Inferred fish behavior and its implications for hydroacoustic surveys in nearshore habitats

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Abstract

Population availability and vessel avoidance effects on hydroacoustic abundance estimates may be scale dependent; therefore, it is important to evaluate these biases across systems. We performed an inter-ship comparison survey to determine the effect of vessel size, day-night period, depth, and environmental gradients on walleye (*Sander vitreus*) density estimates in Lake Erie, an intermediate-scaled system. Consistent near-bottom depth distributions coupled with horizontal fish movements relative to vessel paths indicated avoidance behavior contributed to higher walleye densities from smaller vessels in shallow water (i.e., < 15 m), although the difference decreased with increasing depth. Diel bank migrations in response to seasonally varying onshore-to-offshore environmental gradients likely contributed to day-night differences in densities between sampling locations and seasons. Spatial and unexplained variation accounted for a high proportion of total variation; however, increasing sampling intensity can mitigate effects on precision. Therefore, researchers should minimize systematic avoidance and availability related biases (i.e., vessel and day-night period) to improve population abundance estimates. Quantifying availability and avoidance behavior effects and partitioning sources of variation provides informed flexibility for designing future hydroacoustic surveys in shallow-water nearshore environments.

Key words: hydroacoustic survey, diel migration, vessel avoidance, nearshore habitats, environmental gradients, Lake Erie, walleye behavior, Bayesian

1. Introduction

Hydroacoustic surveys are a common tool for informing management of fish populations (Rudstam et al. 2009, Kubečka et al. 2009). A fish population is available to a hydroacoustic survey when a high proportion is within the survey area, and advantageously distributed within the water column (Simmonds et al. 1992, Simmonds and MacLennan 2005). However, if population availability changes across the survey (Comeau and Boisclair 1998, Lawson and Rose 1999, Neilson et al. 2003, Gorman et al. 2012a), the utility of hydroacoustics as an assessment tool is limited. Fish availability and avoidance have been extensively studied in marine (e.g., De Robertis et al. 2008, Fréon et al. 1993, Olsen 1990, Rose 2003) and small freshwater systems (e.g., Draštík and Kubečka 2005, Draštík et al. 2009, Muška et al. 2013, Wheeland and Rose 2014). However, intermediate-scaled systems, such as coastal ocean areas and the Laurentian Great Lakes, which support important fishery production, have received less attention

Diel migrations and system scale can affect population availability to hydroacoustic surveys, biasing abundance estimates. Many organisms undertake diurnal vertical migrations in response to changing abiotic and biotic conditions within the water column (Arhenstorff et al. 2011, Mehner 2012). In particular, movements into and out of the near bottom "acoustic dead zone" can drastically reduce abundance estimates (Lawson and Rose 1999, Neilson et al. 2003, Ona and Mitson 1996). In nearshore areas, some fishes move horizontally between onshore and offshore habitats (i.e., diel bank migrations) to reduce predation pressure, or access optimal foraging, growth, and reproductive habitats (Fréon et al. 1993, Comeau and Boisclair 1998, Gorman et al. 2012a, Cott et al. 2015). Seasonally and spatially dynamic nearshore areas, forming turbidity and temperature gradients (Schertzer et al. 1987, Binding et al. 2012), can influence fish movements. The juxtaposition of nearshore and offshore environments in intermediate-scaled systems may create mismatches between temporal-spatial scale of diel migrations and hydroacoustic surveys, negatively biasing abundance estimates.

Vessel avoidance can also contribute to biased abundance estimates across system scales. Fish avoid sampling vessels using auditory and visual cues (Mitson 1995, Mitson and Knudsen 2003, Lévénez et al. 1990, Fréon et al. 1993). Therefore, proximity between vessels and fish in shallow water (e.g., small systems or nearshore areas; Draštík and Kubečka 2005, Wheeland and Rose 2014) or due to near surface distributions (Neproshin 1979, Olsen 1979, 1990, Soria et al. 1996) likely intensifies avoidance behavior. However, conditions indirectly related to vessel noise, light, and proximity, such as fish species and size, water temperatures (Neproshin 1979), life stage (Misund 1990), and time of day (Neproshin 1979, Fréon et al. 1993) may modulate vessel avoidance behavior. The mechanisms (i.e., diel migration and avoidance) affecting availability are difficult to differentiate across scales but have similar effects, biased abundance estimates.

Hydroacoustic surveys in intermediate-scaled systems, such as the Laurentian Great Lakes, primarily focus on pelagic forage fishes in deep water (Rudstam et al. 2009), while large predatory fishes in shallow water are not generally targeted. Lake Erie walleye (*Sander vitreus*), a large predatory fish, are important to the Great Lakes region, supporting lucrative commercial and recreational fisheries (Locke et al. 2005, and Roseman et al. 2010). As a result, the population is monitored through a large-scale multi-jurisdictional gill net survey to provide relative abundance estimates used for making management decisions (e.g., quota allocation; Hatch et al. 1987, Vandergoot et al. 2010, Pandit et al. 2013). There is growing interest among fisheries managers in using hydroacoustics as a survey tool; however, habitat use and life history characteristics present a challenging scenario for hydroacoustic monitoring. For example, the walleye population migrates annually between shallow habitats in the western and central basins, and deeper habitats throughout Lake Erie and into Lake Huron (Wang et al. 2007, Pandit et al. 2013). The population is most available for survey when concentrated in the relatively shallow nearshore waters of the western and central basins during the fall, when environmental conditions are less dynamic (Schertzer et al. 1987, Binding et al. 2012). However, during this time, walleye may move vertically into the water column at night to forage (Kelso 1978, Berger et al. 2012), and it is not clear how this behavior may affect vessel avoidance in shallow waters. Additionally, walleye may engage in diel bank migrations to forage in shallow nearshore areas (Kelso 1978), which would make some portion of the population inaccessible to hydroacoustic surveys at night. Therefore, it is unclear how walleye behavior over day-night periods and in response to sampling vessels may affect availability to hydroacoustic surveys.

We were interested in how walleye availability and avoidance behavior may influence estimates of stock abundance. We used vessel comparison surveys in Lake Erie's western and central basins to, 1) quantify differences in walleye density estimates between two survey vessels and day-night sampling periods during summer and fall, and 2) detect relationships between environmental gradients, such as turbidity, temperature, forage fish abundance, and walleye distributions during summer and fall seasons to inform survey timing and extent. This research directly informs future hydroacoustic assessment of Lake Erie walleye, and generally informs avoidance and availability concerns of other fishes in the nearshore waters of intermediate-scaled systems.

2. Methods

2.1 Survey design

We conducted vessel comparison surveys during day and night at two locations in Lake Erie (i.e., Huron and Cleveland; Figure 1A and B) using paired vessel transects similar to previous vessel comparison studies (Keiser et al. 1987, De Robertis et al. 2008). Several other survey designs exist to compare vessel effects (e.g., follow-the-leader, De Robertis et al. 2008, Ona et al. 2007; transect-repeat, Wheeland and Rose 2014; mobile-stationary, Ona et al. 2007), but due to the scale and multiple objectives in our study, we felt that paired vessel transects were best suited. Bottom habitat conditions were uniform across survey locations (silty/mud bottom; 10 – 20 m deep). We oriented sampling transects onshore to offshore, following potential temperature and turbidity gradients during both seasons, to mitigate any confounding environmental effects. During each survey, we sampled with two different sized vessels including the U.S. Geological Survey (USGS) Muskie (large vessel; ~21.3 m) and the Ohio Department of Natural Resources – Division of Wildlife (ODNR-DOW) Almar (small vessel; ~ 9.1 m) near Huron, and the USGS Muskie and ODNR-DOW North River (small vessel; ~ 9.1 m) near Cleveland. Both smaller ODNR-DOW vessels were of the exact same hull, engine, and propulsion design. During a single sampling event, we collected data along four 8-km north-south transects with two traveling offshore, followed by two traveling back toward the shore. Hydroacoustic data were collected simultaneously from each vessel along paired transects (Figure 1C). Vessel-specific transects were spaced 400 m apart, similar to other vessel comparison studies (Keiser et al. 1987) and twice the distance of maximum reported pre-vessel avoidance effects in marine systems (200 m; Ona and Godø 1990), to limit vessel interference while sampling the same population (Mitson 1995). Although we assumed minimal interaction between vessels, we could not definitively exclude the possibility, as we did not have vessel specific radiated noise signatures (sensu De Robertis et al. 2008) nor information on walleye noise tolerances. We first sampled during daylight hours, then repeated the same transects a few hours later, thus completing one vessel comparison survey at a given location. Night sampling began thirty minutes after sunset (Fréon et al. 1993). We sampled Sandusky sub-basin near Huron, OH between the 10 and 15 m depth contours during the fall 2013, and the Central Basin near Cleveland, OH between the 15 and 20 m depth contours during the summer 2015. Huron was surveyed on November 21-22, 2013 corresponding with walleye migration back to spawning habitats and fall ODNR-DOW gill net sampling. We surveyed Cleveland on July 1-2, 2015 corresponding with the summer open lake migration period. This experimental survey design allowed us to evaluate multiple factors of interest (i.e., vessel, day-night period, onshore-to-offshore interval, and depth layers) using a single statistical analysis (ANOVA) at each sampling location.

2.2 Environmental data

We collected water column profiles of temperature and turbidity (nephelometric turbidity units – NTU) prior to the start of the survey, at the break point between the nearshore and offshore transects, and at the end of the offshore transects (Figure 1). We used average water temperatures, from start to break point and break point to end, to adjust speed of sound and absorption coefficients for nearshore and offshore hydroacoustic transects during hydroacoustic data analysis. Temperature and turbidity were compared to walleye distributions to infer habitat use.

2.3 Hydroacoustic data collection

Hydroacoustic data were collected with BioSonics DTX echosounders (BioSonics, Seattle, WA, U.S.A.) and downward facing circular ~200 kHz split-beam transducers. Data collection settings were identical at both survey locations including; -10 dB (re: 1 µPa at 1m depth) reduced power output, -100 dB collection threshold, 0.2 ms pulse durations, and 10 pings-per-second (pps). Transects were traversed at approximately 8-10 km/h, depending on wind direction and wave interference. Transducers were towed alongside vessels at approximately 1.5 m depth using a BioSonics towfish. We calibrated each system prior to the surveys using the standard sphere method (Foote et al. 1987). See *Appendix A* for transducer specifications and calibration results.

2.4 Species composition

To inform species composition from the hydroacoustic surveys we used data from the ODNR-DOW fall western and central basin gill net survey (here forward, gill net survey) and the ODNR-DOW open lake creel survey (here forward, creel survey). We used a subset of data from the 2013 gill net survey, encompassing the area surrounding hydroacoustic sampling near Huron. This portion of the survey included 12 sites (Figure 1B), each sampled with a suspended (1.8-m below surface) multi-filament gill net approximately 396.5 m by 1.8 m with graded mesh sizes ranging from 51 to 127 mm (stretched measure; described in Vandergoot et al. 2011). Three of these sites also included a bottom set monofilament gill net approximately 182.4 m by 1.8 m with graded mesh sizes ranging from 32-127 mm (stretched measure; described in ODW 2016). Gill nets were set overnight, and fish species were measured for total length (to the nearest mm; TL). These sites were sampled between the 1st and 10th of October, and characterized the fall (October-November) fish community near Huron. We generated a length frequency histogram of fish ≥ 300 mm for comparison with size structure from hydroacoustic surveys. This gill net survey underrepresented fish < 300 mm (i.e., reduced selectivity; Vandergoot et al. 2011); therefore, we excluded those fish from comparison. In summer 2015, we relied on recreational fisheries reports and the creel survey to identify high walleye concentrations in management District 2, spanning Huron to Fairport Harbor, encompassing Cleveland (Figure 1B).

2.5 Hydroacoustic data analysis

Hydroacoustic data were analyzed in Echoview 5 software (Echoview Software Pty. Ltd., Hobart, Australia) using single echo detection (SED) variables and fish tracking algorithms to identify individual fish targets and estimate mean target strength (TS). We excluded the top 2.5 m of the water column from analysis including 1.5 m tow depth and twice the transducer nearfield range (~ 0.5 m). We applied a 0.3 m bottom exclusion line, to assure single targets were independent of the near bottom "acoustic dead zone". Most SED filter criteria followed recommendations from the Great Lakes Standard Operating Procedures (Parker-Setter et al. 2009) including; 6 dB pulse length determination level, 0.6 minimum and 1.5 maximum pulse lengths normalized to that of the transmitted pulse, 0.6° maximum standard deviation of along-ship and athwart-ship angles. However, since we were interested primarily in large-targets, we increased the TS threshold to -50 dB, and increased maximum beam compensation to 18 dB to improve encounter rates and increase number of SEDs per fish (DuFour et al. 2017). Fish tracking algorithms included a minimum of 1 SED and 1 ping per fish track, and a maximum gap of 2 pings between SEDs. We manipulated the fish track detection settings to improve the automated detection of individual fish including, sensitivities to along-ship and athwart-ship directions (i.e., alpha and beta values), target gate exclusion distances, and relative weighting among along-ship and athwart-ship axis, range, TS, and ping gap (see DuFour et al. 2017). Algorithm settings provided consistent visual agreement between grouped SEDs and automated fish tracks.

Established TS-total length equations for Lake Erie's western and central basin fish community were not available to apportion hydroacoustic among species. We generated length frequency histograms for fish tracks between -36 to -26.5 dB mean TS for comparison with community composition and size structure from the ODNR-DOW gillnet survey. Distinct changes in TS count frequencies from each hydroacoustic survey corresponded with changes in total length frequencies from the ODNR-DOW gillnet survey, near 400, 500, and 600 mm (Figure 2). Therefore, we matched corresponding TS and total length measurements to estimate a TS-total length equation for the Lake Erie western and central basin fish community (*sensu* MacLennan and Menz 1996, Mehner 2006). We regressed corresponding points using (Eq. 1):

Eq. (1) $$TS_i = \beta * log_{10}(TL_i) + b + \varepsilon_i$$

where, TS is target strength in dB (re: 1 µPa at 1m depth), TL is total length in cm, β is the slope, b is the intercept, and ε_i are normally distributed residual errors. We freely estimated both slope (β) and intercept parameters (b) in this equation. However, given the small number of replicates and limited size ranges in our samples, we also estimated the intercept parameter (b) assuming a constant slope (i.e., 20; Foote 1987, and MacLennan and Menz 1996) (Eq. 2).

Eq. (2) $$TS_i = 20 * log_{10}(TL_i) + b + \varepsilon_i$$

Moving forward, we considered two length groups: small targets from 300 to 400 mm TL comprised of a mixture of species, and large-targets ≥ 400 mm (i.e., -33.3 dB mean TS) primarily represented by age-2+ walleye (i.e., the spawning stock; Vandergoot et al. 2010).

We separated hydroacoustic data into onshore-to-offshore intervals and depth layers for subsequent analysis. Each transect was partitioned into 1000-m elementary distance sampling units (EDSUs). We categorized EDSUs based on their relative location to shore, ranging from 1 (onshore) to 16 (offshore). We also separated each EDSU into 5-m depth layers creating 1000- by 5-m cells. We counted large-targets (i.e., ≥ -33.3 dB mean TS or 400 mm) and estimated wedge volume sampled (an Echoview output) per cell, allowing us to make inferences on density. In addition, we exported horizontal and vertical trajectories for fish tracks ≥ -33.3 dB mean TS to document potential avoidance related movements. Horizontal trajectories were measured with angles relative to the acoustic beam axis where 0˚ defines movement towards the ships bow, 90˚ towards starboard, 180˚ towards aft, and 270˚ towards port. Vertical trajectories are measured relative to a plane normal to the acoustic beam axis where 0˚ defines no change in vertical movement, 90˚ defines upward movement, and -90˚ defines downward movement.

We estimated average forage fish densities at each day-night sampling interval using echo-integration. We used SED filter criteria recommended by the Great Lakes Standard Operating Procedures (Parker-Setter et al. 2009) including; 6-dB pulse length determination level, 0.6 minimum and 1.5 maximum pulse lengths normalized to that of the transmitted pulse, 0.6° maximum standard deviation of along-ship and athwart-ship angles, and 6-dB maximum beam compensation. We restricted SED TS-measurements between -60 and -40 dB mean TS, approximating the size range of preferred walleye forage (i.e., ~25 to 178 mm; Hartman and Margraff 1992) based on Love (1971). In addition, we restricted volume backscattering strength (S_v) to greater than -66 dB using the minimum uncompensated TS threshold setting in Echoview (Rudstam et al. 2009). To remove S_v bias from larger non-forage targets we set an upper limit at -46 dB on a separate Echoview variable using the minimum uncompensated threshold setting, and used a linear minus operator to subtract these returns from the -66-dB limited variable. This produced a virtual forage fish variable including only S_v returns from the target size range (i.e., -60 to -40 dB, or ~25 to 178 mm), which corresponds to forage fish sizes preferred by walleye (Hartman and Margraff 1992). For each 1000- by 5-m cell we divided the mean area backscattering coefficient (ABC) by the mean backscattering cross-section (σ_{bs}) and multiplied by 10,000 to generate an areal density estimate (fish/ha). We averaged cell density estimates from vessels and depth layers at each sampling location, and report day-night density estimates for 1000-m onshore-to-offshore intervals.

2.6 Statistical analysis

We used a Bayesian hierarchical Poisson ANOVA (Qian and Shen 2007) to quantify densities and infer differences in availability due to diel movements and avoidance (Table 1). A Poisson distribution described the random component of our positive count response variable, fish per cell. We used Bayesian hierarchical methods to improve parameter estimates and provide richer inference about the data. Bayesian methods can improve estimates from studies that do not meet traditional ANOVA criteria (i.e., balanced data, and no correlation among treatments; McCulloch 2005) by batching parameters together and assuming correlation through prior distributions (Gelman and Hill 2007). In addition, these methods place emphasis on estimation rather than hypothesis testing; therefore, we can directly compare effect magnitudes (Gelman 2005). The greatest benefit comes with inference, where we calculated the marginal posterior differences between jointly distributed treatments and make probabilistic statements about effects (Qian et al. 2009).

The ANOVA model (Eq 3.) included two primary factors of interest (day-night period and vessel), which we assumed relate to differences in diel availability and vessel avoidance behaviors. Walleye may rise into the water column at night to forage (Kelso 1978, Berger et al. 2012), which would change their proximity to passing vessels and potential avoidance behavior. Therefore, our initial assumptions were that foraging walleye were more active during the night-period, and likely to be off-bottom and available to hydroacoustic surveys. In addition, we assumed that visual perception increased during the day-period, and would cause increased visual avoidance, while a large “noisier” vessel would cause increased vessel avoidance. We also included two spatial factors (depth layer and onshore-to-offshore intervals) that may quantify distributional variability, while also relating to habitat preferences. Finally, we acknowledged that the two main factors of interest (vessel and period) might be dependent on each other as well as the individual spatial factors (depth layer and onshore-to-offshore interval); therefore, we included two interactions. The interaction between vessel, period, and depth layer may signal changes in avoidance behavior across vessel and period treatments that related to diel vertical movements. Additionally, availability and avoidance behavior may change across environmental gradients, which commonly occur along Lake Erie’s shoreline (Schertzer et al. 1987, Binding et al. 2012). The interaction between vessel, period, and onshore-offshore intervals may signal changes in availability or avoidance behavior across vessel and period treatments associated with these gradients.

Eq. (3) $$C_i \sim Poisson(\lambda_i * vol_i)$$

$$log(\lambda_i) = \alpha + \beta1_j + \beta2_k + \beta3_l + \beta4_m + \beta5_{jkl} + \beta6_{jkm} + \varepsilon_i$$

$$\beta1-3,5,6 \sim normal\left(\mu.\beta_{1-3,5,6}, \sigma.\beta_{1-3,5,6}\right)$$

$$\beta4 \sim car.normal\left(\mu.{\beta_4}^{CAR}, \tau.\beta_4\right)$$

$$\varepsilon_i \sim normal(0, \sigma.\beta_\varepsilon)$$

where, α represents the intercept or overall mean, $\beta1_j$ represents vessel main effects, $\beta2_k$ represents day-night period main effects, $\beta3_l$ represents depth layer main effects, $\beta4_m$ represents the onshore-to-offshore interval main effects, $\beta5_{jkl}$ represents vessel-period-layer interaction, and $\beta6_{jkm}$ represents vessel-period-interval interaction. We included an extra parameter (ε_i) to account for overdispersion in the count data (Kéry 2010). We used normal prior distributions for parameters α and $\beta 1 - 3, 5, 6, \varepsilon_i$, with low information hyper-priors for means (e.g., $\mu.\beta_1 \sim normal(0{,}0.01)$) and standard deviations (e.g., $\sigma.\beta_1 \sim uniform(0{,}3)$). To account for serial correlation in the onshore-to-offshore intervals, we used a conditional autoregressive (CAR) model prior. The CAR model assumes a normal prior for each interval, with the hyper-prior mean expressed by the mean of adjacent intervals and hyper-prior precision set as a low information gamma ($\tau.\beta_4$; see Qian et al. 2005). We included wedge volume sampled (vol_i; per 10,000 m^3) as an offset, allowing us to make inferences about fish densities rather than counts.

We ran separate models for each location (Huron and Cleveland; Table 1). Parameter estimates were generated using the Markov chain Monte Carlo (MCMC) sampling program OpenBUGS (Lunn et al. 2009) called from R (R Core Team 2016) through the R2OpenBUGS package (Sturtz et al. 2005). Each model included three mixing chains with 3,000 iterations each and a 1,000 iteration burn-in period. Each mixing chain was thinned to every 10th sample and model convergence was assessed by viewing chain history and the $\hat{R}$ statistic (Gelman and Hill 2007). We reported the marginal posterior estimates for each factor on the scale of interest (fish/10,000 m^3). In addition, we calculated the marginal posterior differences (MPD; Eq. 4) between jointly distributed treatments for vessel and day-night period factors as a measure of effect strength.

Eq. (4) $$MPD = \beta_{1_i} - \beta_{2_i}$$

where, β are the jointly distributed posterior estimates from vessel or day-night period factors and 1 and 2 represent levels within each factor (e.g., large vs. small or day vs. night). Subscript i

represents the individually correlated MCMC samples from each posterior distribution. The proportion of MPD values above or below zero indicates the effect strength and direction.

3. Results

3.1 Species composition

The fishery independent gill net survey indicated a distinct size structure and species composition for fish between 300 and 910 mm near Huron, when the hydroacoustic survey occurred (Figure 2 – Huron-GN). "Other" fish species (e.g., white bass [*Morone chrysops*] and gizzard shad [*Dorosoma cepedianum*]) dominated (~87%) the catch between 300 and 400 mm TL, whereas, walleye were predominant (~93%) between 400 and 910 mm TL. At sizes greater than 400 mm, there were distinct changes in count frequencies at 480 mm and 600 mm, possibly representing abundant walleye cohorts. Mean TS frequency distributions from hydroacoustic sampling (i.e., "unknown") showed declining abundance with size (Figure 2 – Huron-HA and Cleveland-HA), and similar characteristic break points that corresponded with those from the gill net survey. Near Huron, size frequency changes at 400, 480, and 600 mm corresponded with -34.20, -31.75, and -29.30 dB mean TS, respectively. Although, lower than expected fish abundance was observed below -34.2 dB mean TS. Unfortunately, we did not have fishery independent species composition or length data from Cleveland. However, 2015 recreational fishing reports and creel surveys indicated a concentration of walleye near Cleveland during July, as the largest recreational (58,078) and charter (3,601) walleye harvest occurred during July in District 2 between Huron and Fairport Harbor encompassing the Cleveland sampling location (ODW 2016). Interestingly, the length frequency distribution from 2015 hydroacoustic sampling near Cleveland (Figure 2 – Cleveland-HA) was similar to the 2013 fishery independent gill net catch data near Huron showing consistency in Lake Erie community size structures; with corresponding size frequency changes at -33.50, -31.50 and -28.95 dB mean TS.

We generated a TS-total length equation based on corresponding mean TS estimates and total length ($log_{10}(cm)$) measurements (MacLennan and Menz 1996, Mehner 2006) from the Lake Erie western and central basin fish community ($TS = 27.1 * \log_{10}(TL) - 77.4$). Using the same data, the constant slope model produced a higher intercept ($TS = 20 * \log_{10}(TL) - 65.4$), similar to other published studies (Figure 3). The catch data and TS-total length analyses with constant slope suggested age-2+ walleye dominated the community at sizes larger than -33.3 dB (i.e., ≥ 400 mm) near Huron and Cleveland; therefore, subsequent analyses focused on this size group.

3.2 Environmental data

Environmental characteristics varied by sampling location and dates (Table 2). November water temperatures near Huron were cool and isothermal (mean - 7 ˚C), while July water temperatures near Cleveland were warmer (range 17-22 ˚C) with a decreasing onshore-to-offshore gradient. Turbidity measurements were similar between survey locations at the nearshore (mean ~14 NTU) and mid-interval (mean ~5 NTU) points, but differed at the furthest point offshore. Forage fish densities were low and patchily distributed near Huron, ranging from 19 fish/ha (interval 7-Day) to 374 fish/ha (interval 7-Night; Figure 4 - Huron). Forage fish densities were on average ~30x greater near Cleveland, ranging from 183 fish/ha (interval 16-Night) to 19,995 fish/ha (Interval 1-Night; Figure 4 – Cleveland) with fish concentrated in the nearshore intervals. Forage fish distributions near Cleveland exhibited a strong decreasing offshore gradient. Both displayed similar distributional patterns between day-night sampling periods, but lower densities during the day.

3.3 Hydroacoustic data analysis

In total, we collected 128 km of paired-vessel hydroacoustic transect over the two locations and periods. The data were comprised of n=64 EDSUs for each location, with half collected during the day and half collected at night. These efforts produced a total n=1,717 large acoustic targets (i.e., ≥ -33.3 dB or 400 mm), with more targets observed on small vessels and more targets observed at night (Table 3). Higher total counts occurred near Cleveland (n=1,064) compared to Huron (n=653); however, deeper water increased hydroacoustic sampling volume contributing to greater counts. Large-targets consistently moved perpendicular to survey vessel paths (Figure 5A), with ~66% of fish moving horizontally in regions between 60˚ to 120˚ and 240˚ to 300˚. Large-targets vertical movement was minimal (Figure 5B), with ~76% of fish showing no vertical change and ~19% upward and downward movements within 10˚ of a plane normal to the acoustic beam axis.

3.4 Statistical analysis

Vessel size and day-night period related factors explained a small proportion of total variation (reported as ln[standard deviation]; Figure 6) in walleye densities, ranging from 8 to 10% near Huron and 3 to 17% near Cleveland. Conversely, spatial factors including interval and layer explained a larger proportion of total variation near Huron (16 and 21% respectively) and Cleveland (17 to 27% respectively). Both survey locations included large amounts of unexplained variation (Huron – 21% and Cleveland - 22%), while uncertainty in variance components was greater near Huron.

Walleye densities encountered by the small vessel were twice as great as the large vessel near Huron, but both vessels were similar near Cleveland (Figure 7A and C). In shallower water near Huron, the small vessel encountered 0.505 fish/10,000 m^3 more than the large vessel, on average. A high proportion of the MPD (marginal posterior difference) was greater than zero (Figure 7B), suggesting a 89% probability that the smaller vessel encountered higher walleye densities. In deeper water near Cleveland, the small vessel encountered only 0.010 fish/10,000 m^3 more than the large vessel, on average. A small proportion of the MPD was greater than zero (55%; Figure 7D), suggesting no difference in walleye densities between vessels. Day-night patterns in walleye densities differed between locations (Figure 8A-D). At Huron, densities were higher at night, with a mean difference of 0.361 fish/10,000 m^3 (84% of MPD > 0). At Cleveland, densities were lower at night, with mean difference of -0.766 fish /10,000 m^3 (99% of MPD < 0).

Walleye consistently occupied near bottom depth layers at each location (Figure 9). Densities gradually increased with depth layer at Huron, with the highest density in the 10-15 m layer, near the lake bottom (mean=1.90; 95% CI=0.77-3.33; Figure 9-Huron). The magnitude of increasing densities with depth layer was not consistent across all vessel-period-depth conditions, as we observed the greatest mean densities from small vessels at night in the 5-10 m (mean=2.30) and 10-15 m (mean=8.55) depth layers (SN; Figure 9-Huron). Near Cleveland, targets densities were very low in the upper depth layers (0-15 m; Figure 8-Cleveland), with high densities near bottom in the 15-20 m layer (mean=3.42; 95% CI=1.80-5.44) depth layer. Similar to Huron, the magnitude of increasing densities with depth layer was not consistent across all vessel-period-depth conditions. However, near Cleveland we observed greater mean densities during the day from both small (mean=5.04) and large (mean=4.23) vessels at the 15-20 m layer, and slight increases from the small vessel in 5-10 and 10-15 m layers (SD and LD; Figure 9-Cleveland).

Walleye densities were greater nearshore at both locations (Figure 10). Near Huron, the highest density (mean=1.90, 95% CI=1.10-3.09) was observed at interval 4 gradually decreasing to the lowest density (mean=0.30, 95% CI=0.14-0.56) at interval 16 (Figure 10). The magnitude of decreasing densities with onshore-to-offshore intervals was not consistent across all vessel-period-interval conditions. We observed the greatest difference nearshore between main effects and small vessels at night (SN; Figure 10-Huron), while interaction and main effects became more similar offshore. Near Cleveland densities were similar across intervals 1-8 with the highest density (mean=1.45, 95% CI=0.98 -2.06) observed at interval 6, followed by a precipitous decline toward the lowest density (mean=0.27, 95% CI=0.16-0.42) at interval 15 (Figure 10-Cleveland). Again, the decreasing density pattern with onshore-to-offshore intervals was not consistent across all vessel-period-interval conditions. However, at Cleveland we observed greatest differences from interval main effects nearshore from small and large vessels during the day (SD and LD; Figure 10-Cleveland), while densities became more similar offshore across conditions.

4. Discussion

Vessel related avoidance and population availability to hydroacoustic surveys have been studied extensively in deep water marine systems (e.g., De Robertis et al. 2008, Fréon et al. 1993, Olsen 1990, Rose 2003), and small shallow freshwater systems (Draštík and Kubečka 2005, Draštík et al. 2009, Muška et al. 2013, Wheeland and Rose 2014). However, hydroacoustic surveys in intermediate-scaled systems (e.g., Laurentian Great Lakes) comprised of both deep and shallow water habitats have received less attention despite the importance of these habitats to fishery production. This study quantified potential availability and avoidance biases in hydroacoustic surveys for Lake Erie walleye, a large migratory predator fish (Roseman et al. 2010) in shallow nearshore waters (i.e., < 20 m). We found substantial differences in walleye densities that were attributable to avoidance (i.e., vessel) and availability (i.e., day-night period). Although spatially related factors (e.g., interval and layer) accounted for the most variability, researchers should first minimize bias from systematic vessel and period factors to generate the best available stock abundance estimates. Likewise, hydroacoustic surveys targeting large mobile fishes in comparable shallow water settings (e.g., reservoirs, large lake nearshore areas, or marine coastal waters) should consider avoidance and availability biases when generating population abundance estimates.

We used a fishery-independent gill net survey, fishery-dependent creel survey reports, and a TS-total length analysis to inform species composition and size structure of the Lake Erie fish community (McClatchie et al. 2000). These surveys did not allow definitive quantification of walleye proportions at each sampling location (*sensu* Warner et al. 2009 or Yule et al. 2013) as they broadly overlapped spatially and temporally with our hydroacoustic surveys. However, gill net catches near Huron and creel harvest reports surrounding Cleveland (ODW 2016) indicated walleye concentrations, matching expected walleye distributions based on well-established Lake Erie walleye ecology (Kershner et al. 1999, Wang et al. 2007, Pandit et al. 2013). Additionally, similarities in size structures across surveys allowed us to infer walleye abundance above 400 mm (-33.3 dB mean TS). We used corresponding changes in total length frequencies from the fishery-independent gill net survey and mean TS frequencies from hydroacoustic surveys, and generated a TS-total length equation for the Lake Erie western and central basin fish community (MacLennan and Menz 1996, Mehner 2006), assuming constant slope ($TS = 20 * \log_{10}(TL) - 65.4$). This relationship was similar to TS-total length equations produced for other large target (i.e., > 400 mm), physoclistous fishes in marine systems; using similar methods (i.e., paired acoustic-trawl surveys, *in situ* TS measurements, and fixed slope TS-total length equations). Although the species of interest were different (e.g., Pacific walleye pollock [*Theragra chalcogramma*] and Atlantic cod [*Gadus morhua*]), estsimated intercept parameters were similar among studies (b = -65.4, Traynor 1996; b = -66, Rose and Porter 1996; b = -64.9, Ermolchev 2009) over size ranges comparable to those observed in our study (i.e., > 300 mm), lending credence to our initial equation for Lake Erie walleye. Although the similarities are promising, we must continue to refine this relationship by increasing the pool of paired gill net and hydroacoustic samples from the system. Nevertheless, we moved forward with a general assumption that the walleye population strongly influenced large-target communities at both locations and seasons at sizes greater than 400 mm (-33.3 dB mean TS).

Fish avoid highly visible survey vessels, and those generating high-intensity low-frequency noises (Mitson 1995, Mitson and Knudsen 2003, Kipple and Gabriele 2007). Near surface pelagic fishes in deep water may display a “fountain pattern” of avoidance at distance (Olsen 1990, Soria et al. 1996), while swimming down as a vessel passes over (Olsen 1979, Misund 1997). Draštík and Kubečka (2005) showed that fish in shallow water moved horizontally to the vessel path, up to 15 m away from small vessels (i.e., 5-6 m), with decreased densities near the vessel. In our study, horizontal movement and lower densities indicated increased avoidance of the larger vessel in shallow water (i.e., ≤ 15 m). Although we observed horizontal movement of fishes in deeper water (i.e., ≤ 20 m) as well, differences in density estimates between vessels were marginal. Consistently higher walleye densities near bottom (15-20 m depths) partially explained this pattern, as avoidance behavior presumably decreased with distance from sampling vessels (Neproshin 1979, Draštík and Kubečka 2005, Wheeland and Rose 2014). Hydroacoustic survey efforts in the Laurentian Great Lakes (Rudstam et al. 2009, Warner et al. 2009) and other intermediate to large-scaled systems (De Robertis et al. 2008) often target pelagic schooling fishes in deep waters, where avoidance and availability may be less of a concern depending on depth distributions. However, in small (Draštík and Kubečka 2005, Wheeland and Rose 2014) and intermediate-scaled systems (Gorman et al. 2012b) where target species seasonally occupy shallow nearshore habitats, researchers should avoid this type of systematic bias by adjusting timing and vessel size when possible.

The proportion of nearshore to offshore habitat increases as system scale decreases; therefore, bias related to diel bank migrations may increase as well. Fréon et al. (1993) suggested diel bank migrations contribute limited bias in marine settings, restricted to shallow water coastal areas (e.g., Gulf of Curiaco, Venzeuela) which make up a small proportion of large-scale surveys. Within the Laurentian Great Lakes (i.e., Lake Superior), Gorman et al. (2012b) indicated that up to 25% of nearshore species engaged in diel bank migrations, likely reducing the effectiveness of daytime nearshore monitoring efforts (Yule et al. 2008). Additionally, several studies in smaller freshwater lakes and reservoirs note extensive diel movements of fish between pelagic and littoral zones, contributing bias and uncertainty to hydroacoustic abundance estimates (Comeau and Boisclair 1998, Draštík et al. 2009, Muška et al. 2013). Lake Erie represents an intermediate-scaled water body, with a high proportion of nearshore habitat (i.e., < 15 m). In our study, we saw greater walleye densities during the night near Huron (fall), but greater during the day near Cleveland (summer), potentially due to diel onshore-to-offshore migrations driven by optimal foraging habitat and thermal preferences (Sims 2003). Lake Erie walleye use a range of thermal habitats to optimize forage and growth conditions (Hartman and Margraff 1992, Kershner et al. 1999) with the greatest variation in observed thermal range occurring in July (~16-24 °C; Peat et al. 2015). We observed onshore-to-offshore temperature, turbidity, and forage fish gradients near Cleveland (summer); consequently, walleye may have moved onshore into warmer waters with high forage fish densities during the night to feed and aid digestion, then moved offshore to cooler deeper waters closer to physiological optimum during the day (18-22 °C, Christie and Reiger 1988). Conversely, the relatively uniform temperature conditions and patchy forage fish distributions near Huron (fall) may have limited diel bank movements. Given the limited temporal scale of our sampling (i.e., a single 24 hour period) we recommend additional studies to determine magnitude and frequency of walleye diel-bank migrations. Additionally, we suggest future surveys consider seasonal foraging ecology of nearshore target species in intermediate-scaled waterbodies.

Changes in seasonal or diel depth distributions can influence population availability to hydroacoustic surveys. For example, near surface pelagic fishes are more likely to avoid survey vessels, while fishes in the first five meters of the water column may be completely unavailable depending on transducer depth and nearfield properties (Misund 1997). Additionally, benthic oriented species may be unavailable to hydroacoustic surveys if they reside in the near bottom "acoustic dead zone" (Ona and Mitson 1996, Lawson and Rose 1999, Neilsen et al. 2003). Walleye were predominantly bottom oriented with the highest densities in the deepest layers across all sampling conditions, consistent with known preferences for low ambient light conditions (Ryder 1977, Lester et al. 2004). Although some short-term foraging related vertical movements likely occur (Kelso 1978, Berger et al. 2012), we did not observe substantial shifts in walleye depths that may affect near surface avoidance behaviors. Given that walleye were benthically oriented, it is possible that movements into or out of the near bottom "acoustic dead zone" caused vessel or diel related differences, with availability increasing or avoidance decreasing as fish moved into or remained within the water column. However, unlike studies in deeper systems requiring longer pulse durations resulting in larger near bottom “acoustic dead zones”, our study occurred in shallow water (max 20 m), used short pulse durations (0.2 ms), and used a small bottom exclusion zone (0.3 m), which presumably minimized near bottom “acoustic dead zone” related effects. Additionally, we would expect decreasing ambient light conditions to drive vertical movements and thus only occur during night (Kelso 1978, Mehner 2012) at both sample locations. Similarities in depth distributions but differences in day-night patterns between locations indicated two independent mechanisms. We suggest increased vessel avoidance in shallow-water during the day near Huron, and diel bank migrations out of the sample area during the night near Cleveland; however, direct conformation of these mechanisms was not possible.

Spatial extent and sampling intensity are important considerations when developing hydroacoustic surveys (Simmonds and MacLennan 2005), in particular for seasonally dynamic intermediate-scaled systems. Lake Erie walleye are migratory, ranging throughout Lake Erie and into Lake Huron during the summer (Wang et al. 2007), but concentrating in the shallow nearshore waters of Lake Erie’s western and central basins as water temperatures cool during the fall (Roseman et al. 2010). Decreasing onshore-to-offshore turbidity gradients corresponded with decreasing onshore-to-offshore density patterns in our study and were consistent with observed historic gill net studies (Pandit et al. 2013). These patterns were not surprising as walleye consistently exhibit preferences for higher turbidity habitats throughout their range (Ryder 1977, Lester et al. 2004), gaining a foraging advantage in low light conditions (Vandenbyllaardt et al. 1991). Given the consistency between previous literature and our observations, seasonal temperature and turbidity patterns may be useful metrics in delineating timing and extent of future hydroacoustic surveys. The next phase in development of a hydroacoustic survey for Lake

Erie walleye involves apportioning effort across the survey area. Spatially related variation (e.g., interval and unexplained) contributed a high proportion of total variation in measured walleye densities indicating that walleye were patchily distributed. This would suggest reasonable precision in stock abundance estimates might require a high degree of spatial coverage (Aglen 1989, Godlewska et al. 2009), although this level of analysis was outside the scope of the current study. Nevertheless, a variance partitioning analysis applied to preliminary surveys, such as this, can help inform sampling extent and intensity during the next steps in full-scale hydroacoustic survey development.

5. Conclusion

Minimizing availability and avoidance related biases are a priority for hydroacoustic surveys designed to estimate stock abundances (Misund 1997, Simmonds and MacLennan 2005, Parker-Setter et al. 2009). However, the magnitudes of and mechanisms contributing to biases may change with species, season, diel periods, and scale. We targeted a large migratory predator fish (walleye) in the shallow nearshore waters ($\leq$ 20 m) of an intermediate-scaled water body (Lake Erie), and found that vessel avoidance and seasonal foraging behaviors contributed to biased density estimates. As a result, we suggest sampling during the fall, a less dynamic period, to limit diel related availability biases. However, during the fall walleye concentrate in nearshore waters of Lake Erie's western basin, therefore, we suggest sampling from small vessels at night to limit potential vessel related avoidance biases. We found consistent relationships between onshore-to-offshore turbidity gradients and walleye densities indicating turbidity may be a useful metric for delineating future survey extent. Spatial factors contributed a high degree of variation to density estimates; therefore, we also suggest future work identify sampling intensity needed to achieve reasonable levels of precision in abundance estimates. Many ecologically and economically important fishes seasonally occupy nearshore habitats; therefore, within the Laurentian Great Lakes and other intermediate-scaled systems, we suggest that application of hydroacoustic technologies begin with evaluating avoidance and availability related biases under survey conditions.

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Table 1. Description of Bayesian hierarchical Poisson ANOVA model factors and treatments.

Huron	Cleveland	Factor	Levels	Description
x	x	Vessel ($\beta1_j$)	ODNR-DOW Almar/North River	Small vessels; 9.1 m
			USGS Muskie	Large vessel; 21.3 m
x	x	Period ($\beta2_k$)	Day	Period beginning 30 min after sunrise and 30 min before sunset
			Night	Period beginning 30 min after sunset and 30 min before sunrise
x		Layer (H) ($\beta3_l$)	1-3	5 m depth layers at Huron; surface-1 to bottom-3
	x	Layer (C) ($\beta3_l$)	1-4	5 m depth layers at Cleveland; surface-1 to bottom-4
x	x	Interval ($\beta4_m$)	1-16	Relative EDSU distance from shore; onshore-1 to offshore-16
x	x	Interaction l ($\beta5_{jkl}$)	12 or 16	Vessel*Period*Layer
x	x	Interaction 2 ($\beta6_{jkm}$)	64	Vessel*Period*Interval

Table 2. Water column averaged environmental conditions from each sampling location and relative distance from shore.

Environmental variable	Shore*	Huron	Cleveland
Temperature (°C)	Near (1)	7	21
	Mid (8)	7	20
	Off (16)	7	18
Turbidity (NTU)	Near (1)	14	14
	Mid (8)	5	5
	Off (16)	6	1

*Sampled intervals noted in parentheses

Table 3. Large-target (> -33.3 dB) counts observed by each vessel, period, and sampling location.

Vessel	Period	Huron	Cleveland	Total
ODNR-DOW	Day	76	419	495
Almar/North River	Night	450	175	625
USGS	Day	53	281	334
RV Muskie	Night	74	189	263
	Total	653	1064	1717

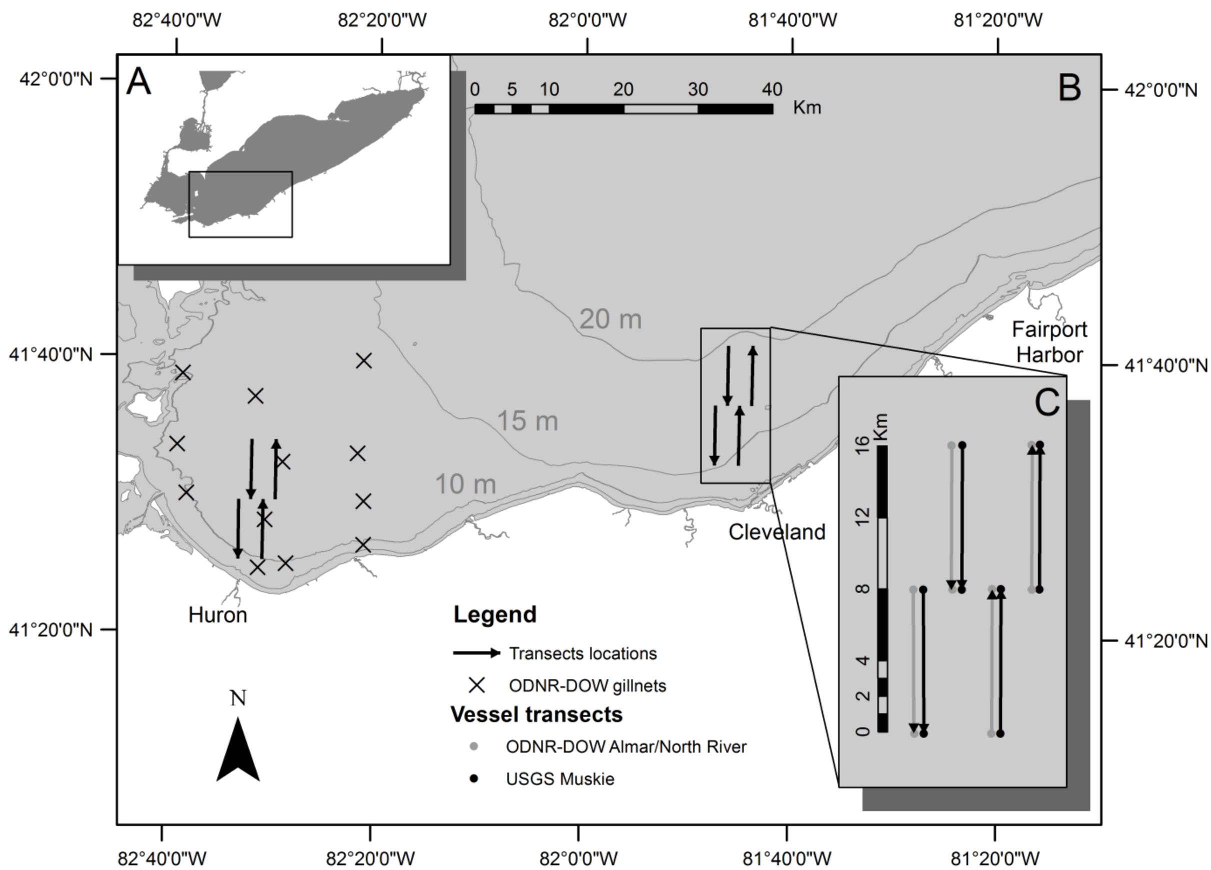

Figure 1. Sampling extent in Lake Erie's Sandusky sub-basin and central basins (A) including hydroacoustic surveys near Huron and Cleveland, OH (B). Hydroacoustic survey paths denoted by offshore to onshore transects at each location (B; black arrows), each comprised of paired vessel specific transects (C; black and gray dots and arrows). Fishery independent gill net sampling locations are designated by x's (B) and fishery dependent creel survey coverage spanned District 2 from Huron to Fairport Harbor.

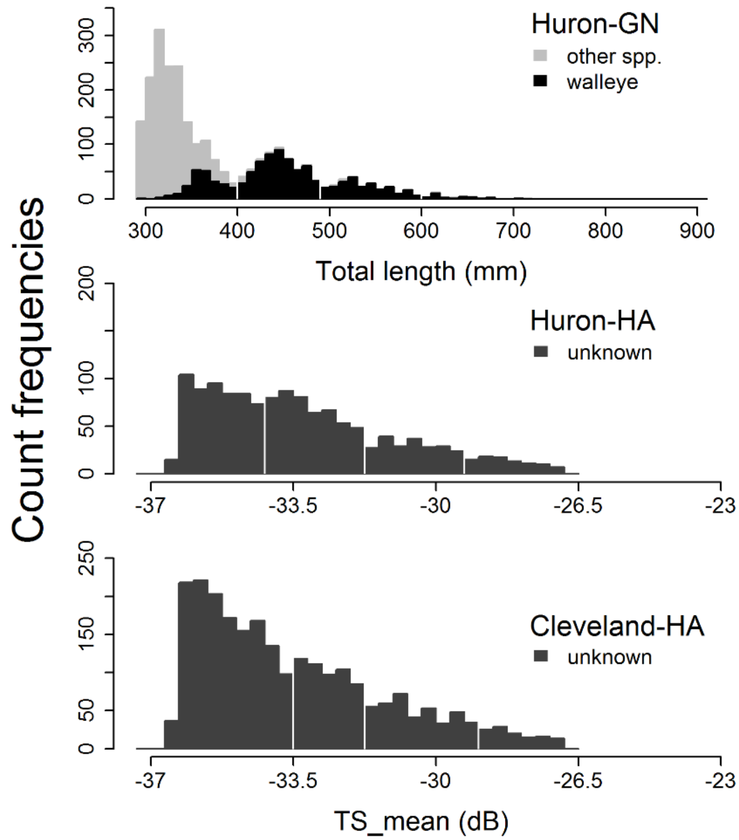

Figure 2. Stacked bar graphs depicting size distribution and species composition for gill nets near Huron and mean target strength estimates (dB) from hydroacoustic sampling near Huron and Cleveland. Vertical white lines highlight similar changes in size frequencies among gill net and hydroacoustic histograms.

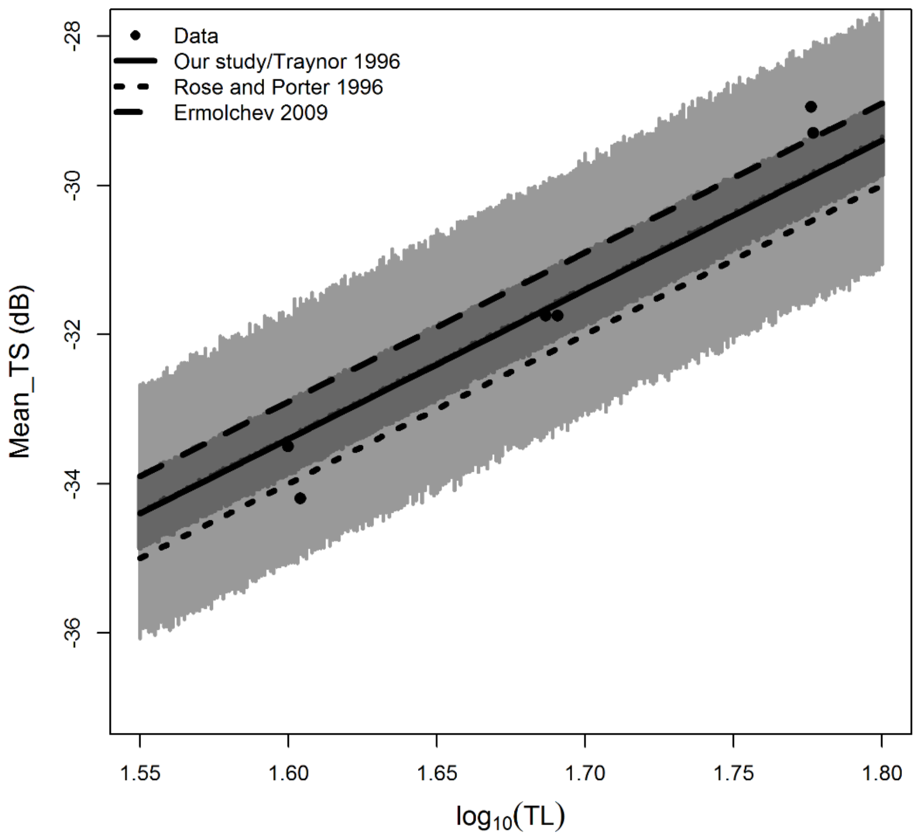

Figure 3. Mean TS estimates for Lake Erie walleye based on corresponding TS and total length frequency histograms. Black dots represent the corresponding TS-total length sizes from the hydroacoustic and gill net surveys (denoted by vertical white lines in Figure 2). The solid black line represents the estimated TS-total length relationship assuming a constant slope ($TS = 20 * \log_{10}(TL) - 65.4$), with dark and light gray bands represent the 50 and 95% credible intervals. Our estimate matched (solid black line, Traynor 1996) and were similar to those derived for marine fishes of similar size (dotted black line, Rose and Porter 1996; dashed black line, Ermolchev et al. 2009).

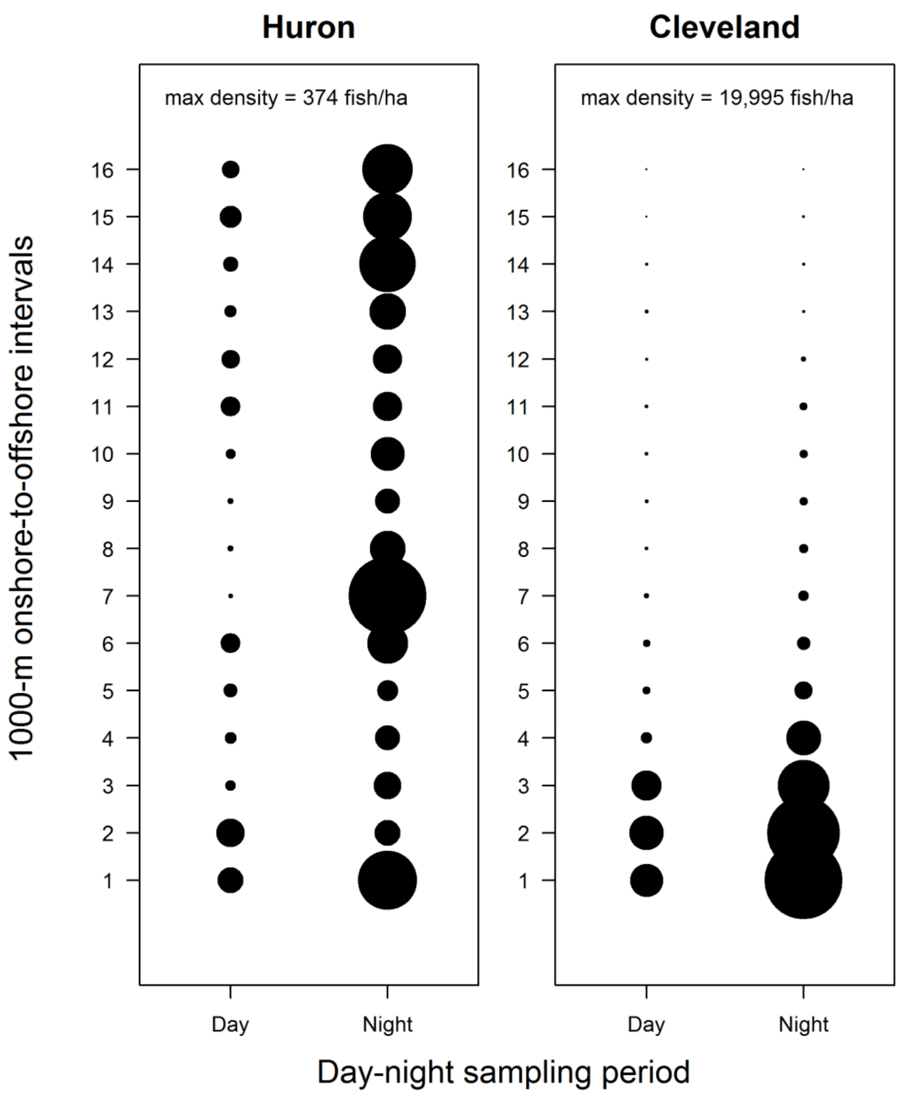

Figure 4. Forage fish density estimates (fish/ha) from hydroacoustic surveys for each location, diel-period, and onshore-to-offshore intervals, averaged over vessel and depths. Density is relative to dots size. Scales are different between locations, with max density at Huron = 374 fish/ha and max density at Cleveland = 19,995 fish/ha.

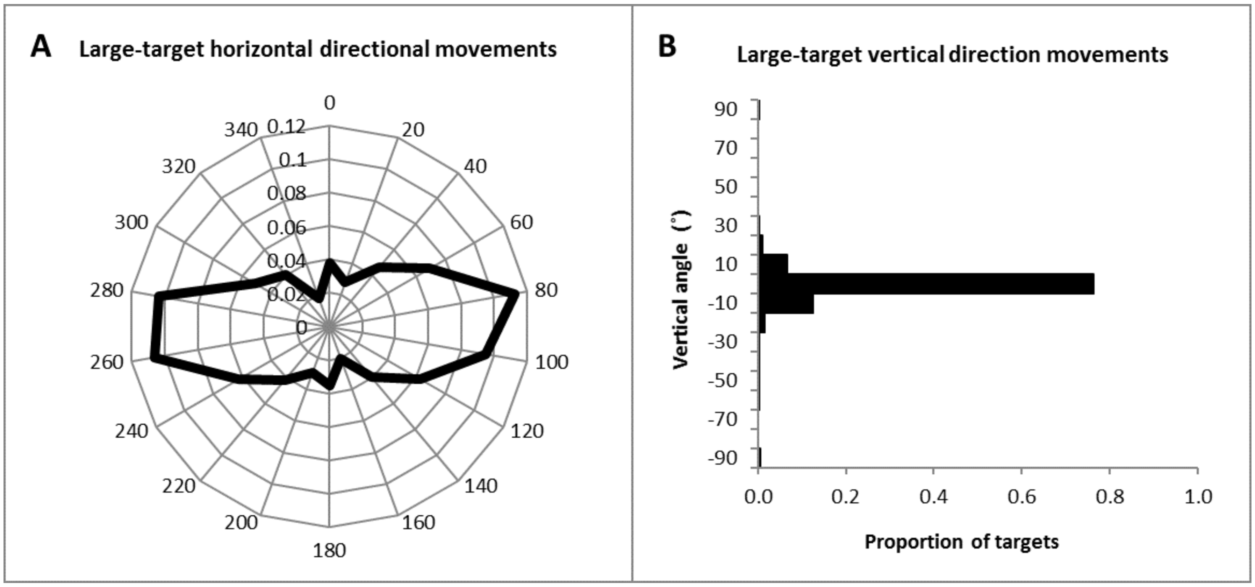

Figure 5. Horizontal and vertical movements of large-targets (i.e., ≥ 400 mm or -33.3 dB) over all survey and sampling conditions. For horizontal movements (A), the circular dial represents 360˚ angle relative to the acoustic axis, and the distance from center represent proportion of targets. For vertical movements (B), the x-axis represents proportion of targets, and the y-axis represents angular difference from the acoustic beams horizontal plane.

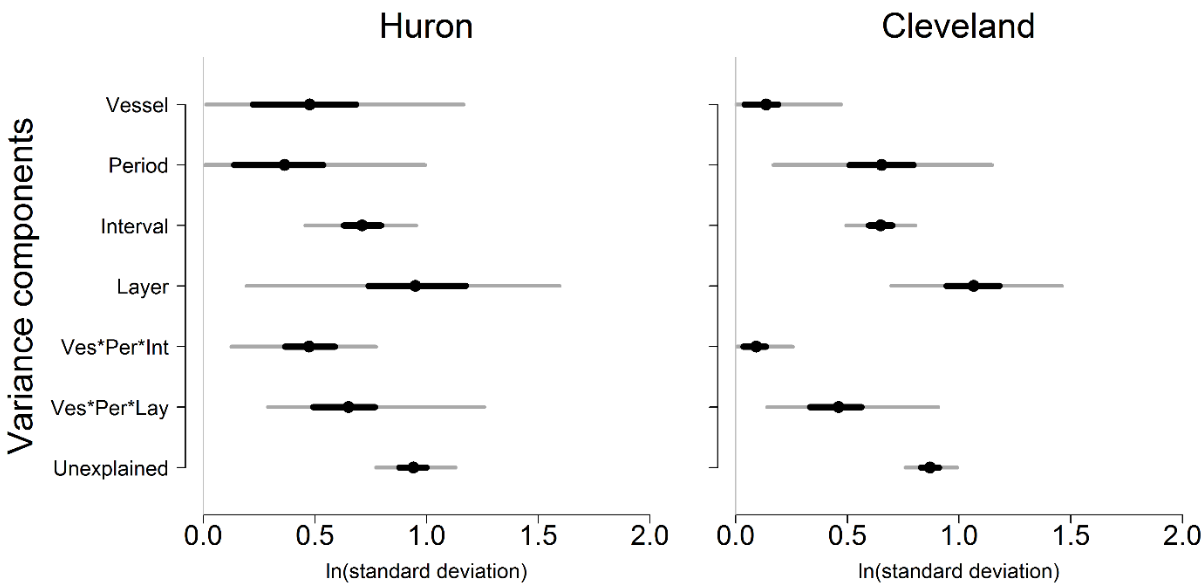

Figure 6. Variance components displayed as the natural log of standard deviation, representing the proportional contribution from each factor near Huron (A) and Cleveland (B). Black circles represent the mean posterior distribution estimates, while black and gray bars represent 50 and 95% credible intervals, respectively.

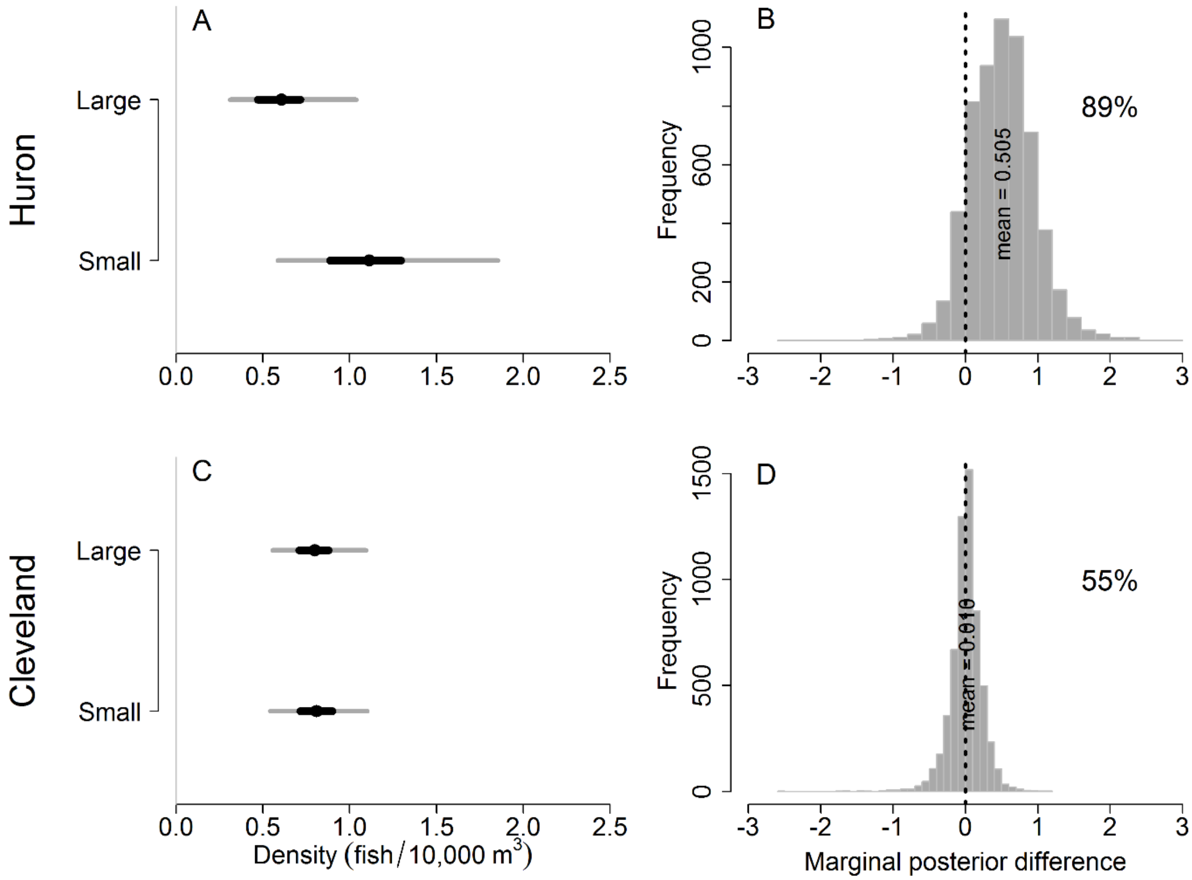

Figure 7. Comparison of estimated vessel main effects near Huron and Cleveland presented as density (fish/10,000 m^3). In panels (A) and (C), black circles represent the estimated mean, while black and gray bars represent 50 and 95% credible intervals, respectively. In panels (B) and (D), histograms represent the marginal posterior difference (MPD) between vessels (small-large) at each location, relative to no difference (0; dashed vertical line). Percentages represent the proportion of the MPD greater than 0.

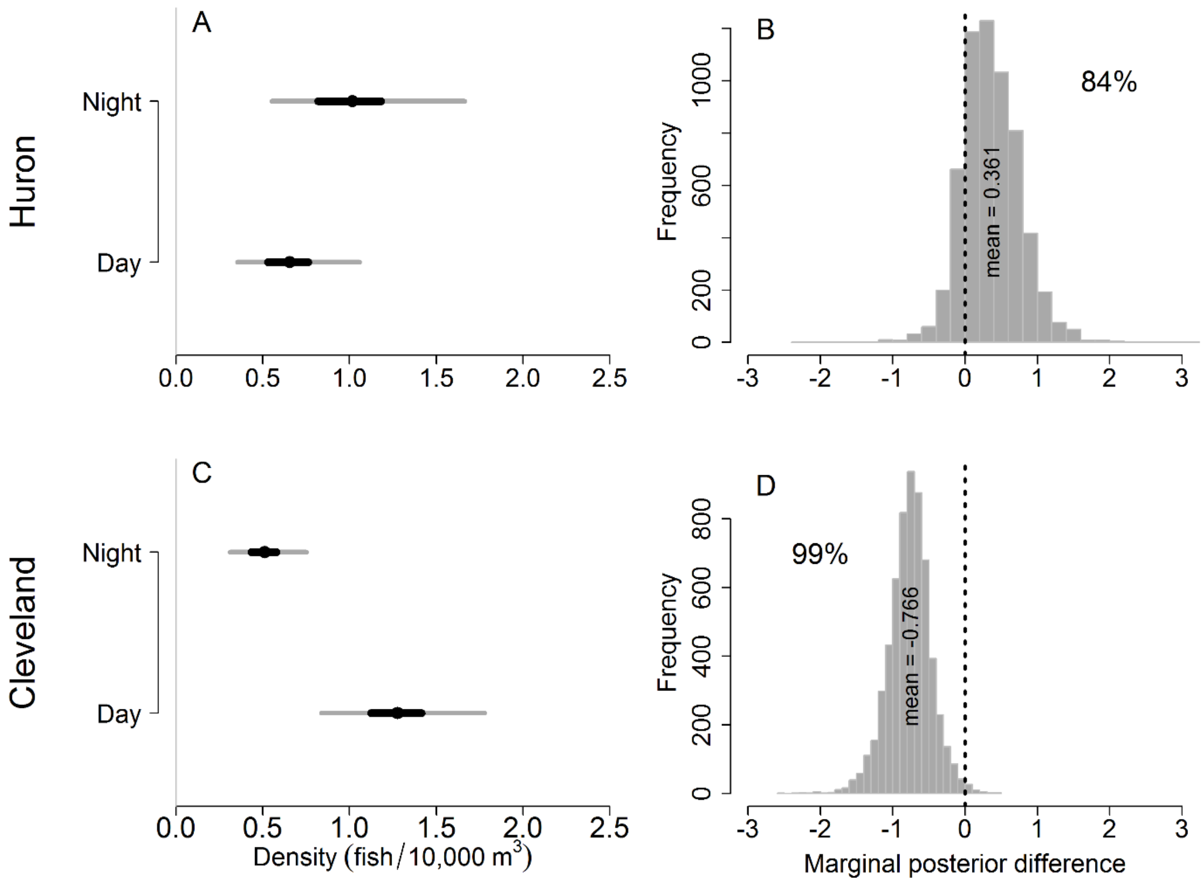

Figure 8. Comparison of estimated period main effects near Huron and Cleveland presented as density (fish/10,000 m^3). In panels (A) and (C), black circles represent the estimated mean, while black and gray bars represent 50 and 95% credible intervals, respectively. In panels (B) and (D), histograms represent the marginal posterior difference (MPD) between periods at Huron (night-day; B) and Cleveland (day-night; B), relative to no difference (0; dashed vertical line). Percentages represent the proportion of the MPD greater than 0.

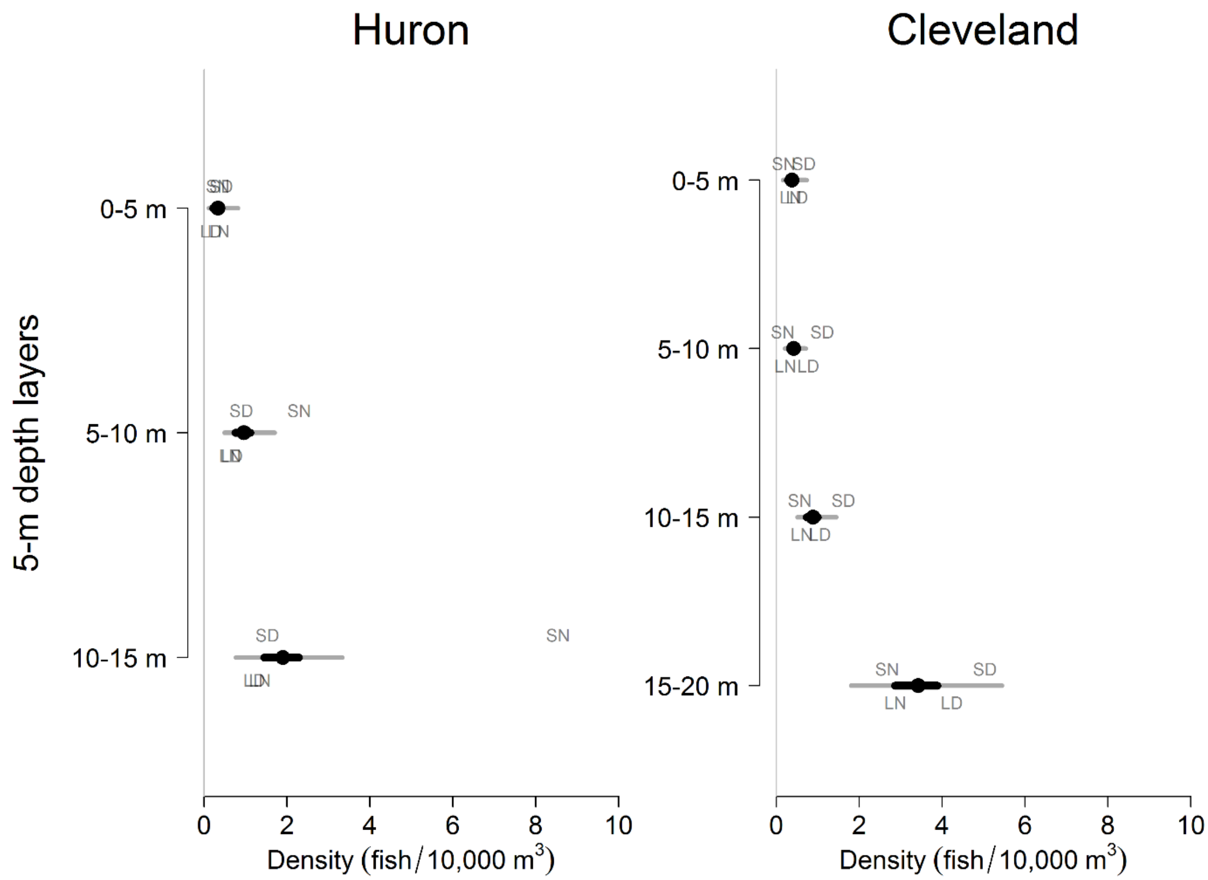

Figure 9. Comparison of estimated depth main effects and vessel, period, and depth interactions effects presented as density (fish/10,000 m^3) near Huron (A) and Cleveland (B). Black circles represent the estimated mean of depth main effects, while black and gray bars represent 50 and 95% credible intervals, respectively. The estimated mean of interaction effects are designated by SN, SD, LN, and LD representing vessel (small-S or large-L) and period (day-D or night-N).

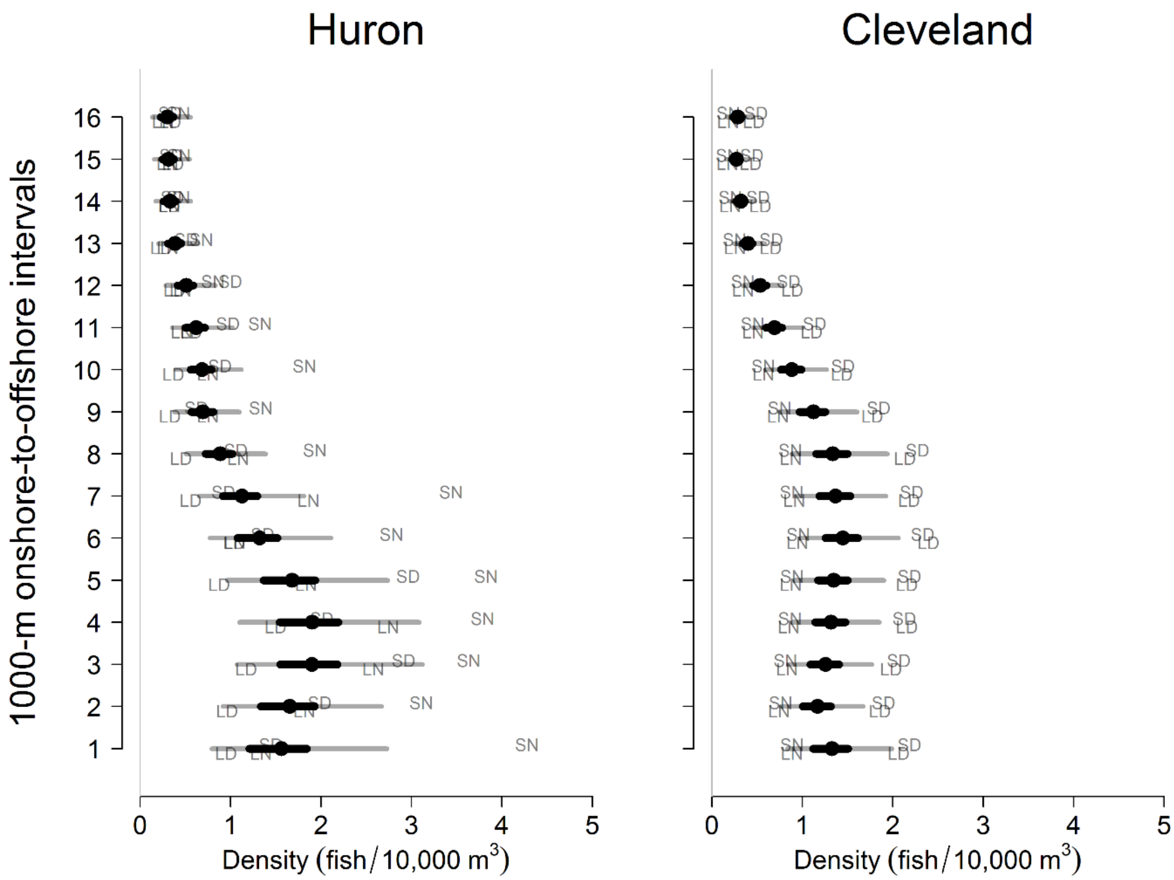

Figure 10. Comparison of estimated onshore-to-offshore interval main effects and interval, period, and depth interactions effects presented as density (fish/10,000 m^3) near Huron (A) and Cleveland (B). Black circles represent the estimated mean of depth main effects, while black and gray bars represent 50 and 95% credible intervals, respectively. The estimated mean of interaction effects are designated by SN, SD, LN, and LD representing vessel (small-S or large-L) and period (day-D or night-N).