Notes

Discovery of an Undocumented Lake Sturgeon Spawning Site in the Headwaters of the Niagara River

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Abstract

Information about spawning fish is important to stock-assessment data needs (i.e., recruitment and fecundity) and management (i.e., habitat connectivity and protection). In Lake Erie, information about Lake Sturgeon *Acipenser fulvescens* early-life history is available for the Detroit River and Lake St. Clair system in the western basin, but fisheries biologists know comparatively little about Lake Sturgeon in the eastern basin. Although researchers have summarized historical spawning areas, no known natural Lake Sturgeon spawning site is described in Lake Erie proper. Researchers documented a remnant population of reproductively mature Lake Sturgeon near the headwaters of the Niagara River in eastern Lake Erie in 2011. Researchers hypothesized that a spawning site was likely in the immediate vicinity of the Niagara River headwaters near Buffalo Harbor, New York; however, its exact location was unknown. We attempted to locate spawning sites near the confluence of the Niagara River using egg traps at three potential spawning sites. We identified Lake Sturgeon eggs at one of these sites using morphological and genetic techniques. Lake Sturgeon eggs collected on one sampling trip began to emerge when placed in preservative, confirming that eggs deposited at this site are fertilized and viable, and that the area supports viable embryos. This discovery fills data gaps in the early-life history for this population, which has domestic and international management implications with respect to proposed recovery targets, stock assessment models, habitat remediation efforts, and status determinations of a protected species in a geographic region designated as an Area of Concern by the International Joint Commission.

Keywords: *Acipenser*; early-life history; egg traps; Lake Erie; Lake Sturgeon; spawning site; Niagara River

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Introduction

Lake Sturgeon *Acipenser fulvescens* are the largest and longest-lived freshwater fish endemic to North America, and have suffered precipitous population declines throughout their distribution (Scott and Crossman 1973; Pikitch et al. 2005). Detailed accounts of Lake Sturgeon declines in Lake Erie implicate the commercial fishery of the late 1800s to early 1900s (Koelz 1925). Population recovery failure in the following century has been linked to migratory barriers, changes in water quality, pollution (Rochard et al. 1990; Auer 1996), invasive species, and degradation of nearshore spawning and nursery environments (Koonce et al. 1996).
Additionally, the species’ life history characteristics of slow growth, delayed maturation, infrequent spawning periodicity, and a generally skewed sex ratio presumably exacerbated population declines and slowed recovery (Golder Associates Ltd. 2011). Contemporary recovery strategies are predicated on habitat remediation, reduction of legacy pollutants, elevated public awareness, and improved ecological function (IJC 2012; Lake Erie LaMP 2002; Golder Associates Ltd. 2011). However, important information gaps, particularly with respect to the early-life history of Lake Sturgeon, limit the efficiency and implementation of current recovery strategies.

While researchers have well documented detailed information pertaining to Lake Sturgeon life history in other regions of Lake Erie (McKinley et al. 1998; Hughes et al. 2011), information on the Lake Sturgeon population(s) of the eastern basin of Lake Erie is particularly limited. Spawning locations in the eastern basin are unknown and early-life history information is data deficient. In 2014, multiple agencies initiated a broad scope to quantitatively describe life history parameters of eastern Lake Erie Lake Sturgeon. The present study describes an ancillary goal to fill data gaps related to early-life history of eastern Lake Erie Lake Sturgeon by identifying one or more spawning sites at the headwaters of the Niagara River where sexually mature adult Lake Sturgeon are known to congregate annually during the spawning period. By describing the discovery of areas where we observed Lake Sturgeon egg deposition near the upper Niagara River, we fill data gaps emphasized in the New York State (NYSDEC 2017) and Ontario (Golder Associates Ltd. 2011) recovery plans for Lake Sturgeon. This provides baseline knowledge about Lake Sturgeon spawning locations where management agencies can focus habitat assessment and remediation efforts—elements that are emphasized in both recovery plans. Our spatial observations also provide explicit information about where researchers should direct survey efforts for eggs, larvae, and juveniles in the upper Niagara River. Lastly, this discovery serves as the first reported area of Lake Sturgeon egg deposition for the entire eastern basin of Lake Erie.

Lake Sturgeon in eastern Lake Erie have only been captured in an area southwest of Horseshoe Reef and the Black Rock Lock Canal Entrance Channel (Figure 1), locally known as the North Gap (Legard 2015) near the Buffalo Harbor. Unfortunately, knowledge gaps about the location of suitable Lake Sturgeon spawning and rearing habitat features near the headwaters of the Niagara River (see Golder Associates Ltd. 2011) narrow our understanding of potential habitat variables driving adult Lake Sturgeon aggregating behaviors. Documentation of spawning location is important for identifying, protecting, or improving Lake Sturgeon habitat. To date, researchers have identified no suitable spawning or rearing habitats in the headwaters to the Niagara River. In the present study, we describe a broadened research approach to detect Lake Sturgeon spawning areas in the headwaters of the Niagara River using egg traps to capture Lake Sturgeon eggs at several sites in the immediate vicinity of the adult capture site. We discuss the results in the context of recovery management implications and future research needs.

Figure 1. Map of study area: headwaters of the Niagara River and adult Lake Sturgeon Acipenser fulvescens capture site during the annual Lake Sturgeon spawning run in May and June of 2017. The spring-spawning Lake Sturgeon adult capture site from 2012–2017 encompassed by the polygon at (C). We chose three strata based on habitat characteristics consistent with Lake Sturgeon spawning preferences such as depths < 4m, gravel-dominated substrate, and relatively high velocity flows. Locations from north to south: Bird Island Reef (A), Middle Reef (B), and the North Gap break wall area (C) at the south end of the North Gap region. The circles indicate location of egg trap sets and the triangles indicate locations where egg traps contained Lake Sturgeon.
Study Area

The headwaters of the Niagara River are fed by eastern Lake Erie waters flowing north into a shallow outer harbor proximate to a lock system known as Black Rock Lock. The western extent belongs to Canada and the eastern, to the United States (Figure 1). The upper Niagara River is approximately 35 river kilometers upstream and south of Niagara Falls. The river feeds into the Niagara escarpment, over Niagara Falls, and through the Niagara Gorge, a geologic feature created by the gradual recession of the falls since the last ice age (Calkin and Brett 1978).

The Great Lakes Water Quality Agreement (US EPA 2015) identifies the Niagara River as an Area of Concern. This designation signifies that certain beneficial uses of the Niagara River have become impaired due to anthropogenic factors, most notably postindustrial waste with prolonged degradation times and destruction of habitat. The International Joint Commission identified the Niagara River as having 6 of the possible 14 Beneficial Use Impairments, including fish and wildlife habitat degradation and population loss, and reproductive impairments due to the deteriorated biological and physical environment (IJC 2012). Within the Niagara River Area of Concern, many contaminated sites occur along the eastern branch of the upper Niagara River extending from Niagara Falls and proceeding south along the lock system to the area known as South Gap in Lake Erie proper (IJC 2012). Hereafter, we refer to the study area as the headwaters of the Niagara River. This area is of particular importance from several perspectives: 1) the area supports an extant Lake Sturgeon population of unknown abundance and trend (LELSWG 2016; Legard 2015) that was historically referenced at the height of commercial exploitation (Koezl 1925); 2) the upper Niagara River region represents a high priority in the context of environmental habitat degradation, species ecology, and native species restoration (IJC 2012); 3) the area is an interface between limnic Lake Erie proper and shallow, fast-flowing, riverine waters—features consistent with Lake Sturgeon spawning preferences (Bruch and Binkowski 2002; Johnson et al. 2006); and 4) there is considerable international interest in the area as a shared connecting waterway between Lake Erie and Lake Ontario, and as such management decisions are subject to a collaborative process between the United States and Canada per existing ratified treaties (Root and Bryce 1910).

Methods

We sampled with egg traps at several sites in the headwaters of the Niagara River. We based site selection on published accounts of Lake Sturgeon spawning habitat preferences. Criteria are outlined by Johnson et al. (2006): shallow in depth (< 4 m) with substrate dominated by gravel in areas of high flow (> 0.4 m/s). We initially identified six potential spawning habitats in our study area that met most of these criteria based on professional judgement. Specifically, we looked for shallow areas (< 4 m) where passive boat drift was rapid relative to other areas investigated, though we did not quantitatively measure current velocity. We chose locations dominated by gravel substrate. We also considered the presence of reproductively mature Lake Sturgeon. Due to logistical limitations, mainly concern for the researchers’ safety in swifter current in the mainstem, we eliminated three candidate locations and were left with three sites occurring within 2 km downstream of the adult capture site near the North Gap. One of these sites, the North Gap break wall area (Figure 1), did not meet the depth or qualitative flow criteria but we retained it due to the prevalence of expressing, reproductively mature adults in the immediate vicinity. We used ArcMap 10.4.1 for Desktop (ESRI 2015) to generate polygons of our three sites using a bathymetry raster of the river confluence (NOAA 2017). These polygons corresponded to Bird Island Reef (221,745.93 m²), Middle Reef (84,904.98 m²), and the North Gap break wall area (11,815.21 m²; Figure 1).

We used standard furnace filter (HD Supply, 6.1 × 110 m) to construct egg traps secured to welded steel frames similar to the design of Nichols et al. (2003). We deployed our traps in groups of three connected by a polypropylene line (i.e., a “gang”), with each downstream end of the gang attached to a buoy (~ 6 kg buoyancy) by a stainless steel cable (6–15 m long depending on water depth). The upstream end attached to a 4.5-kg claw anchor. We deployed gangs when water temperature at depth reached 10°C prior to the observed Lake Sturgeon run in May when researchers typically observe and capture mature individuals at the North Gap area. We sampled with egg trap gangs for 6 wk, approximately the duration of the spawning run (based on observations in previous years). These seasonal parameters coincided with the documented spawning temperature preference between 9 and 21°C documented for the Winnebago system (Bruch and Binkowski 2002). Although we did not measure actual water velocities, we observed differences in passive boat drift at different sites during the vessel survey. Depth also differed among sites ranging from approximately 2 to 6 m. Substrate composition appeared to qualitatively differ among locations based on our professional judgement with sampled sites being dominated by gravel and cobble (3-cm) substrate.

We deployed and retrieved gangs of egg traps once a week at each site. Placement each week was haphazard at each site due to difficulties maneuvering sampling vessels into shallow, fast-moving waters. Deployment by wading was logistically infeasible and determined to be unsafe. The number of gangs that we deployed was roughly proportional to the area of identified habitat, (i.e., we deployed more gangs at larger sites and fewer at smaller sites). We deployed five gangs on Bird Island Reef, five gangs on Middle Reef, and two gangs near the North Gap break wall per week. This corresponded to weekly egg trap areas of 3.47 m² at Bird Island Reef and Middle Reef and 1.39 m² at the North Gap break wall per sampling week. Upon retrieval, we removed the furnace filter from frames, placed each filter in a separate plastic
189-L plastic bag, labeled, and affixed a new piece of furnace filter to each frame prior to redeployment. We examined the retrieved furnace filter material for the presence of eggs following collection. We removed all observed eggs with forceps and placed them in 15-mL falcon tubes with 95% non-denatured ethanol. We identified Lake Sturgeon eggs based on morphological traits (sensu Wang et al. 1985; Eckes et al. 2015). Of the traps from which we collected putative Lake Sturgeon eggs, we selected one to two eggs per trap for genetic species identification to validate morphological identification. To minimize the risk of external contamination and polymerase chain reaction (PCR) inhibition, we removed the egg membrane and extracted DNA from the inner contents of each egg using the Chelex method. We submerged the egg material in 190 mL of a solution containing 5% Chelex 100 resin beads and 2% proteinase K. After a 3-h incubation at 55°C, we heated the samples at 105°C for 8 min, and vortexed and centrifuged them. We removed the supernatant containing the DNA and used it directly in PCR.

We sequenced a 652-bp region of the mitochondrial cytochrome c oxidase subunit I (COI) gene. The COI gene is the basis for the Barcode of Life database, which contains sequence data to a wide variety of reference species. We amplified the 652-bp COI region using universal fish primers (Univ_Shi_F and Univ_Shi_R) designed by Shokralla et al. (2015). Each 25-μL PCR reaction contained 2 μL of the undiluted DNA extract, 4.5 μL PCR buffer (5X), 2.5 μL MgCl₂ (25 mM), 0.5 μL dNTPs (10 mM), 0.25 μL of each primer (10 μM), and 0.125 μL Taq polymerase (5 units/μL). The thermal profile consisted of an initial denaturation step of 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 54°C for 40 s, and 72°C for 1 min, and a final extension step of 72°C for 10 min. We then visualized the PCR products on a 2% agarose gel to confirm amplification success. We labeled PCR products using the BigDye Terminator version 3.1 Cycle Sequencing Kit (Applied Biosystems, Inc.) and bidirectionally sequenced them on an ABI 3130 capillary sequencer. We inspected chromatograms and assembled them into contigs in Sequencher version 4.5 (GeneCodes Corp.). We aligned the resulting sequence data against reference sequences in the National Center for Biotechnology Information database using the nucleotide Basic Local Alignment Search Tool for highly similar sequences (Altschul et al. 1990). Additionally, the sequences were aligned to the Barcode of Life Database, version 3, by searching the species-level barcode records (Ratnasingham and Hebert 2007). Once we confirmed morphological identification techniques using the resulting genetic sequence data, we paired Lake Sturgeon eggs to the gang, site, date, and weekly average water temperature to determine depositional trends and timing in relation to known Lake Sturgeon spawning preferences.

Results

The combined sampled strata area of Bird Island Reef, Middle Reef, and the North Gap break wall was 318,465.19 m². We set 67 gangs of egg traps between May 5 and June 7, 2017 (Figure 1). We set 27 at Bird Island Reef, 28 at Middle Reef, and 12 near the North Gap break wall. In total, we collected 2,728 eggs from furnace filter materials. We identified 86 eggs as Lake Sturgeon eggs, all originating from 12 gangs collected at the Bird Island Reef site (Data S1, Supplemental Material; Figure 1). Lake Sturgeon eggs collected at Bird Island Reef on June 1 contained emerging Lake Sturgeon larvae after we immersed them in the ethanol preservative, indicating that these eggs had been fertilized and were viable at the time of capture. We selected a total of 13 putative Lake Sturgeon eggs for genetic species identification, which spanned 12 different egg traps. We obtained COI sequences for all but one sample, which did not successfully amplify (Data S2, Supplemental Material). We recovered sequences at lengths of over 555 bp for 11 samples, and 403 bp for one additional sample. All sequences obtained from putative Lake Sturgeon eggs matched to Acipenser fulvescens with 100% identity in both the National Center for Biotechnology Information and Barcode of Life databases. We found the genetic distance between Lake Sturgeon and its closest relative, the Shortnose Sturgeon Acipenser brevirostrum, to be 2.09% at the COI gene region, based on the Barcode of Life database. Due to the high variability of COI, and the lack of other congeneric species in the area, it is not likely that the samples were misidentified. Collection trends of eggs from all species indicate that there were fewer eggs overall at the North Gap break wall than at either Middle Reef or Bird Island Reef (Table 1). Bird Island Reef had the greatest number of eggs deposited and was also the largest area surveyed. Across all sampling sites, we identified Lake Sturgeon eggs only at the Bird Island Reef site. Total Lake Sturgeon egg deposition at Bird Island Reef was low, though it varied dramatically by sampling week. Figure 2 shows two distinct peaks of Lake Sturgeon egg frequencies at sampling weeks 3 and 5, which corresponded with water temperatures of 11–14°C.

Discussion

Our discovery confirms that Lake Sturgeon are spawning at Bird Island Reef, which has direct implications for informing stock assessment metrics, management recovery goals, and protection initiatives. Future assessments of habitat quality and connectivity could

| Location                  | Sample size | Total eggs | Lake Sturgeon eggs |
|---------------------------|-------------|------------|--------------------|
| North Gap break wall      | 12          | 3          | 0                  |
| Bird Island Reef          | 27          | 2,004      | 86                 |
| Middle Reef               | 28          | 721        | 0                  |
also impact habitat remediation planning as well as
dredging activities as prescribed in the Remedial Action
Plan for the Niagara River Area of Concern in early
remediation phases (NYSDEC 2012). This is information is
particularly relevant if there is poor Lake Sturgeon access
to habitat or lack of connectivity following the egg and
larval drift periods. It is uncertain whether Bird Island
Reef represents a large contribution to the eastern Lake
Erie Lake Sturgeon population, but the proximity of reef
to the river confluence in an Area of Concern warrants
further investigation of this reef and immediate areas to
quantify available spawning habitat and address recruit-
ment bottlenecks if they exist. Index surveys for Lake
Sturgeon eggs, larvae, and juveniles along with habitat
assessment of possible rearing and nursery areas could
address this research need.

Although we observed some eggs at the North Gap
break wall, the area may be used less for spawning than
the other two sites. The area near the North Gap break
wall is deeper (mean depth ~ 5 m) relative to the other
two sites. It lacks the current velocity, spatial heteroge-
neity, and dominance of clean coarse gravel substrate of
both Bird Island Reef and Middle Reef; however, the
density of mature Lake Sturgeon near North Gap makes
the area relevant to spawning activity. While we have
consistently captured sexually mature adult Lake Stur-
geon at this site in the past, we propose that the area
may serve as a staging area prior to spawning,
particularly for males actively searching for females
(Bruch and Binkowski 2002).

Lake Sturgeon eggs on Bird Island Reef were identified
within the temperature range (9–16°C) reported for other
Lake Sturgeon populations in the Great Lakes (LaHaye et
al. 1992; Bruch and Binkowski 2002; Roseman et al. 2011).
Although we did not quantitatively measure current
velocity, we did observe, based on passive boat drift, that
both Middle Reef and Bird Island Reef were subject to
greater current velocity than the area adjacent to the
break wall at the North Gap. We acknowledge that
current velocity may differ within the water column, but
given the proximity of these sites to the river headwa-
ters, we were confident that current velocity does
increase near the river confluence where we found eggs.

Previous research from the Des Prairies and L’Assomp-
tion rivers has indicated that Lake Sturgeon prefer velocities between 0.1 and 1.09 m/s for spawning (LaHaye et al. 1992). It is likely that the velocities at Middle Reef and Bird Island Reef match this criterion based on our qualitative observations in these areas. Current velocity 1.7 km downstream of Bird Island Reef measures between 1.2 and 1.5 m/s with maximum of 3.7 m/s (INWC 2014). We also observed small cobbles at these sites, which provides ideal interstitial spaces suitable for Lake Sturgeon egg deposition, aeration, and protection (Bruch and Binkowski 2002; Roseman et al. 2011). We propose that adult Lake Sturgeon are using Bird Island Reef during the egg deposition period because we found Lake Sturgeon eggs at this site. Our observation of larval emergence when we submerged the eggs in preservative indicates that these eggs were fertilized and viable at least until the embryonic and larval periods. Future research in this habitat would determine the importance of Bird Island Reef to spawning and early-life history for the eastern Lake Erie Lake Sturgeon population(s).

Despite the habitat similarities between Bird Island Reef and Middle Reef, we only collected Lake Sturgeon eggs from Bird Island Reef. This is not to imply that Lake Sturgeon may not also use Middle Reef. We visually observed one adult Lake Sturgeon southwest of Bird Island Reef as the sampling vessel drifted downstream following egg trap deployment and recoveries at Middle Reef (though reproductive status of this individual was unknown). There could be a number of reasons that we did not observe eggs on Middle Reef. First, Bird Island Reef is closer to the headwaters of the Niagara River, which is presumably the preferable habitat. In the Wolf River System, Bruch and Binkowski (2002) noted that females preferred to spawn close to the shoreline. This observation would be spatially consistent with the geography of Bird Island Reef, which abuts the Black Rock Lock break wall at its eastern extent. By contrast, Middle Reef is somewhat distant from any shoreline structures, although the reef itself is similarly shallow. Middle Reef and Bird Island Reef may differ slightly in current velocity regime and therein substrate. Bird Island Reef, being more proximate to the confluence of the Niagara River, encompasses an area of higher current velocity (as described above). These quicker velocities not only provide increase aeration to eggs, but also provide cleaner substrates in some cases. This was evident in our egg trap sample collections. On almost all occasions when retrieving egg traps from Middle Reef compared to Bird Island Reef, a small layer of filamentous algae covered egg trap filter materials from Middle Reef. This differed from Bird Island Reef where egg traps were relatively clean of algae but did contain some Dreissena spp., mussel debris. There may be a higher risk of egg predation at Middle Reef as compared to Bird Island Reef. Caroffino et al. (2010) demonstrated egg loss variability among traps due to fine-scale environmental factors and predation. If environmental variables or maternal factors influence egg deposition time, emergence, or loss as observed by Duong et al. (2011) on the upper Black River, Michigan, the timing of our egg collection may be mismatched with spawning activity at Middle Reef.

In our study, we limited our observations to the portion of Bird Island Reef flanking the western side of the break wall. However, it is worth noting that the Bird Island Pier divides the reef. The eastern extent of Bird Island Reef is within the Black Rock Lock canal (refer to Figure 1). Prior to the construction of the pier, Bird Island Reef was several feet above the waterline. Workers removed much of the stone for the construction of the Erie Canal and by 1880 it had become a submerged reef (Wooster and Matthies 2008). Thus, the bathymetry of Bird Island Reef fundamentally changed in the 1800s. It is unclear whether the use of Bird Island Reef by spawning Lake Sturgeon has occurred in response to recent habitat deterioration of other proximate, preferred spawning habitat or if the area has been historically important to spawning Lake Sturgeon since the late 1800s. Given the life history and known migration behaviors, it is plausible that Lake Sturgeon would be attracted to Bird Island Reef if their natal spawning grounds became inaccessible or unsuitable. Regardless, Bird Island Reef does have significance to contemporary Lake Sturgeon reproduction.

Lake Sturgeon populations have demonstrated abrupt declines and slow recovery rates throughout the Great Lakes basin in the last 200 y (Pollock et al. 2015). Sweka et al. (2018) demonstrated that given the length of time since the Lake Erie commercial Lake Sturgeon fishery collapse in the late 1800s, Lake Sturgeon populations should have recovered to sustainable abundances (i.e., biomass at maximum sustainable yield), yet researchers have been unable to quantitatively show these recovery signals. Significant data deficiencies in the life history information further complicate the situation. The 2012 Remedial Action Plan for the Niagara River Area of Concern identifies several supportive measures to address data gaps including the need for ongoing collection life history information (NYSDEC 2012). Pollock et al. (2015) reviewed data collection needs for Lake Sturgeon populations in the Great Lakes basin, and also highlighted the importance of filling data gaps in the early-life stages to inform management restoration plans. The New York State Lake Sturgeon recovery plan presents several monitoring goals related to identification of spawning areas and the need for robust juvenile assessments (NYSDEC 2017). Our identification of a previously unknown Lake Sturgeon spawning area fills a life history data gap that may inform future egg and juvenile surveys.

The presence of Lake Sturgeon eggs in high-recreational-use areas in a prioritized Area of Concern underscores the implication for decision makers: how best to balance user group interests with the conservation of a listed species. Although the shallow bathymetry of Bird Island Reef and Middle Reef may offer some respite from recreational boat traffic, Lake Sturgeon conservation and recovery initiatives should include a plan for binational costewardship to reduce impacts on Lake Sturgeon reproductive potential (e.g., habitat loss, fragmentation, recruitment bottlenecks). Future research
including the design and implementation of robust surveys to quantify egg deposition, available spawning and rearing habitat, larval drift, and recruitment processes in the vicinity of Bird Island Reef would directly inform future recovery planning for eastern Lake Erie Lake Sturgeon.

Supplemental Material

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**Data S1.** Egg mat sampling data showing the number of Lake Sturgeon *Acipenser fulvescens* eggs collected in each gang of egg traps (set of three egg traps) deployed in the headwaters of the Niagara River, New York, during 2016.

Found at DOI: [http://dx.doi.org/10.3996/102017-JFWM-087.S1](http://dx.doi.org/10.3996/102017-JFWM-087.S1) (14 KB XLSX).

**Data S2.** Genetic sequence data for eggs collected from egg mat sampling in the headwater area of the Niagara River, New York, during 2016.

Found at DOI: [http://dx.doi.org/10.3996/102017-JFWM-087.S2](http://dx.doi.org/10.3996/102017-JFWM-087.S2) (24 KB TXT).

**Reference S1.** Koelz W. 1925. Fishing industry of the Great Lakes: appendix XI to the report of the U.S. Commissioner of Fisheries for 1925. Report 1001. Department of Commerce, Washington D.C.

Found at DOI: [http://dx.doi.org/10.3996/102017-JFWM-087.S3](http://dx.doi.org/10.3996/102017-JFWM-087.S3) (4040 KB PDF).

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Found at DOI: [http://dx.doi.org/10.3996/102017-JFWM-087.S4](http://dx.doi.org/10.3996/102017-JFWM-087.S4) (8120 KB PDF).

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