Research Article

Impact of the zebra mussel invasion on the ecological integrity of Lough Sheelin, Ireland: distribution, population characteristics and water quality changes in the lake♣

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Abstract

The zebra mussel, *Dreissena polymorpha* (Pallas 1771), invaded Lough Sheelin in the midlands of Ireland in 2001. In order to assess the status of the mussel population in the lake, the distribution, extent of colonisation, abundance, biomass and size-frequency structure of post-settlement stages were studied in 2005 and 2006. In addition, changes to water quality parameters in the lake post-establishment were assessed with reference to the pre-invasion period. Zebra mussels were found throughout the lake at most sites on all main categories of substrates examined (stony and soft substrate; submerged vegetation: Characeae, *Elodea* spp., *Cladophora* spp., *Potamogeton* spp. and *Myriophyllum* spp., and emergent vegetation: *Phragmites australis* and *Schoenoplectus lacustris*). Overall, increases in density and biomass of mussels were recorded from 2005 to 2006. Analysis of physiochemical data show a reduction in chlorophyll *a* with an increase in water transparency, however the total phosphorus concentration remains high. This paper highlights the common misconception that zebra mussel introductions lead to overall improvements in water quality.

Key words: *Dreissena polymorpha*, lakes, population, Sheelin, water quality

Introduction

The zebra mussel, *Dreissena polymorpha* (Pallas 1771), is one of the most notable alien species to invade aquatic ecosystems in recent times (Karatayev et al. 2002; Minchin et al. 2002a). It is responsible for many significant ecological and economic impacts throughout freshwater and estuarine waterbodies in both Europe and North America (reviewed in Karatayev et al. 1997; Munawar et al. 2005; Pimentel et al. 2005; Lovell et al. 2006). Once introduced, mussel populations can expand rapidly to extensively colonise a system, often becoming established as the dominant benthic invertebrate within a few years after initial invasion. Exponential population growth is typically evident within the first few years of colonisation followed by a levelling off (e.g. Burlakova et al. 2006; Lucy et al. 2005; Lucy 2006). This may be preceded by an initial lag phase where the invasion is not detected (Burlakova et al. 2006). In the longer term, population densities can be relatively unstable, fluctuating by varying degrees from year to year (e.g. Stańczykowska and Lewandowski 1993; Burla and Ribi 1998; Hunter and Simons 2004;

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Strayer and Malcom 2006). Densities in excess of 120,000 m^{-2} and a biomass >5kgm^{-2} are possible in lakes (Minchin et al. 2002a; Minchin et al. 2005).

In Ireland, the zebra mussel was introduced around 1994 or earlier (Minchin and Moriarty 1998a; Minchin and Moriarty 1998b). Since then it has extensively colonised many hard freshwater systems (Minchin et al. 2002b; Minchin 2003). It is believed that the mussel was originally introduced into the lower River Shannon region, being inadvertently transported here attached to leisure craft coming from the UK (Minchin and Moriarty 1998b; Pollux et al. 2003; Astanei et al. 2005). The introduction of the zebra mussel to Lough Sheelin most likely occurred in late 2001 (Minchin et al. 2002b; Kerins et al. 2007).

Zebra mussels predominantly live on hard stony substrates but can successfully inhabit soft sediments as well (Marsden 1992; Marsden and Lansky 2000; Coakley et al. 2002). In addition, mussels can extensively colonise submerged vegetation (Sullivan et al. 2002; Burlakova et al. 2006) and attach to hard artificial structures present in the water (Minchin et al. 2002b; Lancioni and Gaino 2006). In some lakes, particularly those without large areas of stony substrate, submerged and semi-submerged vegetation can provide the principal settlement substrate for the zebra mussel (Lewandowski 1982; Ramcharan et al. 1992; Hunter and Simons 2004). Furthermore, they can settle on other fauna, most notably on the shells of unionid mussels (Lucy et al. 2005; Mackie 1993; Maguire et al. 2003). Irish populations are believed to have a typical lifespan of 2 to 3 years or cease growth after that time (Maguire 2002; Lucy et al. 2005).

The magnitude and extent of ecological impacts are primarily related to the abundance and biomass of the resident zebra mussel population, biomass being most relevant, as it corresponds more directly to filter-feeding capacity (Vanderploeg et al. 2002; Burlakova et al. 2006). Being prolific filter-feeders (Reeders et al. 1993; Karatayev et al. 1997), established mussel populations can remove large amounts of seston, including phytoplankton and small zooplankton (Reeders et al. 1993; Wong et al. 2003), from the water column and deposit it on the bottom as faeces and pseudofaeces (Reeders et al. 1993; Vanderploeg et al. 2002). This can result in the suppression of pelagic primary production (Fahnenstiel et al. 1995; Caraco et al.

1997). The associated increase in water transparency allows light penetration to deeper depths which can promote the expansion of submerged macrophytes (Skubinna et al. 1995; Zhu et al. 2006) and the growth of epilithic algae (Lowe and Pillsbury 1995).

The aims of this study were (1) to determine the distribution, extent of colonisation and the population characteristics of the zebra mussel in Lough Sheelin on hard, soft and plant substrates and (2) to evaluate any changes in the principal water quality parameters in the lake post-colonisation. The establishment of baseline invasion data on the zebra mussel will be used to assist with the formation of a long-term monitoring programme to complement existing fish population and physiochemical datasets managed by the Irish Central Fisheries Board.

Material and methods

Study sites

Lough Sheelin (53°48'N, 7°20'W) is situated in the River Inny catchment, a sub-catchment of the River Shannon in the midlands of Ireland. It is a highly alkaline lake (90-220 mg/l CaCO$_3$, Champ 1998), underlain by a carboniferous limestone geology. By Irish standards it is a fairly large waterbody with a surface area of 18.5 km^2, however it is relatively shallow having a maximum depth of 14 metres with approximately 75% of lake less than 6 metres deep (John et al. 1982). The lake floor comprises predominantly of soft substrates such as mud, marl and sand. The shoreline is fringed by stony substrate in all but the southern part of the lake, with more substantive stony areas present in the eastern portion. Generally these do not extend a great distance from the shore. Submerged vegetation, primarily consisting of charophytes (Family Characeae), *Elodea* spp., *Cladophora* spp. and *Potamogeton* spp., are abundant in the shallow southwesterly section of the lake in addition to the western and southern areas nearer the shoreline and in some other sheltered bays. The reed beds, located around the fringes of the lake are of made up of two main species, *Phragmites australis* (Cav. Trin. ex Steud.) and *Schoenoplectus lacustris* (Linn., Pallas).

Lough Sheelin was originally an excellent wild brown trout fishery of good water quality (Champ 1977). However since the early 1970s, the lake has been under considerable environmental pressure from eutrophication, the primary
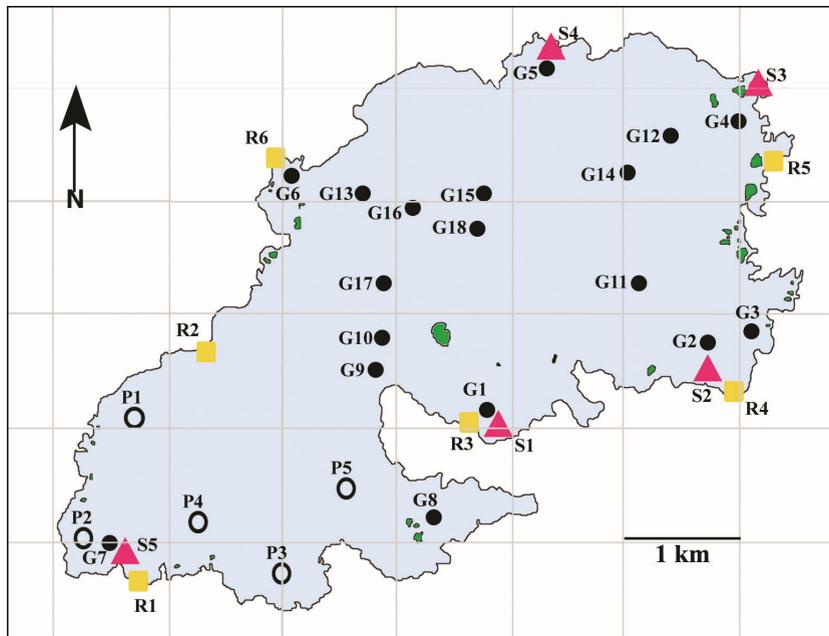
Figure 1. Map of Lough Sheelin showing sites sampled for zebra mussels (▲ stony substrate S1-S5; ● soft substrate G1-G18; O submerged vegetation P1-P5; and ■ reed bed vegetation R1-R6).

source of this pollution originated from intensive agricultural practices, particularly from pig farming and the associated spreading of the resulting slurry in the catchment area (Champ 1993). A brief period of recovery ensued in the early 1990s due to reductions in phosphorus inputs to the lake (Champ 1993). More recently, anthropogenic sources such as local municipal wastewater facilities and local industry may additionally be a contributing factor to the high nutrient load of the lake (Kerins et al. 2007). The lake is particularly suited for zebra mussels, having adequate pH, calcium content, food availability and temperature ranges (Ramcharan et al. 1992; Stańczykowska and Lewandowski 1993; Champ 1998).

Sampling and sample processing

To establish distribution, extent of colonisation and population characteristics of the resident zebra mussel population, four principal substrate types (stony substrate, soft substrate, submerged vegetation and reed beds) were examined for settled juvenile (≥1mm) and adult stages in spring (stony and soft substrates) and autumn (submerged and reed bed vegetation) of 2005

and 2006 (see Figure 1 for a map of sampling sites). Five sites were sampled in the stony substrate (S1-S5) with five replicates taken at three distance intervals (10m, 15m and 25m) following a transect line from the shore using a quadrat square (size 25cm x 25cm). Scuba diving or snorkelling was employed for this. At site S5, due to a lack of adequate stony area, five replicates were randomly taken along a transect line running parallel to the shore at a distance of 5m out (adapted from Lucy 2005). On the soft substrate, eighteen sites (G1-G18) were sampled for zebra mussels using an Eckman grab (size 15cm x 15cm). Six replicates were taken per site (adapted from Marsden 1992). In both the stony and soft substrate sites, a visual estimation of percentage substrate type was used to classify substrate based on the Wentworth scale (Wentworth 1922). In addition, five submerged vegetation (P1-P5) sites were sampled using a double-ended rake thrown out five times from a boat (adapted from Irvine et al. 2001). Retrieved plant material was separated per taxa encountered (Characeae, *Elodea* spp., *Cladophora* spp., *Potamogeton* spp. and *Myriophyllum* spp.). Furthermore, six reed beds (R1-R6) were randomly selected for examination. These were

comprised of *Phragmites australis* and/or *Schoenoplectus lacustris*. Ten random mature specimens of each reed species were individually cut at their base from the outer fringe of the reed bed and carefully removed for further examination (Sullivan et al. 2002). The location of all sites were recorded using a hand held GPS (model Garmin Etrex Summit 3.10).

Tissue blotted dry wet weight was used as a measure for zebra mussel biomass and also for the biomass of submerged vegetation. Mussel density (number/m^2) and biomass (g/m^2) were determined at the stony and soft substrate sites. Size frequency distributions were generated by randomly selecting circa two hundred mussels (if present) and measuring each to the nearest millimetre along the longest axis of the shell.

Physiochemical data were provided by the Central Fisheries Board, which has a long-term water monitoring programme on the lake. Generally, monthly water samples were taken from a mid-lake station. Physiochemical analyses were carried out using standard methods as described in Champ (1998) and Kerins et al. (2007).

Substrate mapping and determination of total abundance, total biomass and filtering capacity of mussel population

A map of the hard and soft substrates in the lake was developed using a combination of direct observations (snorkelling, SCUBA diving, shoreline and boat survey work) and through the grab sampling work. This was integrated with a digitised bathymetric map modified from the Ordnance Survey Discovery Series map 34 and from the bathymetric map in Gargan and O'Grady (1992).

To assess total abundance and biomass of mussels in the lake, mean values were determined per depth interval and proportional area of substrate type, and a weighted average was calculated to produce an overall empirical estimate (adapted from Karatayev et al. 1990 as cited in Lucy 2005; and from Burlakova et al. 2006). As plant sampling for zebra mussels was semi-quantitative, it was not possible to include these in overall calculations of total density and biomass. For overall filtering capacity, an arbitrary rate of 44ml of water filtered per gram of wet total mass per hour was assigned (Karatayev et al. 1997; Lucy et al. 2005). The total volume of water in the lake (88×10^6m^3, Champ 1998) was subsequently divided by the daily filtering rate to provide an estimate of the total filtering capacity of zebra mussels in Lough Sheelin.

Statistical analysis

Potential changes in density and biomass from 2005 to 2006 were evaluated per distance interval and per site using Mann-Whitney U tests. Actual densities were compared to densities predicted using the models in Ramcharan et al. (1992) based on pH, calcium ions, PO_4 and NO_3. Potential changes to physiochemical parameters (chlorophyll *a*, Secchi disc, total organic nitrogen (TON) and total phosphorus (TP)) were assessed by comparing the pre zebra mussel period (1996-2000) with the post-establishment period (2003-2007) using a nested analysis of variance. The relationship between physiochemical variables was also explored before (1991-2000) and after the zebra mussel (2003-2007) establishment using Spearman's Rank Correlations. Assumptions such as normality and homogeneity of variances were tested a priori as appropriate to the statistical test employed. Statistica 8.0 was used for all statistical analyses (StatSoft Inc. 2008).

Results

Zebra mussels were present at all stony substrate sites (S1-S5) and at all soft substrate sites < 6m depth (G1-G9) sampled in spring 2005. In spring 2006, mussels were found at a number of additional soft substrate sites up to 9m depth (G10, G12 and G17). No mussels were located during either sampling period at the deepest, centrally located soft substrate site (G15) which was >9m depth. Stony areas were found to contain densities of zebra mussels three to five times greater than soft substrate sites (2157 ± 416 m^{-2} versus 703 ± 196 m^{-2} in 2005 and 3016 ± 434 m^{-2} versus 587.7 ± 154 m^{-2} in 2006 respectively; Table 1). Biomass was also substantially higher on this substrate (1522 ± 270 gm^{-2} versus 230.7 ± 59 gm^{-2} in 2005 and 2723 ± 344 gm^{-2} versus 207.6 ± 58 gm^{-2} in 2006 respectively; Table 1).

An overall increase in biomass and density were evident on the stony substrates from spring 2005 to spring 2006 (Table 1). However, Mann-Whitney U tests revealed no specific significant differences (P>0.05) for mussel biomass or density on the stony substrate per distance

Table 1. Characteristics of zebra mussels on the principal substrate types.

Year	Parameter	Mean/ Range	Stony substrate	Soft substrate	Characeae	*Elodea* spp.	*S. lacustris*
2005	Biomass† (g/m^2)	Mean	1522 (270)	230.7 (59)	0.43 (0.18)	0.41 (0.22)	1.3 (0.22)
		Range	4.8-9698	0.89-2842	<0.01-1.6	<0.01-3.84	<0.1-6.3
	Density^1 (no.s/m^2)	Mean	2157 (416)	703 (196)	3.6 (1.99)	4.2 (3)	5.98 (1.3)
		Range	32-20288	44.4-11144	0.07-22.7	0.01-52	1-41
	Shell length (mm)	Mean	14.7 (2.3)	9.7 (1.2)	7.4 (1)	8.7 (1.4)	10.6 (0.6)
		Range	3-28	1-26	2-23	2-22	1-22
2006	Biomass† (g/m^2)	Mean	2723 (344)	207.6 (58)	0.22 (0.12)	0.09 (0.06)	3 (0.9)
		Range	112-9490	2.2-3605	<0.01-1.83	<0.01-0.63	0.4-30
	Density^1 (no.s/m^2)	Mean	3016 (434)	587.7 (154)	1.25 (0.71)	0.66 (0.41)	8 (2.58)
		Range	96-13936	44.4-9679.2	<0.01-10.8	<0.01-4.47	1-84
	Shell length (mm)	Mean	16.2 (2.7)	11.5 (0.95)	10.6 (1.1)	10.6 (0.4)	13.2 (1)
		Range	3-31	2-27	1-18	1-20	2-21

Standard error in brackets; [1]for Characeae and *Elodea* spp.=numbers per g wet weight of plant tissue / for *S. lacustris* = numbers per individual plant; †for Characeae and *Elodea* spp.= biomass per g wet weight of plant tissue / for *S. lacustris* = biomass per individual plant; Minimum value in range is minimum non-zero value.

interval at each site. Densities did decrease for sites S1 25m, S2 10m and S3 10m, although this was not found to be significant (Mann-Whitney U, P>0.05). The highest mean biomass and density were found at site S4 in 2005 (3150 ± 780 gm^{-2} and 4851 ± 1453 m^{-2} respectively) and the lowest at site S1 (186 ± 54 gm^{-2} and 485 ± 147 m^{-2} respectively). In 2006, site S5 had the highest mean biomass (5013 ± 1393 gm^{-2}) and S4 the highest mean density (6402 ± 1230 m^2). Again, the lowest mean biomass (589±272 gm^{-2}) and density (555 ± 203 m^{-2}) were found at site S1. At all stony sites with distance intervals (S1-S4), biomass and density successively increased with greater distance from shore and with depth (range 0.2m-2.3m).

On the soft substrate, biomass typically decreased at most sites. However, only G9 experienced a significant decline (from 1630 ± 534 gm^{-2} to 2.22 ± 2.22 gm^{-2}, Mann-Whitney U, P<0.01), whereas G8 was the only site to have a significant increase in biomass (from 39.2 ± 20.95 gm^{-2} to 1722 ± 501 gm^{-2}, Mann-Whitney U, P<0.01). Density was generally stable on the soft substrates with the only changes corresponding to the trends in biomass for G9 (from 7208 ± 2256 m^{-2} to 14.8 ± 14.8 m^{-2}; Mann-Whitney U, P<0.01) and G8 (from 141 ± 72 m^{-2} to 3693 ± 979 m^{-2}, Mann-Whitney U, P<0.01). Indeed, site G9 had the highest biomass and density on the soft substrate in spring 2005. Most other sites had a mean mussel biomass < 300gm^{-2}

and a density of <800 m^{-2}, except for sites G2 (from 1175 ± 591 gm^{-2} and 1243 ± 591 m^{-2} respectively) and G6 (649 ± 223 gm^{-2} and 1680 ± 630 m^{-2} respectively). In spring 2006, the highest biomass and density were recorded at site G8 (see above). For other sites, mean biomass was <150 gm^{-2}, except for sites G1 (872 ± 448 gm^{-2}), and G6 (539 ± 171 gm^{-2}), and mean density typically <130 m^{-2}, except for sites G1 (3012 ± 1525 m^{-2}), G2 (466±357 m^{-2}), G6 (1724±441m^{-2}) and G7 (836 ± 645 m^{-2}).

Zebra mussels were found attached to each of the five main submerged plant taxa in autumn 2005 and autumn 2006. Mussels were present at all submerged sites, except at site P5 in 2006 where no plant material was retrieved. Characeae and *Elodea* spp. represented the principal substrate for attached mussels in both sampling periods. *Cladophora* spp., *Potamogeton* spp. and *Myriophyllum* spp. were relatively uncolonised, however these taxa were not found at all sites sampled. Mean biomass of mussels per biomass of plant and number of individuals per biomass of plant declined in 2006 for both Characeae (49% and 65% respectively) and *Elodea* spp. (79% and 84% respectively). As regards reed beds, *Schoenoplectus lacustris* was utilised for settlement to a greater extent than *Phragmites australis*, with no mussels found on the latter in 2006 and only 1 specimen attached in 2005 at site R6 (Table 1).
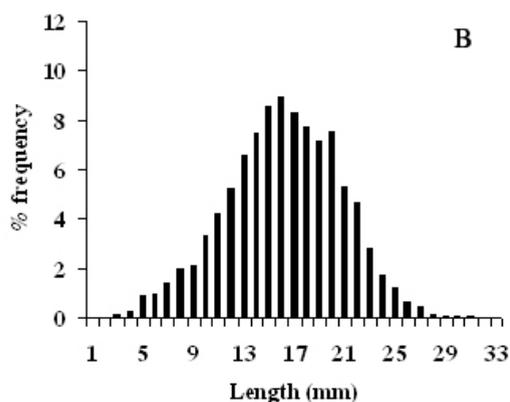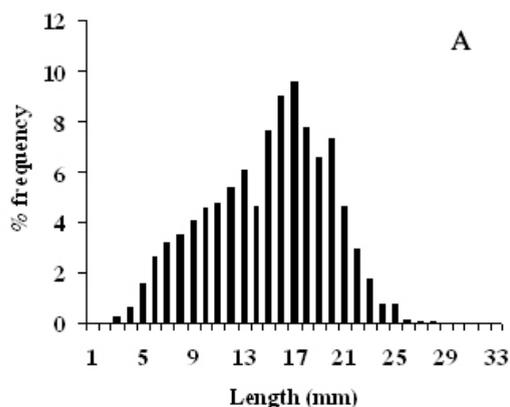
Figure 2. % length frequency of *Dreissena polymorpha* on stony substrates (all sites combined) in spring 2005 (n=5945) (A) and in spring 2006 (n=7300) (B).
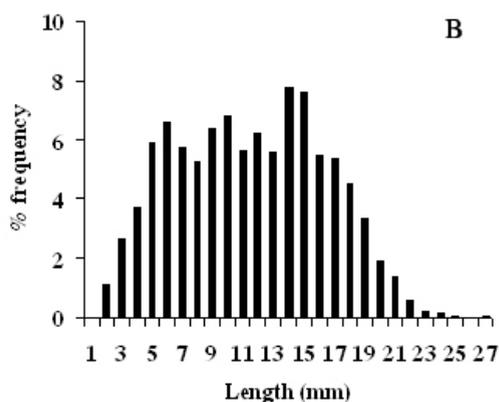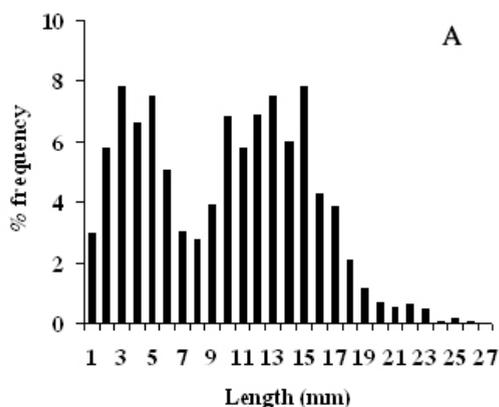

Figure 3. % length frequency of *Dreissena polymorpha* on soft substrates (all sites combined) in spring 2005 (n=1709) (A) and in spring 2006 (n=1348) (B).

Clear age cohorts could not be identified from site specific or overall length frequency distributions, except for mussels on the soft substrate in spring 2005 (see Figures 2A-3B) when all data were combined. This was particularly influenced by site G9, which comprised 57% of the specimens in the overall distribution. Two modes are evident here, representing two possible age classes of approximately 1-7 mm and 8-19 mm respectively (Figure 3A). No unimodal distribution common to all sites was evident. Mean shell length on the stony substrates (14.7 ± 2.3 mm in 2005 and 16.2 ± 2.7 mm in 2006) was greater than on the soft substrates (9.7 ± 1.2 mm in 2005 and 11.5 ± 0.95 mm in 2006) and on the submerged and reed bed vegetation (Table 1).

Models from Ramcharan et al. (1992) applied to the dataset predicted the resident zebra mussel population in the lake would be in the low category (<3000 mussels per m^2), with densities of mussels of 2441m^{-2} in 2005 and 2483m^{-2} in 2006. For these models, pH was entered as 8.19, Ca^{2+} as 41mg/l and PO$_4$ as the average of available readings of 0.0126 mg/l in 2005 and 0.008 mg/l in 2006. Due to a scarcity of information for NO$_3$, a value of 0.417mg/l was assumed in both years.

Estimates for total abundance, total biomass and corresponding filtering capacity for zebra mussels on stony and soft substrates in both sampling periods are given in Table 2. These suggest an increase in total abundance of appro-

Table 2. Total abundance, biomass and filtration capacity of zebra mussels in Lough Sheelin.

Year	Total abundance[1]	Total biomass[1] (kg)	Filtration capacity (m³/day)	Estimated time to filter lake (days)
2005	10.36×10^9	3.73×10^6	3.93×10^6	22.4
2006	16.38×10^9	6.36×10^6	6.71×10^6	13.1

[1] stony and soft substrates

Table 3. Mean values for physiochemical parameters before and after establishment of the zebra mussel.

Parameter	Pre-zebra mussel (1996-2000)	Post-zebra mussel (2003-2007)	Significance
Chlorophyll a (mg/m³)	22.5 (1.96)	10.19 (1.69)	$P<0.0001$
TP (mg/m³)	21.64 (1.41)	34.19 (3.56)	$P<0.01$†
Secchi disc (m)	2.11 (0.085)	2.98 (0.12)	$P<0.0001$
TON (mg/l)	0.81 (0.1)	0.86 (0.11)	$P>0.05$

Standard error in brackets; †only 3 readings in 2000; homogeneity of variance assumptions not met for TP.

ximately 62% from spring 2005 with a similar increase in total biomass of 71%. The increase in total biomass has resulted in a notable reduction in the estimated theoretical time for the zebra mussel to filter the lake (from 22.4 to 13.1 days).

Analysis of the physiochemical data (Table 3) show a significant reduction in chlorophyll a (ANOVA, $F_{1,86}=39.23$, $P<0.0001$) and an increase in Secchi disc values (ANOVA, $F_{1,81}=60.23$, $P<0.0001$), from the period before zebra mussel colonisation to the time since establishment of the mussel. Although a significant increase is evident for TP concentrations (ANOVA, $F_{1,70}=11.05$, $P<0.01$), these data could not be made homogeneous so the result must be treated with caution. Nested ANOVAs are robust to departures from homocedasticity when there are many independent estimates of residual variability (Underwood 1997). However, as only three readings were available for this variable in 2000, this precluded the use of other appropriate statistical tests to evaluate changes to TP. No significant change was detected for TON (ANOVA, $F_{1,82}=0.96$, $P>0.05$).

Spearman's Rank correlations in the pre-zebra mussel period revealed a strong significant negative association between chlorophyll a and Secchi disk ($r_s=-0.705$, df=103, $P<0.05$) and a weak significant negative association between TP and Secchi disc ($r_s=-0.31$, df=94, $P<0.05$), whereas there was a significant, albeit weak, positive association between TP and chlorophyll a ($r_s=0.33$, df=96, $P<0.05$). Post establishment, there was a modest significant negative association between chlorophyll a and Secchi disk ($r_s=-0.55$, df=34, $P<0.05$), however no other significant relationships were evident between TP, chlorophyll a and Secchi disc. No strong or relevant associations were evident for TON in either period when correlated with the other factors (Fowler et al. 1998).

Discussion

Overall, the zebra mussel population appears to be still expanding in Lough Sheelin as evidenced from the 2005 to 2006 data, although some local isolated declines on particular substrates were evident (e.g. at site G9 on the soft substrate). This is common in the years after colonisation although most evident during the initial exponential population growth phase (e.g. Burlakova et al. 2006; Lucy et al. 2005). Indeed, Burlakova et al. (2006) suggest that it can take from 7 to 12 years after the first introduction for a mussel population to reach maximum density in a waterbody.

The biomass and density of zebra mussels on the principal substrates are within the range recorded in the literature for water bodies of similar characteristics (e.g. Burlakova et al. 2006; Stańczykowska and Lewandowski 1993). The latter is somewhat confirmed by the model developed by Ramcharan et al. (1992), where a density category <3000 mussels per m^2 was predicted. Although the model does not take into account substrate type, the predicted densities for 2005 and 2006 are close to the actual average density recorded on the stony substrates, but substantially higher than on the soft substrate.

The overall increase in biomass can be predominantly attributed to observed increases on the stony substrate areas of the lake in spring 2006. This was reflected in the length frequency distributions as a shift from the smaller to larger size mussels on the stony substrate (Figures 2A and 2B). On soft substrates, biomass increased at sites of 0-3m depths but a decrease was evident in the 3-5m depth range. Soft substrate sites located in the vicinity of areas of submerged vegetation growth or close to areas of stony substrate, generally had a higher abundance and biomass of zebra mussels present. Annual plant die-off from year to year most likely facilitates this, as zebra mussels fall onto the soft substrate bottom, attached to dead plant matter, potentially creating a nucleus for future colonisation by other mussels (Ramcharan et al. 1992; Burlakova et al. 2006). Furthermore, the close proximity of vegetation colonised by zebra mussels may act as sources of higher local levels of settling juvenile stages, thus enhancing associated abundance and biomass (Coakley et al. 2002). Although no zebra mussels were recorded at the deepest site in the lake (11.2m depth) in spring of either year, a subsequent diving survey in autumn 2006 confirmed that zebra mussels were present at this site, albeit at a very low percentage cover (1-3%).

The higher number of individual mussels and weight of mussels per gram of plant material found on the Characeae and *Elodea* spp. reflect the relative stability of these submerged taxa. Both are perennial and offer reasonably firm sized substrate for the attachment of juvenile mussels (Lewandowski 1982). Observed decreases in average values recorded in 2006 (see Table 1) are most likely due to the fresh plant growth evident in the 2006 samples. Although not examined, it is reasonable to assume the increase in water transparency post-establishment has resulted in the expansion of submerged vegetation thus providing additional habitat for zebra mussels to colonise. Previous research in the lake has shown that the Characeae beds have retracted in years of low water transparency and a reduction in water quality, only to become eventually re-established after conditions improve (Champ 1993). As regards the emergent reed bed taxa examined, *Schoenoplectus lacustris* was colonised to a greater extent than *Phragmites australis*. These reeds were not as heavily colonised as those reported by Lucy (2005) and Sullivan et al. (2002) in previous Irish lake studies. However it is mentioned that the reed beds were not found to be as important as a substrate for settlement after the initial first years of population expansion (Lucy 2005).

Native unionid mussels, *Anodonta* spp., while subsequently extirpated, have proved to be a significant substrate for settlement of zebra mussels in other Irish lakes (Maguire et al. 2003; Lucy et al 2005). Although few specimens were encountered in Lough Sheelin, all had zebra mussels attached. No live specimens were recorded in the 2006 samples. However it is important to note that a number of predominantly dead *Anodonta* spp. with attached zebra mussels, have been observed retrieved in gill nets during fish population survey work in the corresponding time period. Additionally, a single live *Anodonta* mussel was found during a mid-lake scuba dive in autumn 2006 (personal observations), suggesting native mussels may still persist in the lake in the deeper soft substrate areas. As the *Anodonta* lifecycle involves a parasitic glochi-dial larval stage which can be associated with *Salmo trutta* Linn. (Bauer and Wächtier 2001 and references therein), the migration of these fish from the surrounding feeder rivers into the lake, may help to ensure the presence of an *Anodonta* population, albeit at a substantially lower level than the pre-invasion period.

Apart from soft substrate samples in spring 2005, length frequency distributions showed no clear cohorts to help define age classes. This is due to a number of factors, most notably the occurrence of multiple spawning events resulting in a broad range of time over which mussel settlement can potentially occur in one reproductive season. Furthermore, zebra mussel growth may not be uniform due to local temperature and food differences as well as the slowing of growth with age (reviewed in Karatayev et al. 2006).

The time (22.4 days and 13.1 days in spring 2005 and 2006 respectively) required by the

mussels (on stony and soft substrates) to filter total lake volume, may represent an under-estimate of the actual time of the whole resident population, as zebra mussels on plant substrates were not included in this survey. It must be noted that the influence of seasonal spring water temperatures during sampling (7-10°C) on actual filtration rates, were not incorporated into the estimates, as there is no corresponding filtering rate provided in the literature (Karatayev et al. 1997). The pre-invasion residence time of water in the lake is believed to have been approxi-mately six months (John et al. 1982). Therefore, these filtering estimates serve to illustrate the substantial effect the zebra mussel population may have on suppressing pelagic primary production in Lough Sheelin.

As documented with previous zebra mussel invasions (e.g. Fahnenstiel et al. 1995; Caraco et al. 1997), a significant reduction in chlorophyll *a* (a proxy measure of phytoplankton production) and increase in water transparency, concomitant with the zebra mussel invasion, is evident. However, TP levels have remained high since the mid 1990s (Kerins et al. 2007) and may even be slightly higher than the pre-invasion period. The continuing level of high phosphorus loading to the lake appears to be responsible for this (Kerins et al. 2007). This is unlike some other studies reported in the literature, in which a reduction in TP was observed post-establishment (e.g. Higgins et al. 2008; Maguire et al. 2003). TP is known to be closely related to primary production and thus chlorophyll *a* in lakes (Champ 1998). This relationship has been demonstrated previously in Lough Sheelin (Champ 1993). The positive correlation between TP and chlorophyll *a*, although statistically a relatively weak direct association, is not evident in the post establishment period. If TP continues to remain high, it may become further decoupled from chlorophyll as predicted by Kerins et al. (2007). Interestingly, a previous reduction in TP in the early 1990s corresponded with an improvement in water quality (as measured by chlorophyll *a* and Secchi disc) in the lake (Champ 1993; Champ 1998).

The three primary measures of water quality indicators in Lough Sheelin (TP, chlorophyll *a* and Secchi disc), place the lake into two separate trophic categories, eutrophic as regards TP, and mesotrophic for the latter two parameters, as assessed by current practices (OECD 1982; Toner et al. 2005). This has implications with regard to interpreting and meeting *good ecological status* under the *Biological Quality Elements* as required by European Union Water Framework Directive (2000). Although the Directive makes no explicit mention of invasive species, their introduction is given as an example of a biological pressure and impact in the instructive Guidance document (2003) of the Common Implementation Strategy for the Water Framework Directive (2000/60/EC). The consi-deration of the influence of invasive species in general on aquatic systems has yet to be adequately resolved, although new classification systems to account for this have recently been proposed (Olenin et al. 2007).

The long-term dynamics of the resident zebra mussel population are currently unclear. Stańczykowska and Lewandowski (1993) outline 3 potential scenarios based on long-term observations of density in zebra mussel infested Polish lakes: (1) density will remain relatively stable - (large, deep and mesotrophic or moderate eutrophy lakes); (2) density will be relatively unstable with yearly fluctuations and eventual stability at generally lower densities due to increased eutrophy; and (3) rapid population crash resulting in increased eutro-phication. It is worth noting that if phosphorus inputs to the lake remain high, any sudden decline in the zebra mussel population may result in the re-occurrence of significant eutro-phication problems; the mussels will be unable to partake in their apparent current role to suppress primary production and act as a size-able phosphorus sink. Additionally, this paper highlights the common misconception that zebra mussel introductions lead to overall improve-ments in water quality. In the case of Lough Sheelin, only an apparent improvement was evident, as TP concentrations confirm the lake to be still in a eutrophic state.

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