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Cover Photos: The invasive spiny water flea *Bythotrephes* ensnared on an angling line on Rainy Lake, northern Minnesota (each black dot is an eyespot of a *Bythotrephes*). Branstrator et al. revealed that ensnarement rates of this aquatic invasive species were higher on angling lines than on any of the other gear tested, including downrigger cables, livewells, bait buckets, and anchor ropes. Photo by Jeff Gunderson, retired Director of Minnesota Sea Grant.

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Lines snag spines! A field test of recreational angling gear ensnarement of *Bythotrephes*

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ABSTRACT

Branstrator DK, Dumke JD, Brady VJ, Wellard Kelly HA. 2021. Lines snag spines! A field test of recreational angling gear ensnarement of *Bythotrephes*. Lake Reserv Manage. 37:391–405.

Recreational angling gear is a high-risk pathway of dispersal for the invasive spiny water flea (*Bythotrephes cederströmii*). We measured the number of *Bythotrephes* individuals ensnared on trolled shallow angling lines (3 line materials), a trolled downrigger angling line, a trolled downrigger steel cable, a trolled simulated livewell, a trolled bait bucket, and stationary anchor ropes (3 rope materials) in 2 Minnesota (United States) lakes. The shallow angling lines and the downrigger angling line had the greatest mean ensnarement rates (number of *Bythotrephes* individuals ensnared/transect transit), followed by the downrigger cable and the livewell, followed by the bait bucket and the anchor ropes. Added together, the shallow angling lines (as a mean of the 3 line materials) and the downrigger angling line accounted for 87–88% of the mean total ensnarement rate. Among the shallow angling lines, monofilament and fluorocarbon lines had greater mean ensnarement rates than braided line but the distinction was only statistically significant in one of the 2 lakes. The ensnarement rate of all angling gear combined was positively related to the density of *Bythotrephes* in the water column at the time of study (ambient density). On the downrigger angling line (monofilament), instar-3 *Bythotrephes* were ensnared at a relative frequency disproportionately greater than ambient density would predict, while instar-1 *Bythotrephes* were ensnared at a relative frequency disproportionately less than ambient density would predict. Our results suggest that education and outreach messaging should include instructions on removing *Bythotrephes* from angling lines in addition to the reminder to drain all water.

KEYWORDS
Angling gear; aquatic invasive species; *Bythotrephes*; dispersal; ensnarement

Prevention of propagule dispersal is the most important management strategy in the global effort to minimize environmental and economic impacts associated with nonindigenous invasive species (Leung et al. 2002, Vander Zanden et al. 2010, Sinclair et al. 2020). For many invasive species, human recreation is considered to be the leading pathway of propagule dispersal. In the United States, there is a nationally recognized "Stop Aquatic Hitchhikers!" campaign that directs people to clean, drain, and dry their equipment before moving it between waterbodies. This message is research based and should be effective if followed stringently. Nonetheless, it is broad and fails to emphasize the pathways that pose the highest risk for specific invasive species, and thus where decontamination could be focused or where usage could be minimized or avoided.

The spiny water flea (*Bythotrephes cederströmii*, formerly known as *Bythotrephes longimanus* [Korovchinsky and Arnott 2019], and hereafter *Bythotrephes*) is a nonindigenous aquatic invasive species of considerable concern in North America. Its impacts on food webs pose serious threats to the ecology and recreational value of lakes (Azan et al. 2015), including reductions in the biomass and production of native zooplankton (Pangle et al. 2007, Kerfoot et al. 2016), reductions in the growth rates of sport fishes (Staples et al. 2017, Hansen et al. 2020), and potential changes in water clarity (Walsh et al. 2016). Although *Bythotrephes* has spread to hundreds of lakes in the Midwestern region of North America (Kerfoot et al. 2011, Azan et al. 2015), it still occupies only a fraction of its potential range (Branstrator

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et al. 2006, Walsh et al. 2020), underscoring the value of improving best management practices to prevent its dispersal (Vander Zanden and Olden 2008, Sinclair et al. 2020).

Because *Bythotrephes* is small-bodied (maximum length of about 1 cm), open-water dwelling, widely dispersed in the water column, and often reaches high population densities (10–100 individuals/m^3), it is not amenable to mitigation or eradication once a lake becomes infested. Efforts to control its range focus on expedient and cost-effective ways of eliminating its dispersal. The primary pathway by which *Bythotrephes* is believed to disperse between invaded and uninvaded lakes is on recreational equipment. Evidence that recreational equipment is the primary pathway of dispersal comes from (1) scientific studies that show that rates of human visitation to lakes and associated transport of recreational equipment significantly predict invasion likelihood (MacIsaac et al. 2004, Weisz and Yan 2010) and (2) anecdotal information such as photographs and word-of-mouth testimonials of *Bythotrephes* fouling angling lines and downrigger cables. While aquatic birds are often discussed as couriers of dormant life stages of zooplankton (e.g., as resting eggs that can stick to feet or feathers, or be carried in the gut), there is little support for overland dispersal of *Bythotrephes* by birds (Charalambidou et al. 2003, MacIsaac et al. 2004, Branstrator et al. 2013).

Among the various types of recreational equipment of concern for *Bythotrephes* dispersal, recreational angling gear is considered a high-risk pathway (MacIsaac et al. 2004). Several factors may affect the dispersal risk of angling gear. Thin-gauge gear such as angling line is particularly vulnerable to ensnaring the barbed portion of a *Bythotrephes* tailspine; thus, such gear types may pose the greatest dispersal risk. As *Bythotrephes* grow, they lengthen their tailspine, and this could increase the dispersal risk of angling gear for larger *Bythotrephes* instars. *Bythotrephes* vertically migrate up in the water column on a nightly basis (Young and Yan 2008, Brown et al. 2012), which could increase their contact rates with angling gear during twilight compared to daytime hours. Also, *Bythotrephes* densities vary considerably within and between lakes (Brown et al. 2012, Kelly et al. 2013); thus, dispersal risk of angling gear is likely to be time and location specific.

Previous research has begun to address ensnarement rates of nonindigenous crustacean zooplankton invaders on recreational angling gear. MacIsaac et al. (2004) used surveys of anglers to help rank the risk of angling gear to disperse *Bythotrephes*. They reported that fishing line/nets and anchor ropes were perceived as higher risk whereas livewells and bait buckets were perceived as lower risk, suggesting that differences in ensnarement rate should be expected among different gear types. Jacobs and MacIsaac (2007) measured in situ rates of ensnarement of the fishhook water flea, *Cercopagis pengoi* (hereafter *Cercopagis*), on various brands of commercially available angling line in Lake Ontario. They reported that lines trolled deeper and farther through the water ensnared more *Cercopagis*, and that different brands of angling line ensnared different numbers of *Cercopagis*. We suspect that similar patterns of ensnarement on recreational angling gear exist for *Bythotrephes*; however, a comprehensive study has not yet been conducted. To address this gap, we tested 5 hypotheses in the field: (1) Thin gauge angling lines are more susceptible than other types of angling gear to ensnarement of *Bythotrephes*, (2) ensnarement of *Bythotrephes* on angling gear is positively related to the developmental instar (number of tailspine barb pairs), (3) ensnarement of *Bythotrephes* on angling gear is positively related to the density of *Bythotrephes* in the water column at the time of study (ambient density), (4) ensnarement of *Bythotrephes* on angling gear is greater during twilight compared to daytime hours, and (5) ensnarement of *Bythotrephes* on angling gear differs between lakes.

Methods

We deployed common types of angling gear along transects established in 2 Minnesota (United States) lakes for a prescribed distance or time, and then removed and counted the ensnared *Bythotrephes*. The lakes were Island Lake Reservoir (surface area = 32 km^2, maximum depth = 29 m) in 2017 and Lake Mille Lacs (surface area =

519 km², maximum depth = 13 m) in 2018 (MNDNR 2020). We chose these 2 lakes because of their invaded status, accessibility, and popularity among anglers. *Bythotrephes* was first recorded in the water column of Island Lake Reservoir in 1990 (Gravelle 1990) and in the water column of Lake Mille Lacs in 2009 (MNDNR 2009). Island Lake Reservoir (Secchi depth = 1–2 m) is less transparent than Lake Mille Lacs (Secchi depth = 3–4 m; MNDNR 2009). The reservoir's low transparency is due in part to its tannin staining (total organic carbon = 11.7 mg/L, apparent color = 58 Platinum-Cobalt Scale units; Sorensen et al. 2005).

At the beginning of each field season, we recorded Global Positioning System (GPS) coordinate locations for the start and end positions of 3 transects (each 1 linear km long) and used the same 3 transects every time we visited the lake. In Island Lake Reservoir, the transects were located in the east basin where bottom depth was 7–19 m. In Lake Mille Lacs, the transects were located in the northwest region, near the town of Garrison, where bottom depth was 7–8 m.

We visited each lake on 6 different dates in August and September, the time of year when high but also variable densities of *Bythotrephes* can be expected. On every date we conducted a set of 3 daytime and 3 twilight transect transits, for a total of 36 transect transits (18 daytime and 18 twilight) per lake, or 72 total. Sampling was only conducted when there was very little or no precipitation, wind, and wave action, which ensured that rain and boat motion did not interfere with accurate sample collection. Daytime sampling occurred during 09:00–14:00 h, while twilight sampling occurred during 17:00–22:00 h, with some adjustments, especially to twilight sampling times made in late September when daylight hours diminished. We elected to contrast these 2 time periods because *Bythotrephes* are known to engage in diel vertical migration, rising up in the water column on a nightly basis (Young and Yan 2008, Brown et al. 2012), and people commonly target twilight for angling, suggesting the potential for an interaction with time of day relevant to ensnarement rate. Generally, a set of 3 transect transits required 3–4 h to complete.

We collected vertical profiles of water temperature and dissolved oxygen concentration with a YSI 85 hand-held meter at increments of 1 m at either the start or end position of every transect transit.

On each transect transit we deployed 10 gear types (Table 1). We deployed 7 gear types at the start position and trolled them from a boat moving at 3 km/h to the end position, where we stopped the boat and retrieved the gear. Exposure time was 18–20 min. We deployed 3 anchor ropes at the start position, which were left unattended. The anchor ropes were exposed for 1.5–2.5 h with a few exceptions.

Shallow angling lines

We spooled angling lines on 3 matching rods that were 2.3 m (7 ft 6 in) long with 3 matching bait casting reels (Shakespeare Ugly Stick). Angling lines were 4.5 kg (10 lb) test Berkeley Trilene XL Smooth Casting (hereafter monofilament), 4.5 kg (10 lb) test Berkley Trilene 100% Fluorocarbon XL (hereafter fluorocarbon), and 13.6 kg (30 lb) test Sufix Performance Braid Digital Y6 Braiding (hereafter braided). Each angling line was 0.25 mm (0.01 inch) diameter. We outfitted the terminal end of each angling line with an 85 gm (3 oz) weight tied to a swivel. At the start of a transect transit, 10.7 m (35 ft) of angling line was paid out on each reel. A preliminary field test determined that with 10.7 m of angling line paid out, the terminal weight rode at 3 m (10 ft) depth in the water column when the boat traveled at 3 km/h. Three rod holders

Table 1. Summary of the recreational angling gear deployed. One of each gear type was deployed per transect transit.

Angling gear	Description
Shallow angling line (monofilament)	4.5 kg (10 lb) test, 0.25 mm (0.01 in) diameter
Shallow angling line (fluorocarbon)	4.5 kg (10 lb) test, 0.25 mm (0.01 in) diameter
Shallow angling line (braided)	13.6 kg (30 lb) test, 0.25 mm (0.01 in) diameter
Downrigger angling line (monofilament)	4.5 kg (10 lb) test, 0.25 mm (0.01 in) diameter
Downrigger steel cable	68 kg (150 lb) test
Livewell simulation	1.6 cm (5/8 in) diameter intake hose
Bait bucket	5.7 L (6 qt) capacity
Anchor rope (twisted nylon)	1 cm (3/8 in) diameter
Anchor rope (braided nylon)	1 cm (3/8 in) diameter
Anchor rope (twisted polypropylene)	1 cm (3/8 in) diameter

secured to the boat stern held the rod tips over the sides of the boat with the lines trailing behind the boat away from the outboard motor. Angling line angles at the point of contact with the water were about 30° from horizontal. We estimated that about 6 m (20 ft) of each angling line was submerged.

We retrieved angling lines at the end of each transect transit. Most ensnared *Bythotrephes* accumulated on the first rod eyelet. We rinsed them into a plastic bag using a stream of water. Using forceps, we manually removed *Bythotrephes* that passed the first eyelet. We preserved specimens in 75% ethanol.

Downrigger angling line and cable

On the boat stern we mounted a downrigger apparatus (Cannon Easi-Troll ST) outfitted with a stainless steel downrigger cable that was 68 kg (150 lb) test and weighted at the terminal end with a 3.6 kg (8 lb) keeled downrigger ball. We used the same brand of rod, reel, and monofilament line used for the shallow angling lines. We clipped the angling line to the cable at the terminal end near the downrigger ball using the same style line release clip that anglers would use when fishing. At the start of a transect transit, we lowered the weighted cable and angling line to 1 m above the lake bottom, as determined by an electronic depth finder that displayed the downrigger ball. We adjusted the depth of the downrigger ball, cable, and angling line periodically while transiting a transect to maintain 1 m distance from the lake bottom.

At the end of a transect transit, we unclipped the angling line from the cable by applying slight tension to the angling line so it would detach from the downrigger ball release clip, and then we retrieved both the angling line and the cable. We removed *Bythotrephes* from the angling line as already described for the shallow angling lines. We removed *Bythotrephes* from the cable by continually spraying it with a stream of water into a Nitex mesh bag immediately before it entered the terminal guide. Using forceps, we manually removed *Bythotrephes* that passed the terminal guide. We preserved specimens in 75% ethanol.

Livewell

We simulated how a boat livewell would be used during trolling by continuously pumping water into a plankton net during a transect transit. Water was pumped from about 0.5 m below the lake surface through a 1.6 cm (5/8 in) diameter intake hose, mounted on the port side of the boat's transom, at a rate of 14.2 L/min. This produced about 256–284 L during the 18–20 min transect transit. We preserved specimens in 75% ethanol.

Bait bucket

We trolled a bait bucket (Frabill Flow Troll, 5.7 L [6 qt] capacity) on the lake surface using a rope (about 1.5 m long) attached to the starboard side of the boat. Water flowed passively through the ventilation holes. At the end of a transect transit, we rinsed the contents of the bait bucket into a Nitex mesh bag. We preserved specimens in 75% ethanol.

Anchor ropes

At the start of each transect transit, we deployed 3 anchor ropes of 1 cm (3/8 in) diameter including 1 of twisted nylon, 1 of braided nylon, and 1 of twisted polypropylene material. Separate floats and weights vertically suspended each rope to cover the entire water column. Ropes were deployed within a 10 m diameter circle.

At the end of the exposure time, we retrieved the anchor ropes by gently coiling them into separate plastic bags, which we stored on ice in a cooler. We processed the anchor ropes within 24 h of retrieval by visually examining each rope with a desktop, lighted magnifying lens. Each rope required 15–30 min to search with a few exceptions. Using forceps, we manually removed *Bythotrephes* and other ensnared organisms (daphniids, isopods, leeches, and mollusks) and stored them in 75% ethanol. For quality control, a subset of the anchor ropes (27% in Island Lake Reservoir and 12% in Lake Mille Lacs) was reexamined immediately by a second researcher. We reduced the level of quality control in Lake Mille Lacs due to the absence of ensnared *Bythotrephes* on the anchor ropes in Island Lake Reservoir.

Ambient density

Simultaneous with the deployment of angling gear from the first boat, from a following second boat we collected *Bythotrephes* from the water column. At 3 locations along each transect transit (both end positions and the middle position), we vertically towed standard zooplankton nets (0.5 m diameter mouth opening, 500 μm aperture mesh) in triplicate from 1 m above the lake bottom to the surface. We collected tows within 15 min of the time that the trolled angling gear had passed the sampling location. We preserved specimens in 75% ethanol.

Laboratory and data analysis

Using dissecting microscopes, we sorted and counted *Bythotrephes* by its 3 developmental instars based on the number of tailspine barb pairs (Branstrator 2005). We included specimens with damaged or missing tailspines in the total counts but not in the instar-specific analysis.

To estimate the density (individuals/m^3) of *Bythotrephes* along each transect transit at the time of angling gear deployment (ambient density) we computed the mean of the triplicate zooplankton net tows collected at each of the 3 locations (both end positions and the middle position) and then computed the mean of those 3 values.

We used SYSTAT 13 for statistical analyses, and a cutoff of $P = 0.05$ for statistical significance.

Ambient density, time of day, lake, sampling date, transect. We used a multiple linear regression model and analysis of variance (ANOVA) and *F* ratio to evaluate the overall effect of 5 fixed-effect, independent variables on the dependent variable "total ensnarement rate." "Total ensnarement rate" was defined as the number of *Bythotrephes* individuals ensnared on a transect transit (number/transect transit) on all angling gear combined. For the 3 shallow angling lines and the 3 anchor ropes, we first computed a mean ensnarement rate for each gear type. The 5 independent variables were "ambient density," "time of day" (twilight vs. daytime), "lake" (Island Lake Reservoir vs. Lake Mille Lacs), "sampling date" (the 6 dates that we sampled, given as 1–6), and "transect" (given as 1–3). We included sampling date as a fixed-effect variable because we were concerned that our sampling efficiency (removal of *Bythotrephes* from angling gear) might have improved as a field season progressed. We included transect as a fixed-effect variable because we always transited the same transects in each lake in the sequence 1–3.

Having found no significant effect of time of day, lake, sampling date, or transect on total ensnarement rate, we thereafter treated the 72 transect transits as independent replicates. We plotted total ensnarement rate as a function of ambient density for the 72 transect transits, and used a simple linear regression model to estimate a best-fit relationship and test for slope = 0 (ANOVA, *F* ratio).

Angling gear. To test for differences in the ensnarement rate of *Bythotrephes* among angling gear types, we first computed a mean ensnarement rate (number/transect transit) for each gear type and then compared the mean ensnarement rates among the shallow angling lines, downrigger angling line, downrigger cable, and livewell within each lake using one-way ANOVA models and Tukey pairwise comparisons. For the shallow angling lines, we used the mean of the 3 line materials. We excluded the bait bucket and the anchor ropes due to their low ensnarement rates (4 total *Bythotrephes* were recovered from all bait buckets and anchor ropes, combined, across the entire study). We also used one-way ANOVA models and Tukey pairwise comparisons to compare the mean ensnarement rates among the 3 shallow angling line materials within each lake. We log10 transformed the data before analysis and evaluated the assumption of homogeneity of variances using Levene's test. Untransformed zero values were included in the calculations of the means but not in the statistical models. In 3 of the 4 ANOVA models, the assumption of homogeneity of variances was met ($P > 0.05$). The exception was the ANOVA model that compared the 4 gear types in Lake Mille Lacs ($P = 0.03$). We considered that result to be marginally statistically significant and not in severe violation of the model assumption.

In order to further evaluate differences between gear types, we tabulated the number of transect transits in each lake for which the ensnarement rate was greater for the shallow angling lines (as a mean of the 3 line materials) than for the downrigger angling line, or vice versa. The classification for each transect transit was categorical as either a “yes” (a greater ensnarement rate for the shallow angling lines) or a “no” (a lesser ensnarement rate for the shallow angling lines). We used Fisher’s exact test to determine whether the proportion of transect transits in the 2 classifications was different between lakes.

Developmental instar. To test for proportional differences in ensnarement frequency among the 3 developmental instars of *Bythotrephes*, we used Chesson’s α (Chesson 1983) to determine whether the relative frequencies of the 3 instars of ensnared *Bythotrephes* on angling gear were proportionate to their relative frequencies in ambient density as

$$\alpha = \left(r_i/p_i\right)/\Sigma\left(r_i/p_i\right), \text{ for i} = 1-3 \qquad (1)$$

where r_i is the number of an instar ensnared on the gear at the end of a transect transit, and p_i is ambient density of an instar along a transect transit. Because *Bythotrephes* has 3 instars, $\alpha = 0.33$ indicates that the relative frequency of an instar ensnared on the gear is proportionate to its relative frequency in ambient density. Values of $\alpha > 0.33$ or $\alpha < 0.33$ indicate a disproportionately greater or lesser relative frequency on the gear compared to the relative frequency in ambient density, respectively. We used Kruskal–Wallis models to compare the α values among the 3 instars in each lake. This nonparametric test was more appropriate than ANOVA because the data failed to meet the assumption of homogeneity of variances (Levene’s test) for the Lake Mille Lacs data. For this analysis we did not merge the data sets for the 2 lakes because the mean proportions of developmental instars between the 2 lakes were notably different.

We estimated α for the downrigger angling line only. In addition, we used box plots to show the relative frequency of *Bythotrephes* by developmental instar ensnared on the downrigger angling line compared to ambient density. The downrigger angling line was one of 3 gear types (with the other 2 being the downrigger cable and the anchor ropes) for which physical exposure spanned the entire water column that we sampled with the zooplankton vertical net tows. This was important because spanning the entire water column eliminated potential bias that could have been caused by vertical spatial variation by instar of *Bythotrephes* at the time of sampling (Brown et al. 2012). There were too few ensnared *Bythotrephes* (with many zeros) on the downrigger cable and anchor ropes to allow for a robust analysis of α for either of those gear types.

Results

The main portion of the water column where we conducted transect transits in Island Lake Reservoir (0–12 m) was well oxygenated (>2 mg/L dissolved oxygen) and 11.9–23.4 C. Deeper regions of the water column (12–19 m), which represented minor portions of the transect transits, were often cooler (but never <11.0 C) and often contained <2 mg/L dissolved oxygen. The water column where we conducted transect transits in Lake Mille Lacs (0–8 m) was consistently well oxygenated (>2 mg/L dissolved oxygen) and 15.6–23.7 C.

Ambient density, time of day, lake, sampling date, transect

A multiple linear regression model, with total ensnarement rate as the dependent variable, was significant overall (ANOVA, $F_{5,66} = 7.4$, $P < 0.01$). Of the 5 independent variables, only ambient density was statistically significant ($P < 0.05$). The P values for the other variables were as follows: time of day ($P = 0.32$), lake ($P = 0.86$), sampling date ($P = 0.69$), and transect ($P = 0.72$). These results do not support the hypothesis that ensnarement of *Bythotrephes* on angling gear is greater during twilight compared to daytime hours, or the hypothesis that ensnarement of *Bythotrephes* on angling gear differs between lakes. However, they do support the hypothesis that ensnarement of *Bythotrephes* on angling gear is positively related to ambient density.

Specifically, total ensnarement rate is predicted by ambient density (Figure 1) as:

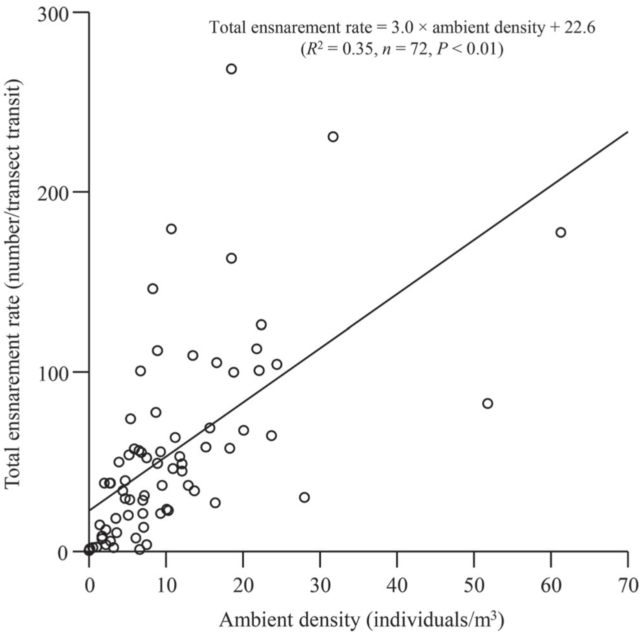

Figure 1. *Bythotrephes* total ensnarement rate as a function of ambient density as defined by a best-fit linear relationship for Island Lake Reservoir and Lake Mille Lacs.

$$\text{total ensnarement rate} = 3.0 \times \text{ambient density} + 22.6 \quad (2)$$

(R^2 = 0.35, $n = 72$ transect transits). The slope of the relationship is significantly different from zero ($F_{1,70}$ = 37.3, $P < 0.01$). Across both lakes, the mean ± 1 standard deviation for ambient density was 11.1 ± 10.6 individuals/m^3 ($n = 72$ transect transits, range = 0.1–61.4), and the mean ± 1 standard deviation for total ensnarement rate was 56.0 ± 54.0 individuals/transect transit ($n = 72$ transect transits, range = 0.0–268.0).

Angling gear

The mean ensnarement rate of *Bythotrephes* ranged widely among angling gear types (Table 2). The general trend in both lakes was that the mean ensnarement rates were greatest for the shallow angling lines (as a mean of the 3 line materials) and the downrigger angling line, intermediate for the downrigger cable and the livewell, and least for the bait bucket and the anchor ropes (as a mean of the 3 rope materials). ANOVA (which excluded the bait bucket and the anchor ropes due to so few individuals ensnared) revealed overall statistical significance among the shallow angling lines (as a mean of the 3 line materials), the downrigger angling line, the downrigger cable, and the livewell in both lakes

Table 2. Ensnarement rates of *Bythotrephes* as number/transect transit presented as the mean ± 1 standard error (n = number of transect transits) for the recreational angling gear tested. For the shallow angling lines and the anchor ropes, values are the means of the 3 materials. Shared letters within lake (column) indicate that the mean values are not statistically significantly different ($P > 0.05$) based on ANOVA and Tukey pairwise comparisons that included 4 variables (shallow angling lines, downrigger angling line, downrigger steel cable, and livewell simulation). We excluded the bait bucket and anchor ropes from the ANOVA models due to the predominance of zero values. The last row represents the sums of the means of the individual gear types.

	Ensnarement rate	
Angling gear	Island Lake Reservoir	Lake Mille Lacs
Shallow angling lines	12.5 ± 1.7 (36) a	37.5 ± 6.3 (36)
Downrigger angling line	37.0 ± 6.5 (33)	14.7 ± 5.8 (35) a
Downrigger steel cable	0.8 ± 0.3 (34) b	6.0 ± 1.8 (36) a,b
Livewell simulation	6.3 ± 1.9 (36) a,b	0.9 ± 0.3 (21) b
Bait bucket	0.0 ± 0.0 (36)	0.03 ± 0.03 (35)*
Anchor ropes	0.0 ± 0.0 (36)	0.03 ± 0.02 (36)*
Total (sum of the means)	56.6	59.2

*Note additional decimal places.

(Island Lake Reservoir, $F_{3,98}$ = 15.2, $P < 0.01$; Lake Mille Lacs, $F_{3,88}$ = 12.3, $P < 0.01$). Tukey pairwise comparisons for Island Lake Reservoir revealed that the mean ensnarement rate for the downrigger angling line was greater than for any of the other 3 gear types. By contrast, Tukey pairwise comparisons for Lake Mille Lacs revealed that the mean ensnarement rate for the shallow angling lines (as a mean of the 3 line materials) was greater than for any of the other 3 gear types. These results support the hypothesis that thin gauge angling lines are more susceptible than other types of angling gear to ensnarement of *Bythotrephes*.

There was a difference between lakes in the actual number of transect transits for which the ensnarement rate was greater for the shallow angling lines (as a mean of the 3 line materials) than for the downrigger angling line. Only 10 of 33 transect transits in Island Lake Reservoir had an ensnarement rate that was greater for the shallow angling lines. By contrast, 29 of 33 transect transits in Lake Mille Lacs had an ensnarement rate that was greater for the shallow angling lines. Fisher's exact test revealed strong statistical departure ($P < 0.01$) from random proportions.

We recovered few *Bythotrephes* from the bait bucket or the anchor ropes (Table 2). Specifically, we recovered no *Bythotrephes* from the bait bucket in Island Lake Reservoir and only one *Bythotrephes* from the bait bucket in Lake Mille

Lacs. We recovered no *Bythotrephes* from the anchor ropes in Island Lake Reservoir and only 3 *Bythotrephes* from the anchor ropes in Lake Mille Lacs, including one on twisted nylon and 2 on braided nylon ropes. However, we recovered a variety of other taxa on the anchor ropes in both lakes, including 10 daphniids (Island Lake Reservoir) and 87 isopods, 53 leeches, and 38 mollusks (Lake Mille Lacs).

Using our results in Table 2, we calculated a mean total ensnarement rate in each lake by summing the individual mean rates for each gear type. This produced values of 56.6 (Island Lake Reservoir) and 59.2 (Lake Mille Lacs) individuals/transect transit. This calculation of the mean total ensnarement rate differs slightly from that presented in the preceding for the entire dataset (equation 2 and Figure 1) where we first calculated a total ensnarement rate per transect transit, not by individual gear type. Using our second formulation (based on Table 2), the sum of the mean ensnarement rates for the shallow angling lines (as a mean of the 3 line materials) and the downrigger angling line accounted for 87% (Island Lake Reservoir) and 88% (Lake Mille Lacs) of the mean total ensnarement rate. Using our results in Table 2, we plotted the projected cumulative percentage of *Bythotrephes* that would be removed from angling gear as it is cleaned (Figure 2). Using greatest percentage ensnarement to prioritize cleaning, our results indicate that shallow and downrigger angling lines should receive the most attention.

There were notable differences in the mean ensnarement rates among the 3 shallow angling line materials (Table 3). For Island Lake Reservoir, the overall ANOVA model was statistically significant ($F_{2,93}$ = 8.2, $P < 0.01$) and Tukey pairwise comparisons indicated that the mean ensnarement rate for monofilament and fluorocarbon was each greater than for braided. For Lake Mille Lacs, the overall ANOVA model was not statistically significant ($F_{2,90}$ = 0.6, $P = 0.55$) despite trends in the same direction as the Island Lake Reservoir results.

Developmental instar

The relative frequency of *Bythotrephes* by developmental instar ensnared on the downrigger angling line departed notably from the relative frequency in ambient density (Figure 3). Most notably, instar 1 was strongly underrepresented on the gear and instar 3 was strongly overrepresented on the gear in comparison to ambient density.

In both lakes, the α values were generally least (below 0.33) for instar 1, intermediate (near 0.33) for instar 2, and greatest (above 0.33) for instar 3. Specifically, in Island Lake Reservoir the mean α values were 0.12, 0.33, and 0.55 for instars 1, 2, and 3, respectively ($n = 30$ transect transits per value); in Lake Mille Lacs the mean α values were 0.03, 0.20, and 0.77 for instars 1, 2, and 3, respectively ($n = 24$ transect transits per value). The distributions of the α values were statistically significantly different within each lake based on Kruskal–Wallis models (Island Lake Reservoir, $H = 51.4$, $P < 0.01$; Lake Mille Lacs, $H = 50.9$, $P < 0.01$). These results support the hypothesis that ensnarement of *Bythotrephes* on angling gear (specifically, downrigger angling line) is positively related to the developmental instar.

Discussion

Transportation of recreational equipment among waterbodies is believed to be the single most important pathway of dispersal for *Bythotrephes* among North American lakes (MacIsaac et al. 2004). To better understand the problem, we tested 5 hypotheses related to the ensnarement rate (number/transect transit) of *Bythotrephes* on recreational angling gear in Island Lake Reservoir and Lake Mille Lacs, Minnesota (United States).

Angling gear

Our results support the hypothesis that thin gauge angling lines are more susceptible than other types of angling gear to ensnarement of *Bythotrephes* (Table 2). Angling lines, whether they were trolled in a shallow fashion behind the boat or lowered with aid of a downrigger that spanned the entire water column, had the greatest mean ensnarement rates among all gear types tested. By contrast, the downrigger cable and the livewell had intermediate mean ensnarement

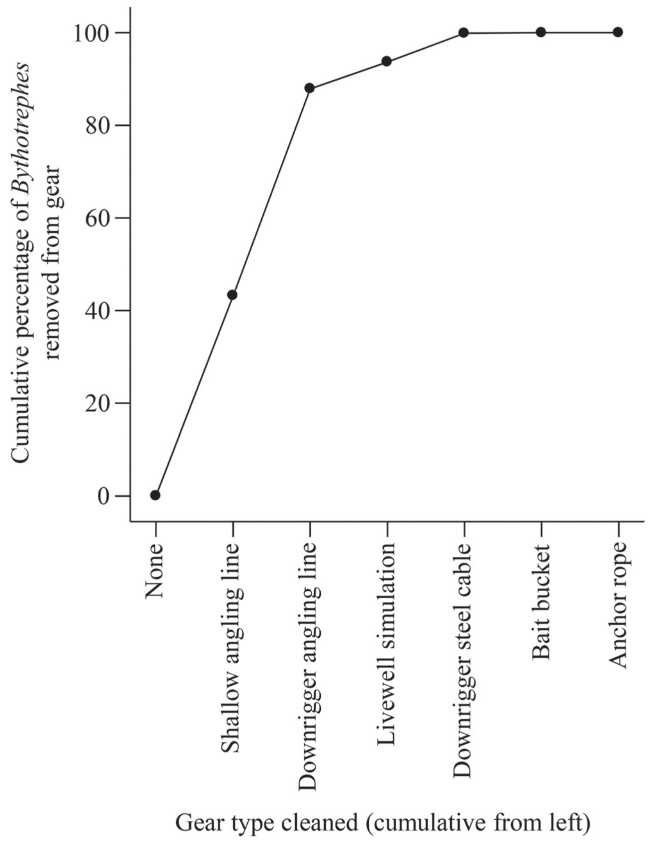

Figure 2. A projection of the cumulative percentage of ensnared *Bythotrephes* that would be removed from recreational angling gear if the gear (*x* axis) were cleaned in sequence from left to right. Numbers are based on the ensnarement rate results in Table 2.

Table 3. Ensnarement rates of *Bythotrephes* (number/transect transit) presented as the mean ± 1 standard error (*n* = number of transect transits) for the 3 shallow angling line materials tested. Shared letters within lake (column) indicate that the mean values are not statistically significantly different ($P > 0.05$) based on ANOVA and Tukey pairwise comparisons.

	Ensnarement rate	
Angling line material	Island Lake Reservoir	Lake Mille Lacs
Monofilament	18.6 ± 3.2 (36) a	38.9 ± 9.0 (36) a
Fluorocarbon	13.1 ± 2.2 (36) a	43.6 ± 8.6 (36) a
Braided	5.8 ± 1.2 (36)	29.9 ± 5.8 (36) a

rates, while the bait bucket and the anchor ropes had the lowest mean ensnarement rates. In a survey of >800 recreationalists in Ontario (Canada), MacIsaac et al. (2004) found that fishing line/nets and anchor ropes were perceived to be more likely than livewells and bait buckets to disperse *Bythotrephes*. A recent survey of Minnesota anglers (MNDNR 2019) found that more than 50% do not believe that angling gear can move aquatic invasive species among waterbodies. Our results indicate that people may not always correctly identify which gear types pose the greatest ensnarement risk.

It is possible that our anchor rope deployments did not sufficiently mimic true anchor rope use by boaters. We attempted to mimic a common usage of anchor ropes by deploying them in a stationary fashion in water with no obvious directional current. It is possible that anchor ropes being dragged behind a drifting boat or deployed in flowing water (e.g., in a river or near a lake inlet or outlet) could yield greater ensnarement rates than we found. Evidence for other groups of biota ensnared on the anchor ropes suggests that chemical toxicity of the rope materials, physical shape or texture of the rope materials, or inadequate methodology to detect ensnared biota on our part are unlikely explanations for the almost complete absence of ensnared *Bythotrephes* on the anchor ropes.

We observed an interesting contrast in our results between the livewell and the bait bucket. Both were deployed near or at the lake surface, but the mean ensnarement rates were much greater for the livewell. One difference was that

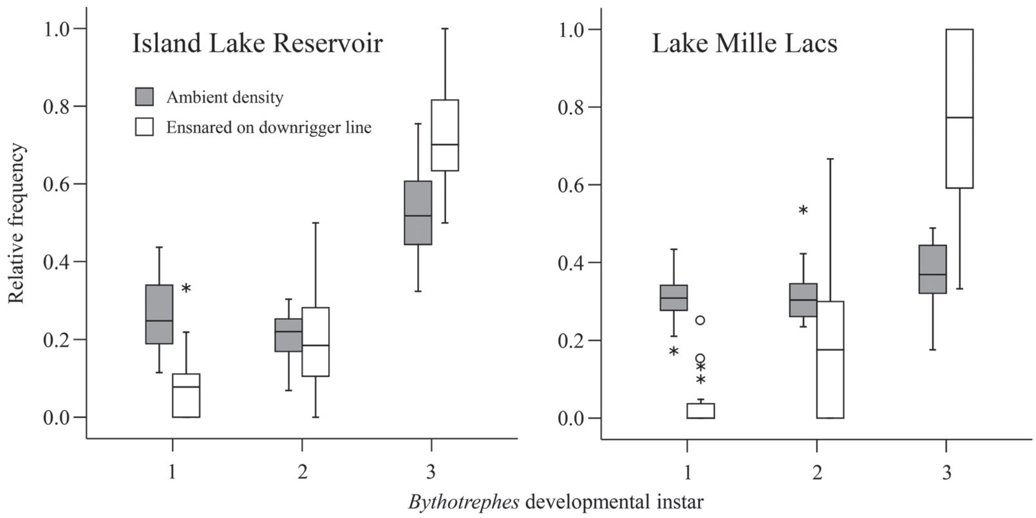

Figure 3. Box plots of the relative frequency (0–1) of *Bythotrephes* by developmental instar in ambient density (gray bar, left) and those ensnared on the downrigger angling line (open bar, right). Centerline = median, box edges = first and third quartiles, whisker ends = range, circles and asterisks = outliers ($n = 30$ transect transits per bar in Island Lake Reservoir, and $n = 24$ transect transits per bar in Lake Mille Lacs). Within each panel, mean relative frequencies (not shown) sum to 1 for each variable across the 3 instars.

the livewell was actively drawing lake water in through an unscreened intake, whereas the bait bucket was accepting lake water more passively through the bucket holes. It is probable that more water and plankton entered the livewell than the bait bucket because water was not pumped into the bait bucket, and because the bait bucket only has holes on the top surface, which reduces water exchange (i.e., water must flow in and out of the same holes, a design feature intended to protect baitfish from being injured from high-volume through flow). A second explanation is that any *Bythotrephes* ensnared in the livewell simulation would have been retained in a net that we installed specifically for capturing plankton. By comparison, *Bythotrephes* initially ensnared in the bait bucket could have been washed back out through the bait bucket holes before the end of a transect transit. A similar phenomenon may occur in real-life ensnarement of *Bythotrephes* in angler livewells, as boat manufacturers build into their livewells overflow drains that may allow some *Bythotrephes* that are pumped into a livewell to passively flush out. Our livewell simulation did not include an overflow drain. We acknowledge that our livewell simulation may represent greater *Bythotrephes* retention than may be experienced by anglers since we captured all *Bythotrephes* entering a livewell, rather than just the individuals retained there. However, we consider our livewell test to still be valuable because boat and livewell designs vary greatly among manufacturers, and there is no way to predict how *Bythotrephes* would interact with many livewell designs once contained within. Thus, our results indicate the ensnarement potential that any livewell could pose.

In addition to the contrasts in the mean ensnarement rates among the gear types, there were differences among the angling line materials (Table 3). Specifically, in Island Lake Reservoir, the mean ensnarement rate for the monofilament and fluorocarbon lines was each greater than for the braided line. The directional trend in Lake Mille Lacs was consistent with that of Island Lake Reservoir in that the mean ensnarement rate was least for the braided line, but there was no statistical difference among the 3 line materials. Monofilament and fluorocarbon lines are made of single-stranded, extruded polymers that have a smooth feel, whereas braided line is made of a multistranded, woven thread that has a rougher texture. Monofilament and fluorocarbon lines also stretch more than braided line before breaking, which would give the line materials different capacities to respond to agitation during trolling and retrieval. Both factors could have influenced the tendency of *Bythotrephes* to become ensnared and remain ensnared. We and others have anecdotally noted that *Bythotrephes* tend to slide on angling line and that this often leads to clumping, which may increase the tendency of *Bythotrephes* to remain attached. Perhaps *Bythotrephes* slid and clumped more frequently on the monofilament and fluorocarbon lines than on the braided line. Jacobs and MacIsaac (2007) measured ensnarement rates of *Cercopagis* on sport fishing lines trolled from a boat in Lake Ontario. Their evaluation of 4 different monofilament line brands showed that the ensnarement rate for Berkeley Trilene XL Smooth Casting, which was the same brand that we used here, was greater than for the other 3 monofilament brands, and that there was considerable variation among all 4 of the monofilament brands they tested. Their study and ours together suggest that the interaction of angling line and ensnarement rate of zooplankton is determined by factors beyond just line material.

Angling lines accounted for the vast majority of ensnared *Bythotrephes* in both lakes. Specifically, the sum of the mean ensnarement rates for the shallow angling lines (as a mean of the 3 line materials) and the downrigger angling line accounted for 87% (Island Lake Reservoir) and 88% (Lake Mille Lacs) of the mean total ensnarement rate. Thus, just cleaning angling lines would remove the majority of *Bythotrephes* ensnared on angling gear (Figure 2). This is an important message to convey to anglers, especially considering that results from a Minnesota angler survey (MNDNR 2019) indicate that more than 50% of anglers may not be thinking about cleaning their gear because they do not believe it can transfer invasive species.

It is prudent to keep in mind that we made specific choices in how we used the angling gear and that these undoubtedly influenced our results. As mentioned, we deployed the anchor ropes in a stationary fashion for 1.5–2.5 h while all other angling gear was trolled for a distance of 1 km from a moving boat for 18–20 min. A host of variables, including the length of time that we deployed the gear, our deployment of the anchor ropes in stationary water (as opposed to in a current), distance from the boat that we trolled the gear, our specific uses of the gear (e.g., trolling as opposed to casting and retrieving angling lines), the types of terminal tackle that we used on the angling lines (e.g., weights as opposed to lures), the lack of any flushing of the livewell (i.e., overflow drains) in our simulation, and the lack of baitfish in the bait bucket, might all have influenced the outcomes. Nonetheless, we believe that our results are a robust index of relative ensnarement rates in relation to how we deployed the gear, and are thus relevant to informing the dispersal risk of angling gear.

Developmental instar

Our results support the hypothesis that ensnarement of *Bythotrephes* on angling gear is positively related to the developmental instar. We tested this hypothesis for the downrigger angling line in both lakes and found that there was a strong and significant trend that indicated that the distribution of the α values was statistically greatest for instar 3 and least for instar 1. These results are consistent with the disproportionate relative frequency of developmental instars ensnared on the downrigger angling line compared to ambient density (Figure 3). During morphological development from instar 1–3, *Bythotrephes* grow progressively in core body size, spine length, and number of tailspine barb pairs (Branstrator 2005). Larger, longer, and more adorned (number of barb pairs) animals present a larger and more complex profile in the water that could increase the frequency of ensnarement on a moving angling line. These same 3 morphological characters could also feasibly increase an individual's retention rate after ensnarement. It seems unlikely that variation in swimming speed could have played a role in the pattern. Swimming speeds of *Bythotrephes* are reported as 16–20 mm/sec (Muirhead and Sprules 2003) with instar 3 being the fastest, but this pace is minimal compared to the velocity that our angling line was moving (2–3 km/h or 555–833 mm/sec).

From the standpoint of dispersal and establishment risk, this result is particularly relevant because instar-3 individuals are the sexually mature portion of a population. When *Bythotrephes* are gravid, instar-3 individuals commonly carry 2–7 offspring (parthenogenetic embryos or resting eggs) per clutch (Branstrator 2005). A strong relationship between propagule pressure and establishment risk has been experimentally demonstrated for *Bythotrephes* in mesocosms (Gertzen et al. 2011, Branstrator et al. 2019). Thus, factors that increase propagule pressure during a dispersal event, including the transport of individuals as embryos or resting eggs, will likely simultaneously enhance establishment risk. This dynamic magnifies the overall threat of dispersal associated with certain types of angling gear such as angling line that selectively ensnares instar-3 *Bythotrephes*.

Ambient density

Our results support the hypothesis that ensnarement of *Bythotrephes* on angling gear is positively related to ambient density. Our results can thus be used to predict ensnarement rate within and among lakes over a range of natural densities of *Bythotrephes* (Figure 1). Because natural densities of *Bythotrephes* commonly fluctuate in lakes by an order of magnitude over short (weekly) time frames (Brown et al. 2012, Kelly et al. 2013), anglers may observe widely different ensnarement rates in the same lake on the same angling gear from week to week. This underscores the need for anglers to avoid vigilance fatigue and to clean gear every time an infested lake is visited. Jacobs and MacIsaac (2007) reported a positive relationship between distance trolled and number of *Cercopagis* ensnared on fishing lines in Lake Ontario. We did not test for an effect of trolled distance on ensnarement rate, and we caution that our results should not be projected to longer or shorter distances because the relationship might be nonlinear and could lead to false predictions. Likewise, if angling gear is periodically retrieved to a boat we suspect that the movement and agitation of the gear could help remove ensnared *Bythotrephes* and reduce total accumulation.

Time of day

Our results do not support the hypothesis that ensnarement of *Bythotrephes* on angling gear is greater during twilight compared to daytime hours. Further investigation of the data did not reveal any reversals in trends in the rank order of the mean ensnarement rates among the gear types in Table 2 when twilight vs. daytime was considered. Sampling even later after dark than we did could reveal different results.

Lake

Our results do not support the hypothesis that ensnarement of *Bythotrephes* on angling gear differs between lakes. There was, however, a notable interaction in ensnarement rate for the shallow and the downrigger angling lines between the 2 lakes. Among other differences, Island Lake Reservoir and Lake Mille Lacs have contrasting presence of cisco (*Coregonus artedi*), a planktivorous predator of *Bythotrephes*. Young and Yan (2008) reported that cisco influence the vertical position of *Bythotrephes,* causing them to occupy shallower portions of the water column during both day and night than they otherwise would in lakes that lack cisco. Our results are directionally consistent with the possibility that *Bythotrephes* were shallower in the water column in Lake Mille Lacs (which supports cisco) than in Island Lake Reservoir (which lacks cisco) in a way that increased their relative exposure in Lake Mille Lacs to the shallow angling lines compared to the downrigger angling line and vice versa in Island Lake Reservoir.

Alternatively, it is possible that the length of line paid out played a role, particularly in Island Lake Reservoir, where more line was typically paid out on the downrigger angling line than the shallow angling lines. In Lake Mille Lacs, however, the length of line paid out (and submerged in the lake during transect transits) was remarkably similar between the 2 gear types, yet the mean ensnarement rate was far greater for the shallow angling lines. We caution that the 2 lakes differ in many ways and that more research is needed to understand how other factors such as bathymetry and water clarity might influence ensnarement rate of *Bythotrephes* on angling gear.

Education and outreach

This study is the first to empirically characterize ensnarement rates of *Bythotrephes* on common types of angling gear. Our results reveal a variety of trends that we believe are relevant to education and outreach messaging around human-assisted dispersal of *Bythotrephes*. In particular, our results demonstrate that angling lines (monofilament, fluorocarbon, and braided) pose major risks for ensnaring large numbers of *Bythotrephes* when trolled in an infested lake.

We caution that turning our results into education and outreach recommendations should be done with consideration for what we measured (ensnarement rate) and what still remains unknown (risk of transfer of living individuals to another lake). Our study did not determine how likely *Bythotrephes* are to survive should they become ensnared and transported on gear. Survival during transport is a critical stage in the range expansion of any invasive species (Sinclair et al. 2020). To this end, we cannot lose sight of the fact that livewells and bait buckets, despite their lesser ensnarement rates measured here, could enhance survival of ensnared *Bythotrephes* if they remain wet for longer periods of time than angling lines.

Bythotrephes are likely to experience a wide range in survival rate depending on whether they remain wet. Research has shown that *Bythotrephes* resting eggs are vulnerable to drying and cannot survive exposure to dry conditions for 6 h or longer (Branstrator et al. 2013). While it is believed that the planktonic stages of zooplankton are far less tolerant of drying than their corresponding resting (dormant) egg stages, this has not yet been tested for *Bythotrephes*. Nonetheless, the absence of a protective carapace around the body of *Bythotrephes* would suggest that tolerance of the planktonic stage to drying is far less than for its resting egg, and thus likely less than 6 h. However, if ensnared individuals remain wet, the window of survival could be prolonged. For example, large masses of *Bythotrephes* clumped on angling line would likely provide a degree of protection against drying that could prolong survival during transfer out of water, particularly during humid or rainy conditions. Likewise, livewells and bait buckets that contain internal crevices that remain damp even after draining could provide safe microhabitats for *Bythotrephes* between lakes. This reinforces the importance of continuing to communicate the imperative to drain all water when leaving a lake. We suggest that wiping down internal crevices after draining would further help remove water and *Bythotrephes*.

In conclusion, our results demonstrate that trolled angling lines are highly susceptible to ensnarement of *Bythotrephes* and thus represent a high-risk pathway of dispersal for this invader. Nonetheless, decontamination of other equipment should not be overlooked. In addition to physical removal or draining water, approaches such as drying equipment surfaces for 6 h or longer (Branstrator et al. 2013) or exposure to lethal levels of heat or chemical disinfectant (e.g., Virkon) for prescribed periods (Branstrator et al. 2013, De Stasio et al. 2019) offer managers and citizens a range of options to decontaminate equipment.

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Authors' contributions

DKB, JDD, and VJB conceived the project. All authors developed the methodology and collected the data. DKB led the data analysis and writing. All authors contributed critically to the drafts and gave final approval for publication.

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