

Research Article

Range expansion of the western tubenose goby (*Proterorhinus semilunaris* Heckel, 1837) in eastern Lake Ontario and the upper St. Lawrence River

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Abstract

The western tubenose goby (*Proterorhinus semilunaris*) has been documented in the Great Lakes basin since the 1990s, when it was introduced to the system via the discharge of ballast water originating in the Ponto-Caspian region of eastern Europe. The first report of this species in the eastern Lake Ontario-St. Lawrence River Basin occurred in 2011, outside of Kingston, Ontario, but beginning in 2016 it has consistently appeared in annual ichthyological surveys in the Thousand Islands region of the upper St. Lawrence River. While these fish have not been detected in great numbers, their presence marks an expanding eastern invasion front into the St. Lawrence River, which could have ecological implications systemwide. Both active adult movement and passive downstream drift of larval tubenose goby coupled with introduction of this species via domestic ballast water discharge within the Great Lakes could be providing a secondary invasion route along the St. Lawrence Seaway.

Key words: Great Lakes, St. Lawrence Seaway, invasive species, vegetation corridors, secondary invasion

Introduction

The western tubenose goby, *Proterorhinus semilunaris* (Heckel, 1837), was first discovered in the Laurentian Great Lakes basin in the early 1990s, where several individuals were found impinged on a power plant intake screen in the St. Clair River (Jude et al. 1992). The source of introduction is believed to be discharge of ballast water from ships that departed from the Black Sea, part of the native range of the tubenose goby (Lelek 1987; Jude et al. 1992). Originally documented upon invasion as *Proterorhinus marmoratus* (Pallas, 1814), further genetic analyses in both the introduced and native regions showed that several genetically distinct species occur in the Ponto-Caspian region, but only a freshwater species, *P. semilunaris*, is present in the Great Lakes system (Naseka et al. 2005; Stepien and Tumeo 2006; Neilson and Stepien 2009). Other species in the genus include freshwater *P. semipellucidus* (Kessler, 1877) from the Caspian Sea basin, an unidentified species from the Kumo-Manych Depression, *P. tataricus* (Freyhof and

Naseka, 2007) from the Crimean Peninsula, the marine *P. marmoratus* from the Black Sea and *P. nasalis* (De Fillippi, 1863) from the Caspian Sea (Freyhof and Naseka 2007; Neilson and Stepien 2009), although Slynko et al. (2013) posit that only two distinct phylogenetic lineages occur, *P. marmoratus* and *P. semilunaris*, based on analysis of mitochondrial DNA containing the cytochrome *b* gene. Studies of mitochondrial genetics of the tubenose goby during the early phases of the invasion of the Great Lakes yielded a single mitochondrial DNA cytochrome *b* gene haplotype, possibly an artifact of the small numbers of tubenose goby sampled, that had not spread very far into the system as a whole (Dougherty et al. 1996; Dillon and Stepien 2001). However, further analyses of genetic material from a larger sample of tubenose gobies in the Great Lakes demonstrated a minimum of three mitochondrial DNA cytochrome *b* haplotypes, indicating a larger, more diverse founding population than previously thought (Neilson and Stepien 2009).

Tubenose gobies are frequently found in shallow littoral waters, in depths less than 1.5 m, with low exposure to wind and wave action (Naseka et al. 2005; Kocovsky et al. 2011; Cammaerts et al. 2012). The tubenose goby is often associated with dominantly rocky substrates, a high diversity of substrate classes, and moderate aquatic macrophyte cover (Jude and Deboe 1996; Kocovsky et al. 2011; Cammaerts et al. 2012). In laboratory experiments, harder surfaces were preferred over vegetative cover as shelter for the tubenose goby (van Kessel et al. 2011); however, they appear to be highly adaptable in mesohabitat (i.e., habitats of moderate size provided by heterogeneity in hydrological conditions and geomorphic setting) use, possibly contributing to range expansion, especially in regions with a broad mix of available habitats (Erős et al. 2005).

Early records of tubenose gobies in the Great Lakes system were associated with dense beds of submersed aquatic vegetation (SAV), including *Vallisneria americana* (Michaux, 1803), *Chara* spp. (Linnaeus, 1763), and *Potamogeton* spp. (Linnaeus, 1753), with high numbers of year-0 fish in these patches (Jude et al. 1995). Macrophyte beds consisting of *Myriophyllum spicatum* (Linnaeus, 1753), *Potamogeton richardsonii* ((A. Bennett) Rydberg, 1905), *Ceratophyllum demersum* (Linnaeus, 1753), *Najas* spp. (Linnaeus, 1753), *Elodea canadensis* (Michaux, 1803), and *Heteranthera dubia* (Jacquin, 1892) have also been used by tubenose gobies; all common species that could provide a diverse array of habitats for these small-bodied fish (Grant et al. 2012). The tubenose goby undergoes a protracted spawning period, likely between June and August, evidenced by presence of recently hatched fish, 5–6 mm in total length (Leslie et al. 2002). Year-0 fish range from 5–40 mm, anything larger is considered age 1+ (Leslie et al. 2002). Dense patches of SAV may serve as spawning and nursery habitat for this species, though information on this

topic is limited. Cover provided by macrophytes in protected shallow embayments appears to be important to these fish. Kocovsky et al. (2011) proposed their use of “vegetation corridors” as a means of spread, as tubenose gobies tend to be affiliated with aquatic vegetation and use it for shelter. These vegetation corridors are shallow areas of aquatic macrophytes, connected to one another along shorelines, coastal wetlands, and tributaries.

Some potential impacts and overlap of diet of the tubenose goby on other aquatic species have been explored in the Great Lakes Basin. In the St. Clair River, tubenose goby diets comprised of aquatic insect larvae (e.g. *Caenis* Stephens, 1835, trichoptera) and small crustaceans (e.g. *Gammarus* J.C. Fabricus, 1775, isopods), indicating potential diet overlap with native darters and logperch (French and Jude 2001). In Europe, tubenose gobies appear to prefer chironomid larvae, as well as isopods, year round (Adámek et al. 2010). The tubenose goby is primarily benthivorous, but may also consume corixids, cladocerans, and copepods (Adámek et al. 2010). In the Great Lakes, tubenose gobies are known to consume the eggs of round goby (French and Jude 2001) and diet analysis revealed presence of zebra mussels in tubenose goby stomachs from Lake Erie (Stauffer et al. 2016).

The range of *P. semilunaris* is also expanding in waterways of Europe, through the Danube, Rhine, Meuse, Moselle, and Main Rivers and associated canals from the Black Sea to the Baltic Sea (Lusk and Halacka 1995; Von Landwüst 2006; Antsulevich 2007; Manné and Poulet 2008; Cammaerts et al. 2012; Janáč et al. 2012). Further documentation of range expansion and predicting areas at risk for invasion is crucial to preventing continued spread and developing management and detection strategies. The objectives of this study are to report on the expansion of tubenose goby into the St. Lawrence River, describe its habitat preferences in this region, and discuss possible sources of introduction.

Materials and methods

Study Area

The upper St. Lawrence River is characterized by a broad diversity of mesohabitats, provided by an archipelago of over 1800 islands and rocky shoals beginning at the confluence of Lake Ontario and the St. Lawrence River. The diverse bathymetry of this region provides a variety of shallow shoals, open and sheltered bays, and drowned river mouth tributaries fringed by extensive coastal wetlands (Roseman et al. 2014). The St. Lawrence River is the natural outlet to the Great Lakes, and the St. Lawrence Seaway spans the entirety of Lake Ontario and the St. Lawrence River, functioning as a major corridor for the transport of nonindigenous species. The focal sites for this study are located near the outflow of Lake Ontario, in close proximity to the largest islands in the Thousand Islands region (Figure 1).

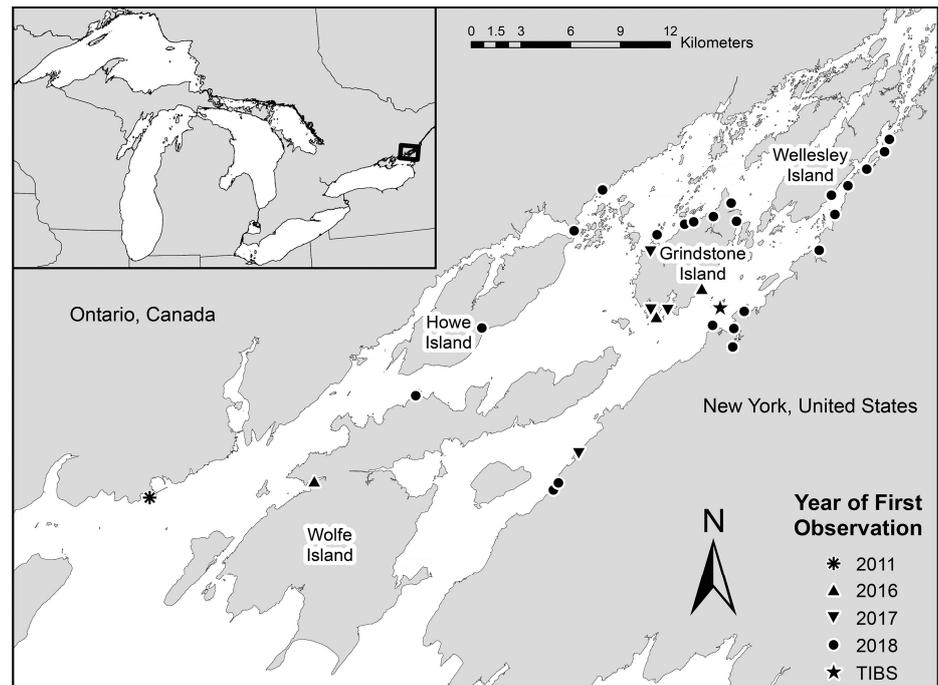


Figure 1. Map depicting discovery sites from 2011–2018 of the western tubenose goby (*Proterorhinus semilunaris*) within eastern Lake Ontario and the upper St. Lawrence River. Inset map depicts relative location of survey area in relation to the Laurentian Great Lakes. The * indicates location of the Thousand Islands Biological Station (TIBS), where the US surveys were based.

Hoop-Netting Wetlands and Tributaries

As part of a long term survey monitoring productivity of northern pike (*Esox lucius*, Linnaeus, 1758), during the month of June, miniature fine mesh (1 mm) hoop nets were set at the mouths of wetland excavations and tributaries to capture northern pike as they emigrate from these sites during their first year of life. These hoop nets consist of four hoops with a central throat, connected to a pair of wings designed to block passage throughout the entire water column. Wing ends were set at the edges of cattail mats, using rebar partially sunken into the substrate. The wings were weighted with lead lines at their base and floats are distributed evenly along the upper portion. To ensure fishing efficiency, the bag end of the net was secured with a small tie and connected to another piece of rebar, to keep the hooped section taut. Nets were checked daily. During 2017 and 2018, three fine-mesh hoop nets were set at a wetland complex in the St. Lawrence River at the southwest head of Grindstone Island, Clayton, New York (Figure 1). Nets were set at the mouths of channels connecting Lindley and Flynn Bays to the north of Club Island (44.24957N; -76.144603W), to capture small-bodied fish. From 2016–2018, nets were set near the mouth of French Creek (Figure 1, Supplementary material Table S1) in natural tributaries to this drowned river mouth system and in recently excavated pothole complexes.

Seining (US waters)

Since 2002, a long-term nearshore juvenile fish and habitat index has been maintained. Seining and quadrat-based vegetation surveys are conducted annually by the Thousand Islands Biological Station, administered by the New York State Department of Environmental Conservation. As part of these surveys, a bag seine is pulled parallel to the shoreline in 30.5 m reaches within coastal embayments of islands and the mainland, following the methods of Farrell and Werner (1999) and Murry and Farrell (2007). From 15 July–15 August 2016–2018, a 9.14 m by 1.83 m long seine with mesh size of 1.6 mm is used to target smaller-bodied fish, specifically year-0 esocids that use these coastal bays as nursery habitat. From 16 August–31 August, an 18.3 m by 2.0 m long bag seine with 6.4 mm mesh was pulled to target larger year-0 esocids in the same sites. Eleven “index” sites are sampled during each period annually, as part of the long-term index; additional exploratory sites are also routinely sampled to compare to the index sites. Between 2016 and 2018, over 40 sites were sampled each year, including several sites along the eastern shore of Lake Ontario and Lake St. Lawrence. Within sampled reaches, substrate class, total macrophyte cover, cover and heights of individual macrophyte species, water depth (m), water temperature (°C) were recorded in six 1 m² quadrats spaced 6.1 m apart, following Murry and Farrell (2007). Tubenose gobies were initially brought back to the Thousand Islands Biological Station (TIBS), Clayton NY, and identified following Scott and Crossman (1998). Year-0 and adult fish were identified following the parameters of Leslie et al. (2002): year-1+ fish exceed 40 mm in total length, while year-0 fish range from 5–40 mm in total length.

Seining (Canadian waters)

Seine surveys were conducted at 61 sites along the north shore of the upper St. Lawrence River from late April to September of 2018. Three seine hauls were conducted at each site using a bag seine (9.14 m × 1.83 m) with a mesh size of 6.35 mm, and habitat was characterized in terms of water quality (temperature (°C)), substrate texture, and submerged aquatic vegetation (species present, maximum height, percent cover). All fish were enumerated and released, with up to 25 individuals of each species randomly selected for total length measurements.

Data Analysis

Data collected in 2018 using the 9.14 m long bag seine in US waters from the confluence of Lake Ontario and the St. Lawrence River to the eastern end of Wellesley Island, NY (Figure 1), were used to assess relationships between tubenose goby presence and several habitat variables. Only sample data that were constrained to this section of the river were used, to ensure sample consistency.

Within each seine haul, mean cover values of each macrophyte species observed within the six sampled quadrats were calculated to describe the habitat covered by the path of the net. Species cover for aquatic macrophytes were manipulated using the Hellinger distance, to address issues of double-absences within abundance-based ecological data with many zeros, without overestimating influence of rare species (Legendre and Gallagher 2001). Indicator species analysis, using package `indicspecies` in R (De Cáceres and Legendre 2009), was performed to identify macrophyte taxa commonly affiliated with either the presence or absence of tubenose gobies. Indicator species analysis may be used to identify specificity and fidelity towards environmental parameters, testing individual species to quantify statistical significance of this association. Higher indicator values indicate stronger fidelity and specificity to a grouping. R 3.5.1 (R Core Team 2018) was used for all statistical analyses.

Results

In American waters of the upper St. Lawrence River, four tubenose gobies were first captured in two sandy bays on the head of Grindstone Island, Clayton NY, on August 18, 2016 in seine hauls associated with the nearshore juvenile fish and habitat index (Figure 1, Table S1). Grindstone Island is the fourth largest island in the Thousand Islands region and has a diverse array of bays, wetlands, and shoals along its coastline. The two bays, Boscobel and Lindley Bay, were dominated by cover of *Chara* spp. Total vegetative cover within the sampled hauls ranged from 30–100%, with a mixture of SAV, including *Najas* spp., *Vallisneria americana*, *Potamogeton richardsonii*, and *Nymphaea odorata* (Aiton, 1789). The substrate in both bays is predominantly silt and sand, with small clusters of boulders present. Boscobel Bay is sheltered, whereas much of Lindley Bay is open to the prevailing winds.

During the 2017 hoop-netting period, two tubenose gobies were captured in nets at the channel excavations connecting Lindley and Flynn Bays. During seining survey, eight individuals, both year-0 and adults, were discovered across four more bays: Flynn, Thurso, and Buck Bays on Grindstone Island, as well as Rose Bay, in Cape Vincent, NY (Figure 1, Table S1). On 25 August 2017, a voucher specimen from Flynn Bay was retained, fixed in 10% formalin and preserved in 70% ethanol. This specimen is housed at the New York State Museum in Albany, NY (NYSM #77503). An exploratory seine in October to examine other bays that could be inhabited by tubenose gobies yielded one adult fish in Boscobel Bay, but no gobies were found in bays further east along the south shore of Grindstone Island. While SAV cover was highly variable among sites during the seining survey, common macrophyte species included *Chara* spp., *Ceratophyllum demersum*, *Nitellopsis obtusa* (N.A. Desvaux) J. Groves, 1919,

Elodea canadensis, *Vallisneria americana* and *Potamogeton* spp. These bays were generally characterized by a broad array of substrates, but most frequently sand, silt, and cobble.

In Canadian waters of the upper St. Lawrence River, 46 tubenose gobies were captured at four seining sites between August 15 and September 4, 2018. The majority of individuals were captured in Quinn's Bay on Howe Island (n = 41), with smaller numbers found in a small embayment on the northeast shore of Wolfe Island (n = 1), the east end mainland launch for the Howe Island ferry dock (n = 3), and the Gananoque Rotary Beach (n = 1). The mean total length of all individuals measured (n = 30) was 3.4 cm. Voucher specimens from each site were fixed in 10% formalin and preserved in 80% ethanol and are stored at the River Institute in Cornwall. Bottom substrates at all tubenose goby locations were dominated by sand and gravel, with some cobble and boulders. Macrophyte cover ranged from 25–75%, and commonly included *Myriophyllum sibiricum* (Komarov, 1914), *M. spicatum*, *Potamogeton pusillus* (Linnaeus, 1753), *C. demersum*, *V. americana*, *E. canadensis*, and *Najas* spp. Tubenose gobies were not detected at eight other downstream sites in the Thousand Islands region between Gananoque and Brockville, Ontario, that were surveyed between July and August 2018.

In 2018, eight adult tubenose gobies were captured in the three hoop nets set in the channel between Lindley and Flynn Bays and one additional adult fish was captured in a net set in a wetland near the mouth of French Creek in Clayton, NY, a new site of discovery for this species. French Creek is a drowned river mouth tributary of the St. Lawrence River; the net was set in a small channel off the main stem of the creek, in a cattail-dominated wetland. During the 2018 seining period, a total of 186 tubenose gobies were captured across 26 sites between 15 July and 25 August. The highest catches occurred in four Grindstone Island bays: Flynn Bay (n = 21), Salisbury Bay (n = 17), Thurso Bay (n = 15), and Lindley Bay (n = 13), and one mainland shoreline near Bartlett Point, Clayton, NY (n = 25). Round gobies (*Neogobius melanostomus* Pallas, 1814) were also present at all sites except for three small unnamed bays on the north side of Grindstone Island that were not extensively sampled. All tubenose gobies captured at Bartlett Point were year-0 fish, this was the only site where exclusively year-0 fish were sampled. Of the 186 fish captured, 73 were year-0 fish.

For 2018 US waters surveys using the 9.14 m long seine, haul data were pooled from sampled bays between the mouth of the St. Lawrence River to Wellesley Island. Bays where tubenose goby were not detected were incorporated. Sites where either age class of goby (i.e., year-0, year-1+) were present typically contained macroalgae taxa, *Chara* spp. and *Nitellopsis obtusa*, or low growing *Najas* spp., while narrow-leaved pondweeds (e.g. *Stuckenia pectinata* (Linnaeus) Börner, 1912, and *P. pusillus* were more

Table 1. Habitat variables associated with the presence and absence of tubenose gobies in US coastal bays of the upper St. Lawrence River in 2018. Mean total cover and water depth are shown, with ranges of values in parentheses. The most frequently encountered substrate classes are listed. Indicator values (0–100) and p-values (** 0.01, * 0.05) of SAV taxa associated with presence and absence of tubenose goby are listed.

	Tubenose Goby Present	Tubenose Goby Absent
Total Cover	86.0% (36–100%)	88.7% (28–100%)
Water Depth	0.82 m (0.55–1.41 m)	0.88 m (0.52–1.57 m)
Substrate	Organic material, silt	Organic material, silt, clay
Macrophyte species	<i>Chara</i> spp. (70.1)** <i>Nitellopsis obtusa</i> (60.9)* <i>Najas</i> spp. (57.9)* <i>Potamogeton zosteriformis</i> (35.0)*	<i>Stuckenia pectinata</i> (63.2)* <i>Elodea canadensis</i> (62.8)* <i>P. pusillus</i> (57.6)**
	Year-1+ Tubenose Goby Present	Year-1+ Tubenose Goby Absent
Total Cover	87.6% (36–100%)	88.1% (28–100%)
Water Depth	0.81 m (0.54–1.41 m)	0.88 m (0.52–1.57 m)
Substrate	Organic material	Organic material, silt, clay
Macrophyte species	<i>Chara</i> spp. (72.0)* <i>Najas</i> spp. (60.5)** <i>N. obtusa</i> (59.6)* <i>Scirpus</i> spp. (25.3)* <i>Spirodela polyrhiza</i> (22.4)*	<i>E. canadensis</i> (62.9)* <i>P. pusillus</i> (56.0)*
	Year-0 Tubenose Goby Present	Year-0 Tubenose Goby Absent
Total Cover	80.1% (37–100%)	88.8% (28–100%)
Water Depth	0.88 m (0.66–1.41 m)	0.87 m (0.52–1.57 m)
Substrate	Organic material	Organic material, silt, clay
Macrophyte species	<i>Schoenoplectus</i> spp. (44.5)* <i>P. gramineus</i> (41.5)*	N/A

frequently observed in sites where tubenose gobies were not detected (Table 1). Splitting the data between year classes, the low growing vegetation generally associated with presence of tubenose goby was again most strongly affiliated with this species, however, a duckweed species, *Spirodela polyrhiza* ((Linnaeus) Schlied, 1839), and the emergent *Scirpus* (Linnaeus, 1753) were also common. No significant indicator values were detected for the absence of year-0 tubenose goby, but emergent *Schoenoplectus* spp. (H.G.L. Reichenbach) Palla, 1888, and *P. gramineus* (Linnaeus, 1753) were strongly affiliated with the presence of this species.

Discussion

The western tubenose goby had not been detected in Lake Ontario or the St. Lawrence River until a single specimen was collected west of Kingston, Ontario in September 2011, (USGS NAS Specimen ID 279264). No further reports occurred until August 2016, when two individuals were captured in a fyke net in Barrett Bay, Wolfe Island, Ontario, Canada (USGS NAS Specimen ID 1454602), and the four individuals described here were captured in seine hauls at two bays (Lindley and Boscobel Bays, Table S1) at the head of Grindstone Island, NY, USA (USGS NAS Specimen ID 1321737, 1321738). Additional detections (of adult fish in 2017 and 2018, and year-0 fish in 2017) indicate that reproduction is probable and that this species could likely continue its downstream spread. In general, however,

Table 2. General chronology of initial records of western tubenose goby (*Proterorhinus semilunaris*) in the Great Lakes Basin. Numbers in parentheses are the corresponding earliest dated record numbers from the U.S. Geological Survey Nonindigenous Aquatic Species Database (USGS 2018).

Water Body	Initial Report	First Sighting Location, Reports
St. Clair River	1990	Belle River Power Plant, St Clair, MI, Jude et al. (1992) (35361)
Lake St. Clair	1993	Macomb County, MI (35537)
Detroit River	1996	River Canard, ON (268972)
Western Lake Erie	1997	Kingsville Marsh, Kingsville, ON (40359)
Lake Superior	2001	St. Louis River, Duluth, MN (153651)
Lake Huron (Georgian Bay)	2011	Outer Harbour, Penetang Harbour, ON (1454351)
Eastern Lake Ontario	2011	Kingston, ON (279264)
Eastern Lake Erie	2012	Grant et al. (2012), (284149)
Headwaters St. Lawrence	2016	Wolfe Island, ON (1454602)

tubenose goby has spread slowly, with a decade-long (2001–2011) gap in notable range expansion (Table 2) and its distribution in the Great Lakes is generally patchy (Kocovsky et al. 2011; Fuller et al. 2018). Our observations of increased catch and new locales from 2017 to 2018 suggest a more rapid expansion is possible and may be ongoing or finally reaching a threshold of detection where the species is less likely to be overlooked.

Kocovsky et al.'s (2011) hypothesis of range expansion of tubenose gobies by active dispersal along vegetative corridors appears consistent with the observed slow invasion pattern for this species in the upper St. Lawrence River. Low-growing *Chara* and *Najas* species have been associated with the presence of tubenose goby since it was first documented in the Great Lakes and complex habitats could be provided by a variety of pondweeds (e.g. *Potamogeton* spp., *Stuckenia pectinata*) and emergent species (e.g. *Scirpus*, *Schoenoplectus* spp.; Jude et al. 1995; Grant et al. 2012). Kocovsky et al. (2011) and Cammaerts et al. (2012) found lower SAV cover values (25–30%) associated with tubenose goby presence, although Grant et al. (2012) reported finding the western tubenose goby in 80% total cover, which is in accordance with our findings. The high values for average SAV cover (80–90%) in sampled reaches of the upper St. Lawrence River certainly could provide nursery habitat and a potential invasion route along these littoral patches of SAV. Furthermore, each fall, annual SAV is uprooted and transported downriver as plants senesce and could present an opportunity for tubenose goby to be transported during this process as these plants move and wash ashore in other locations.

The corridor of islands and shoals in the upper St. Lawrence River could provide the combination of both macrophyte and rocky cover preferred by this species and enable further range expansion. Although the sampled reaches in the Thousand Islands region were not often rocky, this may be an artifact of sampling techniques: the specific species targeted by the seining surveys are more often found outside of coastal wetlands or areas with softer substrates, more focused sampling for tubenose gobies may yield interesting results in the region. Seining has proven to be an effective sampling technique for gobies in wadable waters, but in rocky or more

complex habitats, passive sampling using minnow traps may yield less biased results (Nett et al. 2012). The series of small jumps in individual sightings add further credence to the saltatory spread documented by Kocovsky et al. (2011) and Cammaerts et al. (2012).

The potential for larval drift from ports where domestic ballast water is released may also explain the slow spread of this species. Examining the drift potential of larval fish with similar life histories and patterns of spread is beneficial to further understanding possible risk of range expansion of the tubenose goby. Deepwater sculpin (*Myoxocephalus thompsoni* Girard, 1851) larvae have been found drifting through the Huron-Erie Corridor, which consists of the St. Clair River, Lake St. Clair, and the Detroit River and downstream larval drift of this species and round goby in the Great Lakes have been documented (Hatcher and Nester 1983; Roseman et al. 1998; Hensler and Jude 2007). The discovery of tubenose goby larvae downstream of the mouth of the Detroit River was consistent with this pattern of spread (Kocovsky et al. 2011). The pattern of capture of tubenose goby near the head of the St. Lawrence River (Figure 1) seems to correspond with this downstream, or passive, drift, as well. Exploration of the effects of fetch or wind-mediated drift in more protected bays of the St. Lawrence would be prudent; the effects of current-mediated drift may be lessened by bay geomorphology.

The approximately 250 km trip from areas with known deepwater sculpin populations in Lake Huron to Lake Erie would take less than a week for a larval fish to travel passively in the currents of the Huron-Erie corridor (Roseman et al. 1998). Similarly, larval round gobies in the Great Lakes have been collected over 2 km from known spawning habitat, drifting at the surface at night (Hensler and Jude 2007). This suggests diel vertical migration coupled with passive drift, as only nighttime surveys yielded larval fish (Hensler and Jude 2007). In the Danube River, highest drift rates of larval tubenose occurred at night (Zitek et al. 2004). The findings of Janáč et al. (2013a) supported this, reporting that larval gobies (TL: 5–8 mm) moved primarily at night, with the majority of fish moving either within one hour of dusk or one to 2.5 hours before dawn. Both flooding and faster currents could increase rates of larval drift and potential range expansion, though there is a gap in the literature regarding general drift potential and eventual recruitment of tubenose to new regions (Janáč et al. 2012; Janáč et al. 2013a). Larval drift of tubenose has been posited as one of the key routes of invasion of the Danube and its connected canals (Janáč et al. 2012). This saltatory spread via drift could also explain the recent appearance of tubenose gobies in the headwaters of the St. Lawrence River.

Discharge of ballast water originating in the Black Sea has been accepted as the primary route of introduction for both round and tubenose gobies in the Great Lakes system and ballast water discharge remains a major influence in the secondary spread of invasive species in the region (Jude et

al. 1992). Neither round nor tubenose goby have ever been documented in ballast tanks, although other Gobiid fishes have been found (Wonham et al. 2000). The concepts of ballast water transport or direct attachment of eggs to the hulls of vessels have oft been referenced in literature as means of transport of these invasive gobies, but without scientific evidence, these ideas cannot be fully substantiated (Adrian-Kalchhauser et al. 2017).

In a three-year study of domestic shipping within the Great Lakes and St. Lawrence River, over 200 million tons of ballast water were discharged across 28,000 ship transits (Rup et al. 2010). The amount of ballast discharged within the system by “Lakers,” ships moving exclusively within the Great Lakes and St. Lawrence River, was over twenty times that of ships travelling along the North American coast and transoceanic vessels combined (Rup et al. 2010). Domestic ballast water as a source for secondary invasion across the Great Lakes is viable, though Rup et al. (2010) considered the risk of transport of ballast originating in the St. Lawrence River entering the Great Lakes, following a “common waters” standpoint. The idea of “common waters”, as defined by Adebayo et al. (2014), is that within ports of a single region, fairly consistent community composition should occur, which has been the argument for lax regulations for domestic ballast transport; the assumption of similar taxa presence-absence due to downstream drift and transport isn’t the case. Adebayo et al. (2014) found very low overlap in community composition between port and ballast water samples, suggesting that more stringent ballast water regulations for Lakers and other ships traveling within the system may be necessary to slow or prevent secondary invasion risks. Typical duration of ballast water retention for interregional transport is 3–4 days, while intraregional transport may take less than 24 hours; both transport timeframes are well within bounds for survival of zooplankton and potentially larval fish (Rup et al. 2010).

Rup et al. (2010) examined ports in the Great Lakes that served as both donors and recipients of domestic or coastal/oceanic ballast water from 2005–2007. In Eastern Lake Ontario and the upper St. Lawrence River, a number of ports were denoted as both donors and recipients of domestic ballast, including Bath and Picton, Ontario, just upstream of Kingston, at the head of the St. Lawrence River. Colborne, Ontario served as a recipient port, but is over 100 km from the westernmost site of detection in eastern Lake Ontario and is unlikely to have served as a source for tubenose goby introduction in this region. This mixing of waters via ballast water transport across the Great Lakes could have been a source of introduction for the tubenose goby in eastern Lake Ontario and the St. Lawrence River. Considering the likeliest route of initial introduction was ballast water transport, further secondary invasion facilitated in this manner is feasible. Nighttime surveys or sampling targeting demersal species within ports, as well as surveys of shorelines around ports receiving ballast water discharge, like Bath and Picton, ON, may provide further insight about this possible introduction route.

The range expansion of tubenose gobies is likely due to a combination of both active and passive movement, coupled with inadvertent introduction via domestic ballast water discharge. Hensler and Jude (2007) hypothesized that diel vertical migration of larval round gobies could contribute to ballast water transport of these fish, as ballast is typically drawn up from the water column, rather than within the benthic environment that post-larval fish would occupy, although this has never been validated; presumably this could also occur for tubenose gobies due to their similar life histories. In Europe, they are now distributed across 2000 km along the Danube and connected waterways, from the Black Sea to the North and Baltic Seas (Ahnelt et al. 1998). In larger rivers, they typically demonstrate slower expansion through natural dispersal, but in slower waters, the rate of expansion may increase, since they seem to fare well in calmer waters (Manné et al. 2013). Dams appear to be a minor inconvenience to expansion of territory, as survival of juvenile tubenose gobies passing through dam turbines is high, with 3% mortality associated with this journey (Janáč et al. 2013b). Further downstream expansion of this species along the St. Lawrence River may not be hindered by the presence of large dams. Both downstream and upstream migration across barriers have been recorded (Von Landwüst 2006; Manné and Poulet 2008; Cammaerts et al. 2012).

Looking forward, Lake St. Lawrence, an impoundment between the Iroquois Dam (Waddington, NY, to Iroquois ON) and the Robert Moses-Robert H. Saunders Power Dam, spanning from Massena, NY, to Cornwall, ON., could be at risk for colonization by tubenose gobies. This impoundment is more lentic than the Thousand Islands region and is flanked by agriculture, development, and fragmented wetlands. In Lake St. Lawrence, the backwash created by large ships passing bays that open to the shipping channel could limit the distribution of the tubenose goby throughout this system, as this appears to have contributed to their patchy presence along shipping corridors in Europe (Cammaerts et al. 2012), although secondary introduction via ballast water discharge and the resulting potential establishment of the species in this reach cannot be ruled out. Headwater drawdowns at the Robert Moses-Robert H. Saunders Power Dam are responsible for large daily and seasonal water level fluctuations in Lake St. Lawrence, possibly further limiting their distribution within sparsely vegetated nearshore areas in this reach. To aid in this downstream spread, rocky shorelines in the middle corridor of the St. Lawrence River, a generally straight, featureless section extending from Morristown, NY, to the Iroquois Dam, could harbor fish. However, the Thousand Islands region appears to be at greater risk for further invasion in the coming years.

Ballast water serves as a major vector of nonindigenous species; zooplankton species previously unreported from western Lake Superior were detected in samples of ballast water discharged by ships entering western Lake Superior (Cangelosi et al. 2018). Laker-mediated ballast water

transport across the Great Lakes and St. Lawrence River appears to be a very important pathway for the spread of nonindigenous species, and further regulation of these domestic ships may slow secondary invasion through this system. Continued monitoring of this invasion front and further evaluation of ballast-mediated dispersal of this species would be prudent. Increased regulation of domestic ballast water transport may be a crucial next step to prevent continued secondary invasion of nonindigenous species in the Great Lakes and the St. Lawrence River.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Latitude and longitude coordinates of sites where tubenose gobies have been captured between 2016–2018 in the upper St. Lawrence River.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2019/Supplements/BIR_2019_Goretzke_etal_Table_S1.xlsx