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ORIGINAL PAPER

Potential of passive acoustic recording for monitoring invasive species: freshwater drum invasion of the Hudson River via the New York canal system

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Abstract We conducted a preliminary passive acoustic survey of the occurrence of freshwater drum, *Aplodinotus grunniens*, in the New York State Canal System (NYSCS) to demonstrate the usefulness of underwater sound monitoring in invasive species studies. Data from known populations of freshwater drum in Dale Hollow Reservoir and J. Percy Priest Lake in Tennessee and Lake Champlain in New York were used to validate freshwater drum call characteristics. Similar to more well studied marine members of the Sciaenidae, freshwater drum calls are composed of highly variable trains of 1–119 knocks call^{-1} (mean = 25 knocks call^{-1}), a mean knock period of 33 knocks s^{-1}, mean peak frequency of 400 Hz, and mean duration of 0.8 s. The occurrence of drum chorus calls at many locations within the NYSCS indicates likely spawning throughout the system, and suggests the possibility that individuals have invaded the Hudson River from native populations of Lake Champlain, Lake Erie, and Lake Ontario. We point out that the species has been excluded from the east coast of North America throughout history by geographic barriers, and it would have been impossible for the species to gain entrance to the Hudson without the NYSCS, or direct introduction, and thus it is a true invasive which will likely have a dramatic impact on the Hudson River ecosystem. We suggest that freshwater drum most likely also invaded Lakes Oneida, Onondaga, Cayuga and Seneca through the NYSCS. We conclude that passive acoustic surveys are a highly effective non-invasive tool to monitor the distribution of soniferous invasive organisms in aquatic systems, and promise to be especially useful in documenting the future spread of freshwater drum in the Hudson River system.

Keywords Passive acoustics · Fish sounds · Invasive fishes · Freshwater drum

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Introduction

We first became interested in the potential of passive acoustics as a tool in studies of invasive organisms when we realized that an unknown drum-like fish sound we recorded in a prior study of the Hudson River (see Fig. 2d in Anderson et al. 2008) was likely produced by the freshwater drum, *Aplodinotus grunniens*, which had recently become established in the Hudson River (Mills et al. 1996; Daniels 2001; Strayer et al. 2004; Daniels et al. 2005). Passive acoustics is a powerful new tool to study the ecology of fishes (Rountree et al. 2006; Gannon 2008; Luczkovich et al. 2008). By examining spatial and temporal trends in sound production we can determine spatial and temporal patterns of species occurrence and activity patterns for soniferous fishes in a less invasive and more efficient manner than with conventional methods that require capture of fish. Because passive acoustics have been successfully used to document spatial and temporal distribution of marine species of drum (see review in Rountree et al. 2006), we recognized that passive acoustic monitoring could be an important tool to study the spread of the invasive freshwater drum population in the Hudson River system. However, to our knowledge passive acoustics monitoring of underwater sounds has never before been applied in the study of invasive freshwater or marine species. Further, although freshwater drum are well known to produce sounds as part of their courtship behavior (Rafinesque 1820; Daiber 1950; Trautman 1957; Schneider and Hasler 1960), and in fact Rafinesque (1820) assigned the specific name ‘grunniens’, meaning “grunting”, because of this behavior, acoustic characteristics of the species have only been described in limited detail by Schneider and Hasler (1960). Therefore, digital recordings of their sounds were not available to validate freshwater drum sounds. Consequently, our attempts to get funding for a passive acoustic study of the Hudson River invasion were met with skepticism by local, state and federal agencies.

The freshwater drum has the widest distribution of any New World freshwater fish occurring from Central America to the Hudson Bay, however they have been historically excluded from the entire east coast by geographic barriers (Barney 1926; Lee et al. 1980). Native populations in New York are known from Lake Champlain, Lake Erie, Lake Ontario, and perhaps the Finger Lakes (Barney 1926; Lee et al. 1980; Smith 1985; Carlson et al. 2016). They are thought to prefer deep water and slow currents, but tolerate high turbidity well (Trautman 1957; Pflieger 1975). However, Daiber (1950) concluded that freshwater drum in Lake Erie require shallow areas of lakes with nearby deep water. Although we are not aware of any studies that quantify the salinity tolerance of freshwater drum, Myers (1949) suggested that most freshwater fish of marine origin probably “all retain a high salt-tolerance”, and individuals are occasionally collected in low salinity (<6ppt) estuaries in Louisiana (Perret and Caillouet 1974). The species is primarily a bottom feeder on insect larvae, crustaceans, fish, clams and snails (see review in Becker 1983). Adults and juveniles move into the shallows at night to feed along the shoreline (Rypel and Mitchell 2007). Spawning occurs from May through August at water temperatures of 19–22 °C. They are thought to spawn in open water (Pflieger 1975). Females lay around 600,000 pelagic eggs which are 1.3–1.6 mm in diameter and positively buoyant (Davis 1959; Swedberg and Walburg 1970). The freshwater drum is a moderately large fish reaching a size of up to 18 kg, although it may have reached much larger sizes historically (see review in Becker 1983; the International Game Fish Association records are 95 cm and 24.7 kg). Freshwater drum are a prized game and food fish in many areas of their range, but are not well regarded by anglers in the New York area.

The Erie Canal currently runs 545 km from Lake Erie to the Hudson River, while the Champlain canal runs 96 km from Lake Champlain to the Hudson River. However, it should be noted that most of the approximately 300 km length of the east Erie Canal (from Oneida Lake east) consists of the canalized Mohawk River tributary of the Hudson River. Major lakes associated with the Erie Canal include the Finger Lakes, Oneida Lake, and Onondaga Lake. The Hudson River itself runs 507 km from its source in Lake Tear of the Clouds in the Adirondacks to its mouth at the tip of Manhattan. Tidal freshwater reaches occur from Hudson River Mile (HRM) 150 (241 km) at Troy to approximately HRM 60 (96 km) at Newburgh Bay. Home to more than 200 species of fish, the Hudson serves as a nursery ground for such important fish as sturgeon, striped bass and American shad.

Although freshwater drum have not yet had a significant impact on the Hudson River (Mills et al. 1996), this is likely to change as its distribution inevitably expands and its abundance continues to increase. In the last 20 years the Hudson River drum population has begun to expand south into the tidal Hudson (Daniels 2001; Daniels et al. 2005; Carlson et al. 2016). Within the Hudson River, freshwater drum are now regularly reported as captured in crab pots, gill nets and by anglers north of the Hudson Highlands (Tom Lake, Hudson River Almanac, May 2006, http://www.dec.ny.gov/lands/26150). Two notable reports suggesting that the species is well established in the tidal Hudson are of a 51 cm adult caught 3 September 2006 in Coxsackie, NY at HRM 124 (200 km), and an 8.4 kg adult caught well below the salt front at Croton Point (HRM 34, 55 km) on 12 May 2004. In addition, larval abundance has increased dramatically in the Long River Ichthyoplankton survey (Hudson Valley Generating Companies) and by 2005 had become the 13th most abundant species, indicating the presence of an established and expanding spawning population. Despite these strong warning signs, the invasion of the freshwater drum appears to have attracted little scientific interest other than as a potential predator of the invasive zebra mussel, *Dreissena polymorpha*, (French 1993; French and Love 1995; Morrison et al. 1997; Watzin et al. 2008) even though the Hudson River is well suited to the species which has the potential to become a dominant component of the fish assemblage and significantly impact the trophic structure of the system.

Although it is assumed that freshwater drum gained access to the Hudson River through the New York State Canal System (NYSCS) as a result of recent changes to the structure and management of the canals (Mills et al. 1996; Daniels 2001; Strayer et al. 2004; Daniels et al. 2005; Carlson et al. 2016), little is known about when and how this occurred. Just as importantly, how the canals might have affected the distribution of freshwater drum into other water bodies in the region is uncertain. We suggest, therefore, that a comprehensive survey of the distribution of freshwater drum throughout the region influenced by the NYSCS is needed to help identify both native and introduced populations and how they are spreading through the system.

The purpose of this preliminary study was to determine if passive acoustics could be used as a tool to document the current distribution of freshwater drum within the NYSCS. Detection of a drum call at a location was considered absolute proof that at least one drum was present within the local detection range, but a lack of drum calls provides no information on the presence or absence of the species. However, because freshwater drum sounds had not previously been well studied, we first had to obtain a sufficient description of drum sound characteristics to be confident of their identification. We therefore opportunistically obtained acoustic data of freshwater drum from known native populations to document drum call characteristics, but make no attempt to conduct a statistical comparison among geographic areas. We then conducted two preliminary passive acoustic surveys of selected sites within the NYSCS to document the presence of freshwater drum sounds in the system.

Materials and methods

Recordings from our previous passive acoustic study of the Hudson River (Anderson et al. 2008) were reexamined to obtain suspected freshwater drum sounds for comparison with new recordings from known population areas and from selected sites within the NYSCS (Fig. 1; Table 1). The upper Hudson River site where the drum-like sounds were recorded was located in the Tivoli Bay National Estuarine Research Reserve (NERR) at Red Hook, New York near HRM 95 (123 km). Sampling methods are described in detail elsewhere (Anderson et al. 2008), but briefly a Nomad Jukebox® (Creative Laboratories, LTD) digital recorder was used to capture sounds at a 11 kHz sample rate (16 bit) from a HTI-96-MIN hydrophone (High Tech Industries, Gulfport, MS; sensitivity: Sensitivity −165 dB re: 1 V/μPa, frequency response: 2 Hz to 30 kHz). Suspected freshwater drum sounds were obtained from an 11 h recording starting at 1532 h on 2 September, and an 8 h 45 m recording starting at 1730 h on 9 September, 2003.

Data from a known population of freshwater drum were obtained opportunistically near Nashville, Tennessee. An experienced fishing guide was hired to take us to known freshwater drum "hot-spots" in Dale Hollow Reservoir the night of September 1–2, 2009 (Table 1). Just before sunset we deployed a variable (dial) gain Aquarian (Aquarian Audio Products, Anacortes, WA, USA) hydrophone in the Mitchell Creek area of the reservoir immediately over an aggregation of large fish presumed to be freshwater drum. Acoustic data were captured at 48 kHz, 24-bit, directly to a laptop computer using SpectraPro 332 Professional Sound Analysis software (Sound Technology, Inc.). After recording from the aggregation over a 3 h period, we recorded from five other locations in the reservoir. Further data on freshwater drum were collected from shore and a marina dock in the J. Percy Priest Lake on 4 September 2009 (Table 1).

To examine freshwater drum calls within the NYSCS we conducted a roving survey on July

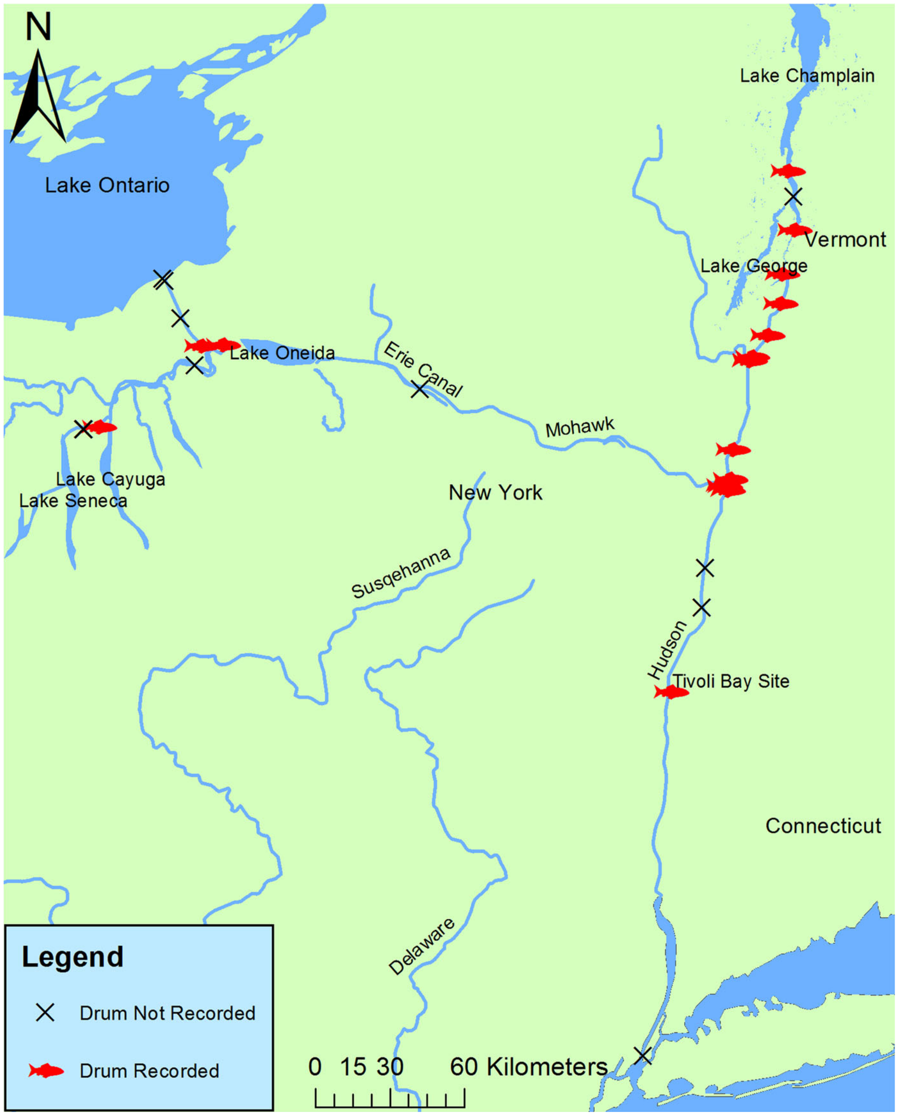

Fig. 1 Freshwater drum sample locations within the New York State Canal System (*fish symbols* indicate locations where drum sounds were observed)

14–16 2010 from the shoreline of Lake Champlain (4 sites), along the Champlain canal (8 sites), the Hudson River between Troy and Stuyvesant, New York (3 sites), and the adjacent Erie Canal (2 sites). We listened for the presence of freshwater drum sounds using the Aquarian hydrophone and amplified headphones for a minimum of 10 min at each site, but discontinued monitoring as soon as 3 min if drum calls were detected (they were sometimes detected immediately). Recordings with the HTI-96-MIN hydrophone of up to 175 min were only made at selected sites (3 within Lake Champlain and 2 within the Champlain canal) where drum were heard (Table 1) in order to obtain data for acoustic description of drum sounds. Acoustic data were captured at 48 kHz with a MOTU Ultralite, 24-bit, 96 kHz, bus-powered firewire audio interface to a laptop computer using SpectraPro. An omnidirectional microphone was used to record voice notes and aerial sounds to a second channel.

A second roving survey was conducted opportunistically on 1–2 August 2013 (field photographs available as Online Resource 1–3). Monitoring was conducted in Lake Ontario near the entrance to the Oswego canal (1 site), the Oswego canal (3 sites), Seneca canal (3 sites), and Erie canal (3 sites). Because

Table 1 Sample locations and monitoring duration for all passive acoustic surveys during this study

Area	Location	Waypoint	Latitude and longitude	Date	Monitored duration (min)	Drum sounds present
New York State Barge Canal Survey						
Lake Champlain	Crown point	NY14	N43°56.816′ W73°24.733′	14 July 2010	175 r	Yes
Lake Champlain	Ft. Ticonderoga Ferry	NY15	N43°51.233′ W73°23.116′	15 July 2010	10	No
Lake Champlain	Putnam Station	NY17	N43°44.092′ W73°22.438′	15 July 2010	28 r	Yes
Lake Champlain	South Bay Fishing Pier	NY18	N43°34.389′ W73°25.886′	15 July 2010	60 r	Yes
Champlain Canal	Lock No. 11	NY19	N43°28.061′ W73°26.133′	15 July 2010	6	Yes
Champlain Canal	Lock No. 9	NY20	N43°21.070′ W73°29.766′	15 July 2010	7	Yes
Champlain Canal	Lock No. 8	NY21	N43°16.322′ W73°34.156′	15 July 2010	15	Yes
Champlain Canal	Lock No. 7	NY22	N43°15.417′ W73°35.019′	15 July 2010	42 r	Yes
Champlain Canal	Lock No. 4	NY23	N42°55.961′ W73°39.236′	16 July 2010	26	Yes
Champlain Canal	Lock No. 1	NY24	N42°49.528′ W73°39.903′	16 July 2010	28	Yes
Champlain Canal	Lock No. 1b	NY25	N42°49.389′ W73°39.851′	16 July 2010	10	Yes
Hudson River	Troy, NY	NY26	N42°47.098′ W73°40.460′	16 July 2010	6	Yes
Erie Canal	Erie Lock No. 5	NY27	N42°48.135′ W73°41.832′	16 July 2010	10	Yes
Erie Canal	Waterford Park near Lock No. 5	NY28	N42°47.951′ W73°41.299′	16 July 2010	3	Yes
Hudson River	Schodack Island State Park	NY29	N42°29.987′ W73°46.601′	16 July 2010	27	No
Hudson River	Stuyvesant, NY	NY30	N42°21.243′ W73°47.342′	16 July 2010	25	No
Champlain Canal	Lock No. 7 entrance by bridge	NY31	N43°15.516′ W73°34.872′	16 July 2010	60 r	Yes
Seneca Canal	Lock No. 4, Waterloo, NY	ECC4	N42°54.060′ W76°51.889′	1 August 2013	6 r	No
Seneca Canal	Lock No. 4b, Waterloo, NY	ECC4b	N42°54.066′ W76°51.979′	1 August 2013	5 r	No
Seneca Canal	Lock No. 3, Seneca Falls, NY	ECS2	N42°54.862′ W76°47.278′	1 August 2013	9 r	Yes
Erie Canal	Lock No. 24, Baldwinville, NY	EC3	N43°09.348′ W76°20.024′	1 August 2013	5 r	No
Oswego Canal	Lock No. 8, Oswego, NY	EO8	N43°27.310′ W76°30.465′	1 August 2013	5 r	No
Lake Ontario	Oswego, NY near Oswego Lock No. 1	EC01	N43°27.799′ W76°31.127′	2 August 2013	5 r	No
Oswego Canal	Lock No. 3b, Futon, NY	EC03b	N43°19.410′ W76°25.091′	2 August 2013	5 r	No
Oswego Canal	Lock No 1. Phoenix, NY	EC04	N43°13.841′ W76 18.307′	2 August 2013	5 r	Yes
Erie Canal	Lock No. 23, Brewerton, NY	EC23	N43°14.302′ W76°11.843′	2 August 2013	6 r	Yes
Erie Canal	Utica, NY	EC05	N43°06.676′ W75°12.878′	2 August 2013	5 r	No
Total	27 sites				594	63% present

Table 1 continued

Area	Location	Waypoint	Latitude and longitude	Date	Monitored duration (min)	Drum sounds present
Tennessee Survey						
Dale Hollow Reservoir	Mitchell Creek site 1	DH174	N36°30.797′ W85°22.458′	1 September 2009	180 r	Yes
Dale Hollow Reservoir	Mitchell Creek site 2	DH175	N36°30.718′ W85°22.331′	1 September 2009	88 r	Yes
Dale Hollow Reservoir	South Fork Kyle Branch	DH176	N36°31.373′ W85°25.242′	1 September 2009	44 r	No
Dale Hollow Reservoir	North Fork Kyle Branch	DH177	N36°31.916′ W85°25.213′	1 September 2009	25 r	Yes
Dale Hollow Reservoir	Pleasant Grove site 1	DH178	N36°31.952′ W85°25.607′	2 September 2009	16 r	Yes
Dale Hollow Reservoir	Pleasant Grove site 2	DH179	N36°32.011′ W85°25.586′	2 September 2009	3 r	No
J. Percy Priest Lake	Visitor Center, Nashville, TN	PP180	N36°09.091′ W86°37.181′	4 September 2009	26 r	Yes
J. Percy Priest Lake	Elm Hill Marina, Nashville, TN	PP181	N36°07.963′ W86°37.265′	4 September 2009	430 r	Yes
Total	8 sites				632	75% present
Previous Hudson River Survey (Anderson et al. 2008)						
Hudson River	Pier 26, New York City, NY	HRM2	N40°43.28′ W74°00.78′	11 July to 9 August 2003	6225 r	No
Hudson River	Tivoli Bay, Red Hook, NY	HRM95	N42°02.883′ W73°55.502′	2-9 September 2003	1485 r	Yes
Total	2 sites				7710	

The presence of freshwater drum as indicated by the occurrence of one or more call is designated by the "yes" in the drum sounds column. Absence of drum sounds are indicated by a "no" which provides no information on the true presence or absence of the species at that location and time. Locations where sounds were also recorded are indicated by an "r" in the monitored duration column of time constraints minimum monitoring time was reduced to 5 min. Sounds were monitored in real time with amplified headphones while simultaneously recording all data with a SQ26-H1 recorder system with a SQ26-08 Hydrophone (Sensitivity = −169.00 re. 1 V/μPa rms) and total system sensitivity of −152.66 dB, re: 100% full digital scale (Cetacean Research Technology, Seattle, WA). Voice notes and ambient aerial sounds were recorded to a second channel from a high definition omnidirectional measurement microphone (frequency response 5 Hz to 30 kHz +1/−3 dB, model M30BX, Earthworks, Inc., Milford, NH).

Post-processing of signals was conducted by listening to all recordings in their entirety while simultaneously viewing the spectrogram and waveform with Raven Pro 1.5 acoustic software (Bioacoustics Research Program 2014) to locate freshwater drum sounds. Sounds were played with the spectrogram zoomed to 0–2000 Hz and a 15 s time display. Spectrogram parameters were set at 1024 point Hann windowed FFTs with 50% overlap. Each drum sound detected was marked with a selection box drawn around its upper and lower frequency boundary and beginning and start times in the spectrogram view. Counts of the number of knocks in each call were made in the waveform view after applying a band pass filter between 100 and 1500 Hz, and the value entered in as a data annotation. Additionally, to obtain accurate temporal data, we adjusted the time boundaries of each selection after filtering and zooming into the waveform to find the start and end of the first and last knock in the call, respectively. The Raven software then automatically calculated basic acoustic parameters of the selected call such as duration and peak frequency (Charif et al. 2010; Table 2), and output data in a tab delineated text file, including any annotated fields (e.g., sound identification and number of knocks). The resulting data set was edited to calculate the knock rate (call duration/number of knocks) and knock period (number of knocks/duration) for each call. Due to the high variation in call parameters within individual recordings, observed differences in calls at different times of the day, and to the limited nature of our non-synoptic data collections, no attempt was made to make geographic or temporal comparisons in call characteristics.

Results

In addition to recording sounds from known populations of freshwater drum, we were able to positively confirm that the drum-like calls were produced by the freshwater drum when a fisherman in a passing boat captured an adult drum during our recording at the South Bay Fishing Pier in Lake Champlain. Sounds characteristics were highly variable within individual recordings and overlapped broadly among sampling locations (Table 2; Fig. 2). A total of 563 drum calls were detected in all recordings combined, but only 301 samples had sufficient signal strength to accurately count knocks (Table 2). Calls consisted of trains of 1–119 knocks (mean 25 knocks/call, with a mean knock rate and period of 33 knocks/s and 0.033 s/knock, respectively, Table 2). Each knock consists of a variable number of pulses (not quantified, Fig. 3). For the 301 isolated calls that could be measured, peak frequency ranged from 188 to 1266 Hz and averaged 400 Hz (Table 2). Low frequency ranged from 41 to 819 Hz and averaged 217 Hz, while high frequency ranged from 330 to 1987 Hz and averaged 844 Hz. Call duration ranged from 0.016 to 4.625 s and averaged 0.84 s (Table 2). Although call parameters varied among locations, we do not report statistical test results because we feel any real location differences are masked by strong temporal (seasonal and time of day) differences and likely fish size class differences in call characteristics which were not controlled for.

Although not quantified, during the day and late evening hours, calls tended to be isolated long-duration disturbance calls (e.g., Fig. 2b, c, audio clips available as Online Resource 5,6). In contrast calls tended to be much shorter during evening chorus periods (e.g., Fig. 2a, audio clip available as Online Resource 4). As the chorus progressed towards sunset, calls became so numerous that they overlap too broadly to allow measurement of individual call characteristics, but a wide variation in peak frequencies is evident in spectrograms of the chorus (e.g., Fig. 4, audio clip available as Online Resource 7).

Despite the limited sampling effort, drum sounds were detected at 17 of 27 sites (63%) visited during the roving surveys including 13 of the 19 canal sites (68%, Table 1, Fig. 1). Specifically, 8 of 8 (100%) Champlain canal, 3 of 5 (60%) Erie Canal, 1 of 3 (33%) Seneca

Table 2 Freshwater drum call characteristics by location (mean and standard error of the mean)

Variable	Dale Hollow Reservoir	Percy Priest Lake	Tivoli Bay	Lake Champlain	Fort Edwards	All
Low frequency (Hz)	150 (13)	170 (5)	176 (18)	368 (10)	249 (7)	217 (7)
Fifth percentile frequency (Hz)	256 (12)	243 (4)	237 (21)	432 (9)	316 (7)	296 (6)
First quartile frequency (Hz)	301 (12)	308 (4)	347 (21)	502 (8)	367 (7)	356 (6)
Peak frequency (Hz)	327 (15)	353 (10)	380 (25)	563 (17)	422 (11)	400 (8)
Center frequency (Hz)	329 (13)	364 (4)	414 (22)	578 (8)	413 (7)	405 (7)
Third quartile frequency (Hz)	367 (14)	430 (5)	505 (27)	663 (10)	480 (8)	468 (8)
95th percentile frequency (Hz)	443 (17)	597 (13)	739 (30)	796 (13)	604 (14)	597 (10)
High frequency (Hz)	787 (39)	726 (22)	1228 (38)	881 (21)	829 (28)	844 (17)
Interquartile bandwidth (Hz)	66 (3)	122 (5)	158 (15)	161 (10)	112 (5)	112 (3)
90% bandwidth (Hz)	187 (9)	354 (13)	503 (26)	364 (15)	288 (13)	301 (8)
Bandwidth (Hz)	637 (38)	556 (24)	1051 (41)	512 (26)	580 (29)	626 (18)
Interquartile duration (ms)	223 (11)	483 (74)	438 (67)	489 (54)	334 (8)	360 (18)
90% duration (ms)	449 (21)	884 (130)	916 (133)	972 (95)	565 (16)	682 (33)
Duration (ms)	566 (25)	1020 (150)	1073 (158)	1160 (114)	632 (19)	804 (38)
Energy (dB)	163 (0.7)	66 (0.9)	86 (1.7)	88 (1.1)	97 (0.8)	109 (2.2)
Aggregate entropy (bits)	2.19 (0.04)	3.12 (0.04)	5.20 (0.15)	3.11 (0.05)	2.71 (0.05)	2.92 (0.05)
Average entropy (bits)	2.03 (0.03)	2.86 (0.04)	5.09 (0.12)	2.80 (0.04)	2.41 (0.04)	2.68 (0.05)
Number of knocks per call	20 (1)	26 (4)	22 (4)	33 (3)	26 (1)	25 (1)
Knock rate (knocks/s)	36.3 (0.4)	24.3 (0.5)	23.0 (2.1)	29.7 (0.8)	41.5 (0.6)	33.4 (0.5)
Knock period (ms/knock)	28 (<1)	42 (1)	50 (3)	35 (1)	25 (<1)	33 (1)
Sample size (N)	92	52	28	48	81	301

Measurements were made according to Charif et al. (2010) with spectrogram parameters set at 1024 point Hann windowed FFTs with 50% overlap

canal, and 1 of 3 (33%) Oswego canal sites, respectively. Drum sounds were heard at 3 of 4 (75%), 0 of 1 (0%), and 1 of 3 (33%) locations for Lake Champlain, Lake Ontario, and the Hudson River, respectively.

Discussion

Sound characteristics

Qualitatively, there is no doubt that the drum sounds recorded in the Hudson River and NYSCS were the same as those recorded from native populations. We have conducted extensive passive acoustic surveys among many types of freshwater habitats throughout the New England area from Maine to New York including the Connecticut, Kennebec, Merrimack, Presumpscot and Saco River systems, and nothing similar to a drum call is found in any other freshwater location in the region (Rountree unpublished data). In fact, we expect that freshwater drum are by far the dominant biological contributors to the underwater soundscape throughout their range, with few other organisms producing sounds of similar magnitude of the drum chorus. The only sounds similar to the freshwater drum are found in marine sciaenids (see below) and the striped cusk-eel (*Ophidion marginatum*, an ophidiid) which enters the lower Hudson River (Anderson et al. 2008). Further, our data on freshwater drum call characteristics agree with data from the Lake Winnebago, Wisconsin population (Schneider and Hassler 1960) where similarly high variations were observed. They reported peak frequencies in the range of 260–400 Hz (compare with our peak frequency ranges of 327–563 Hz, Table 2), with energy between 150 and 2000 Hz (ours between 41 and 1987 Hz), call durations between 0.2 and 5 s (ours from 0.016 to 4.625 s), and knock periods (their pulse period) of 0.0365–0.0602 s (compared to our mean knock period of 0.033 s). Unfortunately, they report

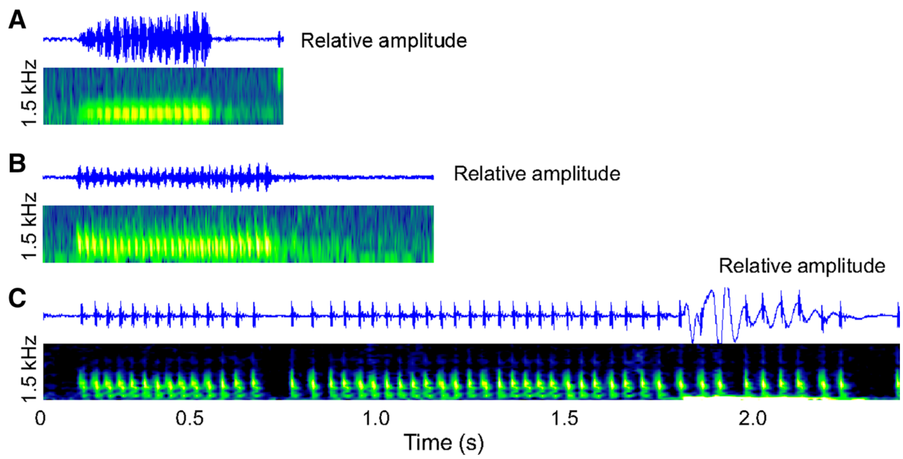

Fig. 2 Examples of highly variable freshwater drum calls (not a reflection of location differences). **a** Isolated 0.7 s call during drum chorus in Dale Hollow Reservoir, Tennessee. **b** Isolated 1.6 s disturbance/agonistic call from Champlain Lock No. C7 in Fort Edwards, New York. **c** Isolated 2.2 s disturbance/agonistic call from Tivoli Bay on the Hudson River. All graphs are on the same temporal scale. *Top figures* in each *panel* represents a relative amplitude oscillogram of the waveform, which are not directly comparable among samples. The amplitude anomaly just before 2 s in the bottom panel is due to a low frequency (peak about 40 Hz) noise artifact. *Bottom figures* are spectrograms showing the lower 0–1.5 kHz frequency of the recording. *Brighter colors* indicate higher amplitudes. Spectrogram parameters: 256 point Hann windowed FFTs with 50% overlap. Audio clips available as Online Resource 4–6

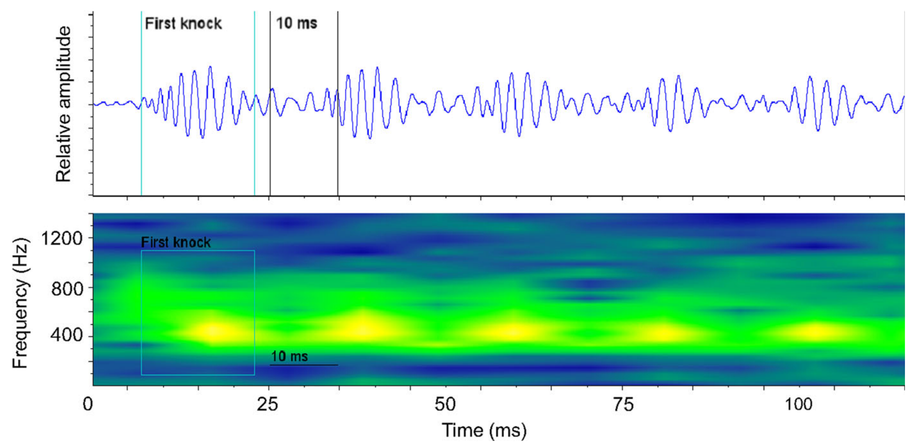

Fig. 3 Example of a freshwater drum call expanded to show the variable pulse number of each component knock. *Top* relative amplitude oscillogram. *Vertical lines* encompass the first knock, and a 10 ms interval. *Bottom* spectrogram of the same signal. The *box* encloses the start and end time, as well as the upper and lower frequency boundaries of the first knock. *Brighter colors* indicate higher amplitudes. Spectrogram parameters: 1024 point Hann windowed FFTs with 50% overlap, 100–1500 Hz bandpass filter

only qualitative estimates of these parameters and do not indicate sample sizes, or provide parameter statistics.

The high variation in sound characteristics observed for freshwater drum is typical of other sciaenids where call parameters are affected by environmental conditions such as temperature, fish size, and associated call behavior (Connaughton et al. 2000; Locascio and Mann 2008; Tellechea et al. 2010; 2011; Ruiz-Blais et al. 2014). Our qualitative observations of differences between calls at sunset and other times of the day are consistent with observations of disturbance and chorus calling in other sciaenids (e.g., Tellechea et al. 2010). During the day and late evening hours, calls occur irregularly as a result of disturbance or agonistic interactions, while calls become short and

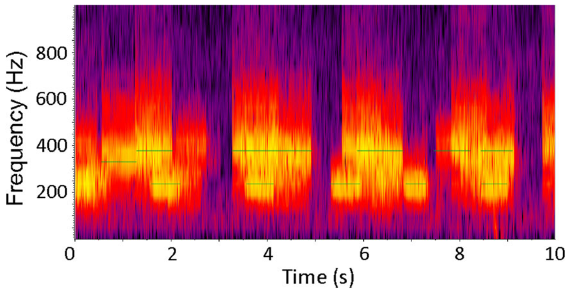

Fig. 4 Example of the spectrogram for a 10 s sequence of freshwater drum chorus calls recorded at the Seneca Canal Lock 3 (spectrogram parameters:1024 point Hann windowed FFTs with 50% overlap). *Horizontal lines* mark the peak frequency of individual calls that vary from 274 to 374 Hz. Audio clip available as Online Resource 7

repetitive during the sunset chorus period. It is important to point out that the high variation in drum sound characteristics observed in this study cannot be simply attributed to environmental effects, as variation within short recordings is greater than expected from environmental effects alone. For example, peak frequency varies by 100 Hz, and durations by as much as 200% in the 10 s recording shown in Fig. 4, and likely reflects repeated calling of two or three different sized individuals. However, such variation can be valuable as it can be used to obtain information of fish size structure and behavior patterns based on passive acoustic data (Luczkovich et al. 2008).

Although there are undoubtedly statistical differences among locations for several of the acoustic parameters measured (Table 2) we feel they most likely result from a small sample size, non-synoptic sampling, high intraspecific variation, fish size variation, and differences in water temperature and other environmental conditions. Therefore, the results from formal statistical comparisons among locations would be misleading. Our study comprised the most rigorous examination of freshwater drum call characteristics to date, but a much larger sample size would be required to examine the effects of time of day, season, location, gender and size class on call characteristics.

Effectiveness of the passive acoustic survey

The passive acoustics survey was far more successful than we expected given our limited sampling effort, and illustrates how powerful the method can be for soniferous organisms. We reiterate, that although the occurrence of drum calls unequivocally demonstrates the presence of drum at a location and time, the absence of calls does not indicate absence of the species. It is important to point out that the presence of chorus activity strongly suggests spawning directly within the canals. Further, in some cases we observed calling right inside the locks themselves, suggesting they do not impede freshwater drum movements. The fact that freshwater drum are present, and most likely spawn, throughout the canal system, suggests that not only do the canals likely serve as vectors for the movement of drum from native populations in Lake Champlain, Lake Erie and Lake Ontario to the Hudson River, but also serve as a seasonal spawning ground. We have demonstrated for the first time that passive acoustics can be used to monitor and track soniferous invasive fishes and other organisms. That result has broad applicability to many other freshwater and marine systems.

How did freshwater drum get into the Hudson River?

Although Barney (1926) first predicted that freshwater drum would invade the Hudson River from Lake Erie, Lake Ontario and Lake Champlain through the canals, currently it is believed that the freshwater drum migrated from the Great Lakes through the NYSCS after first becoming established in the Mohawk River sometime in the last 30–40 years (Mills et al. 1996; Daniels 2001; Strayer et al. 2004; Daniels et al. 2005). The possibility of invasion through the Champlain canal is understood, but does not get much attention. Alternatively, Carlson et al. (2016) suggest some possibility of invasion from salt tolerant individuals that “migrated along the coast from more southern populations.” We dismiss that possibility as there are no known populations of freshwater drum on the entire Atlantic seaboard east of the Appalachians (Lee et al. 1980). Further the species is not likely to be able to survive in high salinity waters for any length of time. However, without actual data on the salinity tolerance of the species, the ability of freshwater drum to expand from the Hudson River into other watersheds on the US east coast cannot be ruled out.

As outlined in detail by Smith (1985) and Daniels (2001), the New York canal system was completed in 1825. The Champlain Canal connecting Lake Champlain with the Hudson River was the first section to be completed and opened in 1819. The Champlain canal thus linked the Hudson River to the St. Lawrence River and to the native drum population in Lake Champlain. The main trunk of the Erie Canal was completed in 1825 and linked the Hudson River to Lake Erie. As Daniels (2001) describes, however, these early canals were largely constructed as shallow ditches (1.2 m deep) that often avoided natural waterways including Oneida Lake. We agree with his assessment that these earlier canals are not the most convincing vectors of fish invasion of the Hudson River and suggest they were probably particularly poor conduits for the freshwater drum, which prefers deep water.

However, the canal system was greatly modified and redesigned in 1918 to take advantage of natural waterways as much as possible. Rivers such as the Mohawk were channelized and lakes such as Oneida Lake were incorporated into the system. Today the NYSCS is a far better potential vector of fish movements due to its increased depth (minimum 3.7 m) and width, reduced number of locks, and use of channelized rivers and lakes (Daniels 2001). Dramatic reduction in commercial shipping in the NYSCS in recent decades, for example from 250,000 tons in 1988 to 800 tons in 2004 for the Champlain canal (Malchoff et al. 2005), may also have had an influence. Large drum year classes in Oneida Lake in the 1970 s appear to be at least partly a response to warm years (Hall and Rudstam 1999) and may have precipitated invasion into the Hudson River at that time.

Our observations of freshwater calls throughout the Champlain Canal, suggests that invasion from the Champlain Lake population may be more important than previously assumed. One fisherman we interviewed during the Champlain Canal survey stated that he had been catching drum there since the early 1990 s. In addition, it is highly likely that freshwater drum spawn directly in the canals, as evidenced by chorus activity, suggesting that eggs and larvae are likely transported through the NYSCS. Because the Champlain canal is shut down and the locks drained each fall, fish in the canals are necessarily migratory. It is also possible that annual draining of the canal may have facilitated movement of drum, and perhaps "trapped" drum in the Hudson River.

However, as Daniels (2001) argues, assumptions regarding the role of the canals in regional expansion of fishes like the freshwater drum should be tested. In fact, we cannot be certain that spread of freshwater drum in the study area has not been influenced by deliberate introductions. For example, Becker (1983) suggests that drum were introduced into the Muen Lake chain in Wisconsin in the 1940 s. Similarly, Wright (2006) notes that 120 adult drum were introduced into the Genesee River by the New York Forest Fish and Game Commission in 1897. Baker (1916) indicates that drum were absent from Oneida Lake prior to 1916, but suggests they would likely be introduced into Oneida Lake where they would thrive on the lake's mussels. And Kirtland (Kirtland 1858 cited in Trautman 1957) discussed the desire to stock Ohio River drum into Lake Erie to improve the food quality of the Lake Erie stock. Now that freshwater drum have been established in the Hudson River, there is a real danger of further spread along the east coast through intentional and accidental introductions of a popular gamefish.

Are other populations in the region invasive?

It is tempting to look to literature surrounding the controversy of whether sea lamprey are native or invasive in the Finger Lakes (Daniels 2001; Wright et al. 1985; Eshenroder 2009; Waldman et al. 2004; 2006; 2009) for clues on the origin of freshwater drum. However, they are very different situations. First freshwater drum are conspicuously large fish, that are readily taken by fishermen, were well known to native Americans, and for which early fisheries existed in nearby Lake Erie, hence arguments that they would be overlooked in early surveys are somewhat dubious. More importantly the biogeography of freshwater drum in relation to glacial history, indicates that they expanded northward from the Mississippi into the Great Lakes as the North American ice sheet retreated during the Pleistocene (Barney 1926; Bailey and Smith 1981). The drum moved into Lake Champlain through the Saint Lawrence, Richelieu and Ottawa Rivers later, after the retreat of the Champlain arm of the sea. Barney (1926) goes on to predict that freshwater drum would likely invade the Hudson River, and thereby gain access to drainages east of the Appalachians through both the Erie and Champlain canals.

Whether the species is native or invasive to the Finger Lakes is uncertain. Most authors appear to assume the species is native to the Finger Lakes (see Carlson et al. 2016), but early accounts from the region are conflicting. Lake Oneida and the Finger Lakes could only have native populations if they were remnants from the original Pleistocene invasion from the Mississippi drainage, or if waterway connections with the Great Lake populations were passable by the drum prior to the construction of canals. Our review of the literature suggests that freshwater drum in the Finger Lakes are most likely invasive.

The only possible natural drum passage into Cayuga, Seneca, Onondaga, and Oneida lakes is the Oswego River, but a natural waterfall and rapids occur less than 1 km upstream from the lake (where the Varick Dam is now located) eliminating the possibility of freshwater drum access to Oneida and the Finger Lakes prior to 1918. Further, since the Oswego River flows north into Lake Ontario, there is no possibility for drum eggs and larvae to disperse into the other lakes. The possibility of remnant native populations also appears unlikely as Barney (1926) does not indicate native populations in the Finger Lakes and reports that freshwater drum were post-glacial invaders of the Great Lakes (see also Bailey and Smith 1981) which suggests they would have been excluded from the already isolated Finger Lakes. Lee et al. (1980) do not show drum collections from the Finger Lakes in their atlas and Smith (1985) shows only recent collections in the Finger Lakes in his distribution maps. Several early authors failed to report freshwater drum in their surveys of Cayuga Lake (Meek 1888; Reed and Wright 1909; Adams and Hankinson 1916). We find it unlikely that all three of these studies would have missed a fish that is so well known from nearby locations and which would have been familiar to local anglers, not to mention the scientists themselves.

In contradiction to this, Surface (1898, 1899) mentions drum in a list of fishes susceptible to predation by lamprey in his account of lamprey impacts on fishes in Cayuga Lake. Greeley (1929) mentions drum as common in Lake Erie and in the mouths of some rivers and creeks in the Erie-Niagara system (see also review by Carlson et al. 2016), but does not clarify if they were present in the Finger Lakes. More directly, Struthers (1929) did not report them among the fishes collected in extensive sampling within the Erie and Oswego canals themselves as well as Oneida, Onondaga, Cross and Neatahwanta lakes. Records from regional State and museum collections provided to us by Doug Carlson (NYSDEC, Pers. Comm.) show only post canal revision (i.e., after 1918) collections in Oneida Lake and the Finger Lakes with two exceptions. One apparently previously overlooked museum record for Rome, New York, deposited by Louis Agassiz in 1854, was presumably from the Mohawk River. A record in the Cornell Museum of Vertebrates of a drum collected in Cayuga Lake by Surface in the same year of his publication (1898) is the strongest evidence that the species is native to the lake, since it occurred before the 1918 modifications of the canals. Also of interest are three records of collections within the canals themselves, two at lock 2 in the Oswego River Canal on separate dates in July 1968 and one in the canal between locks 20 and 21 near Rome, New York in September 1981. The Erie Canal Fishing Derby has been targeting freshwater drum in the western portion of the canal between Tonawanda and Albion since 1990 (Steve Harrington, Derby Coordinator, Pers. Comm.).

Oneida Lake is the closest to any undisputed native population (Lake Erie, Lake Ontario and Lake Champlain). Oneida River flows 29 km from Oneida Lake to join the Seneca River and form the Oswego River which flows another 37 km into Lake Ontario (total about 66 km). Although there were temporary canals connecting Oneida Lake with the Mohawk River as early as 1792 (perhaps accounting for the Agassiz 1854 record at Rome, NY), the original 1825 Erie Canal bypassed Oneida Lake. The Oneida Canal (present from 1835–1863) temporarily connected the Erie Canal with Wood Creek which flows into Oneida Lake from the east, but it was not until the 1918 modification of the Erie Canal that Oneida Lake was fully incorporated into the canal system.

The only detailed examination of Oneida Lake fish prior to the 1918 modification of the Erie Canal was a study of the fish predators of mollusks (Baker 1916). Baker (1916) reported that drum were absent from Oneida, and suggests they should be introduced into Lake Oneida where there would thrive on the abundant mussel population. However, drum were common in Oneida Lake just a few decades after completion of the canal revision in 1918 (see Carlson and Daniels 2004; CNYRPDB 2004). Although circumstantial, taken together, these observations suggest that freshwater drum invaded Oneida Lake and subsequently the Finger Lakes and the Mohawk River after the 1918 reconstruction.

The current distribution of freshwater drum in the region suggests that they are only present in lakes with connections with the NYSCS, being absent in Lake George, and all the Finger Lakes except Cayuga and Seneca, as well as being present in the nearby Oneida, and Onondaga lakes. That distribution is consistent with an invasion hypothesis, however since those lakes with drum may simply be the only ones in which remnants survived from a wider post-glacial distribution, the correlation with the canal system may be coincidental. We suggest that a comprehensive passive acoustic survey of regional water bodies to determine current drum distribution, particularly of spawning locations, together with genetic analyses of individuals from each water body, would be instrumental in determining the native or invasive status of freshwater drum. We also suggest that a comparison of spatial patterns of drum distribution and genetic structure with detailed information on the post-glacial geology and historic waterway management practices in the region can help elucidate factors that contributed to drum expansion in the system and may help to predict the future procession of other invasions.

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