

Research Article

"The day after tomorrow": anatomy of an 'r' strategist aquatic invasion

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Abstract

Invasive alien species, following an arrival, undergo different colonization stages. The full pattern of an invasion is seldom tracked as many studies on invasive processes only take place over a few years. In this study the invasion of the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), was followed for more than a ten-year period. It developed an expansion stage with peak abundance (outbreak) four to six years following arrival. Thereafter the population entered an accommodation stage at a lower level of abundance and biomass. This pattern was repeated for two separate lakes on the Shannon River in Ireland. In concert with the biomass at each invasion stage there were changes to the transparency and chlorophyll a levels of lake water. Based on the results of the current study, revision of the terminology of invasion stages is suggested. Providing some additional insight into the invasion process, it can be accorded with existing frameworks and bioinvasion impact assessment approaches. The sequence of invasion stages with corresponding direct (semi-quantitative) and indirect (qualitative) features as well as examples of empirical evidence is presented in this account.

Key words: *Dreissena polymorpha*, zebra mussel, Ireland, invasion stages, outbreak, accommodation

Introduction

Invasive alien species (IAS) in aquatic ecosystems are often not noticed until such time as their impacts become apparent. Due to infrequent monitoring or poor recognition in the early stage of invasion (Bax et al. 2003; Geller et al. 2010), management methods may not be practical to either eliminate them or otherwise reduce their impact. Early intervention, when populations are still confined to a small area and at a low density, maximizes the probability of effective management and enables a greater range of management options (Simberloff 2001; Darling et al. 2011). Since it is difficult to establish whether an alien species will become a pest or stay benign, it is often unclear whether management measures are required at an early stage.

The dynamics of the invasion process with reference to different states of an invader's population have been addressed many times in the literature, starting from the early works on invasion ecology (e.g., Elton 1958; Williamson and

Brown 1986) and acclimatization of intentionally introduced species (e.g., Karpevich 1960). The proposed theoretical invasion curves generally evolve from a period of low abundance followed by a rapid increase (e.g. Strayer and Malcom 2006; Pace et al. 2010; Moore et al. 2012). Such patterns vary according to intrinsic or extrinsic factors, e.g. changes in the IAS population, changes within the invaded community, cumulative abiotic changes, interactions between the IAS and other variables that control the ecosystem (Strayer and Malcom 2006). Invasions of highly impacting IAS have a series of defined stages (e.g., Williamson 1996; Richardson et al. 2000; Reise et al. 2006; Strayer et al. 2006; Davis 2009; Blackburn et al. 2011), yet there is little agreement as to how these stages should be practically distinguished and named. Most agree to three major stages following arrival: establishment; expansion; and the post-expansion or adjustment phase. The establishment stage involves colonization and self-sustainability from recruitment successes. There is little expansion at this time (Reise et al. 2006; Wang and Wang 2006). The population may

subsequently develop either, a constant linear expansion, or a biphasic expansion with an initial slow linear expansion followed by a more rapid linear expansion, or an exponential increase (Wangen and Webster 2006). The final phase, the adjustment stage (also referred to as ‘saturation’, ‘naturalization’ or the ‘chronic’ phase) is attained when the population stabilizes and the geographical extent of the invasion remains approximately constant (Reise et al. 2006; Wangen and Webster 2006). This normally follows a period of high IAS abundance once confined within its invasive range.

However, invasion stages are of little value to managers since they lack the magnitude of impacts caused by an IAS for each invasion stage. There is also a lack of empirical support on the essential thresholds and attributes for distinguishing each stage of the invasion process (Pace et al. 2010; Strayer et al. 2011). In order to optimize the existing monitoring systems and increasing emphasis given to the bioinvasion issues, a substantial effort is put into development of repeatable, rapid and cost-effective diagnostic tools that are able to identify and quantify ecosystem-wide impact of the established IAS. Rapid assessment methods have proved to be suitable for monitoring purposes, when assessing the environmental status of ecosystems in relation to different anthropogenic impacts. Rapid assessment has been successfully applied for surveillance of marine IAS (e.g., Ashton et al. 2006; Minchin et al. 2006a; Minchin 2007). The approach is based on using surrogate indicators that are easy to access and identify, restricting sampling effort, extrapolating the results (Oliver and Beattie 1996). Therefore, we suggest, that empirical evidence of different invasion stages, once established and properly formalized, can provide sound qualitative and quantitative information on the status of the considered IAS population with relatively small investment of time and effort. Moreover, the approach does not require advanced expertise and may serve for raising public awareness and “citizen science” campaigns. The knowledge on the invasion progress of a particular IAS would enhance management opportunities and help to select an appropriate and timely measure to prevent or mitigate impact. For managers it is also important to obtain reliable and scientifically-based information on when these measures are of no practical value anymore due to IAS having become accommodated within the ecosystem and naturally confined by established ecological relationships.

However, in order to develop such “surrogate indicators” for rapid assessment purposes and understand how an invasion progresses in general, long-term surveillance is needed. Most IAS population studies have been confined to a few years, and most of these are usually undertaken some years after an IAS appears or even decades to centuries later (Strayer et al. 2006; Burlakova et al. 2006; Strayer 2012). In this study we examine the invasion of the zebra mussel *Dreissena polymorpha* (Pallas, 1771) in two lakes on the Shannon River in Ireland over a ten-year period. Taking into account that there are few long-term studies that have followed purposefully and systematically zebra mussel populations from their initial invasion (Burlakova et al. 2006), the reported findings will contribute to the general knowledge on the population dynamics of this IAS. Simultaneously, we followed important features of the invasion process – direct (quantitative and semi-quantitative) and indirect (qualitative) evidences of environmental changes caused by a zebra mussel invasion. We hypothesize, that (i) different stages of invasion could be identified based on population characteristics of IAS and environmental impact magnitude; (ii) given similar environmental conditions, the invasion of IAS will progress in a similar pattern (in terms of impact magnitude, timing and sequence of invasion stages); (iii) there are different qualitative evidences of IAS progress in an ecosystem that are related to the species impact and are typical for a certain stage of invasion. In the current study these hypotheses were tested in relation to a well-known (model) species *D. polymorpha*. However, the presented approach could be applied in a wider sense for invading byssate molluscs in general, or adjusted to other key aquatic invaders, which induce well pronounced environmental impacts at different ecosystem levels. Based on our current findings we suggest adjustments to the terminology of invasion stages which may complement the existing frameworks by adding more details and practicalities.

Methods

Study areas

Lough Derg and Lough Ree, are the most downstream lakes on Ireland’s largest river, the Shannon River (Figure 1), draining 11,250 km² (17%) of the Irish land surface area. While the river’s water transparency is reduced by humic acids from peatland runoff, it is buffered to produce

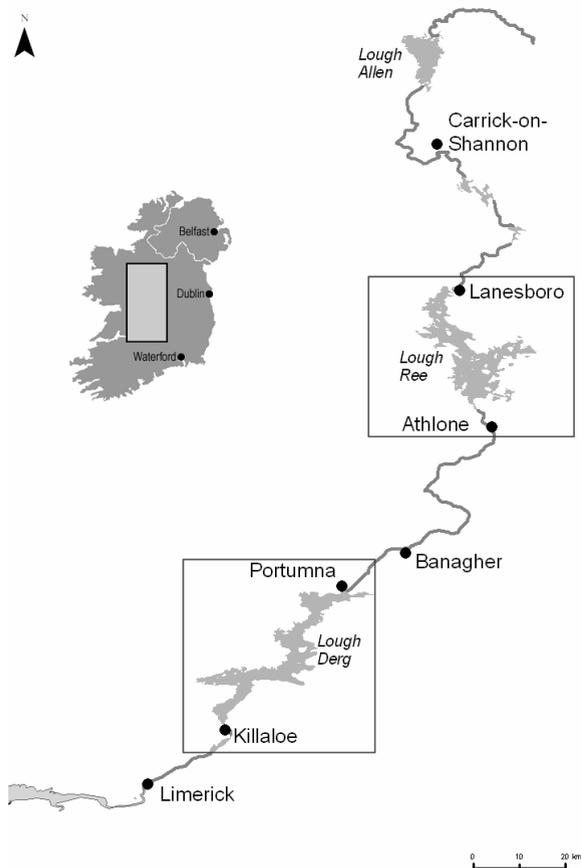


Figure 1. The Shannon river system with two studied lakes – Lough Derg and Lough Ree- indicated.

alkaline conditions as a result of outcrops of carboniferous limestone. The river drops 120 m from its source to the sea with a final 30 m drop at a hydroelectric dam close to the Shannon Estuary (Bowman 1999).

Lough Derg (LD) is at an altitude of 33 m, has a maximum depth of 37 m, a mean depth of 7.5 m and volume of 0.88 km³ with a surface area of 188km². On either side of the lake are small rivers and streams draining into shallow bays. The main axis of the lake, in its most southern region, contains a long narrow trough with depths of 30 m or more (Bowman 1999).

Lough Ree (LR) is at an altitude of 38 m with a maximum depth of 35 m, average depth of 6.2 m and volume of 0.65 km³ with a surface area of 105 km². This lake also has shallow bays on either side where small streams or rivers enter. There are many small shoals and islands. In the south-eastern part of Lough Ree there are some inner lakes in a fen region (Bowman 1999).

Navigation by small recreational craft takes place throughout the main arterial drainage of lakes interconnected by river sections. The Shannon waterway connects to other regions extending to Northern Ireland, Dublin in the east and Waterford in the south (Figure 1).

The zebra mussel was first recorded in Ireland in LD on the lower Shannon River (McCarthy et al. 1998), having most probably arrived in 1993-4 as hull fouling on leisure craft from Britain (Pollox et al. 2003). It spread rapidly to all lakes on the Shannon before, or during, the summer of 1996. As a result all sections of the entire navigation have been exposed to the mussel since then (Minchin et al. 2006b). Patterns in the expansion and development of zebra mussels at specific sites have varied according to their rate of expansion within each lake (Minchin et al. 2002, 2006c).

Sample collection and data analysis

Zebra mussels were collected from vertical surfaces at navigation marks, piles and quays at depths to 3.5m. Eight stations in Lough Derg and four in Lough Ree were sampled annually from 1997 to 2007. Mussels were detached using a 15cm blade with a pocket net mounted on a 4m handle, scraping known distances to provide an estimate of numbers and biomass per m² (Minchin 2007). The average individual biomass was calculated later by dividing the sampled biomass by the mussel abundance. The data on larval abundance was retrieved from the results of the earlier studies in the lakes (Minchin et al. 2005).

The environmental parameters, water transparency measured by Secchi depth and Chlorophyll a (Chl-a) concentration, were selected as response variables of the zebra mussel impact (quantitative evidence) following the biofiltration - the most prominent effect by the zebra mussel. The long-term data were provided by the Irish EPA from a general water quality monitoring program based on 18 stations in LD and 18 stations in LR, all of which are sampled 4 times per year.

The temporal changes within the lake ecosystems were based on quantitative zebra mussel population characteristics (abundance, biomass and averaged individual biomass) and environmental variables (water transparency and Chl-a concentration). We did not take account of the spatial variability of zebra mussel populations but examined the generalized patterns of the invasion process following the likely colonization date.

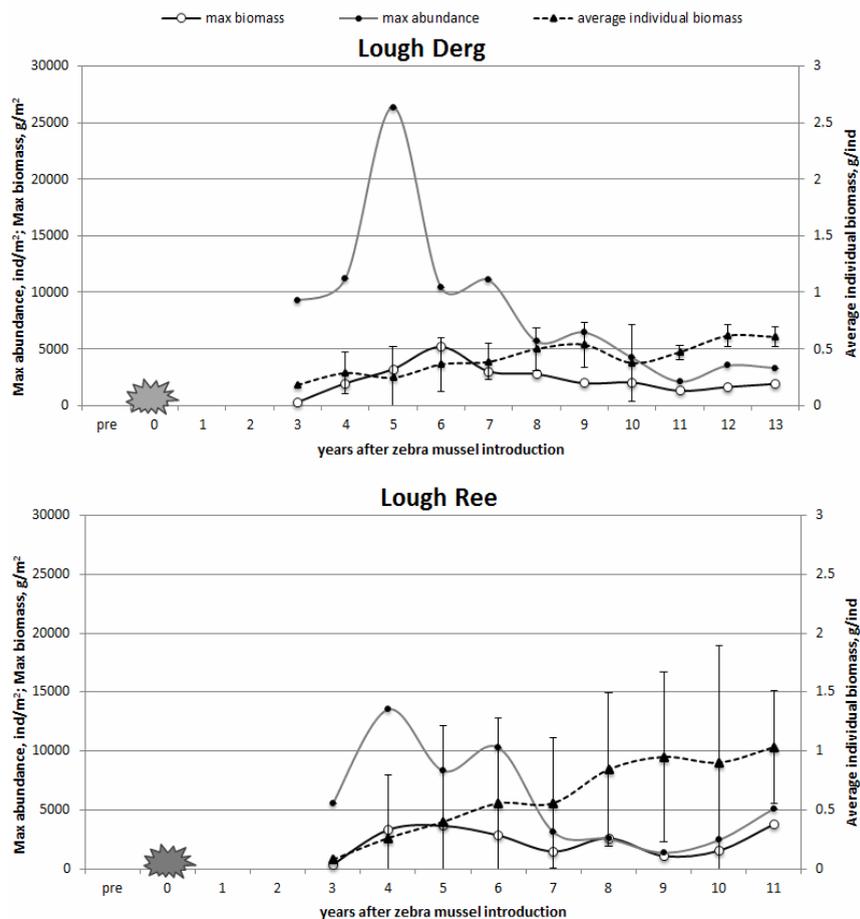


Figure 2. Patterns of zebra mussel population dynamics in two invaded lakes (the explosion icon indicates the year of presumptive introduction of the zebra mussel: 1994 in LD and 1996 in LR). Error bars here represent standard deviation.

The annual maximum abundance and biomass values from each lake and maximum annual Chl-*a* concentration and water transparency for each sampling station were used in the analysis. For reference, the Chl-*a* concentration and Secchi depth data recorded in the lakes prior to the presumptive zebra mussel arrival (in 1992 for LD and 1995 for LR) were used.

A non-parametric Wilcoxon signed rank test was applied to compare changes in zebra mussel population abundance and biomass within the two lakes. Similarities of the variables (zebra mussel population characteristics and environmental variables) were assessed using ANOSIM, and non-metric multidimensional scaling (MDS) procedure, at different periods of the invasion process. The impact of outlier values were downweighted using logarithmic transformation. Environmental variables for the pre-invasion and later invasion stages were compared using a 't'-test.

We accepted a significance level of 0.05 for statistical tests to differentiate between statistically significant and random effects. The statistical analyses were performed using Primer 6 for Windows® and Statistica 6.0TM (StatSoft) software.

Results

There were similar (Wilcoxon signed rank test, $p > 0.05$) trends for zebra mussel maximum abundance and biomass and for the averaged individual biomass (biomass to abundance ratio) for both lakes (Figure 2). Biomass and abundance rapidly increased in years 4 to 6 following arrival, and then declined. Although the peak abundance in LD was almost twice that found in LR, in both cases it coincided with maximum numbers exceeding 10,000 ind/m², biomass of more

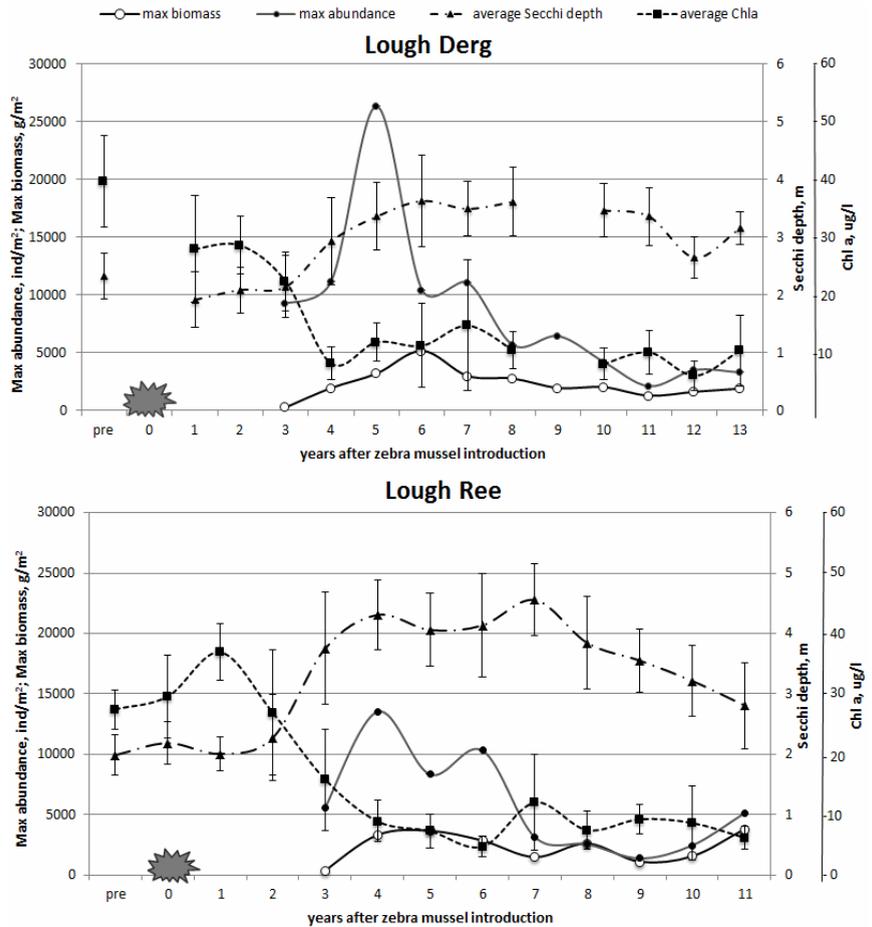


Figure 3. Changes in Chl-*a* concentration and Secchi depth in response to the zebra mussel invasion in two invaded lakes (the explosion icon indicates the year of presumptive introduction of the zebra mussel: 1994 in LD and 1996 in LR). Error bars here indicate standard deviation.

than 2,000 g/m² and approximately twofold change in water quality parameters. The mean biomass of individual mussels gradually increased within both lakes during the study period. Changes in water transparency and Chl-*a* concentration were consistent with the mussel population dynamics in both lakes, where increases in transparency corresponded with the increase in zebra mussel biomass and decrease in the levels of Chl-*a* (Figure 3).

We distinguished three separate invasion stages by using the similarity analysis of ecosystem state for different periods following the zebra mussel introduction (Figure 4). The main factors influencing the similarity within a group of samples were: mussel abundance (~45% contribution), biomass (~35% contribution) and Chl-*a* levels (~15% contribution). The most distant group corresponded to the third year following arrival, when high numbers of mussels coincided with

comparatively low biomass due to dense settlements of young individuals. Some changes in transparency and Chl-*a* concentration took place at that time, although reported values were still within, or close to, the natural range observed in the lakes before zebra mussel invasion.

For three to four years after initial discovery, zebra mussel populations in both lakes increased in numbers and biomass, and consisted of a high proportion of young individuals (as it is evident from the average individual biomass curve, Figure 2). The greatest abundance was registered during this stage. Peaks in abundance and biomass coincided with changes in water quality (Chl-*a* and transparency). Apart from these, this stage had the highest variation in the measured values (evident from the SD bars, Figures 2 and 3). The final and subsequent stage revealed stabilization of zebra mussel populations at lower densities, with a prevalence of larger individuals. At this stage,

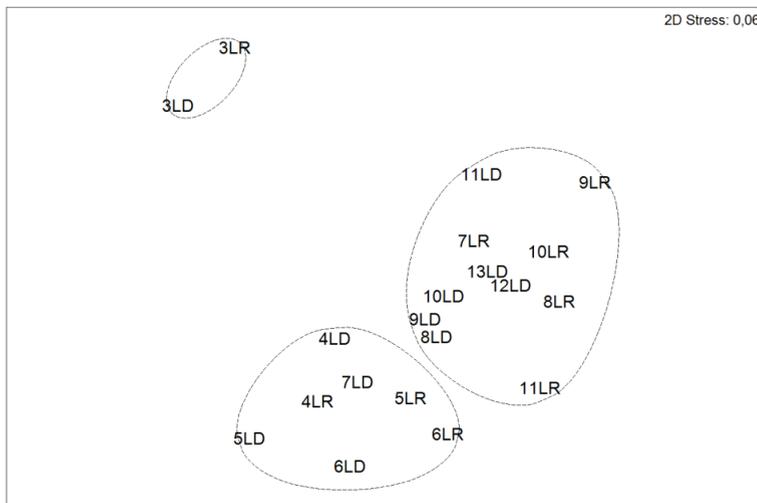


Figure 4. Non-metric multidimensional scaling plot of similarities in ecosystem state (based on zebra mussel abundance, biomass, averaged individual biomass, Chl-*a* concentration and Secchi depth) at different periods after the zebra mussel introduction (ANOSIM: Global $R = 0.781$, $p = 0.001$). Numbers indicate the year after the zebra mussel introduction (as in Figure 3), letters next to figures indicate the lake (LG – Lough Derg, LR – Lough Ree), dashed line bands the group of samples at 95% similarity level.

the effects of the zebra mussel on Chl-*a* concentration and water transparency also stabilized but did not revert to pre-invasion levels (t test, $p < 0.001$).

Discussion

We have shown three separate stages of zebra mussel invasion in two Irish lakes: 1) arrival and early expansion, 2) outbreak and 3) accommodation. These stages had features that were identifiable from direct observation within the lakes (Table 1). Of these, the outbreak stage had three separate phases, late expansion, peak abundance (over a one to two year period) and early decline.

Arrival and early expansion

The arrival and establishment of an IAS is the least distinct stage with little measured impact on the ecosystem. The small numbers present at such a time are usually overlooked and their time of arrival is often vaguely known. Time lags normally follow a period of establishment (Crooks 2005; Wang and Wang 2006; Wangen and Webster 2006) and population expansion may not occur for some time (Strayer et al. 2006). This lag is mainly driven by biological traits, environmental or biotic conditions, demographic constraints (Crooks 2005; Reise et al. 2006; Larkin 2012) or the Allee Effect – the positive correlation between population size or density and the mean individual fitness (Allee 1927). In the case of long time lags, an expansion may not be expected and will greatly depend on the recruitment

ability of successive generations. In the case of ‘r’-strategists, such as *Dreissena*, which can reproduce within a year of colonization the eradication of the established population is nearly impossible. This is because their pelagic larvae become widely dispersed downstream and by wind generated currents in lakes (Lucy et al. 2008). Similarly to other European and North American ecosystems (Burlakova et al. 2006), in LD and LR, it took mussels three years to expand sufficiently to result in the changes to the ecosystem without a perceptible lag phase. Eradication as a result is only possible when its distribution is confined to that period soon after arrival, unless it becomes confined within a small unconnected waterbody. Initially, the abundance of the zebra mussel in the two studied lakes was low and recorded for a few localities (Minchin et al. 2002, 2006c). Settlements were sparse on stones and living unionids (Table 1, Figures 5a and b). However, following the progress of the invasion, let us assume that the expansion starts within this benign stage, therefore we define this as an *early expansion phase*. In contrast to *establishment* and *lag phases*, the *early expansion* implies dynamics within the IAS population and seems to be more appropriate for successful ‘r’-strategist invaders that enter this phase within a short time.

Outbreak

For managers and policy makers the outbreak stage is of most interest when environmental or societal impacts are of concern (Reise et al. 2006).

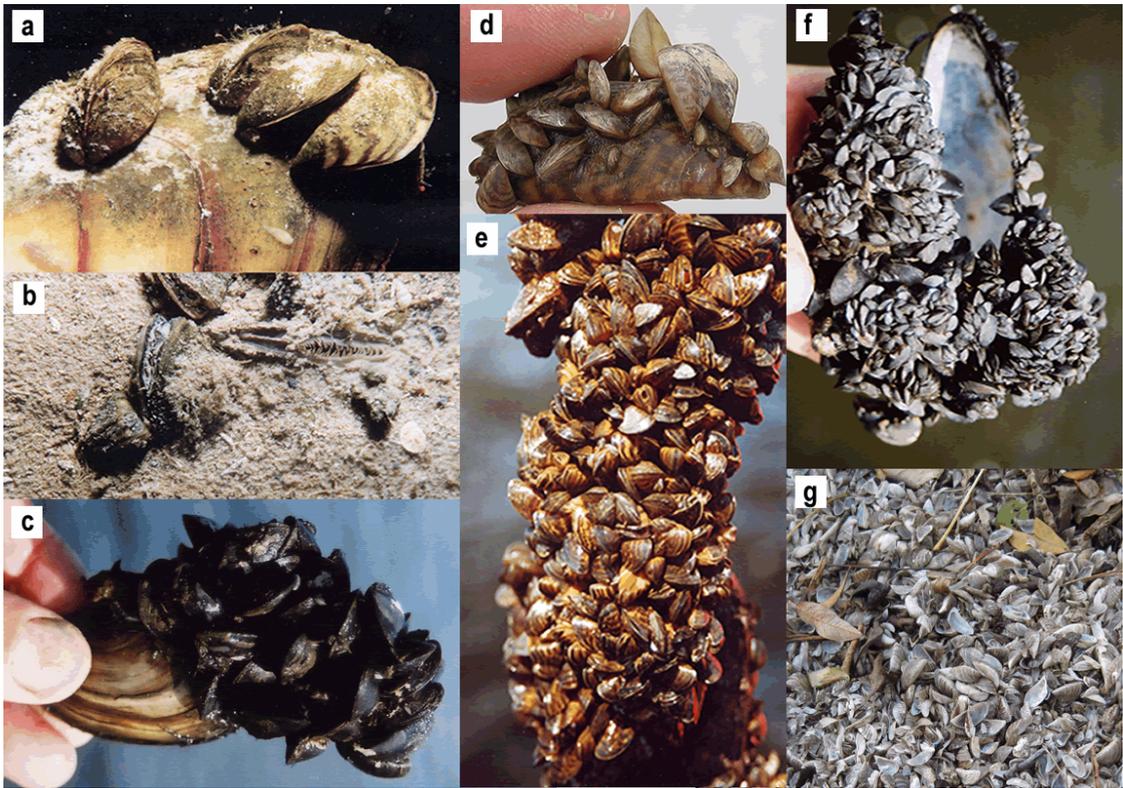


Figure 5. Empirical evidence typical to different stages of the zebra mussel invasion (examples from the two studied lakes): a, b – arrival and establishment; c, d – expansion; e, f – outbreak; g – accommodation (Photographs by D. Minchin). See also Table 1 for additional explanation.

This stage has three successive phases: *late expansion*, *peak abundance* and *early decline*. The late expansion phase was a time when zebra mussels occurred at all sampling stations within the lakes. Large and small mussels were present but with a low average individual biomass (below 5 g/ind) combined with sharp increase in abundance (Figure 2) resulting from strong recruitment. This phase corresponded with a noticeable decline in Chl-a concentration, increase in water transparency, fouling of most unionids, modification to soft and hard substrates and formation of specific zebra-mussel associated communities (Table 1, Figures 5e and f). These results are consistent with the other studies in Irish lakes and elsewhere (e.g. Berkman et al. 1994; Burlakova et al. 2000; Karatayev et al. 2002; Minchin et al. 2002; Lucy et al. 2013). Generally, at this stage eradication is impractical but prevention of an invasive species spread involving public awareness is a policy generally accepted in both North America and Europe (Anderson 2005; Genovesi 2005; Lodge et al. 2006; Olenin et al. 2011).

Peak abundance followed late expansion with a difference in mussel abundance between the two lakes that might have been due to the extent of the sampling and local variability. Nevertheless the patterns remained the same with biomass being a better descriptor (Figure 2) in relation to environmental alterations (Figure 3). The important finding was that in both lakes the start of the outbreak coincided with maximum reported abundances and biomass exceeding 10,000 individuals per m² and 2,000 g per m² – these values could be indicative thresholds for managers interested in determining the species status. At this stage, characterized also by the twofold change in the water quality parameters, the species should be qualified as invasive with appropriate management measures designated for its containment and mitigation of impact as necessary. However we should keep in mind that localized species impact (at the level of communities or habitats) may be asserted at much lower numbers. For instance, in an earlier study the biomass threshold at which habitat engineering impact

Table 1. Direct and indirect evidences of the zebra mussel invasion process. In column 1, the stages defined in the current study and their correspondence with abundance and distribution rates (ADR range A to E) and biopollution levels (BPL range 0 to 4) (Olenin et al. 2007¹) and invasion phases described by Blackburn et al. 2011² (range C0 to E) are presented where applicable.

Stages	Direct evidence	Indirect evidence
Arrival, establishment ADR=A; BPL=0 ¹ C3 ²	Low abundance of larvae and adults (single to few specimens) occurring at a single or few localities, no impacts noted	Sparse settlements on hard substrates and some unionids (Fig. 5 a-b).
Expansion ADR=B-C; BPL=1-2 ¹ D1, D2 ²	Low to moderate abundance abundances (not exceeding 10 000 ind/m ²) and biomass (below 2 000 g/m ²) observed in many places; large and small individuals present; declines in Chl- <i>a</i> noticed, however concentrations are still close to the natural variation.	Appear on most unionids; form clumps on hard and soft substrates; attach to live zebra mussels or empty shells; druses with infaunal and epifaunal associates; mussel shells appear on exposed shores (Fig. 5 c-d).
Outbreak ADR=D-E; BPL=3-4 ¹ E ²	High larval abundance (>1 000 per m ³) and heavy (>10 000 ind/m ²) settlements; prevalence of small individuals; biomass/abundance ratio low (mean individual biomass <<0.5 g); peak abundance followed by peak biomass; notable water clearances and Chl- <i>a</i> alterations (twofold and more comparing to natural background values).	Dense settlements on rushes and reeds, mussel and unionid shells cast upon shore (Fig. 5 e-f); ultimate loss of unionids; many heavily fouled vacant unionid shells; mussels colonize soft sediments; typical mussel community evolves; extensive mussel shell windrows on exposed shores; macrophytes extend range to deeper water.
Accommodation ADR=C-D; BPL=2-3 ¹	Biomass/abundance ratio increases (mean individual biomass 0.5 g or more); population fluctuations stabilize; decline of maximum abundance and biomass below 10 000 ind/m ² 2 000 g/m ² correspondingly; moderate larval abundance (tens to hundreds); transparency and Chl- <i>a</i> still differs from the natural background values, but less than during the outbreak stage.	Shells and clumps observed widely in deeper water; low densities on rushes and reeds; unionid shells mostly buried; unionid shells seldom cast ashore; mussel shell accumulations on exposed shores (Fig. 5 g); associated communities present; extensive shell deposits in sediments; high percentage cover on solid surface; bird predation noted; macrophytes remain in deeper water.

of zebra mussel asserts was defined as 200 g/m² (Zaiko et al. 2009). This corresponds to several zebra mussel clumps that provide habitats for bottom dwelling fauna and form species-specific community, replacing the native ones dominated by unionids (Lucy et al. 2013).

The typical qualitative evidences of the outbreak stage in LD and LR were heavy settlements with clear prevalence of small individuals were observed on rushes and reeds during peak abundance (Sullivan et al. 2010). Larvae were abundant (reaching 2,000 ind/m³ densities during the summer peaks) and widely distributed with downstream dispersal (Minchin et al. 2005). The formation of extensive encrustations and druses of mussels evolved new communities that included the tube building IAS *Chelicorophium curvispinum* (Lucy et al. 2004; Minchin and Zaiko 2013). Unionid shells, with mussel byssal plaques, were cast ashore along with mussel shells to form windrows (Table 1, Figure 5g). The populations of mussels then enter a decline that results from feedback mechanisms which probably include competition for space and food and decrease in reproductive potential and settlement success (Strayer and Malcom 2006; Pace et al. 2010).

Accommodation

After the biomass and abundance of mussels has declined it entered a more stable population state. This arises from the regulatory effects that modify the abundance by either top-down or bottom-up regulations within an ecosystem, or both (Reise et al. 2006; Moore et al. 2012). Some irreversible changes to the ecosystem have taken place such as the loss of unionids (Minchin and Zaiko 2013; Lucy et al. 2013). However the niches of extirpated species might become recolonised from the adjacent areas, e.g. the feeder streams and rivers where populations survive as could happen in the course of time (Strayer and Malcom 2007).

In LD and LR, zebra mussel shells and small druses were still widely distributed at this stage. Yet, there was an evident decline and stabilization in maximum abundance and biomass values along with a clear increase in biomass/abundance ratio (Figure 3). Reeds and rushes had only small settlements of mussels and were often devoid of small mussels. Unionid shells became buried in sediments and biodeposits and were seldom seen in the more extensive windrows of mussel shells onshore. Mussel shells formed a significant

component to shallow water soft sediments. A small increase in Chl-*a* and decrease in water transparency was evident (Figure 3). Macrophytes extended their range into deeper water and increased in abundance in shallow water (Minchin and Zaiko 2013).

The *accommodation stage* does not imply an end to the invasion process. While reverting to a pre-invasional state is most unlikely, a further outbreak stage may occur due a natural cyclic behavior of an IAS population (Strayer and Malcom 2006). Therefore any alien species that has already shown its ability to expand should be monitored in relation to potential new outbreak events.

Significant changes to the two lakes have taken place with total loss of formerly abundant unionids (Minchin et al. 2006c; Minchin and Zaiko 2013). However the niches of the unionids, and other suspension feeders, have become occupied by the mussels and invading populations of the Asian clam, *Corbicula fluminea*. For many species a single high-abundance phase is apparent (Zettler et al. 2002; Gomoiu et al. 2002; Strayer and Malcom 2006; Moore et al. 2012), which appears to be the case to-date in the Shannon since the accommodation stage has lasted 12 years without a further outbreak stage, with populations remaining at comparatively moderate levels (DM pers. obs.). However there have been further modifications resulting from the recent expansion in the population of *C. curvispinum* in LD whose muddy tubes cover mussel surfaces potentially reducing mussel settlement success. In addition, long term ecosystem effects will now be more difficult to ascribe to a single species following the recent arrival and early expansion stage of the suspension feeding Asian clam, to both lakes (Minchin 2014).

We reported a similar zebra mussel invasion pattern for two separate lake systems. Based on these results, the invasion process was divided according to different invasion stages. We were able to distinguish the late expansion, outbreak and early decline in both lakes and provide information on the characteristics of each stage based on direct observations in the field. In addition we determined and elaborated on the characteristics of the accommodation stage, that is generally overlooked in other studies and proposed schemes of invasion dynamics (e.g. Richardson et al. 2000; Alimov and Bogutskaya 2004; Blackburn et al. 2011).

The suggested adjustments of the terminology of invasion stages can be easily absorbed within existing frameworks of invasion processes (e.g. Blackburn et al. 2011) and bioinvasion impact assessment approaches (e.g. Olenin et al. 2007) (Table 1). For instance, defining the outbreak stage with three subsequent phases compliments and elaborates on the broad '*Spread*' phase determined as dispersal and environmental adaptation in the bioinvasion framework by Blackburn et al. (2011). Linking together those different approaches may help to make bioinvasion impact and risk assessments more robust and consistent.

Although our results showed that abundance of IAS is not always the best predictor of the population status and the invasion stage achieved (as in the case of the beginning and the end of the outbreak stage, at a time when populations might be similar in number but differ in size structure), we find that impact magnitude relates to the species abundance. In the Biopollution Assessment (BPL) method (Olenin et al. 2007), the abundance and distribution range was suggested as a key parameter determining largely the entire impact assessment. We find that it can serve also as a semi-quantitative indicator of invasion stages (Table 1) when following key aquatic invasions. This could be a handy approach taking into account that BPL is under consideration as a standardized indicator for Descriptor 2 (Non-indigenous species) within the Marine Strategy Framework Directive and might be included into national monitoring programs (Olenin et al. 2010).

The indicative thresholds in the current account provide direct evidence of the zebra mussel invasion stages for two separate lakes. These values were consistent with the results of earlier studies conducted in LD, LR, and other Irish lakes (Minchin et al. 2002, 2006c; Minchin and Zaiko 2013). However, specific thresholds need to be determined for other IAS and for zebra mussels within other aquatic ecosystems with different environmental conditions. Therefore further work might be required to reveal the invasion stages of other impacting IAS and whether these follow a similar pattern.

We believe that combining qualitative and quantitative distinction of invasion stages can facilitate the understanding of invasion process by managers, decision makers and general public, will result in a better awareness of risks posed by IAS and periods when maximum economic impact may prevail (Minchin and Moriarty 2002). The sequence of invasion stages with corresponding features presented in Table 1 and Figure 5

provides the example of the detailed zebra mussel invasion ‘anatomy’, and might be extrapolated for other invasive byssate freshwater molluscs. Assuming, that many “key IAS” with high impact ability could result in readily observed environmental change during their invasion process, a similar approach to identifying the invasion stage should be of value to managers. It is clear that these qualitative evidences can vary among ‘r’-strategists according to their taxonomic and functional group. It is of special value in determining stages for those alien species with a previous invasion history from elsewhere or those expected to arrive. The approach suggested here will provide the basis for tracking an invasion process, risk assessment or prediction of invasion consequences.

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