples for *Chaoborus*, and examining the contemporary isotopic food web to augment our understanding of brook trout isotopic data previously collected. The goal of our analyses was to answer three interlinked questions: 1) has the biotic community of Honnedaga continued to recover from acidification, 2) what effect has the colonization of vertebrate and invertebrate zooplankton predators had on zooplankton community composition and 3) how has the recovering brook trout population been influenced by these changes.

METHODS

Study location.—Honnedaga is a relatively large, deep lake in the southwestern Adirondacks with a surface area of 312 ha and a maximum depth of 55.8 m. The lake is steep-sided with significant depth throughout much of its area and exhibits strong stratification throughout the summer months with significant cool, well-oxygenated volume below the thermocline.

Honnedaga's watershed is small relatively to the lake's volume and dominated by thin glacial till, making the lake particularly sensitive to acid deposition (Schofield 1965). Prior to the introduction of rainbow smelt in 2015 Honnedaga's fish community consisted solely of native brook trout.

Zooplankton sampling and analysis.—Zooplankton sampling was conducted during July and August of each year using vertical plankton tows at a fixed site in the deepest portion of the lake during early afternoon. Two replicate samples were collected on each date with a 0.5-m diameter 153- μ m mesh zooplankton net with a tow depth of 25-50 m, depending upon the occasion

(Figure 1). Collected zooplankton were preserved in 95% ethanol prior to laboratory analysis. At each zooplankton sampling event we also measured secchi depth and collected a surface water sample for later measurement of chemical variables including pH, DOC, and calcium. We enumerated zooplankton species composition and size by diluting each sample to a known concentration before measuring all individuals within a 1 ml sample using a 18-150x power dissecting microscope and a digitizing tablet. This subsampling process was then repeated until a total of at least 100 individuals had been counted, identified, and measured. We then estimated the weight of each counted individual using standard length-weight relationships (Watkins et al. 2011) and used the resulting weights in combination with observed density, the number of samples counted, sample concentration, net diameter, and tow depth to calculate a per-L estimate of lakewide biomass for each species identified.

In order to better understand the presence and relative densities of *Chaoborus* species over time we re-analyzed each sample by placing the entire sample into a gridded petri dish and counting the total number of chaoborid larvae observed using a dissecting microscope. All larvae observed were removed from the sample for identification to species and later stable isotope analysis. Using similar calculations to the main zooplankton analysis we calculated a per-L density for chaoborid larvae using the known tow volume. *Chaoborus* are difficult to sample effectively due to their patchy distribution and the diel migration patterns undertaken by some species (Wissel et al. 2003), therefore our zooplankton sampling methodology was not ideal for characterizing *Chaoborus* density. However, since our sampling extended well below the thermocline and was repeated over many years we consider this sampling approach as a useful index of abundance over time.

We analyzed differences in zooplankton community between years using non-metric multidimensional scaling (NMDS) to cluster samples based on per-species biomass estimates (mg / L) in order to discern whether distinct temporal patterns would emerge. The NMDS algorithm is widely used in community ecology as non-metric methods avoid problems associated with non-linear community changes associated with underlying variables (Prentice 1977). We chose to scale along four dimensions after iteratively testing different values and finding that these produced low stress satisfactory for interpretation (~0.10 for multiple runs) (Kruskal 1964) without a surfeit of weakly-informative “nuisance dimensions” that have the potential to bias group testing (Legendre and Gallagher 2001). Analysis was performed in R version 3.5.2 (R Core Team 2018) using the “MASS” (Ripley et al. 2013) and “vegan” (Oksanen et al. 2010) packages.

Fish community sampling.—We sampled littoral fish assemblages each spring using nighttime boat electrofishing along the entire shoreline. Each survey occurred on two or three consecutive nights, depending on weather, in the fourth week of May using two netters and consistent gear (Figure 1). As Honnedaga consistently exhibits very stable, low conductivity (Mean: 14.4 uS/cm, SD: 2.4) we standardized our surveys to use 60 Hz pulsed DC at 1061 V and a duty cycle of 25%, consistent with established sampling techniques for low conductivity waters (Reynolds and Koltz 2012). We standardized our catch by shoreline length to obtain a relative index of abundance for each species that was free from bias due to gear saturation (Marcy-Quay et al. 2019).

We also conducted fall surveys using trap nets to target brook trout spawning assemblages. Fish were captured in six Oneida-trap nets deployed for two or three nights during the third week of October at consistent sampling sites (Figure 1). In addition to all measuring and

weighing all fish captured during these surveys, a subset of 20 fish (10 male and 10 female) were kept for subsequent determination of age, muscle-tissue water content, and stable isotope ratios.

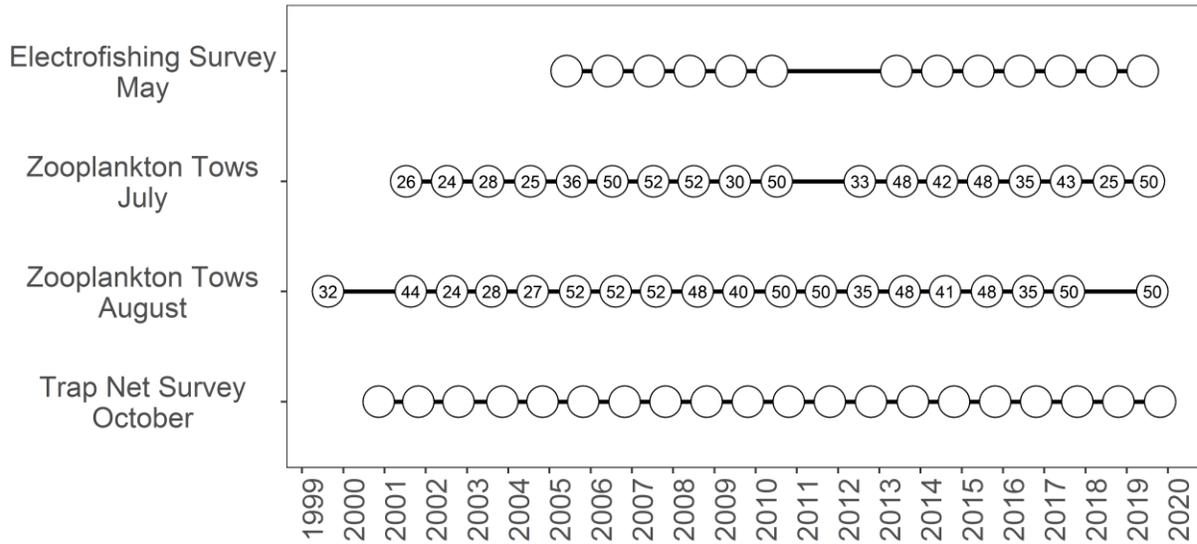


FIGURE 1. Honnedaga Lake sampling timeline. Points represent individual sampling events while lines connect gear/season combinations. Depth of each zooplankton tow (in meters) is displayed within the point for that event.

Stable isotope analysis.—For fish stable isotope analysis we used white muscle from the mid-body of individuals longer than 150 mm. To better understand the structure of the non-fish food web we collected samples of other potential food sources during spring 2019 including crayfish, aquatic insect larvae, isopods, and zooplankton. Additional samples of zooplankton and Chaoborus were extracted from stored zooplankton samples. While ethanol preservation can affect ^{13}C and ^{15}N (Feuchtmayr and Grey 2003) studies suggest that for zooplankton the effect on both elements is minimal (Syväranta et al. 2008). Due to their smaller size, food web samples were analyzed whole with the exception of crayfish for which we used muscle tissue extracted from the tail. All samples were dried at 40°C prior to being ground and homogenized. A 0.8-1.2

mg portion of each sample was weighed and encapsulated using 4x3mm tin capsules (EA Consumables) before being submitted to the Cornell University Stable Isotope Laboratory for analysis using their ThermoFinnegan Delta Plus mass spectrometer. After analysis, samples with a C:N ratio of greater than 3.5 were corrected for lipid content using the mathematical normalization suggested by Post et al. (2007) following the recommendation of Skinner et al. (2016).

RESULTS

Water chemistry.—Water chemistry values improved throughout the study period with mean summertime surface pH rising to 6.0 (SD: 0.11) for the period from 2015-2018 (Figure 2). Measurements of DOC exhibited a corresponding increase to a mean value of 1.8 (SD: 0.2) for 2015-2018. Levels of calcium in the water showed no clear pattern with an overall mean of 1.40 (SD: 0.24). Secchi depth declined sharply during the study period, from values above 20 m to a mean of 10.2 (SD: 2.8) during the final three years. Along with depth, qualitative assessments of color shifted from “dark blue” or “blue” during the early part of the study period to “light green” or “green” during the latter portion, suggesting increases in phytoplankton biomass.

Fish and Chaoborus indices.— Brook trout CPUE rose gradually from the beginning of surveys in 2005 until 2015 (Figure 3), followed by a slight decreasing trend. A total of 4931 fish were captured during the study period, with a mean size of 305 mm (SD: 96) and no evident trend in size between years. Of the 21 zooplankton samples analyzed from 1999-2019, no *Chaoborus* were found in any samples prior to 2010; individuals were detected in all samples after that point with the exception of the final year of data analysis (2019). We noted a clear trend in *Chaoborus* abundance with low relative densities in 2010-2014, a sharp peak in 2015, followed by a decline to very low relative densities in 2019 (Figure 3). A subset of *Chaoborus* from each year were

identified to species and classified as *C. punctipennis*. Springtime electrofishing surveys began detecting rainbow smelt in 2016, after which CPUE has increased exponentially (Figure 3). Presence of multiple age classes and mature smelt in spring surveys confirm that the introduced population is successfully reproducing.

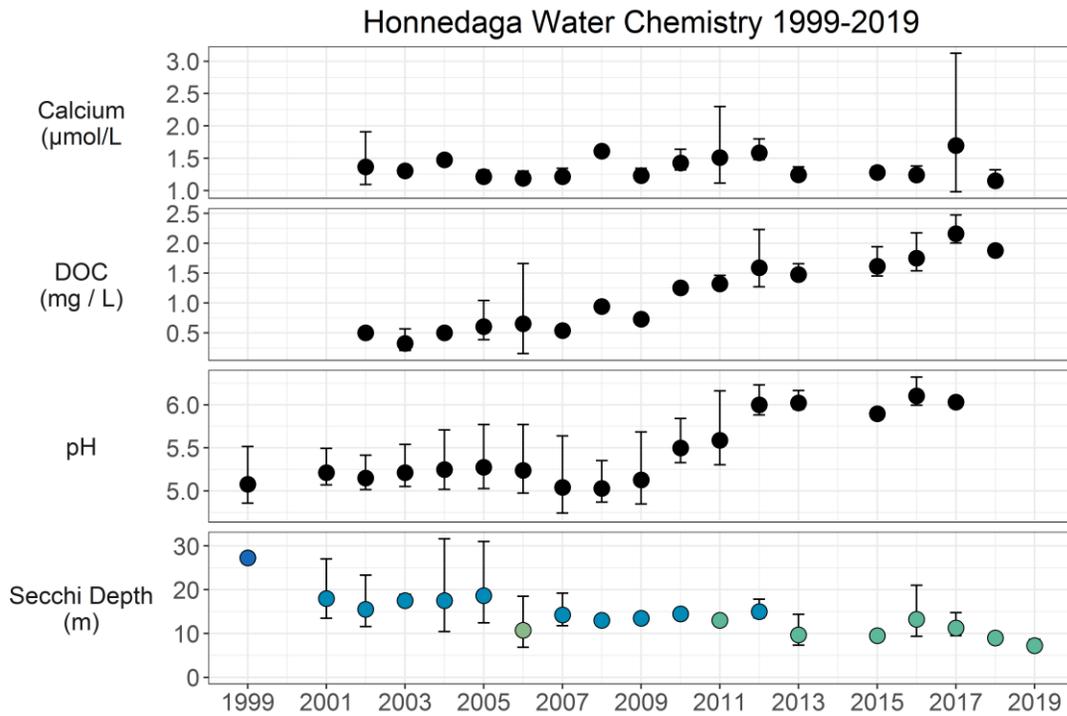


FIGURE 2. Water chemistry from summer (July-August) sampling on surface waters in Honnedaga lake from 1999-2019. Points denote means with error bars indicating two standard deviations above and below. Fill color of points for secchi depth readings illustrate the qualitative assessment of disk color at time of sampling.

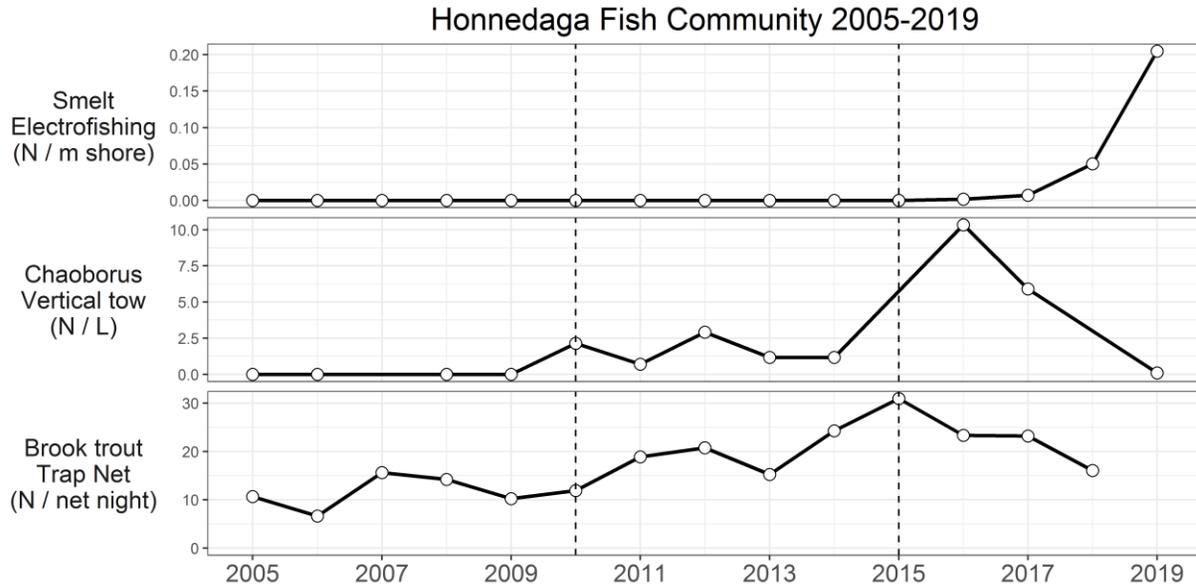


FIGURE 3. Relative biomass of fish species and *C. punctipennis* in Honnedaga Lake from 2005-2019.

The NMDS scaling algorithm successfully converged with multiple runs achieving a stable stress value of approximately 0.10. Visual inspection indicated that clustering along axes one and two displayed strong temporal trends while axes three and four were less evidently differentiated. We applied grouping data to the resulting scaled points to perform a permutational multivariate analysis of variance in order to test the hypothesis that per-species biomass differed between three distinct groups of years based on observed predator communities: pre-2010 period dominated by brook trout, the 2010-2017 period with *Chaoborus p.* but not substantial smelt presence, and the 2018-2019 period characterized by high smelt densities. This analysis indicated that the groups were significantly different ($P < 0.001$) and explained a small proportion of the variation in observed densities ($R^2 = 0.23$). Correlation of relative density for each species with scaling dimensions identified clear drivers of each axis (Table 1). Axis one correlated strongly with shifts between biomass of *L. minutus* and three larger species, *D. catawba*, *M. edax*, and

H. gibberum while axis two correlated with shifts in dominance between *L. minutus* and *B. longispina*. Axis three correlated strongly with two species, *D. pulicaria* and *D. thomasi*, but in opposite directions suggesting a competitive tradeoff between them. Finally axis four correlated strongly and in opposite directions with the large predatory copepod *E. lacustris* and the large predatory cladoceran *P. pediculus*.

Stable isotopes.—Isotopic analysis of the Honnedaga food web showed strong differences in $\delta^{13}\text{C}$ signature between littoral and pelagic food sources as well as pronounced trophic enrichment of $\delta^{15}\text{N}$ (Figure 5). Benthic aquatic insects (Chironomidae, Ephemeroptera, Odonata, Plecoptera, Trichoptera), isopods (Asellidae), and crayfish (*Cambarus bartonii*) exhibited relatively enriched $\delta^{13}\text{C}$ signatures with crayfish having the highest values for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, likely reflecting their omnivorous diet and potential for terrestrial foraging. Isopods had lower mean $\delta^{15}\text{N}$ values consistent with their detritus-heavy diet relative to aquatic insects that may be omnivorous or predatory depending on species and size. Values of $\delta^{13}\text{C}$ were notably depleted for *Daphnia p.* and *Chaoborus p.* with means approximately 5‰ below those for littoral sources. Values of $\delta^{15}\text{N}$ for *Chaoborus p.* were enriched relative to *D. pulicaria* but only by 1.4‰ on average, less than the 2.5-3.4‰ generally expected for trophic enrichment. This may reflect differing $\delta^{15}\text{N}$ values for other potential prey item, such as copepods, or result from degradation during storage which is known to produce unpredictable results (Feuchtmayr and Grey 2003; Syväranta et al. 2008). Ratios of carbon differed markedly for smelt between 2017 and 2019 with an average enrichment of 3.2‰ for the latter year. There was no significant difference in smelt $\delta^{15}\text{N}$ values between the two years. Brook trout also exhibited trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ over time that neatly corresponded to the year groupings employed in the zooplankton analysis: pre-2010, 2010-2017, and 2018-2019. Mean $\delta^{13}\text{C}$ was depleted by -0.9‰ between the

pre-2010 and the 2010-2017 groups, while mean $\delta^{15}\text{N}$ was enriched by 1.6‰. Continued enrichment of $\delta^{15}\text{N}$ was evident in the 2018-2019 group with mean values 0.5‰ higher than those for 2010-2017; conversely, $\delta^{13}\text{C}$ was sharply enriched with a mean value 1.7‰ higher than that for 2010-2017.

TABLE 1. Pearson correlation coefficients for the relative biomass of each species and the non-metric multidimensional scaling axes.

Species	Axis 1	Axis 2	Axis 3	Axis 4
<i>Bosmina longspina</i>	-0.36	-0.81	-0.02	0.09
<i>Daphnia catawba</i>	0.44	0.19	-0.19	-0.23
<i>Daphnia galeata mendotae</i>	0.18	-0.03	0.23	-0.02
<i>Daphnia pulicaria</i>	0.34	0.21	0.65	-0.12
<i>Diaacyclops thomasi</i>	0.18	0.17	-0.65	0.13
<i>Diaphanosoma sp.</i>	0.08	-0.15	0.26	-0.26
<i>Epischura lacustris</i>	-0.03	0.21	-0.12	-0.54
<i>Holopedium gibberum</i>	0.52	-0.20	-0.32	-0.03
<i>Leptodiptomus minutus</i>	-0.61	0.62	-0.22	0.00
<i>Mesocyclops edax</i>	0.48	0.17	0.10	0.40
<i>Polyphemus pediculus</i>	-0.17	0.25	0.00	0.54
<i>Sida crystallina</i>	-0.03	0.12	0.31	-0.10

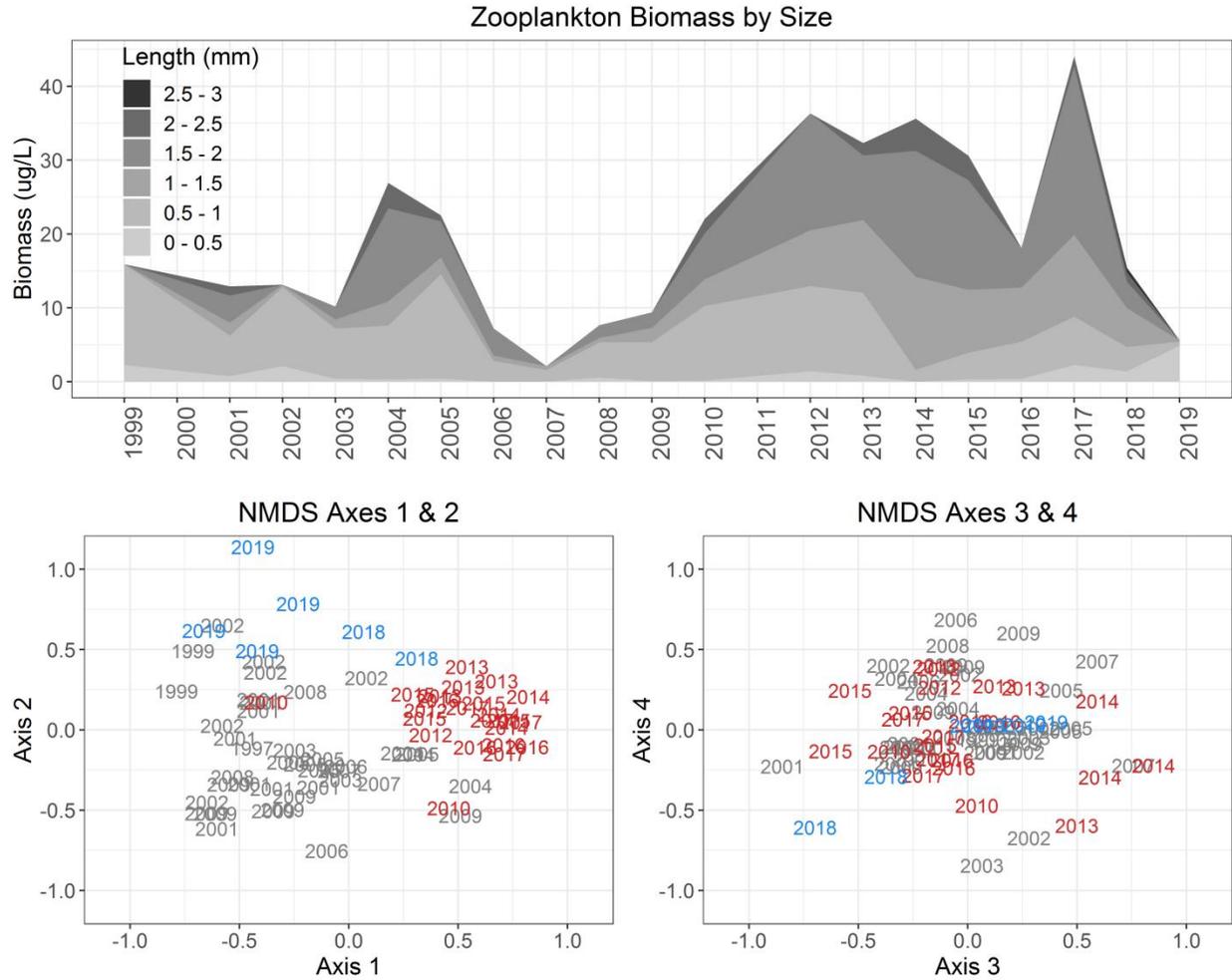


FIGURE 4. Total per-liter zooplankton biomass and non-metric multidimensional scaling (NMDS) results for per-species per-liter zooplankton biomass in Honnedaga Lake from 1999-2019. Total per-liter biomass is separated by year and length category while NMDS results are separated by sample and labeled by year. Colors indicate membership in each of three periods: pre-*Chaoborus* (gray, 2005-2009), *Chaoborus* and pre-smelt (red, 2010-2017), and both *Chaoborus* and smelt (blue, 2018-2019).

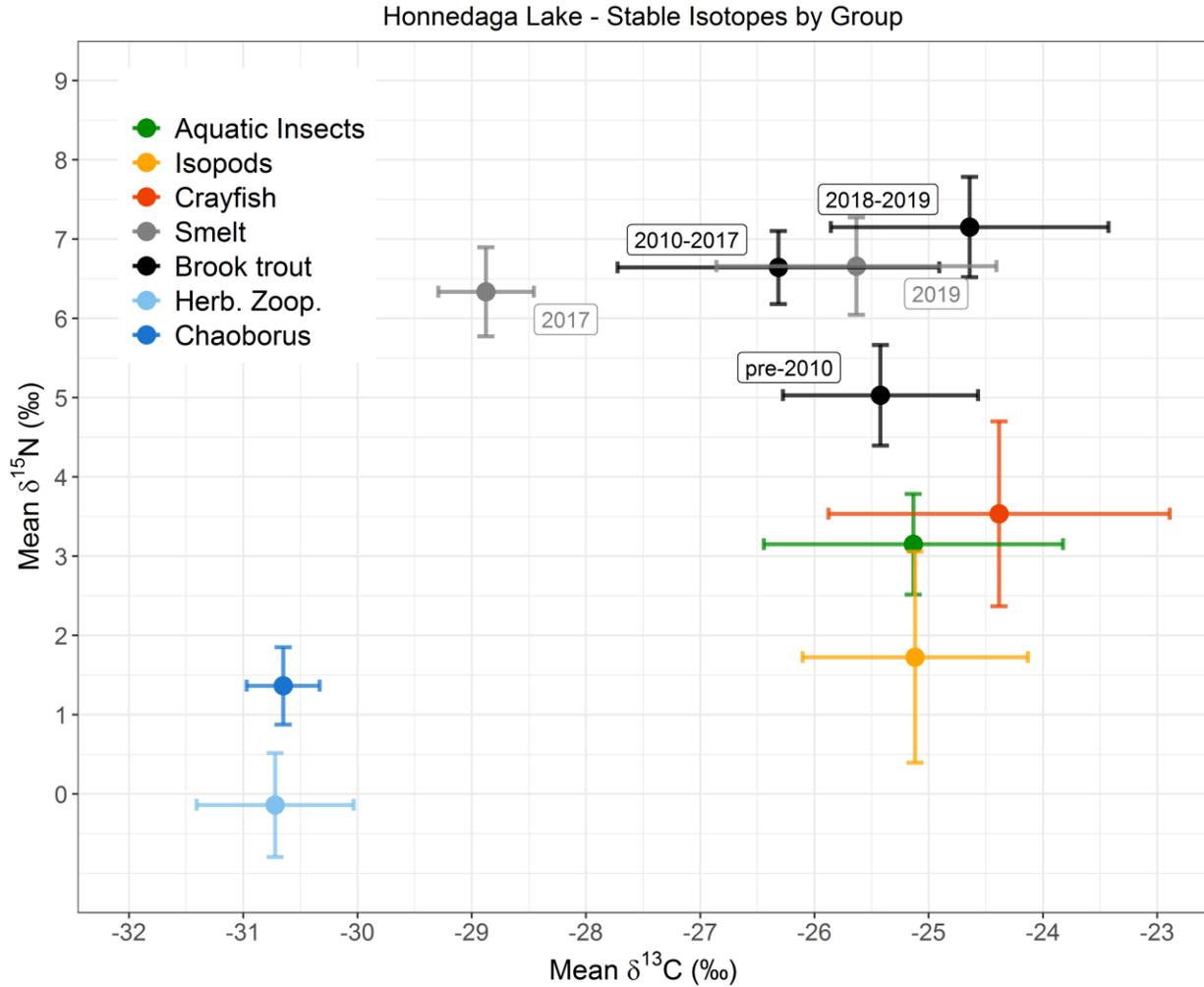


FIGURE 5. Ratios for the stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) for food web components from Honnedaga Lake. Points represent mean values while bars indicate one standard deviation. Food web components are denoted by color with isopods (gold), aquatic insects (green), and crayfish (red) representing samples collected during spring 2019. Herbivorous zooplankton (light blue) and *Chaoborus* (dark blue) represent stored samples from 2007-2019 (zooplankton) and 2012-2017 (*Chaoborus*). Rainbow smelt (gray) are separated and labeled by year (2017 or 2019) while brook trout (black) are separated and labeled by period.

DISCUSSION

We observed strong shifts in biomass and composition of the Honnedaga Lake zooplankton community coincident with changes in the relative density of two novel zooplankton predators. One predator, *Chaoborus*, appeared in the lake in 2010 as it recovered from acidification; the other, non-native rainbow smelt, was unintentionally introduced in 2015. The appearance of *Chaoborus* contributed to development of a zooplankton community typical of lakes that have recovered from acidification (Keller et al. 2007). This was reversed by the introduction of rainbow smelt, returning the zooplankton community to a condition resembling conditions when the lake was acidified.

In 2010, the appearance of *C. punctipennis* led to a zooplankton community that was more diverse than in prior years and dominated by large-bodied species, resembling a community in lakes that were no longer acidified. Although this could be attributed to a slight rise in pH between 2009 and 2010, pH levels remained below the 6.0 threshold specified by Havens et al. (1993) for widespread zooplankton recovery from acidification. In addition, many acid-sensitive species (e.g. *E. lacustris* and *M. edax*) were present in low numbers prior to 2010, suggesting that chemical incompatibility alone does not explain these shifts. Instead, colonization by *C. punctipennis* likely contributed to dominance by large zooplankton by simultaneously releasing them from both competition with smaller species and piscine predation. *C. punctipennis* have been reported to selectively feed upon small prey, particularly as late instars selecting smaller individuals due to gape limitations and handling efficiency (Swift 1992). The appearance of high densities of *H. gibberum* is consistent with the potential dominant influence of *C. punctipennis* on the zooplankton community because these gelatinous zooplankton are difficult or impossible for *C. punctipennis* to handle (Swift 1992)

Drivers behind the timing of *C. punctipennis* colonization are unknown, but the species disperses readily and is present within many regional waters. Therefore, this organism could have easily reached Honnedaga Lake after a shift to changing environmental conditions such as the observed increase in mean DOC concentrations to nearly double previous values coincident with the first detections of *Chaoborus*. Changes in DOC are often linked to watershed pH (Driscoll et al. 2016) with widespread increases associated with recovery from acidification (Leach et al. 2019). Dissolved organic carbon has a strong, nonlinear effect on UV attenuation with a critical threshold between 1-2 mg/L, below which 1% attenuation depths quickly increase and extend to depths greater than 20 m (Williamson et al. 1996). *Chaoborus* larvae are known to be sensitive to UV exposure, with ambient surface levels resulting in mortality (Persaud and Yan 2003). The observed shift in DOC values within the most critical range for UV attenuation could have increased survival of *Chaoborus* in Honnedaga Lake after 2009. Regional studies have shown links between DOC and *Chaoborus* abundance (Wissel et al. (2003) although the range of values included in their study (1.4-12.4) was well above most values measured in Honnedaga. Improvements in pH and monomeric aluminum concentration were also observed during this period that could have contributed to *Chaoborus* survival, but previous studies suggest that *C. punctipennis* is relatively tolerant of both acidification and aluminum levels (Havas and Likens 1985; Price and Swift 1985).

As has been observed with prior introductions of planktivorous fish, the introduction and subsequent establishment of rainbow smelt during the last few years of this study rapidly changed both food web linkages and the overall zooplankton community. To some degree, predation by smelt resulted in a zooplankton community that resembled waters heavily impacted by acidification (i.e. low diversity and dominance by small, acid-tolerant species). This

zooplankton community broadly resembled that of the lake prior to colonization by *Chaoborus*, though NMDS results indicate that it differed in species composition from that earlier time period with the majority of biomass consisting of *B. longispina* rather than *L. minutus*. The propensity of rainbow smelt to select large-bodied prey is well-documented (Johnson and Goettl 1999), but the decline in *L. minutus* may reflect a preference by smelt for copepods or higher order effects due to changes in community interactions. In addition, smelt appear to have greatly decreased *C. punctipennis* abundance; the observation of enriched $\delta^{15}\text{N}$ and depleted $\delta^{13}\text{C}$ ratios in smelt collected in 2017 suggest that their diet was dominated by *Chaoborus*. In particular, their $\delta^{13}\text{C}$ ratios were approximately 2.0‰ higher than those measured for *Chaoborus* and ~4.0‰ lower than the mean values for littoral invertebrates. Likewise $\delta^{15}\text{N}$ enrichment of smelt in 2017 suggest a mean prey $\delta^{15}\text{N}$ ratio of 3.0-3.5‰. Taken together these signatures suggest a heavily pelagic prey base with a higher aggregate trophic level than could be explained by zooplankton augmented by littoral invertebrates alone. Isotope ratios for smelt in 2019 much more closely resemble those expected from a littoral diet, mirroring the decline in relative abundance of *Chaoborus* and supporting the theory that smelt reduced *C. punctipennis* to the point of rarity.

We found isotopic evidence for diet adaptation in brook trout in response to each colonization event. Incorporation of *Chaoborus* into fish diets appears to have been relatively quick with a pronounced enrichment in $\delta^{15}\text{N}$ noted in 2010, the first year that we detected *Chaoborus* in our zooplankton samples (Figure S1). Changes in $\delta^{13}\text{C}$ were not noted until 2011, likely due to differential turnover of ^{13}C in muscle relative to ^{15}N (Perga and Gerdeaux 2005). Our findings suggest that brook trout were much slower to begin consuming smelt. Isotopic ratios for trout remained very similar to those of smelt throughout the 2015-2017 period with

nearly identical $\delta^{15}\text{N}$ values. However, beginning in 2018 brook trout began to show enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values comparable to those for smelt, suggesting that they had begun engaging in widespread piscivory.

Our findings support prior observations that changes to mid-level consumers in lake ecosystems can strongly impact aquatic food webs by altering zooplankton communities (Walsh et al. 2017). Metrics based on these communities, such as species richness, are often used in assessments of ecosystem recovery and are important in evaluating responses to management efforts, such as those enacted to reduce acidification (Keller et al. 2002). However, consideration of mid-level invertebrate predators is often haphazard or non-existent in studies investigating differences in zooplankton communities across gradients of acidification. For example, Yan et al. (2008) explored long-term trends in community changes in response to predators and chemical variables but did not directly consider *Chaoborus* abundances despite stating that they were a principle invertebrate predator in the lakes they studied. Similarly, while Gray et al. (2012) did include *Chaoborus* densities in their analysis and found them to be weakly predictive of cladoceran community composition, they did so without consideration of species. However, genus-level information about *Chaoborus* is likely be a poor predictor as there is considerable variation between species in diet (Fedorenko 1975; Croteau et al. 2003), diel behavior (Carter and Kwik 1977), and ability to co-exist with fish (Wissel et al. 2003).

Gray et al. (2012) also pointed out that their *Chaoborus* densities were collected 3-4 years after zooplankton sampling and might therefore be influenced by increasing DOC and associated reductions in UV exposure, but concluded that the mean increase of 0.97 mg/L was unlikely to affect abundance. However, the initial DOC values for many of their study lakes were at or lower than 2.0 mg/L, the threshold below which even very small shifts in DOC can

radically change UV attenuation (Williamson et al. 1996). This dynamic may explain why Gray et al. (2012) found DOC to be a strong predictor of zooplankton community composition, as well as the decoupled zooplankton recovery observed by Leach et al. (2019) in browning lakes throughout the region. Ultimately our results suggest that *Chaoborus spp.* may be important drivers zooplankton community composition and especially relevant in the context of both recovery from acidification and widespread increases in browning.

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APPENDIX

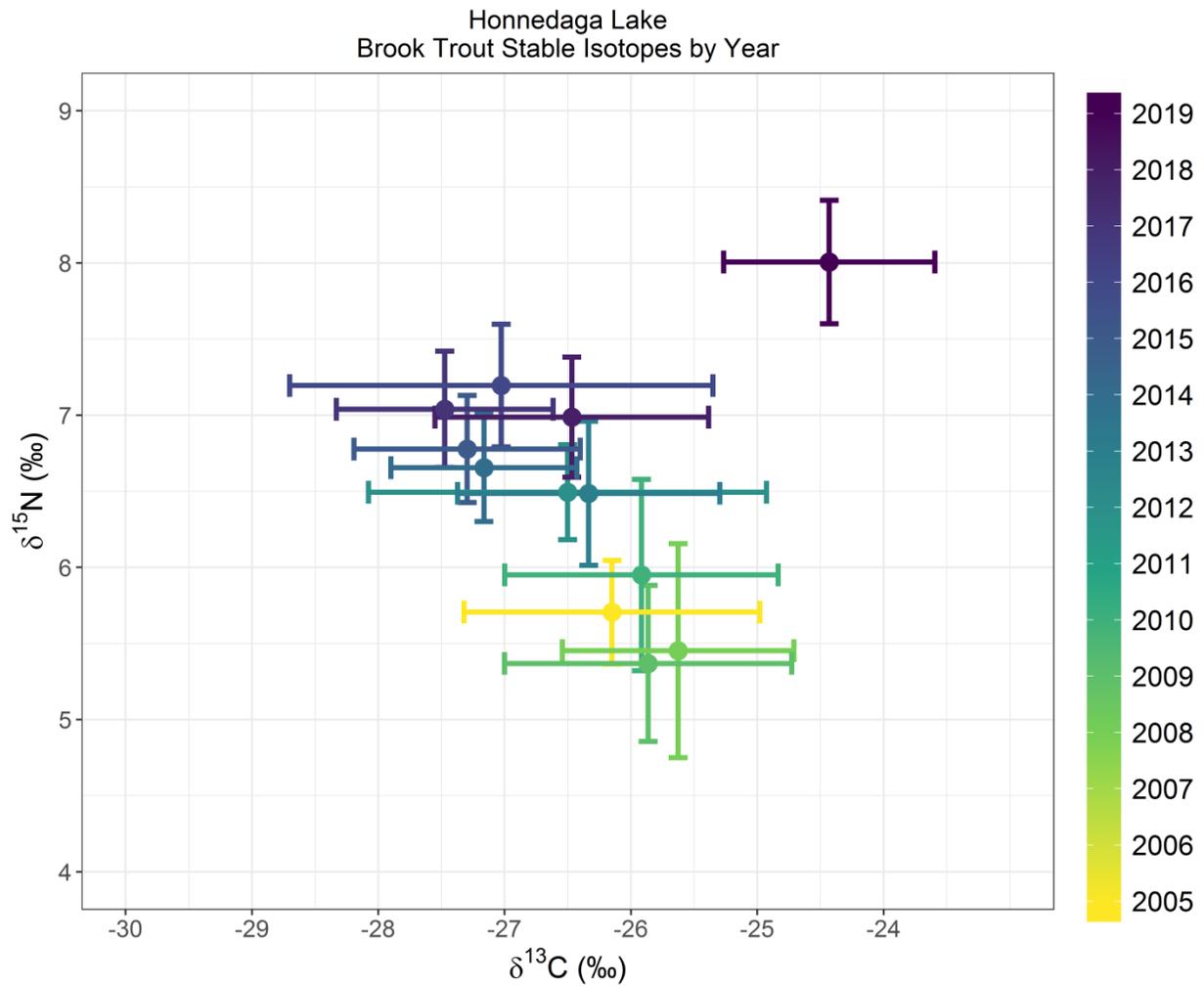


FIGURE S1. Ratios for the stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) for brook trout from Honnedaga lake. Points represent mean values while bars indicate one standard deviation.

**CHAPTER 4 – DIEL MOVEMENT BY WHITE SUCKER (*CATOSTOMUS
COMMERSONI*) IN CONNECTED NORTHERN LAKES: IMPLICATIONS FOR
CONNECTIVITY AND ECOSYSTEM DYNAMICS**

ABSTRACT

Although consistently repeated daily habitat shifts by fish can expose or protect individuals from a variety of threats and influence nutrient transport between systems, logistical constraints make individual horizontal movement difficult to study on short time scales. As a result, diel movements by fish are often poorly documented. Suckers (Catostomidae) are a key group of fish that have been examined with this in mind, as many species are large, long-lived, and comprise a large proportion of biotic biomass in many waters. Previous studies in rivers have shown that multiple sucker species exhibit complex, diel movement. We investigated the prevalence of short-term movement by the widely distributed white sucker (*Catostomus commersoni*) in an interconnected northern lake system using a combination of PIT-tagged fish and mark-recapture abundance estimation. Our results indicate that white suckers engaged in inter-lake movement on a repetitive and distinctly directional diel basis. Overall, these findings highlight the potential influence of extensive, yet generally unobserved, movement within connected lake systems on the biology and management of these and other fishes.

INTRODUCTION

Horizontal movement of fishes within freshwater systems has long been recognized as important to conservation and management (Gerking 1959), yet presence and scope of such behavior is poorly documented and often controversial. This is true even in relatively simple stream habitats where theories as to the prevalence and scope of movement

have been actively debated (Gerking 1959; Gowan et al. 1994; Rodríguez 2002). The highly variable results of such investigations may in part be due to the complex mechanisms driving movement that likely involve an intersection of extrinsic environmental conditions and intrinsic individual traits (Rasmussen and Belk 2017). This latter category includes attributes of individuals such as sex and condition, as well as less obvious inter-individual differences in behavior that can potentially affect both individual movement and the behavior of social groups (Jolles et al. 2017). In addition to being species-specific, movement may therefore vary greatly depending on the system involved and even the genetic makeup of individuals in the population (Rasmussen and Belk 2017). Such variation presents a challenge when making conservation decisions involving connectivity because prevailing insights are generally limited to easily observed large-scale spawning movements of charismatic species such as salmonids (Fullerton et al. 2010). By contrast, the ecosystem dynamics of more cryptic foraging dynamics are likely as important (Roach et al. 2009; Jardine et al. 2012), but seldom have been recognized.

Movement is fundamentally associated with optimal foraging and energy management. For example, a predator can increase prey encounter rates and enhance foraging opportunities by moving to new locations or moving through an area as rapidly as possible, while balancing movement costs against the energetic costs involved (Ware 1978). Conversely, increasing foraging area or speed also carries the potential for increasing predation risk (Brönmark et al. 2013). Rennie et al. (2008) postulated that this balance explained sexual dimorphism in walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*), with females growing faster due to the riskier high-intensity feeding activity necessary to support their energy-intensive gonad development. In heterogeneous habitats such as rivers, movement can allow individuals to thermoregulate, either to fine-tune metabolism (Westhoff et al. 2016) or avoid lethal

temperatures (Berman and Quinn 1991). Fish may also employ movement to achieve an optimal blend of both foraging opportunities and metabolic efficiency. Armstrong et al. (2013) observed that juvenile coho salmon (*Oncorhynchus kisutch*) alternated between feeding on sockeye salmon (*Oncorhynchus nerka*) eggs in cold downstream waters and resting in warm upstream waters despite the two habitats being nearly one kilometer apart. On a larger scale, movement related to foraging or spawning can result in the transfer of nutrients within and between systems (Flecker et al. 2010; Childress and McIntyre 2015).

Seasonal or diel movement of individuals results in spatially and temporally heterogeneous distributions that can complicate assessment efforts and expose populations to a variety of threats. Seasonal migrations to limited habitats, such as spawning grounds, leave fish vulnerable to a variety of factors that can impede these movements, including losses of connectivity (McCully 1996) and changes to temperature (Crossin et al. 2008) or flow regimes (Dudley and Platania 2007). These mass movements can also make populations highly vulnerable to harvest at locations often targeted by commercial and recreational fisheries (Selgeby 1982). Likewise, assessments that target these aggregations through seasonal surveys or the use of angler data can often result in biased, hyperstable estimates (Erisman et al. 2011). Beyond aggregation effects, the scale, frequency, and speed of movement can also strongly influence the capture efficiency of many sampling techniques by changing both encounter and retention rates (Rudstam et al. 1984). Thus understanding the spatial ecology of a fish population is vital to conservation and management (Cooke et al. 2016).

Unfortunately, logistical constraints make individual horizontal movement difficult to study on short time scales. While mass diel vertical (Hasler and Villemonte 1953) and horizontal (Hasler and Bardach 1949) movements in lakes have been recognized for over 70 years, large-

scale individual-based studies in freshwater systems are rare (Booth et al. 2013). Technological constraints are partially responsible. Although both radio and acoustic telemetry can provide high frequency position determination, they require either large amounts of human effort or extensive automated systems (Lucas and Baras 2008). Furthermore, depth-based attenuation of radio tags tends to limit their applications in deeper lacustrine environments (Stasko and Pincock 1977; Freund and Hartman 2002) while acoustic tags suffer from ultrasonic interference in flowing waters (Shroyer and Logsdon 2009). One alternative to these techniques is passive integrated transponder (PIT) telemetry, which provides point-based individual movement for a relatively low per-individual cost. This approach is increasingly being used in river systems, for example to identify previously unrecognized short-term movement of sucker populations in the Gila River (Booth et al. 2013). Regardless of technique, most studies of non-spawning fish movement have focused on relatively well-defined water bodies such river networks or single lakes. However, many freshwater ecosystems are mosaics of diverse, interconnected habitats with linkages that vary depending on species and timing (Schofield et al. 2018). Chains of connected lakes are a common example. Studies of game fish in these connected ecosystems suggest that muskellunge (*Esox masquinongy*) travel freely between waters, yet some species like walleye may behave as relatively isolated populations (Weeks and Hansen 2009).

Suckers (Catostomidae) represent a promising group in which to study fish movement as many species are large, long-lived, and often maintain high biomasses in the waters they inhabit (Quist and Spiegel 2012). Like salmonids, spawning migrations of iteroparous suckers have been shown to represent a sizeable nutrient subsidy to tributary ecosystems (Childress and McIntyre 2015). Studies of Sonoran sucker (*Catostomus insignis*) movement in streams using PIT arrays have also revealed a high degree of non-spawning movement, including nocturnal foraging

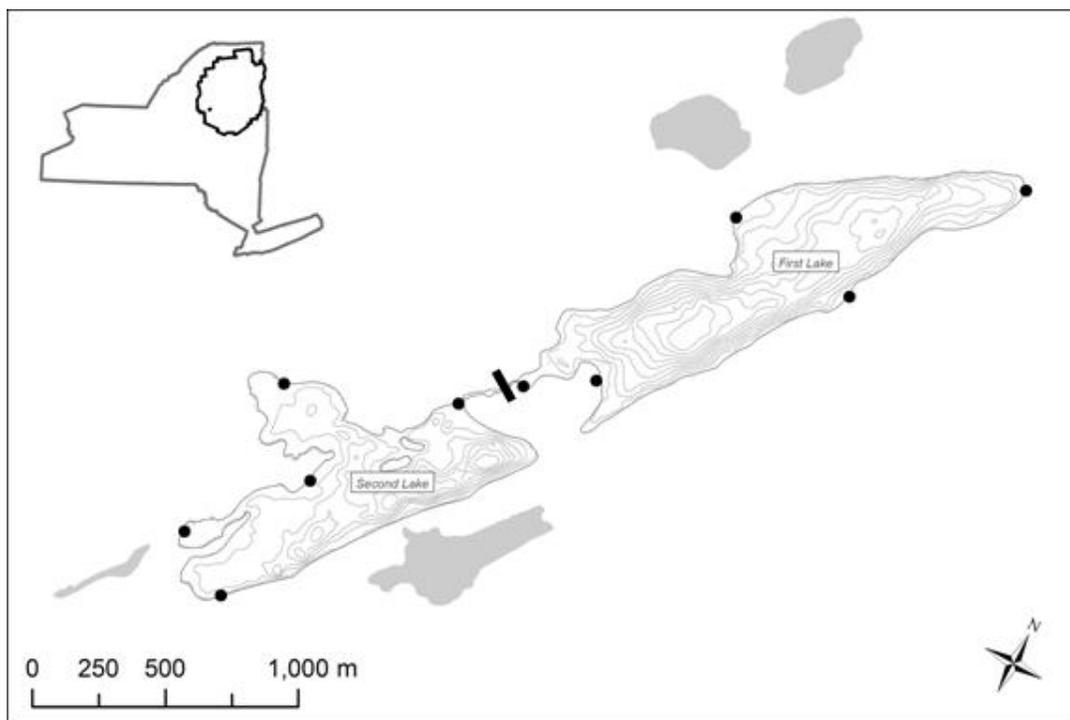
behaviors that structure benthic habitat and play a significant role in organic matter transport (Booth et al. 2020). Similar behavior has been observed in other sucker species, including a stream population of northern hog sucker (*Hypentelium nigricans*). Matheney and Rabeni (1995) observed that these fish exhibited both strong diel patterns of activity, foraging in deep pools during the day and resting in shallow riffles at night, and localized home ranges with repeated use of the same pools and riffles throughout the season. Short-term movements may be typical of sucker populations, but intensive studies to date have only focused on stream populations.

We sought to investigate the scope, timing, and magnitude of short-term movement by white suckers (*Catostomus commersoni*) in First and Second Bisby lakes, an interconnected northern lake system. White suckers represent an important study species for such an investigation as they are abundant generalists that inhabit streams, rivers, and lakes from northern Canada to the American South. In small northern lakes, white sucker often comprise the majority of piscine biomass (Flick and Webster 1992; Brodeur et al. 2001), therefore their movements are likely to play an important role in trophic dynamics. Ultimately our objective was to use a combination of PIT telemetry and mark-recapture modeling to answer three primary questions: 1) does substantial non-spawning movement occur between First and Second Bisby lakes?, 2) what is the timing and frequency of any such movement?, and 3) is the abundance and magnitude of population movement of white suckers large enough to influence ecosystem processes?

METHODS

Study location.— The Bisby chain of numbered lakes is located in the southwestern Adirondacks (Figure 1). The main portion of the chain is comprised of two oligotrophic lakes, First and Second Bisby lakes. First Bisby has a surface area of 63 ha and a maximum depth of 31 m while

second is slightly smaller with an area of 50 ha and a maximum depth of 19 m. The two lakes are connected by a short (200m long), narrow (mean stream width ~4m), shallow (average depth 1m), low-gradient channel through which fish can move throughout the year. Third and Fourth Bisby Lakes lie downstream of Second Bisby but are generally not passable by fish due to a low dam between Second and Third Lakes and the absence of a deep enough connection between Third and Fourth. Both First and Second Bisby Lakes support self-sustaining wild populations of lake trout (*Salvelinus namaycush*), brook trout, white sucker, smallmouth bass (*Micropterus dolomieu*), central mudminnow (*Umbra limi*) and creek chub (*Semotilus atromaculatus*). In addition, First Bisby is stocked with Atlantic salmon (*Salmo salar*) each year.



MAP 1. First and Second Bisby lakes. Inset map depicts study site location within New York State and the Adirondack Park (black outline). Contour lines within study lakes represent 3 m depth intervals, nearby non-study waterbodies are depicted in solid grey. Points represent standardized trap net sampling locations. Black bar depicts location of stream-width PIT array.

Fish sampling.— We captured white suckers in First Bisby Lake during the spring and fall months of 2015-2018 using a combination of Oneida-style trap nets, gill nets, and littoral boat electrofishing, as well as by gill netting in Second Bisby Lake. All captured fish were measured, weighed, and scanned for previously implanted tags. Fish larger than 150 mm in length that had not been previously tagged were anesthetized prior to having a 23 mm HDX PIT tag (Oregon RFID) implanted in their body cavity. Tagged fish were monitored until they were fully recovered, then were released at the site of capture. White suckers captured during their spring spawning run were also evaluated for ripeness, i.e. whether gametes could be expressed and sexed according to gamete type and/or the presence of tubercles (indicating male individuals).

To estimate the abundance of white suckers we used a pre-existing dataset of marked fish caught during annual surveys from 2003-2007. We chose to use this dataset, rather than information from our contemporary surveys, because it represented a set of multi-year sampling events conducted with consistent gear at fixed locations in both lakes. For mark-recapture modeling we further restricted the data to only fall captures, eliminating the potential for bias due to spawning-related movements (a concern for early spring surveys). Our movement data suggested that only fish larger than 250 mm were moving with any frequency, therefore we used data from tagged fish with a length of at least 250 mm. Each survey in this dataset consisted of a single sampling occasion in late September with ten nets emplaced for two nights at consistent locations in First and Second Bisby Lakes (Figure 1). Captured fish were handled as described previously with the exception of tagging being accomplished using a numbered spaghetti tubing tag (Floy Tag Co) anchored in the base of the dorsal fin rays (White and Beamish 1972).

PIT array.— To assess movement between the two lakes we installed a stream-width PIT array at the narrowest point of the connecting channel. This array consisted of a multi-antenna HDX PIT reader (Oregon RFID) driving three sequential antennas, each made up of a single 4 m x 0.5 m loop of 12-ga copper wire affixed to a rectangular frame of treated lumber. Antennas laid flat along the bottom of the channel in order to allow passage of boats and were capable of detecting tags throughout the water column, which had a mean depth of 0.6 m over the antennas. The array operated continuously from May to October during 2016-2017 and from May through June of 2018 before several power system failures made operation erratic. The array logged the time and position (i.e. detection antenna) of each detected tag and its unique ID, allowing direction of travel to be inferred from the individual's sequence of travel through the array.

Mark-recapture.— Because PIT array data ultimately suggested a high degree of movement between the two waters we treated both lakes as a single population. Abundance was estimated using the POPAN formulation of the Jolly-Seber model (Schwarz and Arnason 1996) that allows for the estimation of N , apparent survival (ϕ), capture probability (p), and probability of entry into the population (p_{ent}). The latter term encompasses both permanent immigration and recruitment, although in our system recruitment is the only feasible form of entry into the population. Apparent survival similarly includes both loss due to death and permanent emigration, the latter possible during high water events when individuals could potentially go over the dam to Third Bisby Lake and be unable to return. We verified the suitability of our data using goodness of fit tests (Pradel et al. 2003) before fitting a set of models encompassing all potential combinations of constant and time-varying parameters. Ultimately the model that included constant ϕ and p_{ent} but time-varying p had the lowest AIC value, therefore we used results from that model fit for all subsequent analyses.

Software.— All statistical analyses were conducted in R version 3.5.2 (R Core Team 2018). Mark-recapture models were fit using the “marked” package (Laake et al. 2013) with goodness of fit assessed with the “R2ucare” package (Gimenez et al. 2017). Data manipulation was performed using “dplyr” (Wickham et al. 2015) and plotting carried out with the “ggplot2” (Wickham 2011 p. 2) and “grid” (Murrell 2002) packages.

RESULTS

During the 2015-2018 surveys we captured a total of 386 unique individuals, of which 295 were PIT tagged (i.e. were ≥ 150 mm in length) (Table 1). Detection of individuals at the channel array began shortly after the first tagging occasion and continued throughout the study period. While the greatest amount of movement occurred during the May spawning season, steady movement persisted through fall during 2016 and until August in 2017 (Figure 2). A complete cessation of movement was noted between August and early-September 2017. This gap in detections was not due to array failure as other tagged fish (smallmouth bass) were detected by the array during this period. Instead, the most likely explanation is that the very low water levels observed during August 2018 made movement undesirable or impossible. Movement was very closely correlated with light levels during all years and seasons with the bulk of movement occurring just after dusk and just prior to dawn (defined as the beginning and end up nautical twilight, respectively) and shifting in parallel with the solar cycle throughout the year.

TABLE 1. Number of white suckers captured during seasonal sampling of First and Second Bisby lakes in 2003-2009 and 2015-2018. Fish from 2003-2009 were captured in both lakes using trap nets, while fish from 2015-2018 were captured in First Bisby using a multiple types of gear.

	2003	2004	2005	2006	2007	2008	2009		2015	2016	2017	2018
Spring		512	275	217	443	624	273		13	102	88	78
Fall	418	424	262	201	596				136	43	48	12

The direction of movement was nonrandom during the two daily periods. The vast majority of moving fish passing the array at dusk went from Second Bisby to First while the majority of fish transiting during the dawn hours transited from First Bisby to Second. Analysis of individual tag data showed that the majority of individuals moving into First Bisby each evening returned the following dawn, though only a subset of tagged individuals engaged in this diel movement. Among this subset of frequently moving individuals, diel movement was repeated throughout the season and often for multiple days in a row (Figure 5). The greatest number of recorded diel movements in a season for an individual was 48, with a further 10 occasions where the individual stayed in First Bisby Lake for one to three days prior to returning. A few individuals in the dataset (tags T189666 and T285141) appeared to engage in a limited degree of diel movement in the opposite direction, spending the majority of their time in First Bisby and occasionally venturing to Second Bisby for short stints. Diel movement patterns were also repeated across multiple years, with many individuals displaying the same pattern in successive years or across all three. Interestingly, the size distribution of moving individuals was not representative of the larger population and primarily consisted of larger individuals. Of the 28 individuals that engaged in some form of diel movement, none were smaller than 200 mm. Low numbers of 200-299 mm fish engaged in diel movement (1.1% and 5.9% of the tagged 200-

249 and 250-300 mm, respectively) while larger size classes were far more likely to move (Table 2). The greatest movement was observed in the 450-500 mm size group where 43.3% of tagged individuals engaged in diel movement during one or more years.

The fall 2003-2007 fall dataset included 585 Floy-tagged individuals that were used for POPAN abundance estimation (Table 1). Finally, an additional 1983 fish were captured and tagged during spring surveys conducted from 2004-2009. Although data from spring surveys conducted during those same years were not used for population estimation, these data were included in analyses of spawning timing, size distribution, and individual growth. The size distribution of fish within the population suggested the presence of at least three cohorts, as well as a less differentiated group of fish in the 400-500 mm size range (Figure 3). Growth data from recaptured individuals showed rapid growth during the summer months for smaller size classes with a mean rate of 0.52 mm/day (SD = 0.09) observed for fish in the 100-200 mm size class. Growth subsequently slowed in larger size classes, with some individuals in all classes 300 mm or larger showing no growth (or even apparent declines) in length over summer months. Conversely, tagged fish from all size classes grew very little over winter months, adding an average of 0.03 mm/day (SD = 0.10). Relative proportions of ripe individuals from all sampling events indicated a peak spawning time of approximately May 14-15th, although ripe individuals were captured during all surveys which stretched from May 10th to May 29th (Figure 4). The relative proportion of ripe individuals declined sharply by May 22nd, suggesting that the majority of spawning takes place prior to that date. This timing is typical of described white sucker spawning phenology for the region (Morse 2007).

TABLE 2. Mark recapture estimates, population size distribution, distribution of fish engaging in diel horizontal movement (DHM), and expanded estimates of numbers and biomass of moving fish.

	Length Category					
	250-299 (mm)	300-349 (mm)	350-399 (mm)	400-449 (mm)	450-499 (mm)	500-549 (mm)
Estimated N	471 (274-812)	348 (202-599)	118 (68-203)	70 (41-121)	92 (53-159)	72 (42-124)
Population Size Distribution	0.40	0.30	0.10	0.06	0.08	0.06
Proportion of tagged fish engaging in DHM	0.06	0.11	0.23	0.13	0.43	0.25
Estimated N engaging in DHM	28 (16-48)	25 (14-43)	18 (11-31)	4 (3-8)	31 (18-53)	4 (2-6)
Estimated biomass engaging in DHM (kg)	5 (3-9)	8 (5-14)	9 (5-16)	3 (2-6)	34 (20-59)	6 (3-10)

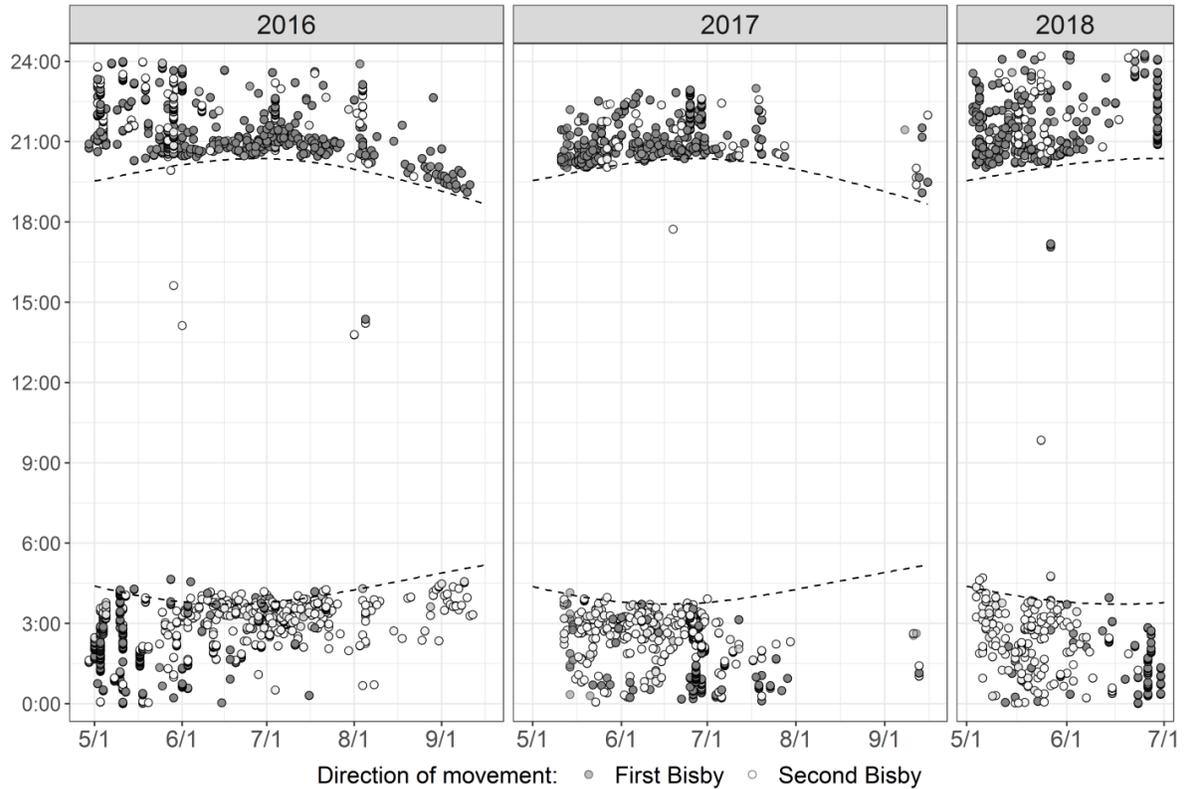


FIGURE 1. Records of individual movements across the PIT array between First and Second Bisby lakes by year, date, and time of day. Direction of movement, determined by the sequence of antenna detections within a five minute period, is depicted by shading with grey points denoting movement into First Bisby and white points detecting movement from First to Second Bisby. Date (X-axis) spans the array's operating period for each year. Time of day (Y-axis) is depicted in Eastern Standard Time. A dashed line indicates the beginning and end of nautical twilight for each day

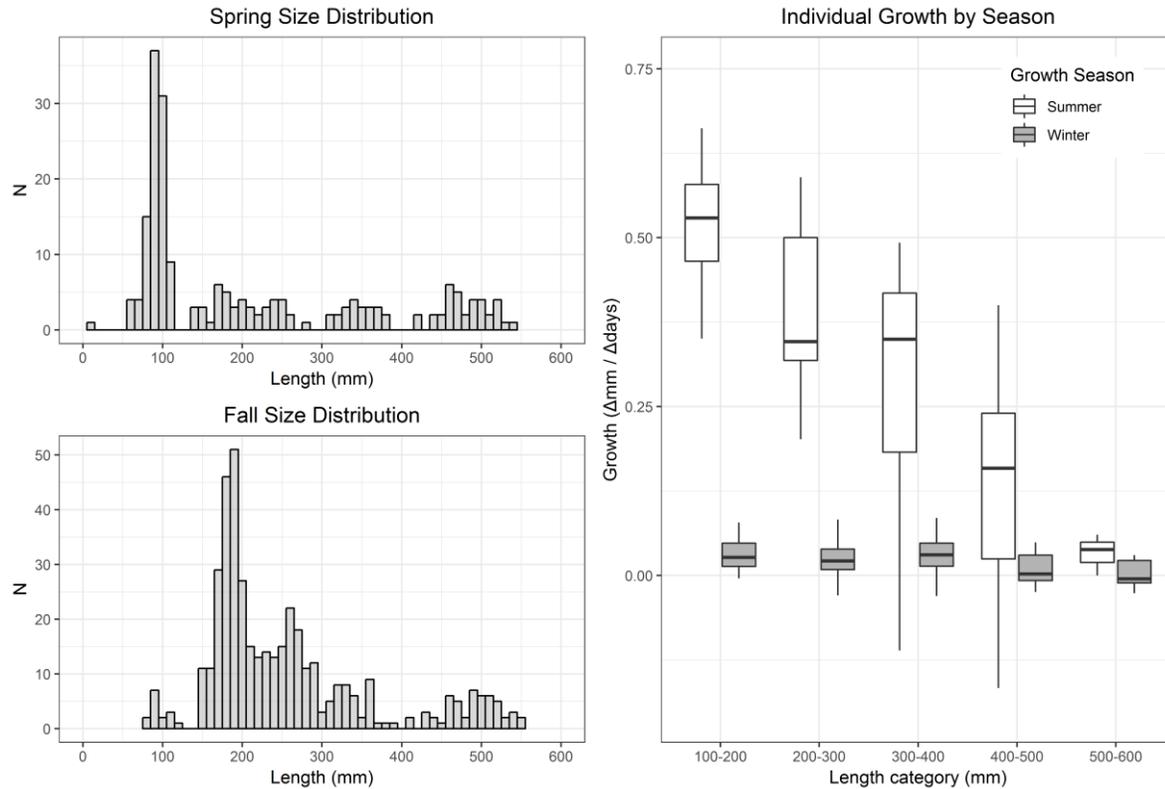


FIGURE 2. Size distribution and individual growth of white sucker captured during spring and fall trap net occasions. Size distribution represents number of fish captured within each 10 mm bin. Individual growth reflects change in size of tagged individuals recaptured within one year over either a summer growing season (spring capture and fall recapture) or winter (fall capture and spring recapture).

Mark recapture estimates indicated that the total population of white suckers ≥ 250 mm in First and Second Bisby lakes numbered approximately 1173 individuals (95% CI = 681-2020). The estimate of average annual survival was 0.49 (0.34-0.64) while the probability of entry into the population during a given year was estimated to be 0.23 (0.17-0.30). Capture probability estimates fluctuated between years and ranged from 0.18 to 0.33 aside from the initial, non-identifiable probability. These results suggest an adult density of 10.3 fish per hectare (95% CI = 6.0-17.9) in the combined lake system. Assuming that the size distribution of fish captured in

trap nets is representative of the larger population, we calculated the relative proportion of the population within each 50 mm size class. We then further applied the proportion of PIT tagged fish that engaged in diel movement within each size class to arrive at an estimate of 109 fish (64-188) engaging in regular diel movement during a given year (Table 2). Using estimated numbers within each length group, the median length for each group, and a standard length-weight relationship for white sucker (Murphy et al. 1991), we calculated the biomass of suckers engaging in diel movement to be approximately 65 kg (95% CI = 38-114).

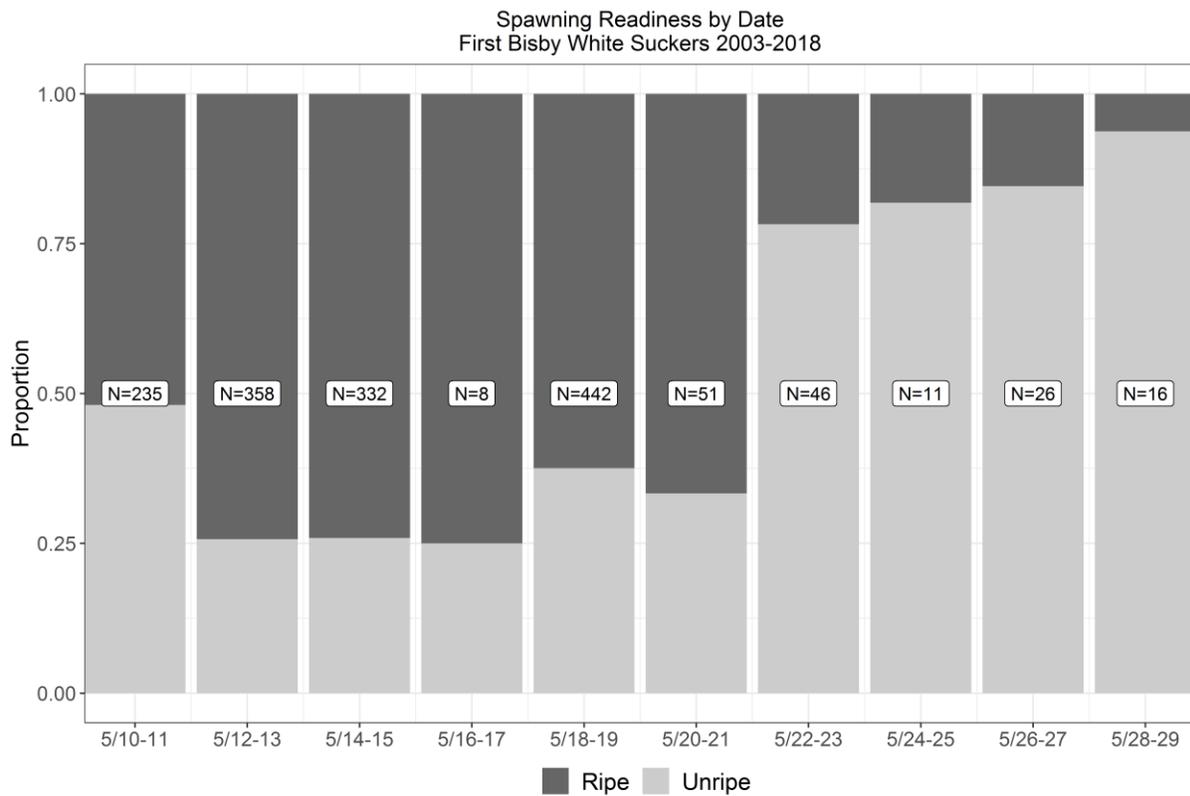


FIGURE 3. Proportion of ripe and non-ripe (pre- or post-spawn) fish within two-day capture windows from the earliest to latest dates of spring capture within First and Second Bisby lakes.

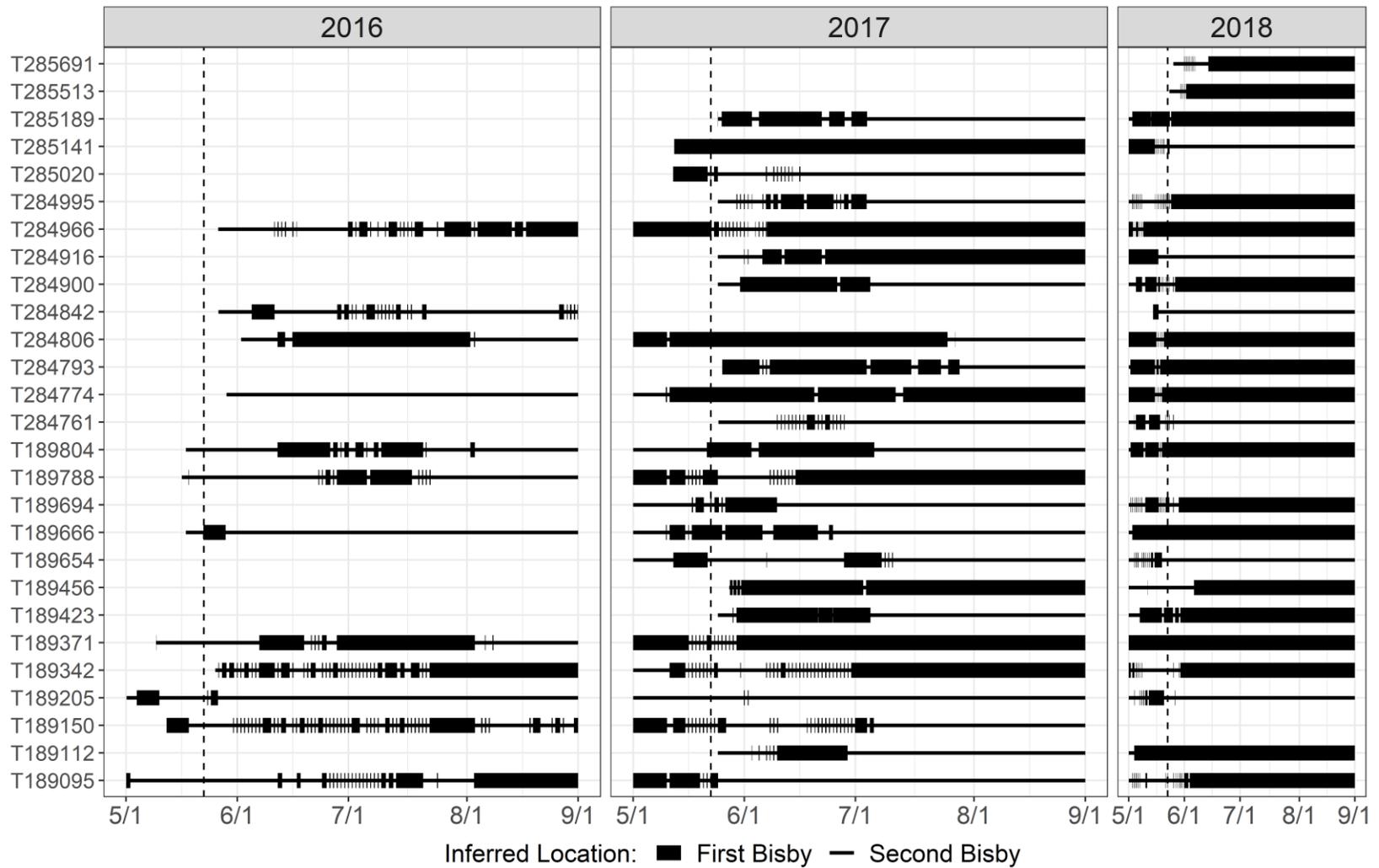


FIGURE 4. Movements by date and time (decimal days; X-axis) for individual tagged fish exhibiting some degree of diel movement. Line thickness represents lake of residence, inferred from directional movement across the stream-width array between First and Second Bisby. The dashed line indicates May 22nd, the date by which historical captures indicate most fish are no longer ripe (i.e. in spawning condition).

DISCUSSION

We found that white suckers moved between study lakes throughout the ice-free season and did so on a repetitive and distinctly directional diel basis. These findings are similar to those reported by Booth et al. (2013) for Sonoran suckers and desert suckers in a New Mexico river. Together, these studies in divergent ecosystems suggest that small-scale movement may be prevalent in catostomids inhabiting a wide range of environments. Our results also suggest that inter-lake movement has a distinct individual component, with some tagged fish engaging in the same repetitive movements each year while others only exhibited movement during the spawning season. Individual variation in movement may be an adaptation to facilitate dispersal, with "explorer" phenotypes most likely to colonize new habitats (Rasmussen and Belk 2012) and discover optimal foraging locations (Gowan and Fausch 2002). Thus the variation in observed activity may be due to intrinsic traits (i.e. "personality") rather than extrinsic factors, although the repetitive nature of inter-lake excursions supports the notion that movement between lakes confers some benefit.

Feeding behavior is one obvious explanation for diel movement between waters. White sucker are known to feed upon a wide range of diet items, from benthic invertebrates and detritus to pelagic zooplankton (Saint-Jacques et al. 2000). Historical diet studies of Second Bisby Lake white suckers suggest that these fish predominately feed upon chironomid larvae and cladocerans, alternating between the two sources throughout the season (Alexandersdottir 1975). The permanent connection between First and Second Bisby Lakes seems to foster similar communities of zooplankton and benthic macroinvertebrates, therefore movement is unlikely to be a strategy for targeting prey resources unique to each lake. However, such movement may still allow individuals to target underexploited patches (Ward et al. 2006), particularly if moving

fish are larger and therefore able to cover greater distances more efficiently than their smaller competitors (Gerritsen 1984). If individuals are simply using First Bisby as an expanded foraging territory, the repetitive return movements to Second Bisby we observed may reflect the usage of a regular refuge habitat as has been observed in other species (Matheney and Rabeni 1995; Booth et al. 2013). Alternatively, circadian rhythm studies of white sucker suggest that they actively engage in diel patterns of behavioral thermoregulation (Kavaliers 1982); the shallower benthic habitat of Second Bisby Lake may represent an optimal combination of metabolic efficiency and predator avoidance.

Beyond individual fitness, inter-lake foraging movement may influence the flow of energy within and between these lakes. Estimates of consumption derived from radioisotope tracing of individuals from the Ottawa River suggest that adult suckers can consume 0.024 gram of food (dry weight) per gram of dry body weight during a typical day (Rowan and Rasmussen 1996). Assuming an estimated body water content of 80% (Marcy-Quay, unpublished data), large white suckers engaging in diel movement may consume 300-550 g dry weight of prey in First Bisby Lake each night. Because these fish spend the majority (~18hrs) of each day in Second Bisby, the bulk of the energy from those diet items is likely transferred to Second Bisby during elimination and excretion. However, the impact of diel movement may extend beyond nutrient transfer. Booth et al. (2020) suggested that benthic foraging by suckers in desert streams may suspend organic matter and create complex bottom morphologies that influence benthic macroinvertebrate communities, effectively acting as "ecosystem engineers". Similar effects have been seen in lakes populated by smallmouth buffalo (*Ictiobus bubalus*) which can influence nutrient cycling through feeding-related sediment disturbance (Shormann and Cotner 1997).

Thus differential foraging activity resulting from inter-lake movement may affect lake-wide food webs through multiple pathways.

Movement between waterbodies is important in the context of lake ecosystem connectivity, particularly actions that may influence fish passage. Concerns about fish passage are often considered only in river systems with large seasonal migrations (Anderson et al. 2018). However, a growing body of evidence suggests that connectivity on much smaller spatial and temporal scales is important (Fullerton et al. 2010). It has been well established that the loss of these linkages in connected lake systems has the potential to disrupt metapopulation dynamics and increase the probability of extinction for isolated population fragments (Hurd et al. 2016). Similarly, connectivity losses that constrain fish movement can alter trophic dynamics by forcing species to shift to alternate food sources when their preferred prey are exhausted (Roach et al. 2009). Despite the great prevalence of connections between lakes, many small lakes have traditionally been considered as isolated systems, though mounting evidence shows that fishes often engage in frequent movement when connections exist (Daniels et al. 2008). Our results reinforce these findings and highlight the potential importance of inter-lake fish movement on shorter timescales than has been previously considered in interconnected lake systems. The presence of such linkages is especially important in the context of smaller systems where seemingly routine actions such as culvert installation and water level management have the potential to substantially alter cryptic connectivity.

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