

Research Article

Natural dispersal of the introduced Asian clam *Corbicula fluminea* (Müller, 1774) (Cyrenidae) within two temperate lakes

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Received: 8 February 2018 / Accepted: 27 April 2018 / Published online: 4 July 2018

Handling editor: David Wong

Abstract

The Asian clam *Corbicula fluminea* has spread rapidly through western Europe and was first recorded in Ireland in 2010. Since then it has been found within four different river catchments including four localities along Ireland's largest river, the Shannon. While three of these Shannon occurrences may have been due to introductions with angling equipment or leisure craft, subsequent expansions will have resulted from natural spread. The dispersal of this clam within two temperate lakes of > 100 km² was examined over a six year period to the autumn of 2016. Downriver and down lake water flow and currents generated by wind result in young clams being distributed by means of a byssal dragline that would appear to explain the distributions obtained.

Key words: spread, current, dragline, byssus, wind, invasion front, Ireland

Introduction

The Asian clam *Corbicula fluminea* (Müller, 1774) is native to Southeast Asia, Australia and Africa (Karatayev et al. 2007), and since the early 1900s it has spread through much of North America (McMahon 1983). Almost seventy years later it invaded South America (Boltovskoy et al. 1997) where it expanded into tropical environments (Bagatini et al. 2007). It was first recorded in Europe in Portugal and France during 1980 (Mouthon 1981) and has since spread through the river and canal network to most of Western Europe and, *via* the River Danube, as far as the Black Sea (Son 2007). In 1998 it was recognised in Southeast Britain (Howlett and Baker 1999) and spread, most probably *via* canals and navigable rivers, within the midlands of Britain (Willing 2011). The species is of concern as it can behave as an ecosystem engineer causing significant impacts on the environment as well as industry (McMahon 1983; Johnson et al. 1986). These impacts are mainly due to rapid increases in biomass but also population collapses (McMahon 1999; Sousa et al. 2009) with economic consequences (Isom 1986).

In April 2010, the Asian clam was first encountered in southeastern Ireland by Sweeney (2009). In a subsequent survey of this region, Sheehan et al. (2014) found clams at densities of up to > 17,000 m⁻² within the upper tidal freshwater areas of the Barrow and Nore rivers. It may have been present here since 2006 or earlier (Caffrey et al. 2011). In August 2010, the species was found in the upper Shannon River at densities of 400 m⁻² to 750 m⁻² (Hayden and Caffrey 2013), 50 km upstream of Lanesborough (Figure 1). In January 2011 it was found in the mid-lake region of Lough Derg where it may have been present since 2007 (Minchin 2014a) (Figure 1). In the following year a separate concentration was located at Lanesborough (Figure 2) at the most northern end of Lough Ree, and another in the lower Shannon River extending into Upper Lough Derg (Minchin 2014b). Since then it has been found within two separate catchments north of the Shannon (Caffrey et al. 2016; Minchin 2017). The clam is expected to become more widely spread on account of its wide range of physiological tolerance (Lucy et al. 2012). This clam is brooded within the demibranchs of adult gills until released as a post-veliger stage, so lacks a veliger pelagic

existence within the water column (Britton and Morton 1982). Here we trace the dispersal of *C. fluminea* within two Irish lakes, most probably by water currents and the possession of a byssal thread which acts as a dragline. This account includes the earlier distributional account of Minchin (2014b).

The sampling regions

Upper Lough Ree: Lough Ree has a surface area of 105 km², a mean depth of 6.2 m, a maximum depth of 35 m and is the second largest lake on the Shannon River (Figure 1). An extensive survey of the entire lake for *C. fluminea* took place in 2012. Clams were found only within a small bay at the northern end through which the river Shannon flows (Minchin 2014b). Substrates in this bay range from cobbles and stones in the main channel, where the depth is close to 6 m, to mud and emergent macrophytes in the shallows. The specific source of the clams, sampled in October 2014 by Caffrey and Millane (2014), was within a power plant discharge canal running parallel to the river leading to the bay; depths here are < 1 m to 2 m and the substrates consist of large stones, pebbles and sand. This is an area fished by anglers. The area south of the navigation cut in this study (Figure 2) was examined in June 2016 at depths of up to 3 m.

The River: A section of the river Shannon with a gradient of ~ 3 m over a distance of 60 km links Lough Ree to Lough Derg (Figure 1). Water flow is generally slow except within narrow and shallow channels. Sediments vary from a bedrock of carboniferous limestone, glacial stones, gravels, crumb-peat and plant detritus to sands and muds. Depths vary along the section, up to 14 m in riverbed depressions. From 2012 to 2016, clams were found from 22 km upstream of Lough Derg to the lake entrance.

Lough Derg: Lough Derg has a surface area of 118 km² and mean depth of 7.5 m (Figure 1). We identified two areas where clams were concentrated. The first, termed the river/upper-lake concentration, was continuous from the river above Lough Derg (see above) to almost a third of the way down the length of the lake (Stations 1–5, Figure 3). The second, termed the mid-lake concentration (Stations 8 and 9, Figure 3), was located in January 2011 (Minchin 2014b). Depths in the former region gradually increase from ~ 4 m to 24 m and in the latter from 3 m to 25 m. Depths further south, in the region of Station 10, where there is a glacial trench, extend to 37 m.

Supplementary material for all regions sampled is included in Table S1.

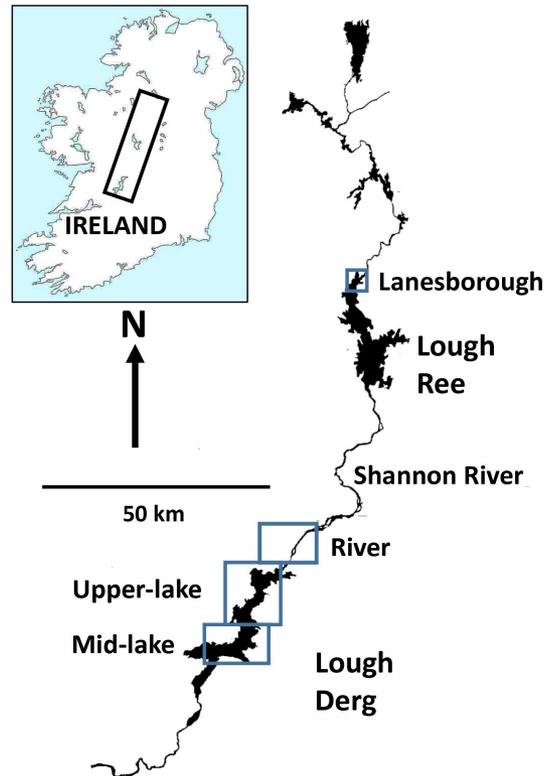


Figure 1. The Shannon River showing the navigation sections surveyed for the Asian clam.

Methods

Sampling in Lough Derg took place from January 2011 to October 2016. Visits to Lough Ree were made in 2012, 2015 and 2016. Altogether the studies involved > 2000 dredge and grab samples.

The dredge was a 5 mm stainless steel mesh basket with a 260 mm diameter “mouth”, 180 mm diameter bottom and 300 mm height; and weighted on one side with lead (Minchin 2014b). It was deployed from a vessel at a speed that would cut grooves in the sediment without becoming buried. On retrieval, samples were flushed in lake water. In 2012, the entire expanse of both lakes, and the river section in between, was surveyed to determine overall clam distributions (Minchin 2014b). The ranges of the different concentrations were recorded in 2012 and 2015 based on the dredge samples.

A Van Veen grab, with an 18 cm × 14 cm (0.025 m²) “bite”, was used to estimate clam densities. Retrieved samples were washed using a 2 mm sieve. Numbers of grab samples ranged from 15 to 64 for each of the Stations 1 to 10 in the river and Lough Derg (Figure 3).

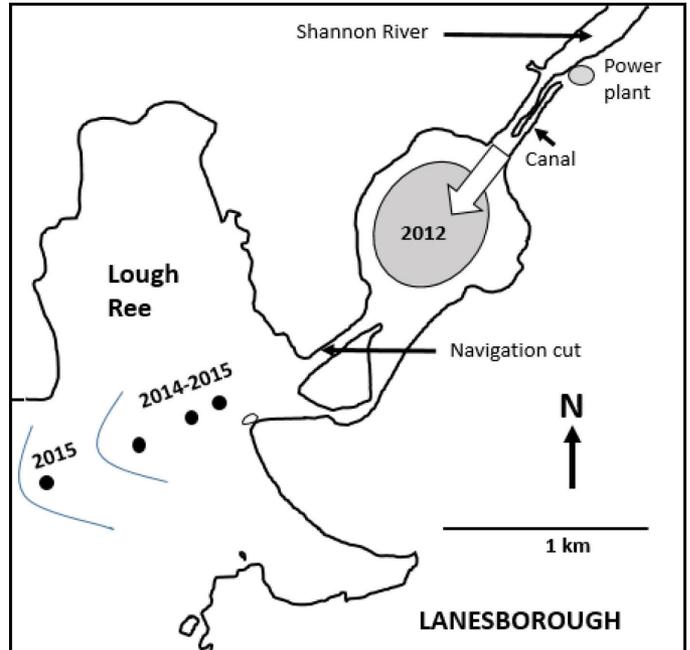


Figure 2. Upper Lough Ree shows the known presence of clams in 2012 (grey shading) and where the clam year-classes have extended their range into Lough Ree (dots) with likely extent of these. The warm water discharge from the power plant is indicated by the canal.

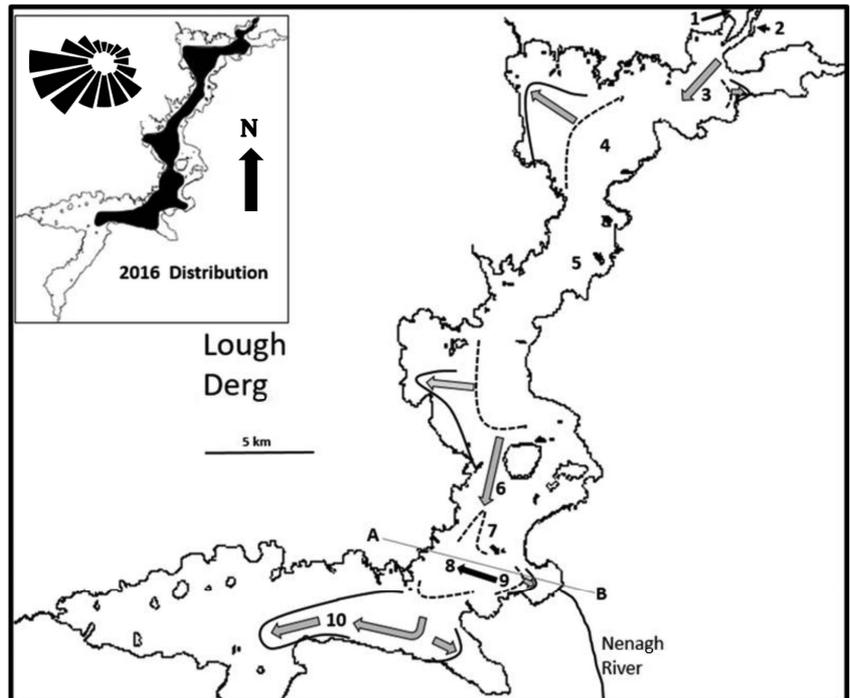


Figure 3. Range distribution in 2012 (dashed lines) and 2015 (solid lines) from the full extent of the ranges in these years. Upper Lough Derg concentration includes Stations 1–5, mid-Derg concentration, Stations 8 and 9. Arrows indicate pathways of spread. Black arrow indicates mid-lake main study area. All station numbers refer to grab samples. A–B transect refers to Figure 8. The inset shows the distribution in the lake by 2016 together with wind rose.

Each of the sampling areas represented by Stations 8 and 9 were about 1 hectare in extent whereas for all other Stations the sampling took place over areas greater than this (Station regions 1–7 and 10).

Corbicula fluminea undergoes reproduction by means of androgenesis (Pigneur et al. 2011). On account of the genetic similarity we refer here to *C. fluminea* as “concentrations” as these would appear

to be part of the A/R European clonal lineage (Pigneur et al. 2014) with this same lineage occurring in Ireland (R. Sheehan, pers. comm.).

Clams were measured for shell-length using Vernier callipers.

Results

Over the study period, *C. fluminea* increased its range, abundance and density in Lough Derg and extended its range in Lough Ree. Small clams often became entangled by their byssus (Figure 4) in the dredge mesh, despite being smaller than the mesh size. Occasionally, clams < 5mm were found attached to drifting plant materials (Figure 5). The largest clams with a byssal thread were 8 mm, found attached to shells or pebbles. None were found attached to floating matter nor in mid-water. Clams were associated with a wide variety of substrates: clay, mud, crumbed peat, plant debris, shells, sands, gravels, pebbles, stones, cobbles and boulders. Finer sediments tended to occur in deeper water or sheltered shallows.

Spread of clams downriver and down lake

A widespread dredge survey throughout Lough Ree during 2012, involving > 200 stations, failed to recover any clams except in a small bay connected to the main lake *via* a navigation cut (Figure 2). By June 2016 the clams had extended their range southwards from the navigation cut by > 1 km (Figure 2). There were two size classes: 6–9 mm and 11–14 mm, representing two year-classes, with the smallest furthest to the south at depths of 2.8–3 m.

Lough Ree lies directly downriver from the Lanesborough power station where there is a warm-water discharge canal running parallel to the river (Figure 2). *Corbicula fluminea* had been found here in 2014 (Caffrey and Millane 2014) and in May 2015 the canal continued to support a dense concentration of clams.

In 2012, in the Shannon River upstream of Lough Derg, clams of ≤ 10 mm made up approximately 20% of samples taken in grabs and dredges (Figure 3), whereas in 2014, in the lake itself immediately below the inlet, they exceeded 60% (Figures 6A and 6B).

The 2012 survey of Lough Derg located two discrete concentrations of *C. fluminea* in the upper and mid-sections of the lake, separated by a distance of ~ 4 km (Figure 3). By 2015, these concentrations had merged, the gap being filled by clams representing the 2013 (Station 6) and 2014 (Station 7) year classes, with modal sizes 5–7 mm and 9–10 mm according to their age. The mid-lake concentration at the Dromaam Deep site at this time consisted of

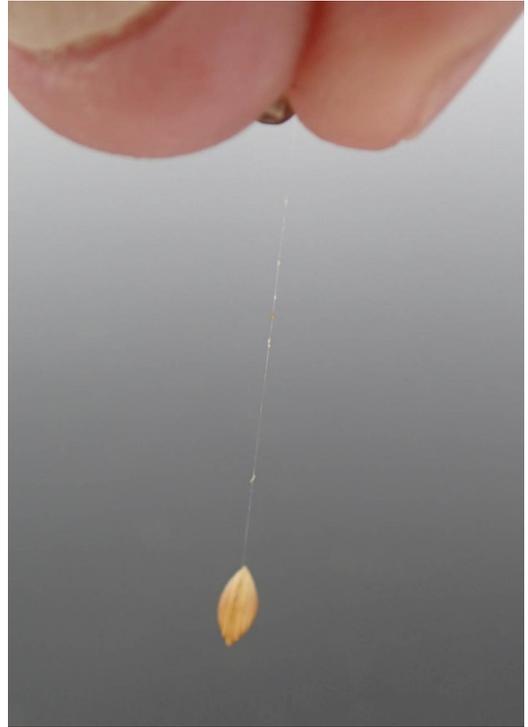


Figure 4. A byssal thread of a clam removed from the mesh of a dredge. Photo by Dan Minchin



Figure 5. An 8 mm clam attached by a byssal thread to drifting plant material retrieved using a dredge. Photo by Dan Minchin.

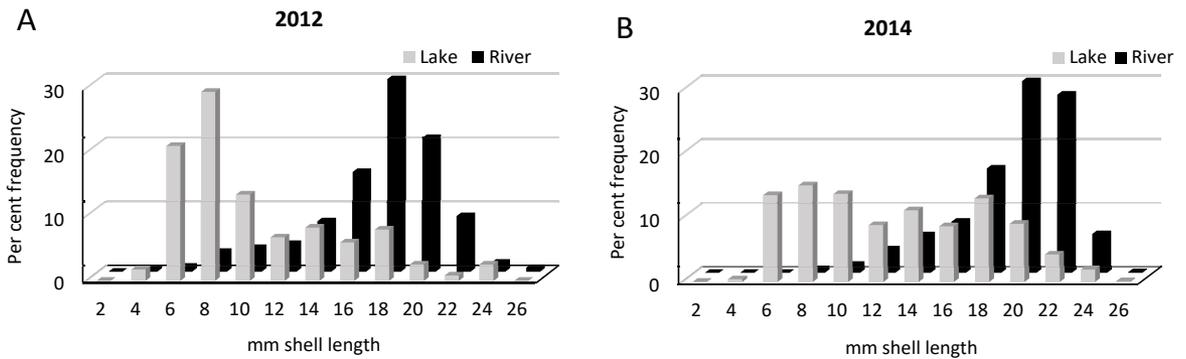


Figure 6. Size distributions of clams within the river and the region below where it enters the lake for 2012 (A) based on numbers 542 (lake) and 829 (river) and 2014 (B) based on numbers 1372 (lake) and 1067 (river).

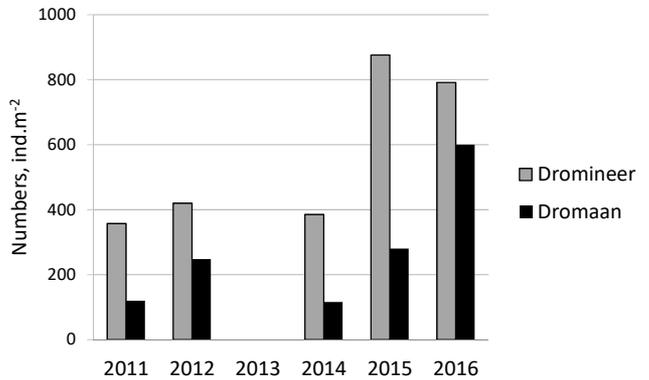


Figure 7. Estimates of density m⁻² at two selected sites in Lough Derg by year, except for no collection in 2013. Grey: Dromineer Bay (Station 4) at 5 m and black Dromaam Deep (Station 3) (20+ m). Based on thirty grab samples.

larger individuals (with a modal size of 19 mm at Station 8), representing the year class before the two concentrations merged. Figure 3 shows the extent of the concentrations for 2012 and 2015.

In September 2015, the southwards expansion of clams in Lough Derg had advanced ~ 5.5 km down-lake since 2012, to a depth of 37m. These clams were 2–7 mm (2014 year class) and 8–14 mm (2013 year class) in size. By 2016 clams had colonised almost two thirds of Lough Derg, from the upstream Shannon River southwards, a linear distance of ~ 42 km, but no further southward spread was noted. The shallowest location with clams (2.8 m depth) was east of Station 9.

Spread of clams from and within bays of Lough Derg

Clams dispersed down-lake in both loughs Ree and Derg, and in the latter case there was a spread into bays on either side of the main lake axis. In 2011, they were abundant in the shallow Dromineer Bay (Station 9, Figure 3) with the smaller clams (modal

size 6 mm) present at the deeper (20 m+) Dromaam Deep (Station 8) 2 km to the west. By 2016 clams at the Dromaam Deep had become larger.

From July 2012 to September 2015, there was a range expansion of ~ 2 km into bays on the west side of Lough Derg, compared with ~ 0.5 km to bays on the eastern side.

Density of clams

In 2012, clam densities in the river and upper Lough Derg (Stations 1 to 5) ranged from 62 to 335 m⁻² according to the nature of the river, lake sediments and currents; over stony substrata only occasional individuals were retrieved. Grabs were most successful in the river (e.g. Station 2) where densities in soft sediments were > 1100 m⁻² in July 2012 and two years later exceeded 1800 m⁻². In upper Lough Derg, samples were mostly from soft sediments and in 2012 densities here ranged from 60 to > 100 m⁻². By 2014, at Station 5, this had increased to > 650 m⁻². With respect to the two principal mid-lake study areas,

over the period 2011 to 2016 the density at Station 9 (Dromineer Bay) increased by a factor of 2 and by even more at the deep-water Station 8 (Figure 7). Further down the lake, behind the diffuse front, Station 10 had the lowest density ($\sim 20 \text{ m}^{-2}$), consisting of small clams.

Discussion

Juvenile bivalves are known to produce a byssus (Yonge 1962) and post-larval stages use a byssal thread as a means of dispersal (Sigurdsson et al. 1976). The threads are produced by *C. fluminea* (Kraemer 1979; Minchin 2014b) in the early parts of their life which help in their dispersal by water currents. The distribution in our two study lakes is more likely to have occurred by this process than by other means. Since no dredging or commercial fishing takes place in the areas studied, the spread of *C. fluminea* is almost certainly due to natural processes. While entanglement of the byssus, or mucus, thread of small clams on bird's feet is a possible means of spread (McMahon 1999), clams do not occur within the wading depths of birds in the Shannon region. This contrasts with the freshwater tidal area of the upper Barrow Estuary $> 100 \text{ km}$ to the south-east, where clams become exposed at low water. Tufted duck *Aythya fuligula* (Linnaeus, 1758) are frequent visitors to the Shannon and dive to feed on zebra mussels (De Leeuw 1997) and perhaps clams. Diving ducks are known to prey upon the related *C. japonica* (O.F. Müller, 1774) in Japan (Yamamuro et al. 1998) but are unlikely to be distributed alive as the duck *Aythya affinis* (Eyton, 1838), when fed the related *C. manilensis* (Philippi, 1844), had no intact clams in the faeces (Thompson and Sparks 1977). Internal transport of clams by birds is unlikely to take place due to body their temperatures of $36\text{--}37 \text{ }^\circ\text{C}$ (Bevan and Butler 1992), exceeding the tolerances of clams (McMahon 1999; Rajagopal et al. 2000). Aquatic mammals such as otters do feed on clams (Edelman et al. 2015) but otters also have high body temperatures of $38 \text{ }^\circ\text{C}$ (Kruuk 1995). Otters are known to have fed on *C. fluminea* elsewhere on the Shannon River (Hayden and Caffrey 2013). Fish do feed on *C. fluminea*. The North American blue catfish *Ictalurus furcatus* (Valenciennes in Cuvier and Valenciennes, 1840) can pass living clams through the gut provided temperatures are below $21 \text{ }^\circ\text{C}$ (Gatlin et al. 2013). Most fishes in the Shannon catchment are cyprinids (Delanty et al. 2016; Kelly et al. 2013) with the ability to crush molluscs by means of pharyngeal teeth. It is unknown whether they feed upon, or have the ability to crush, large clams. Trout, *Salmo trutta* Linnaeus,

1758, are not known to feed on clams nor is the eel, *Anguilla anguilla* (Linnaeus, 1758), which have a preference for chironomids (Ilarri et al. 2014).

An orientated, up-current pedal movement in clams (McMahon 1991) most probably assists in the dispersal of adult clams. This activity was not examined in this study but it might account for the small localized eastward spread of the clam up-current from Station 9. In a North American study, *C. fluminea* was apparently spread up-stream at least 1.2 km per year (Voelz et al. 1998), perhaps by fish. However, the sizes of the clams undertaking such movements were not reported. A possible transport mechanism might be the snagging of young clams by their byssal threads on the gill-rakers of migrating fish. Such a mechanism is unlikely to explain the pattern of spread in the Shannon. Small scale dispersal has been studied in a river in the southern United States using tags; this showed that clams of 12 mm seldom moved more than 30 m in seven months (Cianciolo 2017).

As *C. fluminea* lacks a pelagic larval stage, we contend its release and spread after brooding at $\sim 250 \text{ }\mu\text{m}$ is governed by local current movements and use of its fine byssal dragline (McMahon 1999). In this study, the byssus threads of clams $\leq 5 \text{ mm}$ were regularly snagged in the dredge mesh, their abundance probably underestimated due to their passing through the mesh or being otherwise displaced. They might also spread by attachment to drifting materials. We occasionally retrieved individuals $< 5 \text{ mm}$ attached to plant material collected from deep water (Figure 5).

Prezant and Chalermwat (1984) suggested dispersal by floatation, based on the production of a mucus string that was capable of lifting clams of 9 to 22 mm in an aquarium. Since the earliest likely date for the arrival of *C. fluminea* in Lough Derg is 2007, there were some hundreds of vertical and horizontal plankton net tows, involved during separate investigations, and no clams were found at the surface nor in mid-water during the day or night. Thus, we have no indication of clam floatation dispersal in Lough Derg. It is also unlikely that "byssopelagic" dispersal takes place (Sigurdsson et al. 1976) and that dragging along the lake floor takes place as evidenced by the capture of many specimens in dredge hauls.

The spread from the Dromineer Bay concentration (Station 9) to the Dromaan Deep (Station 8) $\sim 2 \text{ km}$ to the west (section A–B of Figures 3 and 8), was probably driven by currents from the Nenagh River 1.5 km to the east. Leaf litter and twigs from the river drift along this westward track, past the clam concentration towards the deeper, glacial trench. During flooding, a distinct sediment plume follows this same pathway. Also, prevailing westerly winds might generate

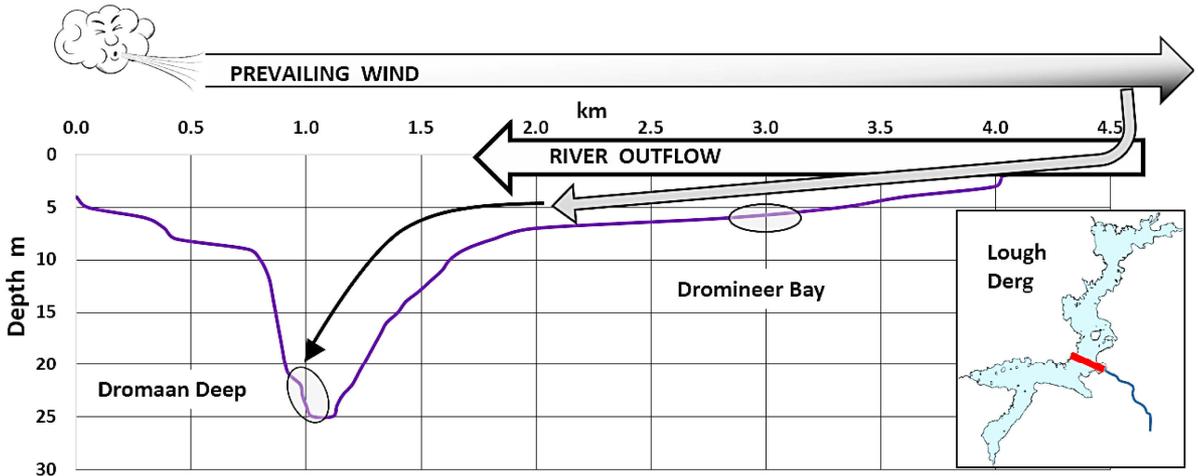


Figure 8. Lough Derg showing transect (inset) and likely vectors generating water currents dispersing small clams from Dromineer Bay (shaded oval) to Dromaam Deep (shaded oval).

an undertow in this direction with the smallest clams being carried to the deeper water. Undertows are known to be generated in lakes, and movements of water following rapid changes in wind direction, with sudden changes in temperature at depths to 20 m, indicate water movements to such depths in Lough Derg (unpublished). Onshore movement of surface water almost certainly results in a near lakebed offshore movement (Greenwood and Osborne 1990) although this is poorly understood in lakes. Langmuir longitudinal slicks (Leibovich 1983), resulting in a downwind drifting of spiral “tunnels” of convergence to shore, are regularly noted on Lough Derg. This is likely to result in a lower water return as an “undertow”, especially under strong wind conditions.

The density of clams at Station 8 over the six year study period increased almost 6 times, whereas in Dromineer Bay (Station 9) it doubled (Figure 7). While the sampling efficiency of the grab is unknown, the results indicate an overall trend of increasing numbers locally. The increased density appears to be due to the additional down-lake spread of small clams from the upper Lough Derg concentration. This generalised pattern of spread down-river, down-lake and into lake bays, observed in Lough Derg (Figure 9), are likely to apply to the future spread of clams in Lough Ree.

The preponderance of larger clams in the river upstream of L. Derg, and greater number of small clams in the lake below the river (Figures 6A and 6B), in two separate years, suggests a general purge of smaller clams to the lake. The low numbers of clams

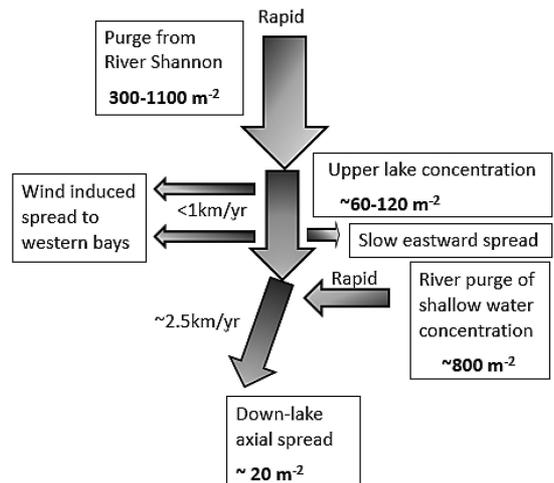


Figure 9. Dispersal scheme of clams in Lough Derg. Estimated density ranges of clams indicated.

entering Lough Ree, taking into account the strong current flow from the river and canal, are less than expected. This might be due to mortalities following their release, which are thought to be high (Franco et al. 2012). The hard substrate in the power plant warm water canal, and strong water flows, may have damaged their small fragile shells. Clams were first discovered in this canal in 2014 (Caffrey and Millane 2014). At this time the clams had already

extended their downriver range as far as the navigation cut. In 2016, the front had extended further south by almost 1 km into Lough Ree, most probably due to water currents.

Densities of *C. fluminea* in Lough Derg are unlikely to attain the 17,000 m⁻² recorded in the Barrow Estuary (Sheehan et al. 2014). This is because in lake ecosystems the greatest densities reported are up to ~ 1,300 m⁻², the higher densities occurring in rivers and canals (reviewed in Lucy et al. 2012). Nevertheless, their biomass, when added to that of the zebra mussel (Zaiko et al. 2014) within the hypolimnion of Lough Derg, could, during a prolonged warm period with slack winds in the late spring and/or summer, lead to de-oxygenation. Such an event arising from increases in temperature (Osman et al. 2015) has been noted in North America (McDowell et al. 2017). In June 2016, following a suspected algal bloom collapse, dissolved oxygen in the hypolimnion of L. Derg declined by ~ 50% over a ten day period (R. Boelens pers. ob.). *Corbicula fluminea* is intolerant of hypoxic conditions (Boltovskoy et al. 1997; Johnson and McMahon 1998; McMahon and Bogan 2001; Mouthon and Daufresne 2006) and extensive die-offs of clams have been recorded (Sickel 1986; Vohmann et al. 2010; Phelps 1994).

The progressive downlake movements are expected to continue. It is unclear what the maximum densities are likely to be but this will probably depend on depth and the nature of the sediments. It is unlikely that *C. fluminea* can be effectively managed as recruitment would appear to take place annually. The natural expansion patterns found in this study are very likely to be repeated elsewhere.

In conclusion, *C. fluminea* expanded its range into and within two Shannon lakes over a six-year period, most probably as a result of human activity but the subsequent secondary dispersal will have been due to water currents, and likely aided by the production of a byssal dragline when ≤ 5mm. Down-river currents carry a preponderance of small clams into lakes. In Lough Derg, the spread appears to be along the central lake axis with a lower spread into bays on either side. The extended range from the river and into Lough Derg is currently the most widespread concentration known in Ireland. The southern-most extension over the six year period was > 5 km. The 4 km gap between the two lake concentrations, determined in 2012, merged within three years. Small clams formed diffuse frontal lines into bays, advancing mainly on the western side; and down lake from where in subsequent years their released brood would enable further expansions. Clams at the most southern front in Lough Derg in 2015 were found at depths up to 37 m. A predicted expansion in

2016, following strong currents from overwinter flooding, did not materialize from these depths. Clams in one shallow bay were probably carried into the nearby deeper water, flushed by river inflow. The colonisation of Lough Ree is at an early stage. Both lakes are considered to be mesotrophic and summertime stratification is usually short-lived and over deeper areas. Nevertheless, following a prolonged period of warm, calm weather in late spring/early summer, the biomass of clams added to those of zebra mussels in the hypolimnion could present a risk of localised mortality followed by de-oxygenation; this would have major consequences for benthic biota.

Acknowledgements

This study, during 2011, 2012 and 2016 was made possible with the financial support from Inland Fisheries Ireland and Waterways Ireland. During 2015 a small grant was provided by the Heritage Council. Our thanks to Rory Sheehan for information on the Irish lineage of *Corbicula*. We gratefully acknowledge the assistance of Marcin Penk during 2014. We also thank Robbie McGrath for providing an ice-breaking service to get access to the lake during a winter. Furthermore we thank the assistance of two referees and the Assistant Editor David Wong for useful comments on our submission. The work was conducted from the vessel *Levitstown*.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Distribution of the principal sites where *C. fluminea* was examined.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2018/Supplements/BIR_2018_Minchin_Boelens_Table_S1.xlsx