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Research Article

Establishment of *Corbicula fluminea* (O.F. Müller, 1774) in Lake Maggiore: a spatial approach to trace the invasion dynamics

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Abstract

We analysed the dynamics of the invasive Asian basket clam *Corbicula fluminea* in Lake Maggiore (Italy), recorded for the first time in August 2010. In order to reveal the extent of its dispersal, we monitored 30 locations along the lake for presence/absence of clams. This assessment of population structure, density and biomass is based on quantitative samples collected along the southern shoreline at four sites with diverse types of habitats. In the present study, the on-going process of *Corbicula* invasion was analysed from a spatial and temporal perspective. We compared density and size structure of the population among the sites (spatial distribution). We attempted to trace the colonization dynamics of the clams, so the invasion dynamics were tentatively reconstructed from spatial distribution of size /age groups and the contribution of the last recruited cohort to total population density along the lake littoral zone. Results from our surveys conducted in 2010–2011 have demonstrated that the Asian clam was well-established in the lake, thus about one-third of the lake (i.e. the southern basin) was already colonized by *C. fluminea* in 2011. Size frequency distribution in autumn 2011 further illustrated reproduction events and new recruitments. Population densities in Lake Maggiore were among the highest ever recorded in an Italian lake. Both the rapid spread of *Corbicula* in the littoral area and the relatively high densities, even at the most recently invaded sites, infer the potential ecosystem impacts associated with a dominant invasive species. Data reported here are not intended to be exhaustive since they concern only two years of investigations, so more detailed studies on both the ecology and invasive habits of this new alien species in Lake Maggiore are planned. The spatial approach used in the present study may clarify the dynamics of this invasion. Future monitoring might help us to disentangle the effects of spatial variability versus temporal succession during the establishment of the invasive species.

Key words: Asian basket clam; size-structure; spatial distribution; population dynamics; Lake Maggiore

Introduction

Records of non-indigenous species (NIS) from aquatic environments are increasing rapidly across the world (DAISIE 2008), not only as a result of escalated human activities but also thanks to increased scientific and public awareness of actual threats of invasive species to biodiversity and ecosystem functioning (Sousa et al. 2011). Invasion ecology has grown immensely in the 50 years since Elton's book on "The ecology of invasions by animals and plants" (Elton 1958) was published (reviewed in Richardson and Pysek 2008; McIsaac et al. 2011). This is becoming an important multi-disciplinary subfield of ecology with growing links to many other disciplines, with continuous improvement of methods and techniques addressing issues related to introduction and establishment of organisms in new locations, their interactions with resident organisms, and the concern of costs and benefits of their presence and abundance with reference to human value systems (Richardson and van Wilgen 2004; Richardson and Pysek 2008). Several aspects of the dynamics of invasions need further investigation (Williamson 1999; Hayes and Barry 2008). Specifically, the dynamics of newly introduced populations have rarely been documented throughout the whole establishment process. As invasive species are hard to detect in the early phase of colonization, they generally attract attention only after the population is established and when their impacts are severe enough. Recent studies confirm that successful establishment of insects, zooplankton, fishes, birds and mammals is correlated with the propagule size (number of organisms introduced in the new environment) and with the propagule number (the number of introduction events) (Kolar and Lodge 2001; Cassey et al. 2004), both incorporated as propagule pressure (Lockwood et al. 2005). Understanding propagule pressure is a relatively new frontier in invasion ecology (Richardson 2004), and provides a key element to explaining why some populations persist while others do not (Kolar and Lodge 2001; Lockwood et al. 2005).

One of the most "efficient" worldwide freshwater invaders, listed among the 100 worst invasive alien species (DAISIE 2008) is the Asian or so called basket clam, *Corbicula fluminea* (O.F. Müller, 1774) (Figure 1). This species underwent a massive global expansion, spreading from its native region (Southeast Asia) to North America (Counts 1986), South America (Ituarte 1994) and to Europe (Araujo et al. 1993). However, the taxonomy and origin of *Corbicula* species established in Europe still seems to be confusing (Sousa et al. 2008a). Thus *C. fluminea* and *C. fluminalis* (Müller, 1774) are frequently mixed together or regarded as different morphotypes instead of different species (Renard et al. 2000; Qiu et al. 2001; Pfenninger et al. 2002; Lee et al. 2005). A complementary genetic characterization is particularly recommended (Wilke and Falniowsky 2001; Sousa et al. 2007), due to the high plasticity of shell morphology (Morton 1987; Baker et al. 2003) induced by different environmental and ecological conditions, both biotic and abiotic (e.g. wave exposure, type of substrate, food and calcium availability and pollutants).

There are many reports on the impacts of *Corbicula* species on specific ecosystem properties (reviewed by Sousa et al. 2008a), such as alteration of nutrient cycling and energy flow (Beaver et al. 1991), phytoplankton depletion (Cohen et al. 1984), resource and space competition with native macroinvertebrates and substrate modification (Werner and Rothhaupt 2007, 2008; Karatayev et al. 2009). Human activities may be also strong impacted, especially due to biofouling (Mattice 1979; McMahon 1983; Darrigran 2002). In contrast to other freshwater bivalves with low tolerance to environmental unsteadiness, *Corbicula* could survive in a wide range of habitat conditions due to its high physiological and ecological plasticity (Byrne and McMahon 1994; Johnson and McMahon 1998; McMahon 2000; McMahon and Bogan 2001; Sousa et al. 2007, 2008a, b). Thus the genus *Corbicula* includes sexual dioecious species (having distinct male and female organisms) and hermaphrodites. The latter could have at least some or all reproducing through a rare form of asexual reproduction, known as androgenesis, in which offspring are clones of their "father" (discussed in details in Pigneur et al. 2011). The same authors claimed the androgenetic lineages of hermaphrodite *Corbicula* as widely distributed in Western Europe compared to their sexual relatives, suggesting that androgenesis would thus play an important role in the invasive success of *Corbicula*, together with high dispersal abilities and r-life strategy (e.g. early maturity, high fecundity, etc.). The ability to couple filter feeding with pedal feeding is most likely to contribute also to the establishment in a novel environment (Hakenkamp and Palmer 1999). Life span varies with habitat, but on average it ranges from 1 to 5 years (Sousa et al. 2008a), even if maximum reported is of approximately 7 years (Hall 1984). Adults can reach lengths up to 5 cm (Hall 1984). Sexual maturation takes from 3 to 6 months, when the shell height reaches 6–10 mm (Williams and McMahon 1989; McMahon 1999). Sousa at al. (2008a) classify clams of 10 mm or greater as adults. The hermaphroditic *C. fluminea* can self-fertilize releasing up to 2000 juveniles per day, with an average annual fecundity of >68000 (Williams and McMahon 1989). Typically, sexually mature individuals reproduce twice a year, initially from spring to summer and again in the late summer to autumn (Britton and Morton 1982). After incubation (brooding) of larvae within the inner demibranch (Figure 1), juveniles are released (c. 250 µm diameter) and able to move actively on the substrate and to drift along rivers. Larvae anchor to sediments, vegetation or hard substrates through a single mucilaginous byssal thread (Britton and Morton 1982). According to McMahon (1999), settled juveniles can grow to > 2 cm shell lengths in 6–12 months. The occurrence of both pelagic and benthic life stages enables *C. fluminea* to spread over long distances by boats, currents, and locally by diffusion. Natural dispersal can occur with water currents (Figuerola and Green 2002)

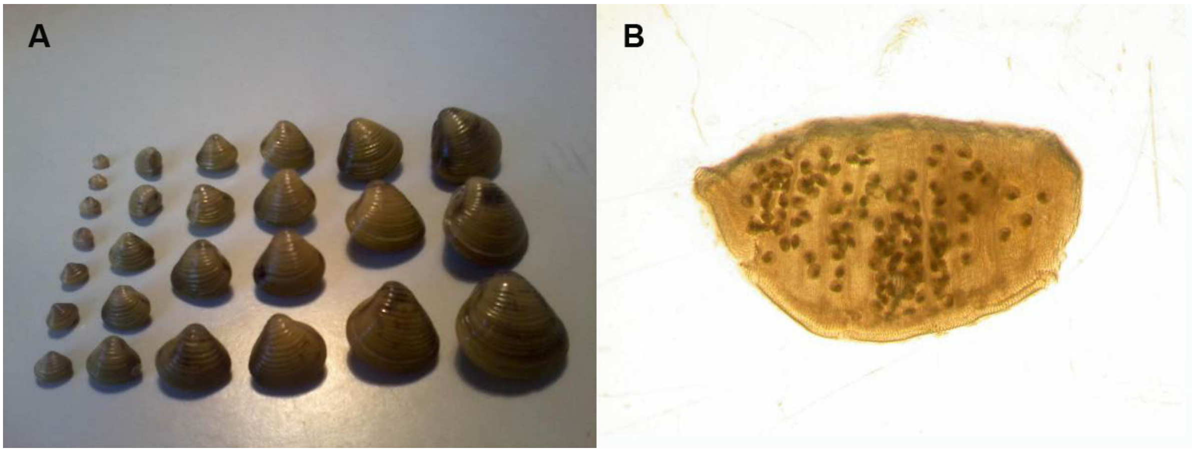

Figure 1. Specimens of *Corbicula fluminea* (**A**) from Lake Maggiore and D-shaped larvae in the inner demibranch of a mature individual (**B**). Photographs by Irene Guarneri.

or when the mucilaginous byssal threads of juvenile clams become entangled in floating debris or on the feet or feathers of waterfowl (McMahon 1999). It is also recognised that the Asian clam has a strong power of locomotion and can move upstream of its own accord (Voelz et al. 1998). All these characteristics are advantageous for the secondary spread of the species already settled in a novel environment. However, its introduction to Europe seemed to be a result of increased international trade, via ballast waters (Karatayev et al. 2007). According to Gherardi et al. (2008), the pathway of *C. fluminea* introduction in Italy is stocking activities, while for *C. fluminalis* is somehow still unknown. Since its first detection in the Po River in the late 1990's (Bedulli et al. 1995; Fabbri and Landi 1999; Mizzan 2002; Cianfanelli et al. 2007), *C. fluminea* has rapidly colonized many waterways in Northern Italy. In the largest Italian lake – Garda , *C. fluminea* was recorded in 2002, and appeared to live in sympatry with *C. fluminalis* detected in 2008 (Ciutti and Cappelletti 2009). *C. fluminalis* was also recorded in a small alpine lake in Trentino province (Northern Italy) (Lori et al. 2005). The establishment process in vast freshwater bodies in Italy is on-going, as we found *C. fluminea* in Lake Maggiore in August 2010. With this study we aimed at reporting the settlement of *C. fluminea* in Lake Maggiore (Northern Italy) by providing the first results of age/size spatial distribution of its populations at different littoral sites in favour of tracing the establishment process of the species.

Methods

Study area

Lake Maggiore (latitude N 45°50'19"; longitude E 8°37'17") is a tectonic-glacially formed lake in the southern side of the Alps, at the border between Switzerland and Italy (Figure 2). It is the second largest and deepest lake in Italy with a surface area of 212.5 km^2, maximum depth of 372 m, and a shore length of 170 km. Input from a catchment area of 6.599 km^2 into the lake occurs directly and through three major (Ticino, Maggia, Toce) and eleven smaller rivers and streams. The Ticino River is the only outflow from Lake Maggiore. With its 170 km of shore line it is an internationally famous European resort. Besides recreational activities (swimming, sport-fishing and yachting), the lake is a water resource for the residents in the area, in terms of fisheries and navigation. The largest proportion of inhabitants is distributed in the southern part of the catchment area, where the main industrial activities are also located. Since the early 1980's the lake underwent a progressive re-oligotrophication and presently is classified as oligo-mesotrophic (Salmaso and Mosello 2010). The wide range of habitats along the shoreline mirrors natural and human-mediated areas, together with features such as wave movements, breakers, littoral currents, and a changing water table. Steep and rocky banks mainly characterize the upper (northern) part of the lake; except for the area of the Magadino floodplain (Canton Ticino, Switzerland). In contrast, the southern

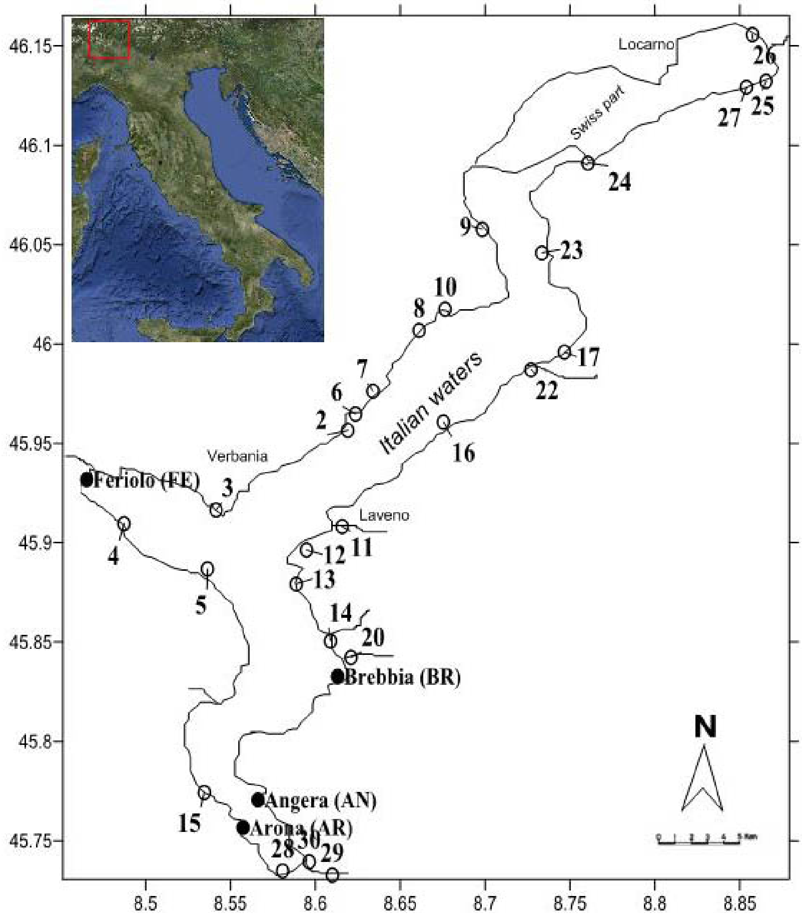

Figure 2. Sampling locations in Lake Maggiore in 2010–2011; ●–quantitative sites; FE= Feriolo; AN= Angera; AR=Arona; BR= Brebbia ○- qualitative sampling (see Appendix 1 for geographic coordinates).

is characterised by gentle slopes with a soft to sandy-gravelly bottom. The lake is already colonised by other alien bivalves- the zebra mussel *Dreissena polymorpha* (Pallas, 1771) and Chinese pond mussel *Anodonta woodiana* (Lea, 1834) (Kamburska et al. 2013).

Sampling strategy

Clams were found accidentally in August 2010 while sampling for littoral benthic organisms. After the discovery of *C. fluminea*, we monitored (presence/absence) a large variety of littoral habitats (in total 30 locations) to trace its diffusion along the shoreline of both the Italian and the Swiss part of the Lake in September 2010 (Figure 2, Appendix 1). Shallow areas were visually inspected, while scuba dive surveys were undertaken in the deeper areas and at tributary infalls up to 15 meters depth.

Four sites were selected for quantitative analyses. Two of these four locations were close to the northernmost limit of *Corbicula* distribution in the lake: Feriolo (FE) on the western, and Brebbia Sabbie d'Oro (BR) on the eastern side of the lake (Figure 2). FE is under pressure of recreational activities (boating, bathing, etc.), while BR is relatively undisturbed area. At both sites, small scale differences in wave intensity resulted in high sediment patchiness. Arona (AR) and Angera (AN), the other two sites (Figure 2), are located in the southern part of the lake basin, where heavy recreational boat traffic is present. The sediment texture is quite dissimilar: a high ratio in silt and terrestrial leaf litter had accumulated at the AR site. In contrast, a deposition of coarser sediment, poor in silt was evident at the (AN) site. Here we discuss data obtained during September-October in 2010 and in 2011. At each site,

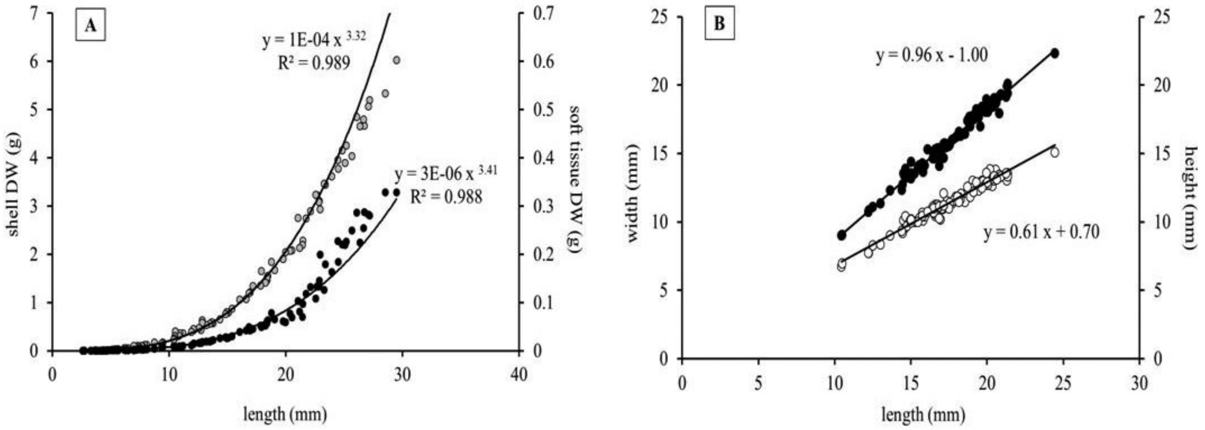

Figure 3. Curvilinear regression lines and equations of *Corbicula fluminea* shell length, mm vs (**A**) shell (empty circles) and soft tissue (black circles) dry weight (DW, g); (**B**) shell width, mm (empty circles) and height, mm (black circles).

bivalves were collected by sieving the sediments through a 0.5 mm^2 mesh size net within 0.5 m^2 quadrat samples, randomly positioned. Samples were taken at least in triplicates, to cover an area between 1.5 to 5 m^2 (< 1.5 m water depth, maximum to 50 meters from the shoreline towards the deep). All of the surface-dwelling and burrowed clams to a depth of *circa* 15 cm within each quadrat were retained, so the density of clams per square meter was calculated. Conventional morphometric characteristics -shell height H (umbo to gape), length L (anterior to posterior margins of the shell) and width W of each specimen were measured using electronic calliper (to the nearest 0.01 mm). Smaller specimens (< 5 mm) were measured later in the laboratory under a stereo-microscope (eye piece micrometre at 25). To determine the biomass of *C. fluminea*, we used in total 250 specimens collected from all four sampling sites. After morphometric measurements, soft tissues from each animal were carefully separated from the shells with dissecting instruments. Both, soft tissues and shells were dried individually at 105°C for 24 hours and weighed for dry weight (DW) afterward.

Data and statistical analyses

Relationships of soft tissues DW and DW of shells to shell L (mm) were nonlinear, so we applied a curvilinear regression model using the method of least squares, a mathematical technique for predicting a dependent variable using an independent variable. The best fitting of data was performed by comparing the AIC (Akaike's Information Criterion) value of the exponential model ($y = ae^{bx}$) with that of the logarithmic model ($y = ax^b$), where y is the DW of either soft tissue or shell (in g), x is the shell L (in mm), a is the intercept, and b the regression coefficient. These two equations (Figure 3a) allowed the calculation of soft tissues DW, the shells of the individuals from each sampling site, and the total biomass (soft tissues plus shells) expressed in $g.m^{-2}$ (Table 1). Morphometric relationships length-width-height of *C. fluminea* was expressed by regression equation (Figure 3b).

Length frequency distribution plots by size classes of 0.5 mm interval starting from 1.0 mm were generated (Figure 4). The age structure was projected based on length-frequency analyses and seasonally oscillating version of von Bertalanffy's growth formula recommended by Cataldo and Boltovskoy (1998). Using our data, the estimated potential size range for one year-old individuals was from 15 to 22.5 mm; for two years a range of 23.5 to 27 mm, and for three years from 27 to the maximum observed 31 mm; growth constant: 0.65 (Cataldo and Boltovskoy 1998). The new recruitments are sized to 14–14.5 mm. We continued testing these intervals with our new monthly data, even if in the case of *C. fluminea* interpretation of growth and definition of age size is still questionable (Fritz and Lutz 1986; Cataldo and Boltovskoy 1998).

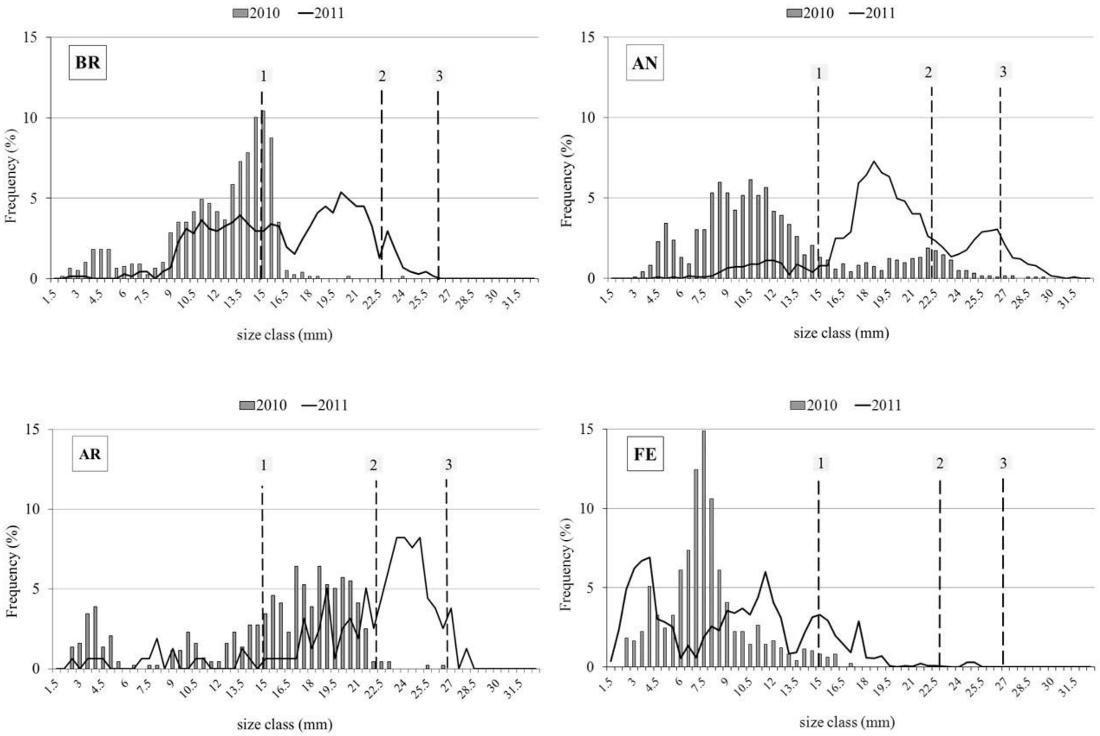

Figure 4. Frequency distribution plots of different size classes of *Corbicula fluminea* in Lake Maggiore in autumn 2010 and 2011 (sampling sites BR-Brebbia, AN-Angera, AR-Arona, FE-Feriolo; Vertical lines and nearby numbers indicate approximated age of cohorts).

Table 1. Descriptive statistics of selected parameters of *Corbicula fluminea* in autumn; sampling sites: BR- Brebbia, AN- Angera, AR-Arona, FE- Feriolo (see Appendix 1 and Figure 1 for geographic coordinates and position); N - number of measured specimens.

site-year (number of replicates)	Density (ind m^{-2})		Biomass ($g.m^{-2}$)		Length (mm)			
	mean	st.dev	mean	st.dev	N	mean	st.dev	range
BR-2010 (4)	1249	904	254	16	1554	12.04	3.5	1.95-23.67
BR-2011 (9)	981	420	1392	645	604	16.31	4.4	2.13-25.5
AN-2010 (2)	1222	102	853	243.8	2444	11.7	5.2	2.74-29.41
AN-2011 (4)	1247	745	3051	1479.4	1247	19.71	4.5	4.06-31.03
AR-2010 (5)	87	33	103	29	437	14.9	5.6	2.19-26.46
AR-2011 (7)	90	78	277	216.1	158	21.09	5.3	2.13-27.83
FE-2010 (3)	655	379	41	16.8	982	7.38	2.7	2.19-16.74
FE-2011 (5)	1148	1123	484	299	1785	8.87	5.02	1.13-24.57

Descriptive statistics (means, standard deviation-st.dev.) of measured parameters (length, density, and biomass) were reported. Using Statistica (data analysis software system), version 7 (STATSOFT, Inc., 2004), a post hoc test (Tukey honest significant difference test) was performed for multiple comparisons to determine significant differences of variable means between groups (sampling sites).

Results

Clams were found initially in August 2010. In total 30 locations were monitored for presence/ absence of *C. fluminea;* specimens were found only at 11 sites (Appendix 1). Our qualitative survey demonstrated that clams were already spread along the southern part of the lake, up to 10 meters water depth. The northernmost distribution limits were the locations Brebbia Bozza on the eastern side, and Suna (sites N20 and N3 on Figure 2) on the western side respectively. Collected clams were attributed to *C. fluminea* according to morphological characteristics, such as shell outline, shape, sculpture, and pigmentation (Lee et al. 2005). Quantitative analysis further revealed the distribution pattern in the lake. Length, density, and biomass of *C. fluminea* population in autumn differed between sampling sites, as well between years, 2010 and 2011 (Table 1). Thus the highest density was registered at BR (1249 ind.m^{-2}) and AN (1222 ind.m^{-2}) locations in autumn 2010, both at the eastern side of the lake. In contrast, *C. fluminea* was much lower at the western side of the lake: at FE twofold lower (655 ind.m^{-2}) compared to BR and AN, while at the AR site it was merely 87 ind.m^{-2}. Clams sized >25 mm were found only at the most southern sites- AR and AN (Table 1). Maximum length reached 24 mm towards the north at BR, and only 16.7 mm at the northernmost site FE. An increasing trend in size appeared following the order: FE<BR<AR<AN. Contrasting size structure (Figure 4) resulted in a distinctive total biomass pattern at four sampling sites. The plentiful population at AN location resulted in highest biomass (853 g.m^{-2}), while equally dense clams at BR reached only 254 g.m^{-2} (Table 1). Although quite abundant at FE site, small sized specimens correspond to the lowest estimated biomass (41 g.m^{-2}), whereas the lowest density at AR attained 103 g.m^{-2} total biomass.

An asymmetric multimodal mode of size distribution appeared at BR, AN, and AR locations, while it was clearly unimodal at the FE site (Figure 4). The proportion of recently recruited individuals to total population density also varied among the sites (Figure 4). Three cohorts were distinguished at AR (< 5 mm, from 9 to 12 mm, >13 mm individuals, the latter most abundant). According to estimated age, clams in the first and second cohort shared 30 % in total density, and corresponded to the new recruitment of 2010. The third cohort (>13 mm) was mainly constituted of one-year olds (about 68%) and two-year old clams, which were only 2 % of the total density. Individuals from 5 to 10 mm in length were missing, but were moderately or well represented at the other three sites. A similar pattern could be recognized at the AN site, where the share of first (4–6 mm) and second (7–14 mm) cohorts of clams was over 75% in total density. The remaining 25 % were composed of one-year (18%), two-year (6.5%) and three -year old (0.5%) clams. The population at the BR site consisted of 61% of younger than one year clams, followed by one-year olds (about 39%), whereas only 0.1% of total clams density was 2 years. The youngest population appeared at FE, where clams younger than one-year comprised 96% of the total density, the rest, 4%, were one-year old specimens (Figure 4).

Corbicula expanded gradually at the north-eastern side of the lake in autumn 2011 (Appendix 1). In that year, the total density of *C. fluminea* population slightly increased except for the BR site. There was a clear upward trend in size of clams shell, concomitant with an increase in total biomass at all sampling sites (Table 1). About 3 kg.m^{-2} of biomass was registered at the AN location, and was also high at the BR site (1.4 kg.m^{-2}). Size frequency distribution plots further exposed a lengthening of size range of individuals collected in autumn 2011 (maximum L= 31.03 mm), e.g. suggesting an intensive growth of cohorts during preceding years including the latest recruitments in 2010 (Figure 4). Small sized organisms, aged up to one year, were again most prevalent at the FE site (about 88 % of the population), while this age group made up around 41 % at BR, and only 10–11 % at AR and AN sites respectively. Tukey honest significant difference test revealed statistically significant differences between the sampling sites in the mean values (2010–2011) of species density at $p < 0.05$ and in maximum length at $p < 0.1$ (Appendix 2a, 2b).

Discussion

Here we report the establishment of *C. fluminea* in Lake Maggiore. Nonetheless the occurrence of *C. fluminalis* could not be excluded as both species for instance seemed to live in sympatry in Lake Garda (Ciutti and Cappelletti 2009). Recently Pigneur et al. (2011) found three West European morphotypes belonging to three distinct nuclear and mitochondrial lineages, so the species status of the morphotypes remains still doubtful. Shells in Lake Maggiore were oval and elongated- an indication of slower growth rates in crowded conditions (e.g. Seed 1968; Stirling and Okumus 1994). Species density we have found in Lake Maggiore (87–1249 ind.m^{-2}) was among the highest ever registered in invaded Italian lakes (Fabbri and Landi 1999; Nardi and Braccia 2004; Ciutti et al. 2007; Pezzi 2008; Ciutti and Cappelletti 2009). In fact, Asian clams densities commonly exceed 1000 ind. m^{-2} (McMahon 2000; McMahon and Bogan 2001; Mouthon 2003; Sousa et al. 2005, 2008b), only occasionally reaching >10000 ind. m^{-2} (Eng 1979; McMahon and Williams 1986; Correa et al. 1992; Boltovskoy et al. 1997) and up to hundred thousand ind.m^{-2} (Cherry et al. 1986; Cohen and Carlton 1995). Such high densities are quite exceptional and generally typical for canals and rivers (reviewed in Lucy et al. 2012). However, amounts of close to 3000 ind. m^{-2} were reported from Lake Constance (Werner and Rothaupt 2007), a lake not far from Lake Maggiore in respect to climatic and trophic history.

Spatial and temporal aspects of invasion dynamics are of particular importance not only to track the spread of a new species, but also to predict its further dispersal. Here we hypothesize that the species first settled in the southern basin of the lake, starting from a population established already in its outlet River Ticino (Nicolini and Lodola 2011). Potential vectors could be of human mediated or natural spread sources. For example activities such as bait bucket introductions, accidental introductions associated with imported aquaculture species (Counts 1886), or as a food item in markets (Foster et al. 2008) are possible. Other noteworthy dispersal agents are water currents or flooding events (Isom 1986). Quite possible the species was conveyed via diffuse upstream movement of its larvae and/or transportation by boats entering the lake through the river outlet. In this respect, the size structure of the population in autumn 2010–2011 is a clue to tracking the settlement process and to reconstruct different phases in the invasion dynamics of the species. Thus the southernmost sites (AR and AN) were found to host the oldest (3 year-old), and the biggest (>26 mm body length) individuals in 2010. The BR location is likely to have established a population ≤2 years ago, while the high frequency of small sized individuals and deficiency of large-sized could suggest that FE was likely the most recently invaded site. The assumption is that *C. fluminea* has been established in the lake for some years and it is likely the spread started after 2007. In spite of such a recent introduction, this species has already populated about one-third of the lake shoreline. Differences in population density and size structure among the sampling locations may not only result from different period of establishment, but also as a consequence of diverse abiotic conditions. For example Boltovskoy et al. (1997) stress the usefulness of population structures as an indicator of overall environmental fitness. Abiotic conditions that might impact population development include redox potential, concentration of nutrients and calcium, water hardness, organic matter, sediment structure and texture, and heat wave (e.g. Sousa et al. 2008a; 2008d). In our case, soft sediments as those at AR are less favourable for *Corbicula* than fine to coarse sandy substrate found in the other sampling locations (Cordeiro and MacWilliams 1999; Paunović et al. 2007; Schmidlin and Baur 2007; Sousa et al. 2008b). A low tolerance to hypoxic conditions (reviewed in McMahon 2000), as at AR, may also explain a higher density of *Corbicula* in sandy- and gravel-rich bottom habitats (AN, BR) where active water circulation oxygenate the sediments. In contrast, the fine black muddy sediment characterizing the AR site, along with a reduced water circulation, suggest that hypoxic conditions are likely to occur. The significance of thermal regimes on the clam's reproduction and growth, together with the importance of food availability for recruitment (Cataldo and Boltovskoy 1998) may also well contribute to current dynamics of *C. fluminea* in the lake, although the species has a relatively faster recovery rate after a disturbance compared to native species of Unionidae (Sousa et al. 2007). Moreover, considering the environmental limits for *C. fluminea* (reviewed in Lucy et al. 2012), it seems none of the recognized factors (salinity, temperature, calcium and oxygen concentration, pH) would limit the spread of the species in the lake. Pronounced new recruitments were manifested at FE site (88% of the population) in autumn 2011, while lower at other locations. This does not imply with certainty, insufficient reproduction or juvenile mortality. Possible explanation could be that juveniles settle in sites not surveyed, possibly in shallow areas with submerged vegetation, and after that migrate to deeper sites (Sousa et al. 2008d). However, clams of previous recruitments, including those of 2010 appeared to be fast growing: as evident by recorded extension of size range and increase in total biomass in 2011.

Our data are not exhaustive, so further investigations into the ecology and invasive behaviour of the Asian clam in Lake Maggiore are planned. However, the rapid spread of *Corbicula* along the littoral area and its relatively high densities, suggest its potential to become a keystone littoral species. The species is likely to continue to expand northwards from the areas where it is presently confined. Recreational boats and anglers in the lake, often accessing river tributaries (Ticino, Toce), contribute also to species proliferation from south to north and to upriver spreading. Many biological invasions do not occur as a gradual expansion along a continuous front, but result from the expansion of satellite populations that become established at ‘invasion hubs’ (With 2002). Eradication of *C. fluminea* from the southern lake basin is almost impossible, so will incur significant costs and will be highly disruptive to the habitat and its associated biota. Methods to control or restrain *C. fluminea* should be focused not only on reducing its density and thus moderating its impacts on the ecosystem, but also to reducing the opportunity for *C. fluminea* to disperse, or be spread, within and outside Lake Maggiore, which is presently acting as an active invasion hub. Still several uncertainties exist about the possible predators that could benefit the high abundance and biomass of *Corbicula* in the lake. The ecological role of *C. fluminea* in the functioning of lake littoral food webs has still to be clarified. Failure to act rapidly to *C. fluminea* could result in the demise of a number of resident protected fish and invertebrate species in the lake as suggested by our recent observation of an average 90% decrease in density of native *Unio elongatulus* in the more heavily colonized sites (Riccardi et al., unpublished data). Understanding the spatial dynamics of invasions can provide key insights into the development of strategies to control invasive species (Florance et al. 2011). Therefore future monitoring might help us to disentangle the effects of spatial variability versus temporal succession in this *Corbicula* invasion.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Records of *Corbicula fluminea* (Lake Maggiore, Northern Italy) in autumn 2010 – 2011.

Appendix 2a. *Tukey* honest significant difference test in mean density (ind.m^{-2}) of *C. fluminea* between the sampling sites.

Appendix 2b. *Tukey* honest significant difference test in maximum length (mm) of *C. fluminea* between the sampling sites.

Appendix 1. Records of *Corbicula fluminea* (Lake Maggiore, Northern Italy) in autumn 2010 – 2011. Locations refer to sites shown in Figure 1 (*-first record; **-quantitative sampling).

N of site	Sampling site, location	Coordinates of the sampling sites in decimal degrees		Record date presence/absence	
		Latitude, N	Longitude, E	Sept-2010	Sept-Oct 2011
1	Feriolo (port, boats) (** FE)	45.931856°	8.4654046°	+	+
2	Sasso di Ghiffa	45.956624°	8.619163°	-	-
3	Suna	45.928278°	8.542491°	+	+
4	Baveno	45.908254°	8.506656°	+	+
5	Stresa	45.886892°	8.536560°	+	+
6	Panizza beach	45.964854°	8.623704°	-	-
7	Oggebio -Sierra beach	45.976358°	8.633968°	-	-
8	Oggebio- la cascata	46.006948°	8.661128°	-	-
9	Cannobio	46.060114°	8.706497°	-	-
10	Cannero	46.017677°	8.676475°	-	-
11	Laveno	45.908196°	8.615809°	-	-
12	Cerro	45.896405°	8.594866°	-	-
13	Reno	45.882404°	8.599486°	-	-
14	Monvalle	45.850651°	8.608947°	-	+
15	Parco Cavalotti Intra	45.780418°	8.542939°	-	-
16	Porto Valtravaglia	45.960799°	8.675460°	-	-
17	Luino	46.002260°	8.739796°	-	-
18	Arona (** AR)	45.75681°	8.557483°	+* Aug 2010	+
19	Angera(**AN)	45.770696°	8.576212°	+	+
20	Brebbia- Bozza	45.842359°	8.621038°	+	+
21	Brebbia- Sabbie d'oro (** BR)	45.832833°	8.6132°	+	+
22	Germignaga	45.995885°	8.721303°	-	-
23	Maccagno	46.045927°	8.733452°	-	-
24	Zenna (border Italy/Switzerland)	46.104111°	8.753814°	-	-
25	Gambarogno (Switzerland)	46.146976°	8.850496°	-	-
26	Reviscài (Switzerland)	46.165635°	8.850482°	-	-
27	Ronco Tenero (Switzerland)	46.145528°	8.847707°	-	-
28	Dormelletto	45.734925°	8.580817°	+	+
29	Sesto Calende	45.732845°	8.61°	+	+
30	Lisanza	45.739491°	8.596393°	+	+
sites where *Corbicula* occurred				11	12
Corbicula absent				19	18

Appendix 2a. *Tukey* honest significant difference test in mean density (ind.m^{-2}) of *C. fluminea* between the sampling sites (BR, AN, AR, FE) (**-significant at p < 0.05*).

sampling site Mean (ind.m^{-2})	BR 1115	AN 1234.5	AR 88.843	FE 901.35
BR		0.927	*0.023 **	0.721
AN	0.927		*0.015**	0.437
AR	*0.023**	*0.015**		*0.049**
FE	0.721	0.437	*0.049**	

Appendix 2b. *Tukey* honest significant difference test in maximum length (mm) of *C. fluminea* between the sampling sites (BR, AN, AR, FE) (**-significant at p < 0.1*).

sampling site Mean (mm)	BR 24.59	AN 30.22	AR 27.15	FE 20.66
BR		0.349	0.820	0.590
AN	0.349		0.736	*0.099**
AR	0.820	0.736		0.264
FE	0.590	*0.099**	0.264	