

Cryptic invaders: nonindigenous and cryptogenic freshwater Bryozoa and Entoprocta in the St. Lawrence River

Kayla M. Hamelin · Rowshyra A. Castañeda · Anthony Ricciardi

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Abstract The distributions of most cosmopolitan invertebrate species are assumed to result from natural processes. Cryptic invertebrates with obscure biogeographic origins are often considered native by default, resulting in potentially severe underestimation of the extent of human-assisted invasions. This problem is exemplified by freshwater Bryozoa (Ectoprocta) and Entoprocta—small and widely distributed invertebrates commonly found in lakes and rivers. A benthic survey of a thermally modified section of the St. Lawrence River revealed the presence of two non-indigenous bryozoans: Carter's moss animal *Lophopodella carteri* (Hyatt) and the crystal moss animal *Lophopus crystallinus* Pallas. Also discovered was a cryptogenic entoproct, the goblet worm *Urnatella gracilis* Leidy. These species were collected as statoblasts and (in the case of *U. gracilis*) colonial fragments downstream of the Gentilly-2 nuclear

power plant at Bécancoeur, Quebec. Local densities of both *U. gracilis* and *L. carteri* increased by an order of magnitude at sites closer to the power plant. The occurrence of *Lophopus crystallinus* statoblasts in St. Lawrence River sediments is the first documented physical evidence of the species in North America. Contrary to the presumed natural Holarctic distribution of *L. crystallinus*, our literature review found that published historical records of *L. crystallinus* in the United States are erroneous or unsubstantiated. We propose that *L. crystallinus* is a western Palearctic species recently introduced to the St. Lawrence River, most likely as statoblasts discharged with ballast water from transoceanic ships.

Keywords Biogeography · Bryozoa · Ectoprocta · Entoprocta · Kamptozoa · *Lophopus crystallinus* · *Lophopodella carteri* · *Urnatella gracilis*

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K. M. Hamelin · R. A. Castañeda · A. Ricciardi (✉)
Redpath Museum, McGill University, 859 Sherbrooke
Street West, Montreal, QC H3A 0C4, Canada
e-mail: tony.ricciardi@mcgill.ca

Present Address:
R. A. Castañeda
Department of Ecology and Evolutionary Biology, University
of Toronto- Scarborough, 1265 Military Trail, Toronto,
ON M1C 1A4, Canada

Introduction

Nonindigenous species—organisms that have spread beyond their historical range directly or indirectly as a result of human activities—are being discovered at increasing rates in inland waters worldwide. In most large lakes and rivers, dozens of nonindigenous invertebrate taxa have been recorded (Ricciardi 2015). These numbers must certainly fall short of reality, as a result of insufficient monitoring, inadequate taxonomic expertise, and incomplete knowledge

of the historical biogeography of many species (Carlton 2009). Indeed, numerous freshwater invertebrate taxa are cryptogenic (that is, their native or nonindigenous origins cannot be confirmed) and perhaps many more are misidentified as natives (“pseudoindigenous”, sensu Carlton 2009). Consequently, the true extent and impacts of freshwater invasions may have been profoundly underestimated.

Small-bodied taxa—such as bryozoans (Ectoprocta), entoprocts, annelids and rotifers, among others that are ubiquitous in lakes and rivers—are remarkably absent from most freshwater nonindigenous species lists (e.g. Mills et al. 1993; Karatayev et al. 2009). Two reasons for this are: (1) their taxonomic resolution is problematic and thus impedes recognition of nonindigenous taxa; and (2) they are believed to be easily transported by processes such as wind and water currents, or carried by migrating waterfowl (e.g. Figueroa et al. 2004), such that they are often assumed to have naturally cosmopolitan distributions (Carlton 2009). Nevertheless, some freshwater bryozoans have well-documented invasion histories (Balounová et al. 2013; Ricciardi and Reiswig 1994; Wood and Okamura 1998), and several other species have disjunct, expanding distributions that suggest recent introductions (Wood 2002; Taticchi et al. 2008).

One would expect bryozoan species introductions to be far more common than records indicate, given that phylactolaemate bryozoans possess highly resistant and abundant resting eggs (statoblasts) that can individually generate a population (Wood 2010). Statoblasts are moved through human activities including inadvertent transport with stocked fish and aquatic plants (e.g. Masters 1940) and ship ballast tanks (Bailey et al. 2005; Kipp et al. 2010). Contrary to the classical view that the cosmopolitanism of bryozoans is the result of natural processes (Bushnell 1973), there is evidence that human-mediated dispersal has played a major role in shaping their contemporary global distributions. For example, transoceanic shipping traffic is the most plausible vector for the introduction of an Asian bryozoan into the Panama Canal region (Wood and Okamura 1998). Statoblasts of eleven bryozoan species, comprising more than 10 % of all described taxa (!), were found in the ballast tank sediments of 33 transoceanic ships visiting the Great Lakes over a two-year period (Kipp et al. 2010); each of these ships was estimated to carry, on average,

nearly one million statoblasts, which could potentially be re-suspended and released during ballasting operations of ships that visit multiple ports within the basin. A few statoblasts from these ships were hatched successfully in informal laboratory trials (S.A. Bailey, Fisheries and Oceans Canada, personal communication). Given the potentially high propagule pressure imposed by ballast water release, among myriad other human vectors, it is rather incredible that only one nonindigenous bryozoan species has been recorded in the Great Lakes-St. Lawrence River system to date (Ricciardi and Reiswig 1994; Ricciardi 2006).

Here, we report the abundance and distribution of nonindigenous freshwater bryozoan and entoproct species in a 4-km thermally modified section of the St. Lawrence River downstream of a nuclear power plant.

Methods and site description

Invertebrate samples were collected within a broader survey assessing the structure of benthic communities downstream of the Gentilly-2 nuclear power plant (G2NPP) on the south shore of the St. Lawrence River ($46^{\circ}23'38''\text{N}$, $72^{\circ}21'12''\text{W}$) near Bécancour, Québec (Fig. 1). The G2NPP facility began operation in 1983 and remained functional until it was decommissioned at the end of December 2012. For decades, the heated discharge from G2NPP was released at temperatures ~ 11 °C higher than the ambient river temperature, which prevented a multi-kilometer section of the river from freezing during winter months (Langlois and Vailancourt 1990; Castañeda and Hamelin unpublished data).

Using a petite Ponar grab (231 cm^2 area), we sampled the benthos along a 3.2 km transect downstream of G2NPP (Fig. 1). This distance encompassed the artificial discharge canal (mean depth 2–3 m) and most of the thermal plume, defined by year-round open water of variable depth (>3 m) driven by both seasonal and tidal influences (Table 1). We collected samples along the length of the transect perpendicular to the isotherms of the thermal gradient. Two benthic grabs were taken at each of 10 stations in June and August 2011, and 30 stations in May and September 2012. Samples were sieved through 0.5 mm mesh and all invertebrates and coarse sediments retained in the sieve were fixed in 75 % ethanol.

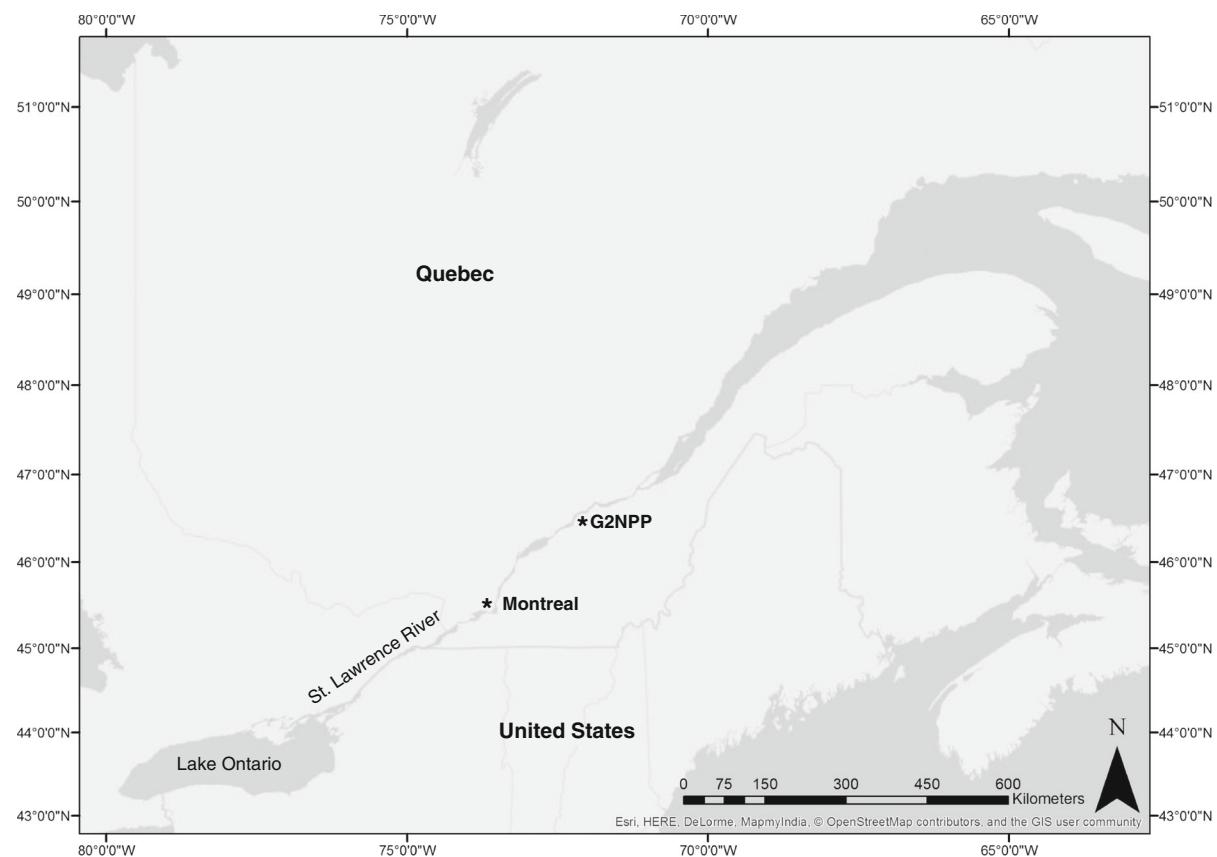


Fig. 1 Map of the study site and location of the Gentilly-2 nuclear power plant (G2NPP) on the St. Lawrence River

Table 1 Physico-chemical variables in the Gentilly-2 discharge canal (“Canal”) and downstream of the discharge canal (“Rest of Plume”), recorded in situ along the sampling transect in August 2011 and May 2012

Variable	Canal		Rest of Plume	
	May	August	May	August
Depth (m)	2.2 ± 0.9	2.6 ± 0.4	4.8 ± 1.1	3.1 ± 1.4
Temperature (°C)	24.3 ± 0.6	30.2 ± 4.8	16.2 ± 2.2	24.8 ± 0.6
Dissolved oxygen (mg/L)	10.7 ± 0.43	7.7 ± 1.0	10.6 ± 0.4	8.4 ± 0.4
Flow velocity (m/s)	0.07 ± 0.04	0.23 ± 0.16	0.07 ± 0.07	0.11 ± 0.14
Sediment grain size (Phi)	2.28 ± 3.22	-0.89 ± 1.75	2.28 ± 2.31	1.27 ± 2.44

Values reported as Mean ± SD

At each station, we measured temperature and dissolved oxygen (mg/L) using a YSI probe, water velocity using a digital flow meter (Swoffer Model 3000), and depth using either a digital depth sounder or weighted measuring tape. The mean grain size (Phi scale) of sediments was estimated following Jones and

Ricciardi (2005). During our sampling period, temperatures were elevated in the canal (mean 24.3 °C in May 2012, mean 30.2 °C in August 2011), and represented an average temperature enhancement of 6–8 °C relative to downstream sites. Large sediments (gravel) were observed close to the power plant

outflow, with smaller sediments and organic debris found throughout the canal, and mixed sediments downstream.

Using a dissection microscope, we manually removed statoblasts and colony fragments from sediments, and identified species following Wood (2010). The analysis of sediment samples is considered to be a reliable method of gaining information on the distributions of bryozoan species that release statoblasts, and may be more accurate for rare species than searching for attached colonies alone (Hill et al. 2007). Moreover, the number of statoblasts and colony fragments (in which an individual was defined to include all branches originating from a shared pedal base) are proxies for local colony abundance (Francis 2001; Hartikainen et al. 2009). Species abundance measures were standardized as statoblast or colony densities per square meter (dividing numbers collected by the area of the grab), for ease of data comparison and interpretation. Density and species composition were examined in relation to the thermal gradient downstream from the G2NPP discharge source.

Results and discussion

Four bryozoan and one entoproct species were collected from the sediment samples. These include two native bryozoans, *Pectinatella magnifica* (Allman) and *Cristatella mucedo* (Cuvier). The remaining species are considered here as either nonindigenous or cryptogenic: Carter's moss animal *Lophopodella carteri* (Hyatt), the crystal moss animal *Lophopus crystallinus* Pallas, and an entoproct—the goblet

worm *Urnatella gracilis* Leidy (Fig. 2). Bryozoan statoblasts were encountered in greater density near the G2NPP discharge source (Fig. 3). Their abundance in the discharge canal was largely dominated by *L. carteri*, an Asian species that has an invasion history in North America and Europe (e.g., Sanzhak et al. 2012; Walker et al. 2013) and is the only nonindigenous bryozoan previously recorded in the Great Lakes-St. Lawrence River system (Ricciardi 2006). It is generally rare, but sometimes locally abundant, in thermally unmodified areas of the river (Ricciardi and Reiswig 1994). The section of the river immediately downstream of the G2NPP appears to support an unusually high number of colonies of *L. carteri* in 2012, as suggested by the concentration of statoblasts in the sediments (Fig. 3). In contrast to the floating statoblasts of other bryozoans, the statoblasts of *L. carteri* and *Lophopus crystallinus* are non-buoyant, and so they may indicate the local presence of the species (Wood and Marsh 1996).

The entoproct *Urnatella gracilis* is native to the eastern and midwestern USA, where it is broadly distributed in flowing waters and occurs as far north as Lake Erie (Rogick 1935; Wood 2010), but is considered nonindigenous in western regions of the continent (e.g. California; Ray 2005). Its occurrence at Bécancour, Québec, represents the northernmost record of its North American distribution. Colony densities at our study sites declined exponentially with distance from the G2NPP, and specimens were rarely encountered beyond the discharge canal (Fig. 4). Segmented stalked specimens (Fig. 2c) were commonly found attached to the shells of another thermophilic species, the invasive Asian clam *Corbicula fluminea*, which



Fig. 2 Examples of specimens collected in the St. Lawrence River near Bécancour, Quebec: **a** *Lophopus crystallinus* statoblast, **b** *Lophopodella carteri* statoblast, **c** *Urnatella gracilis* colony

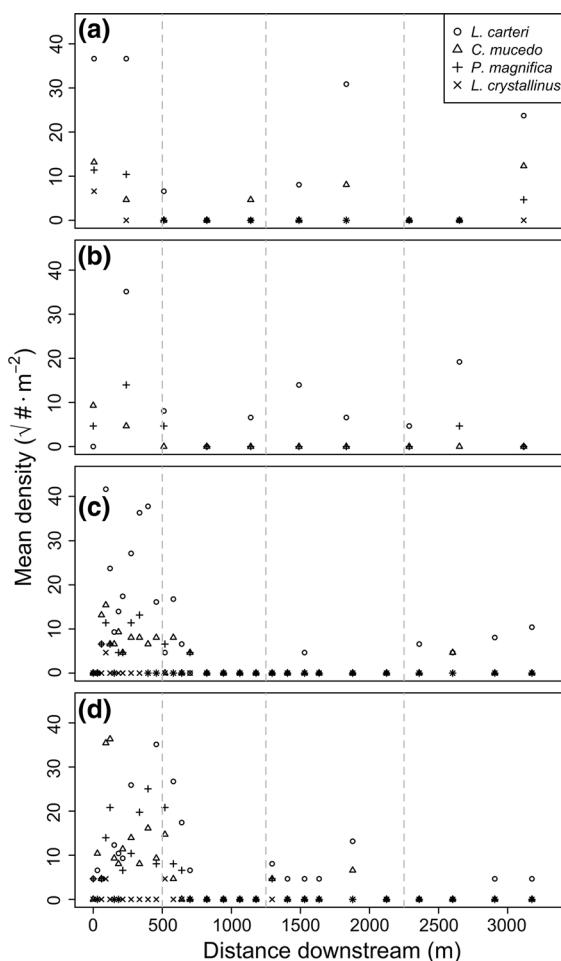


Fig. 3 Statoblast density (square-root transformed) as a function of distance downstream from the G2NPP discharge source in **a** June 2011, **b** August 2011, **c** May 2012, and **d** September 2012. On each sampling date, segments of the discharge plume (indicated by dashed lines) differed in total numbers of statoblasts pooled for all species (Chi square tests; $p < 0.01$), with the highest abundance consistently found in the canal region (0–500 m). Raw data are provided in Supplementary Material

was also abundant in the discharge canal (Simard et al. 2012). No evidence of the occurrence of *U. gracilis* was found beyond the thermal plume or in subsequent benthic collections in other areas of the river (Castañeda and Ricciardi unpublished data). In summer 2013, several months after the closure of the power plant, some colonies were found attached to abandoned Asian clam shells and gravel in the discharge canal, but in dramatically reduced numbers (R. Castañeda, personal observation); we suspect that

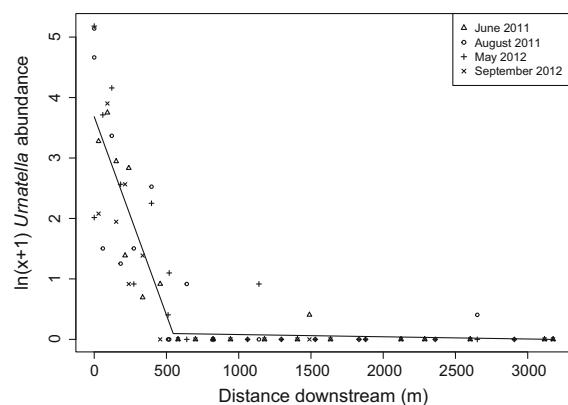


Fig. 4 Numerical abundance of *Urnatella gracilis* colonies (number of colony fragments in individual benthic grab samples) as a function of site distance downstream from the G2NPP discharge source in June 2011, August 2011, May 2012 and September 2012. Least-squares regression lines of counts pooled across sampling dates are shown, with a breakpoint indicated at 547 m (SE = 43), which corresponds to the position of mouth of the discharge canal. Regression line prior to breakpoint: $\log_e(\text{abundance} + 1) = 3.68 - 0.0066 \times \text{distance}$ (adj. $R^2 = 0.80$, $p < 0.05$). The slope of the regression line following the breakpoint is not significant

the population will not persist in the absence of the thermal plume. *Urnatella* was not encountered in a previous survey of bryozoans (including Entoprocta) in eastern Canada (Ricciardi and Reiswig 1994). As such, *U. gracilis* should be considered cryptogenic in the St. Lawrence River. It was possibly introduced through hull fouling or ballast water transport by domestic shipping within the Great Lakes basin (Rup et al. 2010), or by overseas shipping from Europe—where it is presumed to be nonindigenous (see Vranovsky 1994; Protasov 1995; D'Hondt et al. 2002). Its establishment in the St. Lawrence River could have been facilitated by the thermal discharge of the G2NPP power plant, similar to occurrences in northern Europe where the species is largely confined to artificially heated waters (Protasov 1995).

Our most noteworthy finding is that of the crystal moss animal *Lophopus crystallinus*, a species believed to have a natural Holarctic distribution (Massard and Geimer 2008). Five intact statoblasts, which readily identify the species (Fig. 2), were retrieved from different sites within the canal approximately 100–500 m downstream of the discharge source. Given that *L. crystallinus* colonies can tolerate temperatures near 0 °C (Hill and Okamura 2005), they

may also occur in the river beyond the plume. However, in spite of suitable environmental conditions throughout much of the Great Lakes-St. Lawrence River basin, the species was not recorded in previous bryozoan surveys (Rogick 1935; Wood 1989; Ricciardi and Reiswig 1994). We evaluate three hypotheses explaining its occurrence at our study site: (1) *L. crystallinus* is native to the St. Lawrence River; (2) *L. crystallinus* is nonindigenous in the St. Lawrence River, but native elsewhere on the continent; or (3) *L. crystallinus* is nonindigenous to North America.

The biogeographic status of *Lophopus crystallinus*

The putative natural Holarctic distribution of *L. crystallinus* is based on a few historical accounts in the United States, where the species has always been considered rare. In his global review of freshwater Bryozoa, Lacourt (1968) lists North American records of *L. crystallinus* from Lake Erie, the Schuylkill River, and the Illinois River. For the Lake Erie record, he erroneously cites "Rogick 1946", an article that does not exist; presumably, he meant Rogick (1936), who notes different forms of *Lophopodella carteri* statoblasts in Lake Erie and compares them to those of *Lophopus crystallinus* described exclusively from European populations. Neither Rogick nor subsequent researchers collected *L. crystallinus* from the Great Lakes (Wood 1989, 2002). The record for the Schuylkill River near Philadelphia is derived from a very brief report by Joseph Leidy, who mentions that he detected "a species of *Lophopus*" in the river, but "had not yet had leisure to determine its character" (Leidy 1858, p. 190). No illustration or description was provided, and no further details concerning this finding were ever published. Nonetheless, Leidy's comment was noted in a review by Kraepelin (1887)—which was later cited by Lacourt (1968) and others, and thus the record became entrenched in the literature. For the Illinois River record, Lacourt cites Davenport (1899), who lists *L. crystallinus* in an identification key to American freshwater Bryozoa without information on where the species is located. Davenport merely referenced a monograph of freshwater Bryozoa by the American zoologist Alpheus Hyatt (1868), who derived his description of *L. crystallinus* solely from European studies, because he had been unable to locate a specimen in the United

States. Decades later, Kofoid (1908) reported collecting *L. crystallinus* in the form of "small, free-swimming colonies of 5–50 zooids" amongst the plankton drifting downstream of a fluvial lake on the Illinois River in July 1897. He did not mention if there were statoblasts present to verify the identity of the species. It is plausible that these were fragments torn from epiphytic colonies of *L. crystallinus*, if not some other bryozoan; but no specimens exist, and more recent surveys of the Illinois River failed to locate the species (T.S. Wood, personal communication). In his description of the fauna of Lake Mendota, Wisconsin, Muttkowski (1918) mentions that "minute growths of Bryozoa, belonging to the genus *Fredericella*, and probably also to *Lophopus*, occur plentifully on the plants." Apparently, there were no statoblasts to confirm this uncertain identification; it seems more likely to have been a misidentified gelatinous species such as *Cristatella mucedo* or *Pectinatella magnifica*, both which occur in Wisconsin (Watermolen 2004). The last published North American record of *L. crystallinus* is by Cooper and Burris (1984), who reported collecting statoblasts of the species within the Bear Creek watershed in Mississippi in 1976–1977. The authors did not provide any photographic evidence, nor could they offer any specimens for examination (T.S. Wood, personal communication).

The hypothesis that *L. crystallinus* is nonindigenous to the St. Lawrence River is supported by a series of criteria outlined by Chapman and Carlton (1991). Seven of ten criteria are satisfied: (1) The species appears for the first time in a region where previous surveys have failed to locate it (Ricciardi and Reiswig 1994; Ricciardi unpublished data). (2) It is associated with a human mechanism of dispersal: statoblasts of this species were found in the ballast tanks of foreign ocean vessels entering the St. Lawrence Seaway in the early 2000s (Kipp et al. 2010). (3) Its distribution on the continent is highly restricted compared to native species. (4) It has a highly disjunct global distribution, in which it occurs far more broadly in Europe than in North America. (5) It has very limited active dispersal capabilities (Hill and Okamura 2005). (6) Passive dispersal mechanisms are unlikely to account for its occurrence in the river. Although the transport of statoblasts by migratory waterfowl has been documented for other species (Figueroa et al. 2004), there is no published evidence of such long-distance dispersal for *L. crystallinus*, and there are no major flyways

linking the St. Lawrence River and Europe; therefore, a natural trans-Atlantic range expansion is improbable. Finally, (7) species with the closest morphological and evolutionary affinities to *L. crystallinus* occur naturally outside of North America (Wood 2002), further suggesting a nonindigenous evolutionary origin.

A common default assumption is that invertebrate species with global distributions are naturally cosmopolitan as a result of effective dispersal mechanisms operating over long time scales (Carlton 2009). This assumption is more often made for species with a prehistorical presence in a region, but it is sometimes applied to new discoveries of widely distributed species (see Chapman and Carlton 1991). In the case of *L. crystallinus*, unsubstantiated literature records would predispose the interpretation of its recent discovery in the St. Lawrence River to reflect an overlooked native species occurrence within a natural Holarctic distribution. However, prior to our study, there was no physical evidence of the occurrence of *L. crystallinus* in North America. Although *L. crystallinus* appears to have been more abundant throughout its European range in the past than it is presently, it can still be found across mainland Europe and in the U.K. (Hill and Okamura 2005; Hill et al. 2007); whereas in North America there are no credible records of the species—or at least none since 1897, if the Kofoid report were to be accepted (Wood 2010). As such, and given the aforementioned criteria, we conclude that *L. crystallinus* was introduced to the St. Lawrence River by ships from a European population. Furthermore, until contemporary or paleolimnological evidence is uncovered to prove otherwise, we contend that the most appropriate interpretation of the global distribution of *L. crystallinus* is that it is a western Palearctic species.

The occurrence of *Lophopus crystallinus* in the St. Lawrence River is one of a few cases of bryozoans that have anomalous global distributions and have been discovered in regions in which they were previously unrecorded. Other examples include the North American species *Pectinatella magnifica*, now spreading in Europe and southeast Asia (Balounová et al. 2013), the Asian species *Asajirella gelatinosa* discovered as a single population in Panama (Wood and Okamura 1998), and another Asian species *Lophopodella carteri* in North America and Europe (Ricciardi and Reiswig 1994; Wood 2002; Sanzhak et al. 2012). These cases suggest that, although the large-scale distribution patterns of some species can be explained

by passive dispersal with migratory birds (Freeland et al. 2000; Wood 2002), human activities likely play a major role in the cosmopolitanism of freshwater bryozoans, including an unknown number of species that are pseudoindigenous in their present range.

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