MANAGEMENT OF THE IMPACTS OF ZEBRA MUSSELS IN NORTHERN IRELAND AND DETERMINATION OF EFFECTS ON FISH POPULATIONS IN LOUGH ERNE THROUGH ALTERATIONS OF THE FOOD WEB

Final Report

Project CP1149/188

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Executive Summary

1. The zebra mussel was first documented in Lough Erne in 1997 and rapidly colonised the whole system including inflowing rivers such as the River Erne and Woodford River. Early ecological impacts included an increase in water clarity, reduction of chlorophyll *a* concentrations and rapid colonisation of the native *Anodonta* population.

2. The early impacts suggested that zebra mussels were likely to have a significant impact on the ecology of Lough Erne. A three-year study was undertaken to assess both their impacts at higher trophic levels and the implications of zebra mussels spreading to other catchments.

3. Strategies to limit the spread of zebra mussels were developed and the Zebra Mussel Management Strategy for Northern Ireland (2004-2010) was produced. The strategy aimed to minimise the spread of zebra mussels in Northern Ireland through raising awareness, developing policy and legislation, monitoring and research and developing contingency plans for immediate action in the event of further zebra mussel spread.

4. Research focused on determining the effects of the zebra mussel invasion on the six species of fish (roach, bream, perch, pike, eel and trout) that comprise the majority of biomass in Lower Lough Erne. Changes in abundance, population structure and biomass of the six species were quantified.

5. Investigation of foodweb change in Lough Erne included documenting change in phytoplankton and zooplankton abundance and community composition, and impacts on populations of the native mussel *Anodonta* and other benthic invertebrate species. The major dietary components, established by gut content analysis, were determined for the main fish species and the implications of these changes for fish populations were outlined.

6. The zebra mussel population continued to expand, particularly in Upper Lough Erne. Average densities were low compared to some other European and North American waterbodies ranging from <1 to 2,500m^{-2}, however higher densities of over 10,000m^{-2} were documented on some localised areas of hard substrata.

7. The filtering capacity of the native *Anodonta* and the zebra mussel populations were calculated. In Lough Erne, zebra mussels have now effectively replaced *Anodonta* and as a result, bivalve filtering capacity is now approximately twenty times higher. This level of planktivory makes zebra mussels strong resource competitors with unionids, zooplankton, larval and some adult fish.

8. Water clarity has increased and there has been a reduction of about 90% of peak summer maximum chlorophyll *a* concentration, as a result of zebra mussel filtering activity. Qualitative information suggests that there has been little change in community composition as the abundance of all phytoplankton

species has declined. However, monospecific blooms of *Microcystis* have been recorded in 2003 and 2004, which may be related to selective filtration of phytoplankton by zebra mussels. If the *Microcystis* blooms involve toxic strains and become a regular occurrence, this will have human health implications. There has also been an increase in macrophyte growth with more extensive littoral vegetation in the shallow areas of the Erne lake system.

9. There was a significant decline in total zooplankton abundance with copepods, rotifers and cladocerans all affected. The majority of species have declined in abundance. Stable Isotope Analysis of archived samples indicated that in Lough Erne where food limitation has been induced by zebra mussels, zooplankton are utilising a greater amount of allochthonous carbon and this was reflected in a shift in zooplankton $\delta^{13}C$ away from phytoplankton and towards that of allochthonous resources. Zooplankton elemental composition also suggested a switch to a lower quality diet.

10. Since the establishment of zebra mussels the diversity of the benthic invertebrate community has appeared to decrease, though this may not indicate a decrease in overall abundance as zebra mussels, *Gammarus* and chironomids are now highly abundant. The *Anodonta* population has been heavily impacted and extirpation is likely. The long-term survival of *Anodonta* populations in Irish lakes invaded by zebra mussels is unlikely due to zebra mussel fouling impacts, competition for food and resulting decline in *Anodonta* condition.

11. The abundance of zebra mussels mean they now play a significant role in the feeding relationships of the fish of Lough Erne. Zebra mussels are now a substantial component of the diet of all size classes of roach, bream and roach bream hybrids, but not perch or trout.

12. The impact of zebra mussels on the lower trophic levels of Lough Erne has implications for fish populations through modification of habitat, food webs and available resources. The reduction in available zooplankton resources may increase competitive interactions and has the potential to impact on recruitment and growth of zooplanktivorous fish. An abundant zebra mussel population will provide a novel food source for those species that can incorporate zebra mussels in their diet. Species that require clean gravel to spawn may be affected by zebra mussel colonisation of hard substrata. The habitat provided by the zebra mussel colonies with abundant gammarids and chironomids will be beneficial to benthic feeding fish. Habitat provided by macrophyte growth will favour perch over roach, as it is a superior forager within littoral vegetation.

13. There were no clear trends in abundance or biomass over time for pike, bream, roach bream hybrids and trout. However, there were changes in both abundance and biomass of the two dominant fish species roach and perch over time, in particular since the establishment of zebra mussels. The number of perch has increased and the abundance ratio has shifted from 2:1 to 1:1, this is reflected in the population structure of roach and perch. The changes in the lower trophic levels in Lough Erne appear to have benefited perch in competitive interactions with roach.

14. The Lough Erne food web has undergone rapid and extensive ecological change since the establishment of zebra mussels. The reduction in phytoplankton and zooplankton abundance, reduction in diversity of benthic invertebrates and changes to recruitment patterns of the fish populations are likely to be a result of the establishment of zebra mussels; as there is no evidence of major confounding changes in external driving variables of the Erne ecosystem during this period. Light appears to be a crucial factor in determining the impact of zebra mussels on the pelagic lower food web. However, the long-term effects are yet to be determined and will only be ascertained by continued study of the food web.

15. The potential impacts on the fish populations in the most vulnerable lakes are outlined, in particular Lough Neagh, Lough Melvin and the MacNean lakes. Generally, in lakes with high colour zebra mussels may impact the lower trophic levels and reduce the amount of pelagic resources available for fish. In lakes with less peat staining the impact may not be as great. The establishment of zebra mussels in a water body may not reduce the amount of benthic resources available for fish therefore there may not be a reduction in fish production in invaded waterbodies. The fish populations in Lough Erne appear to have responded to the zebra mussel invasion as if to an effective reduction of trophic status. Fish populations in other vulnerable waterbodies may also do so, especially lakes where both perch and roach are present.

16. The implications for the conservation objectives of the ULE Special Area of Conservation and other vulnerable waterbodies are outlined. There may be both negative and positive impacts on the features and conservation objectives and the presence of zebra mussel could lead to some waterbodies no longer being considered to be in favourable condition. Further spread of zebra mussels will also impact on the classification of lakes under the Water Framework Directive. If the current risk assessment guidance is applied, there is a real risk of failing to achieve at least 'good status' of all waterbodies by 2015 due to the presence of zebra mussels.

17. Measures that should be taken to minimise the risk of the spread of zebra mussels to these vulnerable lakes to maintain their integrity and conservation value are outlined in the Zebra Mussel Management Strategy for Northern Ireland.

CONTENTS

1. Introduction

1.1 Invasive species in Ireland

Invasive species are second only to land use change as a threat to biodiversity in freshwater ecosystems and the economic and ecological costs of invasions continue to increase as a direct consequence of expanding transport and commerce (Mack *et al*., 2000; Sala *et al*., 2000). An invasive species (alien, non-indigenous, non-native) is a species or sub species that has moved beyond its normal or past distribution. When species are moved beyond their native ranges the outcome is extremely unpredictable. Many non-native species have no major impacts while others have had catastrophic impacts on ecosystems and native species and economic interests such as agriculture, forestry, infrastructure and public health (DEFRA, 2003). Invasive species can have severe economic consequences; in the US, invasive plant and animal species are estimated to cost the economy $137 billion annually (Library of Congress, 2003).

Ireland has a depauperate fauna compared with continental Europe as a result of its isolation. This isolation has given rise to some unique species and gene pools. Species invasions may therefore be particularly damaging if the few native species are adversely affected. Conversely, vacant habitats or niches may allow integration of species with minimal community disturbance and/or rapid recovery (Dick, 1996). In some cases, native species or established invasive species appear to facilitate establishment of later-arriving non-indigenous species. Synergistic interactions among invaders may well lead to accelerated impacts on native ecosystems, in an '*invasional meltdown*' process (Simberloff & Von Holle, 1999).

Over the last few years invasive species in Ireland have increasingly come to the attention of policy makers. Both the United Kingdom and the Republic of Ireland are contracting parties to the Convention on Biological Diversity (CBD). The CBD is the only global and legally binding instrument to address the issue of invasive species and it requires contracting parties, as far as is appropriate, *"to prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species"*. A review of invasive species in Ireland was jointly commissioned by Environment and Heritage Service and the National Parks and Wildlife Service (Stokes *et al*., 2004). The recommendations are currently under considerations by both Governments.

1.2 Context of project

The zebra mussel *Dreissena polymorpha* is one of the latest and arguably the highest profile addition to the Irish fauna with public awareness campaigns aimed at limiting its spread taking place in both jurisdictions. This invasive bivalve from the Ponto-Caspian region, was first documented in the Shannon (McCarthy *et al.*, 1997). All available evidence suggested that zebra mussels became established in Ireland following importation of boats with living attached zebra mussels. The initial distribution of zebra mussels in Lough Erne suggested that zebra mussels first entered Lower Lough Erne as adults attached to boat hulls. Subsequent inoculations within the Erne and Shannon navigation systems, indicated that the likely means of dispersal of zebra mussels to new waterbodies in Ireland were spawning of attached adults on boat hulls and hull scrapings returned to the water (Minchin *et al.*, 2003).

An initial survey indicated that zebra mussel settlement probably occurred in very small numbers in Lower Lough Erne in 1996 (Rosell *et al.*, 1999). The first large scale survey of zebra mussels in the Erne was carried out in June 1998 and by late 1999 zebra mussels had colonised the whole system, including inflowing rivers such as the River Erne and Woodford River (Maguire, 2002). The size structure of the zebra mussel population suggested that zebra mussels in Lough Erne can grow up to 15 mm yr^{-1} and have a life span of 2.5-3 years or cessation of growth in older mussels. They tend to reach a size of 25-30mm with only a small proportion reaching over 30mm in length. The initial years of the zebra mussel invasion in Lough Erne were characterised by large variations in adult density and biomass among sites and timing of veliger production and abundance. The presence of overwintering veligers indicated that the conditions in Lough Erne are highly suitable for zebra mussels.

Research on the early ecological impacts in the Erne documented increased water clarity and reduction of chlorophyll *a* concentrations, the signature impacts of a zebra mussel invasion. Changes in nutrient concentrations and the reversal of some trends since 1999 showed that zebra mussels have probably had a significant impact on water quality. This is consistent with significant removal of material from the water column to the benthic environment and has been commonly observed in other waterbodies where zebra mussel densities have been increasing. There was rapid colonisation of the *Anodonta* population with a significant decrease in condition of the *Anodonta* population and an increase in its mortality. (Maguire, 2002; Maguire *et al.*, 2003).

1.3 Scope of project

The early ecological impacts suggested that zebra mussels were likely to have a significant effect on the ecology of Lough Erne. It was vital to assess both their impacts at higher trophic levels and the implications of zebra mussels spreading to other catchments. The current study was a three-year project (March 2002-5) which contained two main packages of work focusing on the management of the impacts of zebra mussels in Northern Ireland and determination of the effects on fish populations in Lough Erne through alterations of the food web.

1.3.1 Management of impacts of zebra mussels in Northern Ireland

This element of the work was delivered through a one-year MPhil studentship (September 2002-3) with input from other project staff. The focus of the studentship was developing strategies to limit the spread of zebra mussels in Northern Ireland. The impacts of zebra mussels were reviewed and control and mitigation measures were investigated to inform management advice. An evaluation of the effectiveness of the education and awareness campaign in Northern Ireland was then completed to determine overall level of awareness of the zebra mussel, in both the general public and in organisations which work on freshwater bodies in Northern Ireland. While most people claimed some knowledge of the zebra mussel (87%), only 62% of boaters reported regularly inspecting their boat for zebra mussels before moving it to different lakes (see Sykes, 2003 for further details).

The studentship also involved initial production of the Zebra Mussel Management Strategy for Northern Ireland (2004-2010). The overall aim of the management strategy was to minimise the spread of zebra mussels in Northern Ireland through raising awareness, developing policy and legislation, monitoring and research and developing contingency plans for immediate action in the event of further zebra mussel spread.

The management strategy was based on an understanding of the invasion history, general biology and ecology of the zebra mussel, economic and ecological impacts and control methods. The strategy:

- Identified the most important dispersal vectors in Northern Ireland and mitigating measures
- Prioritised the most vulnerable lakes and preventative measures that are needed
- Outlined possible consequences of invasion in the most important lakes

- Recommended a surveillance programme for further spread
- Made management recommendations to minimise the spread of zebra mussels
- Outlined an implementation table.

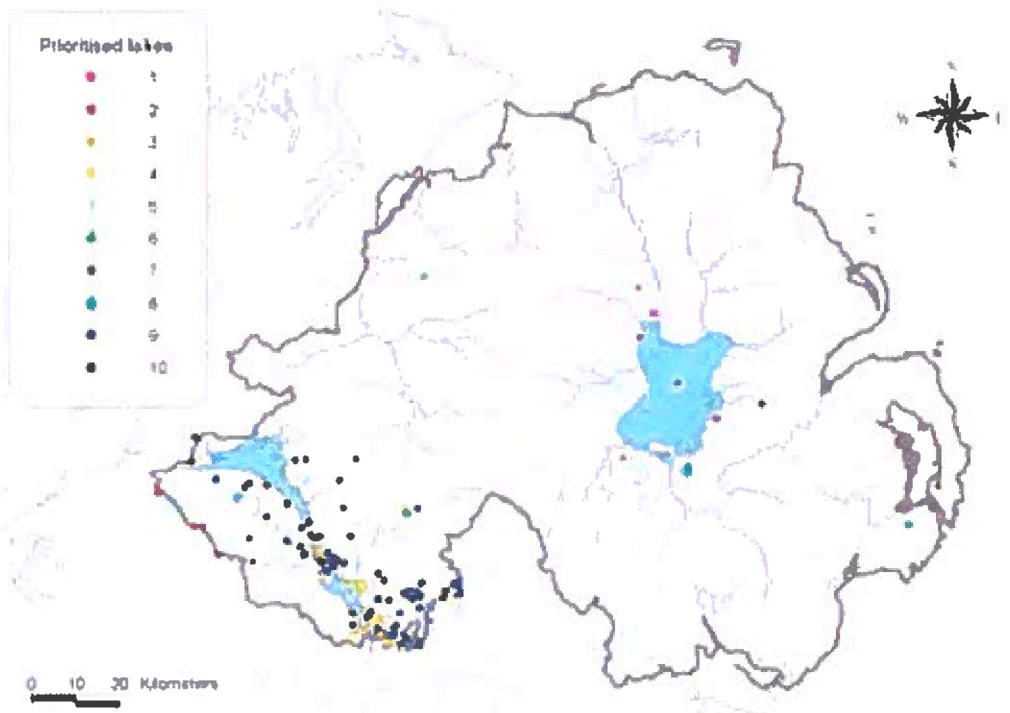


Figure 1. Map showing the location of the top ten vulnerable lakes or groups of lakes (see Maguire & Sykes, 2005 for further details)

The studentship also involved developing an early warning system for the colonisation of Lough Neagh and Lough Melvin by zebra mussels. Early warning systems in the form of spat collectors were deployed in Lough Neagh and Lough Melvin at the start of May 2003. A survey of marinas in Lough Neagh using a small dredge and scrapers was carried out in June 2003. Further dredge samples were taken at Ballyronan Marina, Coney Island, Kinnego Marina and Rams Island during October 2003 and 2004 and no zebra mussels have been found to date although uncolonised *Anodonta* were found at Ballyronan and Coney Island.

OUTPUTS

Maguire, C.M. & Sykes, L.M. (2005) Zebra Mussel Management Strategy for Northern Ireland (2004-2010). Environment and Heritage Service. Department of the Environment (Northern Ireland).

Sykes, L.M. (2003) Developing strategies to limit the spread of the zebra mussel (*Dreissena polymorpha*) in Northern Ireland. MPhil thesis. Queens University Belfast.

1.3.2 Determination of the effects on fish populations in Lough Erne through alterations of the food web.

This element of work was delivered through a three-year Research Fellowship and additional input from project staff, the Department of Agriculture and Rural Development (DARD) and the Department of Culture, Arts and Leisure (DCAL). Research focused on determining the effects of the zebra mussel invasion on the six species of fish (roach, bream, perch, pike, eel and trout) that comprise the majority of the fish biomass in Lower Lough Erne. Changes in the abundance, population structure and biomass of the six species were quantified.

Investigation of food web change in Lough Erne included documenting change in phytoplankton and zooplankton abundance and community composition, and impacts on populations of the native mussel *Anodonta* and other benthic invertebrate species. The major dietary components, established by gut-content analysis, of the six dominant fish species in Lower Lough Erne were also determined and the impact of zebra mussels on fish diets was assessed.

The research is summarised below and further details are presented in Appendices 1-5 (published papers or papers in preparation for publication). The research was then used to inform predictions on the potential impacts of further zebra mussel spread for fish populations in vulnerable lakes. The implications for attaining the conservation objectives of the Upper Lough Erne Special Area of Conservation (SAC) and Area of Special Scientific Interest (ASSI) and conservation objectives of the most vulnerable lakes are discussed. The implications of zebra mussel spread for compliance with European Directives such as the Water Framework Directive and Habitats Directive are also outlined.

This was informed by an international workshop held from 16-17th October 2003 at the Manor House Hotel, Enniskillen funded by Environment and Heritage Service with contributions from Fermanagh District Council, DARD and QUB. Participants at the workshop included scientists and policy makers who are currently, or have previously carried out research on Lough Erne and other Irish lakes; and invited experts. The scope of the workshop was broad and the objectives were:

- To review Lough Erne research in a holistic way, examining both long-term and short-term changes in the ecology of the Lough
- To explore the future development of an ecosystem model to predict future changes
- To examine the implications of zebra mussels for managing the Erne lakes under the Water Framework Directive.
- To develop a consensus on the best future research programme

Further details on the presentations and outcomes of the workshop can be found in the proceedings.

OUTPUTS

Maguire, C.M. (2003) Ecological change in Lough Erne: Influence of catchment changes and species invasions. Proceedings of an International Workshop, 16-17th October 2003, Manor House Country Hotel, Enniskillen.

Maguire, C.M. and Gibson, C.E. (in press) Ecological change in Lough Erne: Influence of catchment changes and species invasions. Freshwater Forum.

2.0 Research Summary

2.1 Introduction

A number of European and North American freshwater communities have experienced profound ecological changes subsequent to invasion by zebra mussels (Karatayev *et al.*, 1997; Heath *et al.*, 1995; MacIssac, 1996). For example, zebra mussels may alter nutrient cycling in a waterbody and their filtering activities often result in reduced concentrations of suspended solids and phytoplankton, alteration of phytoplankton community structure, increases in water clarity and increased macrophyte growth (Johengen *et al.*, 1995; Fahnensteil *et al.*, 1995; Baker *et al.*, 1998). Zooplankton may be suppressed owing to food limitation and smaller taxa may be ingested directly by zebra mussels (Bridgeman *et al.*, 1995; Jack & Thorpe, 2000). Habitat structure associated with, and waste products generated by, colonies of zebra mussels enhance production of many benthic invertebrates (Gonzalez & Downing, 1998; Haynes *et al.*, 1999). Fouling of unionid mussels can dramatically reduce unionid populations (Ricciardi *et al.*, 1996; Strayer, 1999). Changes in fish populations can occur, through colonisation of spawning grounds and the ability of a species to shift feeding behaviour to prey on zebra mussels (Karatayev *et al.*, 1997; Mayer *et al.*, 2001). It is possible that well-mixed or shallow systems invaded by zebra mussels may experience a shift in energy and biomass from pelagic to benthic food webs (Strayer *et al.*, 1999).

2.2 Population dynamics of the zebra mussel

The zebra mussel population in the Erne system was surveyed in June and December 2002 and 2003. Seven of the fourteen sites overlapped with the survey of zebra mussel density and biomass on vertical surfaces carried out by Dr Dan Minchin (Minchin, 2003). Average densities were low compared to some other European and North American waterbodies ranging from <10 to 2,500 no m^{-2}, however higher densities of over 10,000m^{-2} were documented on some localised areas of hard substrata. There was an increase in zebra mussel density from June 2000 to June 2002 and then a slight decrease in 2003 (Figure 2). However, the biomass of the population continued to increase (Figure 3). This was mainly due to expansion of the zebra mussel population in Upper Lough Erne.

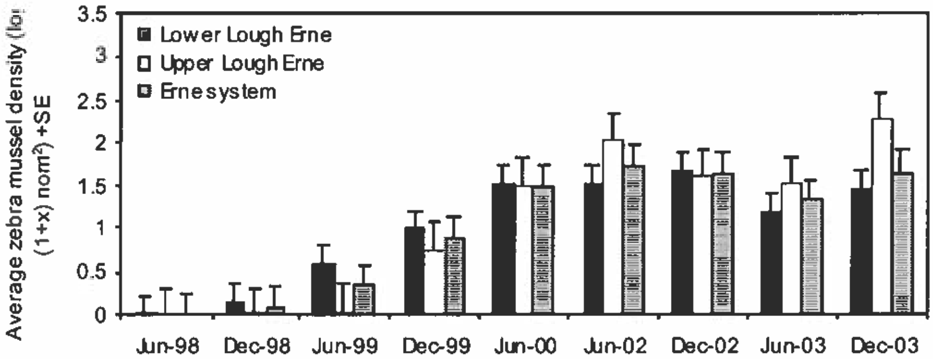


Figure 2. Average zebra mussel density in Lower Lough Erne, Upper Lough Erne and the Erne system (includes River Erne and Woodford River) from 1998 to 2003.

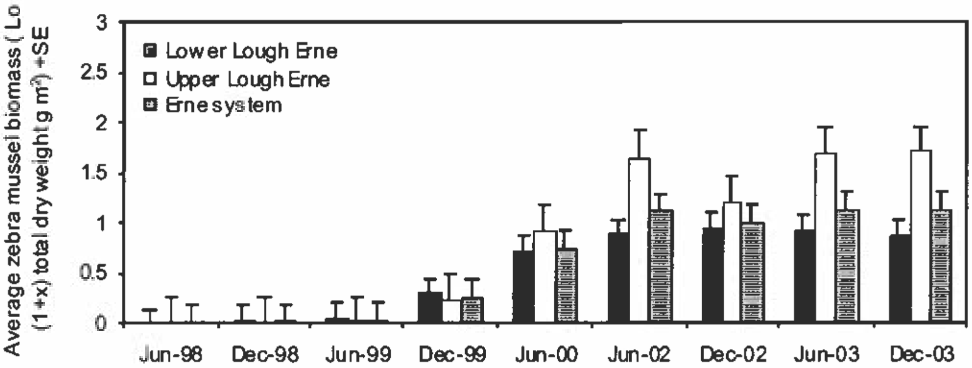


Figure 3. Average zebra mussel biomass in Lower Lough Erne, Upper Lough Erne and the Erne system (includes River Erne and Woodford River) from 1998 to 2003.

2.3 Change in bivalve filtering capacity

The zebra mussel population has continued to expand and this represents a change in bivalve filtering intensity. The total number and biomass of the zebra mussel population in 2003 and native *Anodonta* population (June 2000 data was used) were calculated. RoXanne maps of Upper and Lower Lough Erne were used to calculate the percentage area of hard and soft substrata. Areas above 1.5m and below 20m were excluded as a previous Remotely Operated Vehicle (ROV) survey showed that they did not support many zebra mussels and unionids were not present (Maguire, 2002). The average density and biomass of each species was calculated for each substratum type and then used to estimate the total number and biomass of each species (Table 1).

Table 1. Estimate of the total number and biomass of *Dreissena* and *Anodonta* sp. in Lough Erne.

		Upper Lough Eme	Lower Lough Eme	Upper Lough Eme	Lower Lough Eme
		Average density (no m^{-2})		Average biomass (Kg m^{-2})	
Hard substrata	*Dreissena*	278.2	234.4	0.028	0.025
	Anodonta	0.55	0.25	0.018	0.005
Soft substrata	*Dreissena*	199.3	90.2	0.068	0.017
	Anodonta	1.24	0.57	0.04	0.013
		Total number		Total biomass (tonnes)	
	Dreissena	0.95×10^{10}	1.35×10^{10}	2238	1914
	Anodonta	4.04×10^{7}	4.29×10^{7}	1312	918

The filtering capacity of the population of each species was calculated using equations in Kryger & Riisgard (1988) based on the population structure in Lough Erne. Although this calculation does not take into account factors such as bivalve access to the whole water column, especially when lakes are stratified and that mussels are unlikely to be filtering twenty four hours a day, it does give a relative estimate.

The *Anodonta* population has effectively been replaced by the zebra mussel in Lough Erne (see p19) and the comparison of the filtering capacity of both populations reveals a real difference between species (Table 2). Bivalve filter feeding capacity is now approximately twenty times greater in Lough Erne since the establishment of zebra mussels and this level of planktivory makes zebra mussels strong resource competitors with unionids, zooplankton, larval and some adult fish.

Table 2. Estimated time (days) for *Dreissena* and *Anodonta* to filter the Erne lakes.

	Dreissena	*Anodonta*
Upper Lough Erne	2.45	39.12
Lower Lough Erne	26.9	602.1
Erne system	16	328

2.4 Impact on water clarity and phytoplankton

DARD have maintained a long term monitoring programme of water quality in Lough Erne since 1973 and this data was available to determine the impacts of the zebra mussel invasion on water clarity and phytoplankton (see Appendix 1 for methods). Water clarity in Lough Erne is determined by background colour from humic matter originating from the catchment and suspended particles. Since the establishment of zebra mussel water clarity has increased in Lough Erne and values recorded in 2000 were the highest since records began (Figure 4). In the shallow areas of the lakes water clarity is noticeably greater, whereas in the deeper areas and Broad Lough the change has not been as dramatic due to the background colour.

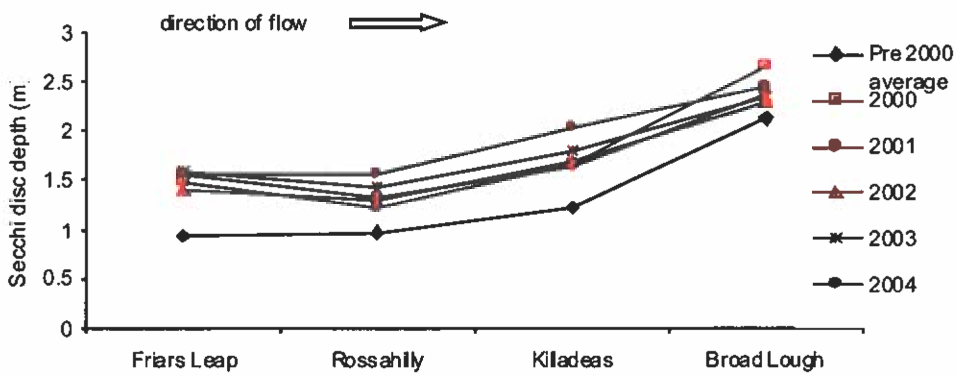


Figure 4. Water clarity after the establishment of zebra mussels compared to the long-term average.

There has been in the Erne lakes, a reduction of about 90% of peak summer maximum chlorophyll *a* concentration, as a result of zebra mussel filtering activity (Figure 5). The effect of zebra mussel grazing on phytoplankton community composition seems to vary amongst waterbodies. The available data on phytoplankton community composition was not sufficiently precise to make quantitative comparisons between years to determine if zebra mussel feeding has had an impact on community composition. However, qualitative information suggests that there has been little selectivity in feeding as the abundance of all phytoplankton species has declined (C.E. Gibson & C.M. Maguire, unpubl. data). There may also be a difference in the impact of zebra mussels on phytoplankton in the shallower margins compared to deeper water. It is likely that cells are advected into the Broad Lough from the margins. Profiles of cell counts in the summer show that there are many more cells in the upper layers, including those of species that are not positively buoyant. Research on sedimentation processes showed that sediment traps only catch a small proportion of the diatom crop (C.E. Gibson, pers. comm.). Studies of vertical chlorophyll profiles and mussel ingestion suggest that mussels refilter the lower portion of the water column more rapidly than phytoplankton are delivered by mixing (Ackerman *et al.*, 2001). Hence mussel consumption of phytoplankton may be constrained by vertical and horizontal mixing of the water column. The sampling sites used in the long term monitoring programme are not located in the margins and so we are unable to differentiate between impacts in the shallow and deeper areas of Lower Lough Erne from the long-term data.

Although zebra mussels do not appear to have altered phytoplankton community composition, monospecific blooms of *Microcystis* sp. were recorded in Lower Lough Erne in 2003 and 2004. While blue-green algal blooms are not a novel occurrence in the Erne lakes, usually they consist primarily of *Anabaena* sp. and *Aphanizomenon* sp., with some *Microcystis* sp. The development of monospecific *Microcystis* sp. blooms may relate to selective filtration of phytoplankton by zebra mussels - a process that depletes the water column of more palatable phytoplankton species and leaves *Microcystis* to accumulate in the absence of competition for light and nutrients. Production of loosely consolidated pseudofaeces also allows viable *Microcystis* to return to the water column for continued growth. The documented increases in *Microcystis* associated with zebra mussel invasions may involve toxic strains only, as zebra mussels have been shown to actively consume non-toxic strains in laboratory studies (Vanderploeg *et al.*, 2001). At present it is not known whether the *Microcystis* blooms in the Erne lakes are comprised of toxic strains, if they are toxic and such blooms become a regular occurrence, this will have human health implications because of the contribution of the Erne lakes to the provision of drinking water.

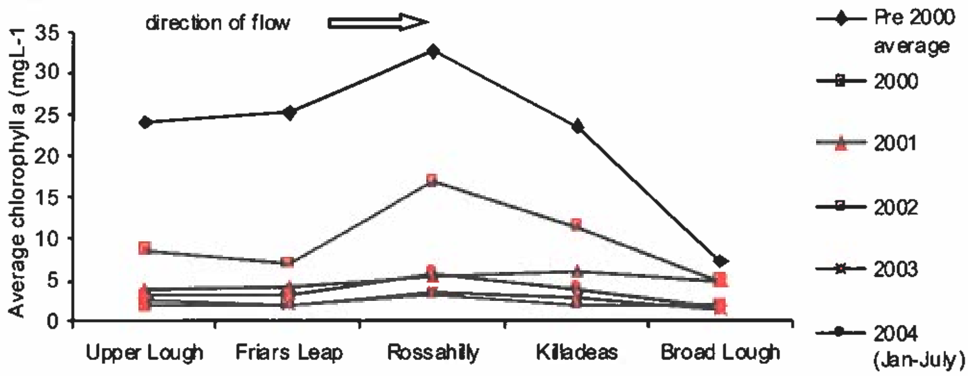


Figure 5. Chlorophyll *a* concentrations in Lough Erne after the establishment of zebra mussels compared to long term average.

2.5 Impact on zooplankton.

Assessment of the zebra mussel impact on the zooplankton population included measuring change in community composition and individual species abundance. Changes in zooplankton abundance were determined by comparing pre invasion (1986-1997) and post invasion (1998-2004) data and samples. Before 1998 the zebra mussel population was low in abundance and was not impacting on water quality, therefore data collected before 1998 was considered to be pre invasion in the analysis (see Appendix 2 for further details).

There are several, not mutually exclusive, mechanisms by which zebra mussels can impact on zooplankton; direct predation, competition for phytoplankton, and by causing a shift in phytoplankton species composition. The mechanisms by which zebra mussels impacted the zooplankton population were investigated using Stable Isotope Analysis (SIA) of archived samples. SIA analysis was provided by Dr Jon Grey, Max Planck Institute of Limnology (see Appendix 3 for further details).

We were constrained in the type of analysis that could be carried out on abundance data due to the lack of replicate samples available before 1999 and some missing samples in the monthly time series. Data was analysed using the Seasonal Mann-Kendall test, an extension of the Mann-Kendall test. This nonparametric test is based entirely on ranks and adjusted to deal with non-normal data, seasonality, missing values, ties, censoring and serial dependence (Hirsch *et al.* 1982; Hirsch & Slack 1984). The test cannot be used for determining when the change took place, only for detecting monotonic trend (gradual or sudden) during an interval of time. The

Seasonal Mann-Kendall test was applied to the data from 1986-2004 to reveal if there was a trend in zooplankton abundance. The same analysis was then repeated separately for the pre-invasion years (1986-1997) and post-invasion years (1998-2004) to determine if the trend or change in values occurred only after the establishment of zebra mussels.

Since the zebra mussel invasion there has been a significant decline in the total zooplankton density in Lough Erne ($p<0.05$) (Figure 6). In other water bodies zebra mussel impacts seem to be selective with the greatest impact on rotifers and cladocerans least affected (Bridgeman *et al.*, 1995; Pace *et al.*, 1998; Jack & Thorp, 2000). In Lough Erne, copepods, rotifers and cladocerans were all affected (Figure 7), although there were differences in impact on different species. While copepod abundance significantly declined from 1986-2004 ($p<0.001$), there was a significant decline pre invasion ($p<0.001$) as well as post invasion ($p<0.05$). This pre invasion decline may be attributable to the decline in zooplankton abundance after the invasion of roach (Rosell & Gibson, 2000). There was a significant decline in rotifer abundance ($p<0.001$) and cladoceran abundance ($p<0.001$) from 1986-2004, although the seasonal Mann-Kendall test was unable to determine if the significant decline was post invasion.

There were significant declines in the rotifer species *Keratella cochlearis* ($p<0.001$), *Keratella quadrata* ($p<0.001$), *Kellicota longispina* ($p<0.001$), *Filinia longiseta* ($p<0.001$), *Polyarthra vulgaris* ($p<0.001$) and there was a significant increase in *Filinia terminalis* ($p<0.001$). There was no significant change in abundance of *Polyarthra dolichoptera*, *Conochilus hippocrepis*, *Brachionus angularis*, *Brachionus calyciflorus* and *Asplanchna priodonta*.

Abundance of both calanoid and cyclopoid copepod species declined, but the greatest decline was in the herbivorous *Eudiaptomus* sp ($p<0.001$). There was a significant decline in *Cyclops* sp ($p<0.001$) and no significant change in abundance of *Eurytemora* sp, although this is only a small component of the copepod community. There were significant declines in abundance of cyclopoid ($p<0.001$) and calanoid nauplii ($p<0.01$). Although there was an overall decline in cladoceran abundance, there was differential impact between species. There was a significant decrease in *Daphnia cucullata var. kahlbergensis* ($p<0.01$) and *Diaphanosoma brachyurum* ($p<0.05$) and a decline in abundance of *D. cucullata*, *D. hyalina*, and *D. hyalina var. galeata* although these were not significant. *Bosmina* sp. and *D. hyalina var.*

lacustris did not decline in abundance. This could be a reflection of greater fish predation pressure on a less abundant zooplankton population causing a shift towards the smaller bodied cladoceran species. Also *Bosmina* is associated with reed beds and macrophytes, both of which have increased since the zebra mussel invasion (see Appendix 2 for further details on individual species).

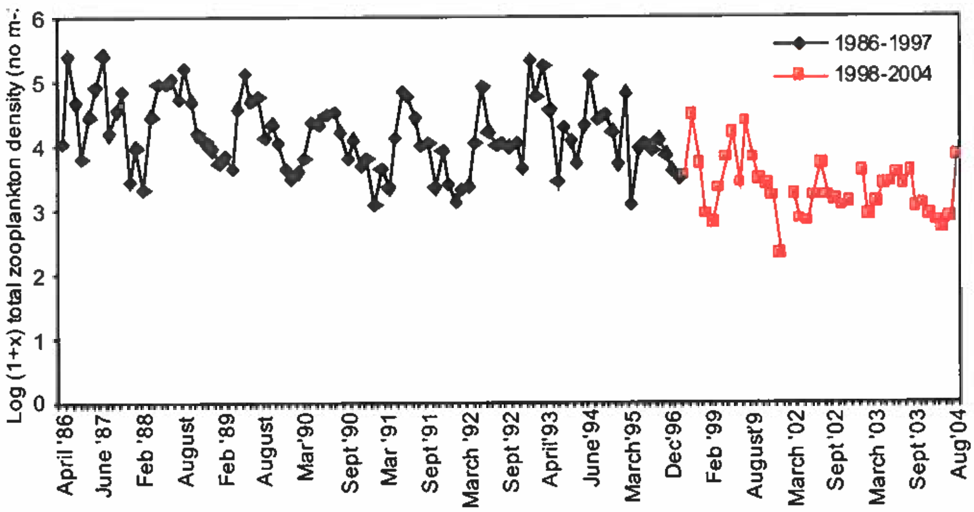


Figure 6. Total zooplankton density in Lower Lough Erne from 1986-1998 (pre invasion) and 1999-2004 (post invasion).

Several reasons have been advanced for why zebra mussels do not consistently have a strong negative effect on zooplankton. These include indirect positive effects on phytoplankton productivity that offset the increased consumption by zebra mussels and physical factors such as mixing that constrain direct effects of mussel filtering on phytoplankton (Noonburg *et al*., 2003). In Lough Erne, phytoplankton abundance has decreased dramatically and because of the background colour from humic matter originating in the catchment, it is unlikely that there has been an increase in the photic zone or corresponding phytoplankton productivity. Zooplankton samples were also taken from the Broad Lough, the deepest point of the lake and stratification of the water column occurs in summer. Stable isotopes were used to investigate the diet of zooplankton population and the impact of the reduction in phytoplankton.

Stable isotopes are increasingly used in food web studies although there are few examples in which they have been used to examine food web response to invasion. The stable isotope analysis (SIA) approach requires that different basal

Carbon and nitrogen stable isotopes of archived zooplankton samples were analysed (see Appendix 3 for methods). Analysis of a series of monthly samples (1992-1996, 1999-2003) revealed significant enrichment of $\delta^{13}C$ of mixed zooplankton ($p<0.05$), *Eudiaptomus gracilis* ($p<0.01$) and *Mysis relicta* ($p<0.05$) post zebra mussel invasion (Figure 8). The results supported our hypothesis and revealed an invasion impact, namely a shift by zooplankton indicating increased assimilation of allochthonous carbon after the establishment of zebra mussels, which would not have been detected by other methods. Changes in zooplankton elemental composition also suggested a switch to a lower quality diet. However analysis of the annual single point time series (1977-2004) showed when phytoplankton was sufficiently abundant in June, zooplankton used this resource and hence did not show a shift in $\delta^{13}C$. Enrichment of mysid $\delta^{15}N$ reflected a shift towards more carnivory.

This study illustrates how stable isotope analysis can be used to determine both the impact of a species invasion upon a food web, and examine the mechanisms of such an impact. In cases where pre-invasion isotope data are not directly available but samples have been archived, then stable isotope analysis may provide a new perspective on food web changes in response to invasion (see Appendix 3 for further details).

The decrease in zooplankton abundance and SIA results indicate the potential for zebra mussels to have a significant impact on phytoplankton and zooplankton abundances in Irish lakes. In Oneida Lake, North America, the establishment of zebra mussels resulted in a decline in chlorophyll *a* concentrations but not in primary productivity as a result of the compensating effect of increased water clarity resulting in deeper penetration of photosynthetically active radiation (Idrisi *et al.*, 2001). The degree of compensation will likely vary among systems depending on a combination of factors, including photosynthetic irradiance (PI) parameter values, light environment, phytoplankton species composition and abundance. Irish lakes with high background colour may not experience a large enough increase in water clarity to result in the compensating increase in photic zone and phytoplankton productivity that has 'buffered' the impact on zooplankton in other waterbodies, resulting in a less abundant zooplankton community with consequences for fish populations.

2.6 Impact on benthic invertebrates.

Zebra mussels can affect benthic invertebrates directly and indirectly, effects are varied and may be beneficial such as generating habitat in the form of shells and causing an increase in benthic organic matter or detrimental, such as competition for food and space and direct colonisation of other bivalve species. Zebra mussels have been shown to have a beneficial effect on amphipods, turbellarians, oligochaetes and chironomids; and negative effect on some gastropods, chironomids and net spinning caddis flies by excluding them from rocky substrates (Botts *et al.*, 1996; Ricciardi *et al.*, 1997).

There was little data available on benthic invertebrates in the Erne system prior to the zebra mussel invasion. Hale & O'Neill (1997) surveyed benthic invertebrates in the Erne lakes by kick sampling at a series of locations around the system. Funding was received from QUB for a summer studentship during 2003 and the survey was repeated and an additional grab survey for benthic macroinvertebrate species was carried out in August 2003.

In the present study only *Chironomidae* and *Gammarus pulex* were found to be present at every kick sample site. Of the 42 taxa recorded by Hale & O'Neill (1997) 24 were not found in the present study. However, we were unable to sample every site in Hale & O'Neill (1997) which may be a contributing factor to the absence of species. The positive effect of zebra mussels on amphipods can be seen in the high abundance of *G. pulex* and *G. duebeni*, and *Asellus aquaticus*. There was a decrease in the abundance of *Planorbidae* which may reflect the exclusion of gastropods from rocky substrates by zebra mussels (Greenwood *et al.*, 2001) (see Appendix 2 for further details).

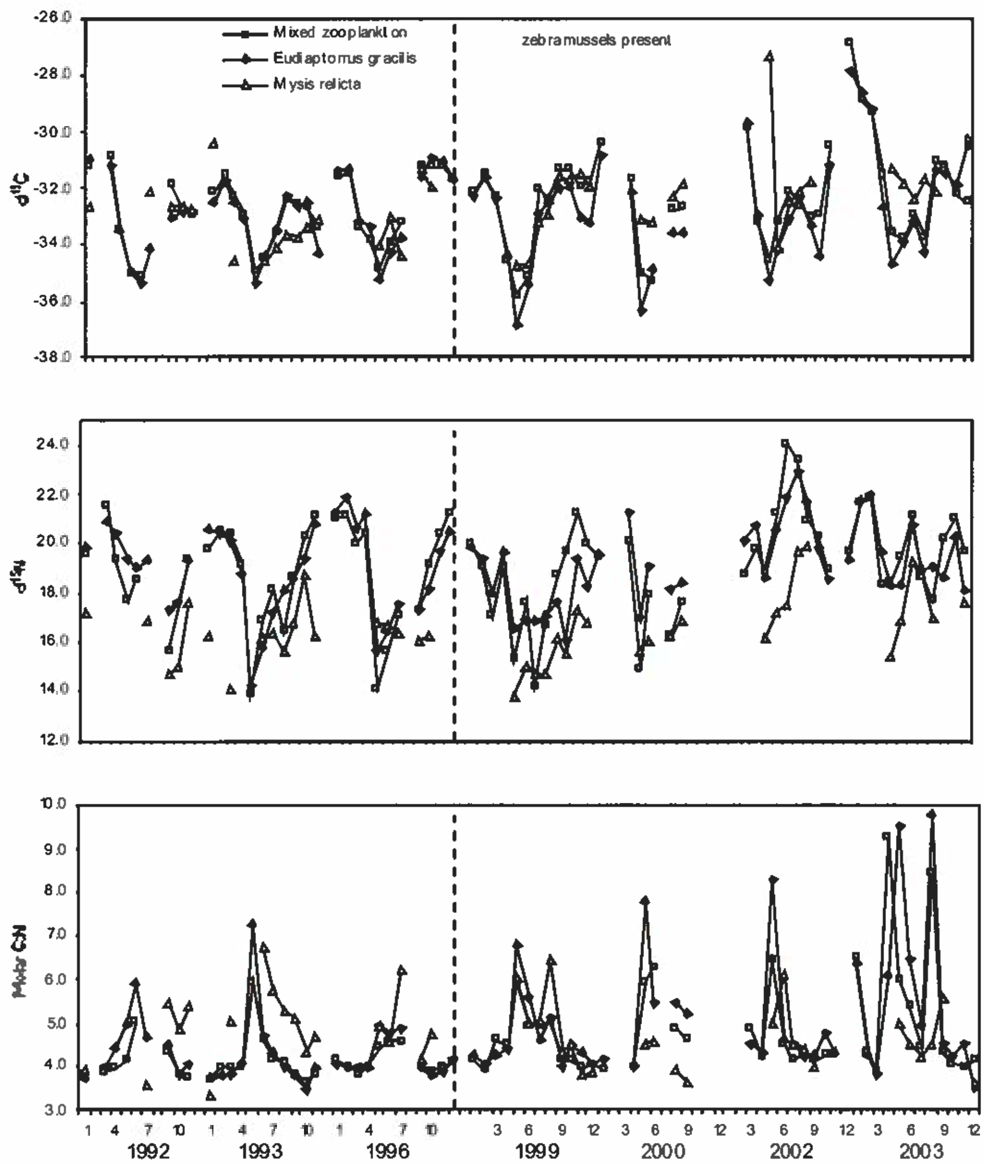


Figure 8. Seasonal time series of $\delta^{13}C$, $\delta^{15}N$ and molar C:N ratios of mixed zooplankton, *Eudiaptomus gracilis* and *Mysis relicta* (1992-1996 and 1999-2003) in Lough Erne. Dashed line denotes invasion and establishment of *Dreissena polymorpha*.

Because only ranked abundances were available from 1997 we were not able to do any multivariate analysis comparing the surveys. The major difference was the presence of *Dreissena polymorpha* in the 2003 samples. We compared the univariate statistics from both surveys (paired t-test) and found that in 2003 there was a significantly lower number of taxa ($t=12.2$, $p<0.0001$, $df=15$) and significantly lower biotic score ($t=10.3$, $p<0.0001$, $df=15$). While the diversity of the benthic invertebrate community has appeared to decrease this may not be indicative of a decrease in overall abundance as zebra mussels, *Gammarus* and chironomids are now highly abundant.

The most visible impact of zebra mussels on benthic invertebrates was the rapid colonisation of the native mussel population. In contrast to the generally similar impacts of zebra mussels on lake ecology in Europe and North America the impact on native freshwater mussels of the family Unionidae may differ markedly between the two regions. Several causal mechanisms of unionid mortality as a result of infestation by zebra mussels have been proposed.

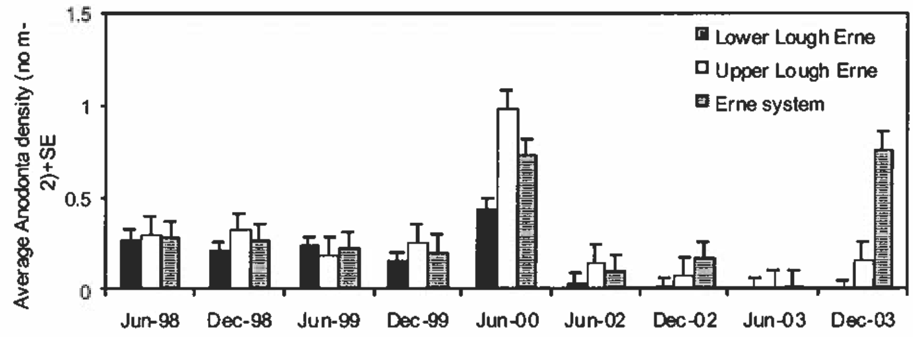
Zebra mussel infestation may: (1) impair locomotion, burrowing and balance; (2) interfere with valve closure, increasing the risk of predation and parasitism; (3) hinder valve opening, impairing feeding, reproduction, respiration and excretion; (4) smother siphons, obstructing respiration and feeding; (5) strip inhalant water of food, reducing food intake; (6) interfere with normal growth, causing shell deformities; (7) generate toxic metabolic wastes (Mackie, 1991; Schloesser & Kovalak, 1991; Mackie, 1993; Schloesser & Nalepa, 1994; Karaytev *et al.*, 1997; Parker *et al.*, 1998; Baker & Hornbach, 2000).

Only three large unionid species have been recognised in Ireland: the swan and duck mussels *Anodonta cygnea* (L.) and *Anodonta anatina* (L.) and the pearl mussel *Margeritfera margeritifera* (L.). Lough Erne has just two species *A. cygnea* and *A. anatina* and unlike in the rest of Europe these species are very difficult to tell apart in Ireland. They also have similar habitats and requirements that may make them equally susceptible to zebra mussel fouling, increasing the risk of extirpation. Research has shown differences in fouling impacts among unionid families with Anodontidae the most vulnerable (Haag *et al.*, 1993)

The severe impact of zebra mussels on native bivalves in North America could not have been predicted from the European experience. If we use invasion history as a predictor there are two distinct invasion histories, that in North America and that in Britain, and one might expect the impact in Ireland to be similar to that in Britain i.e. no major impact or decline in unionids. Unlike most of continental Europe, native species in Ireland have not had prior experience of zebra mussels. The invasion of Lough Erne by the zebra mussel represents the introduction of an important fouling organism into a community that has no evolutionary experience of, and therefore has evolved no behavioural defensive mechanisms against, such fouling.

We hypothesised that the impact on the native unionid species in Ireland would be severe and more similar to the North American experience than a typical European one. The hypothesis was tested using empirical models developed using mainly North American data (Ricciardi *et al.*, 1995) to predict the impact on unionids in Lough Erne (see Appendix 4 for further details).

There was no published information or baseline data on the populations of *Anodonta* in the Erne system prior to the present study of the zebra mussel invasion. The initial survey revealed that the vast majority of the population was uncolonised. Initial recorded *Anodonta* densities were low with an average density of 0.28 m^{-2} (Figure 9). The peak densities recorded in June 2000 can be attributed both to increased sampling efficiency of the dredge and emergence of *Anodonta* from sediments as they became colonised by zebra mussels (Maguire, 2002). By 2003, average density had decreased to 0.07m^{-2} and no live *Anodonta* specimens were recovered at the majority of sample sites (Figure 10). The exception was at the mouth of the River Erne where it flows into the Upper Lough. In 2003 we also documented heavy mortality of a population of very lightly fouled unionids. This phenomenon had also been reported in the Hudson River where it was attributed to competition for food as well as fouling (Strayer & Smith, 1996). It seems likely that mortality of lightly fouled *Anodonta* was due to removal of particulate food by large densities of zebra mussels throughout Lough Erne because a significant decline in *Anodonta* condition was recorded in the Lough after the zebra mussel invasion (Maguire, 2002).



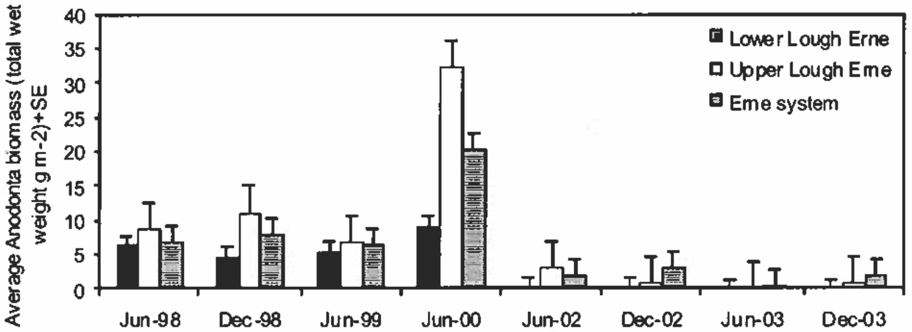


Figure 9. Average density and biomass of *Anodonta* sp in Lower Lough Erne, Upper Lough Erne and the Erne system (includes River Erne and Woodford Rivers) from June 1998 to December 2003.

When the infestation level of zebra mussels on unionids in Lough Erne is compared to data from other ecosystems, Lough Erne stands out (see Appendix 4 for predicted versus observed data). Infestation levels on *Anodonta* in Lough Erne at low zebra mussel densities are higher than the other European and North American waterbodies (Figure 11).

The negative impact on unionids in Lough Erne is not unique in Ireland, a similar pattern of rapid colonisation and extirpation appears to be happening in other Irish waterbodies. None or very few live unionids have been documented in Lough Derg, Lough Key or Lough Ree (Shannon system) in recent years (F. Lucy, pers.comm.). All indications are that the impact on native unionid populations in Ireland is very different from the typical European experience. The lack of evolutionary exposure to zebra mussel populations is an important point distinguishing Irish unionid populations from those in central Europe. Continental European populations of unionids are also more diverse than Irish populations which may provide them with more resistance to zebra mussel invasion. Low species richness is one of the community properties held to increase the chance of species becoming invasive (Mack *et al*., 2000). However, North America has the most diverse unionid populations in the world with 299 species and subspecies and they were heavily impacted (Schloesser *et al*., 1996).

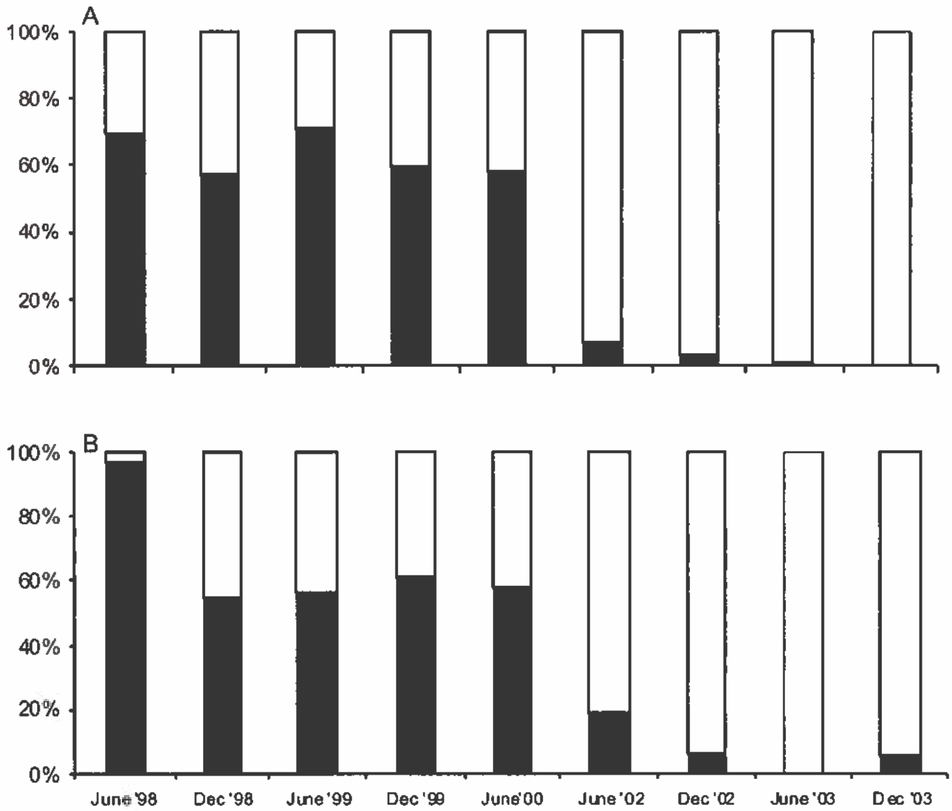


Figure 10. Mortality of *Anodonta* in Lower Lough Erne (A) and Upper Lough Erne (B) indicated by the percentage of live specimens collected (shaded).

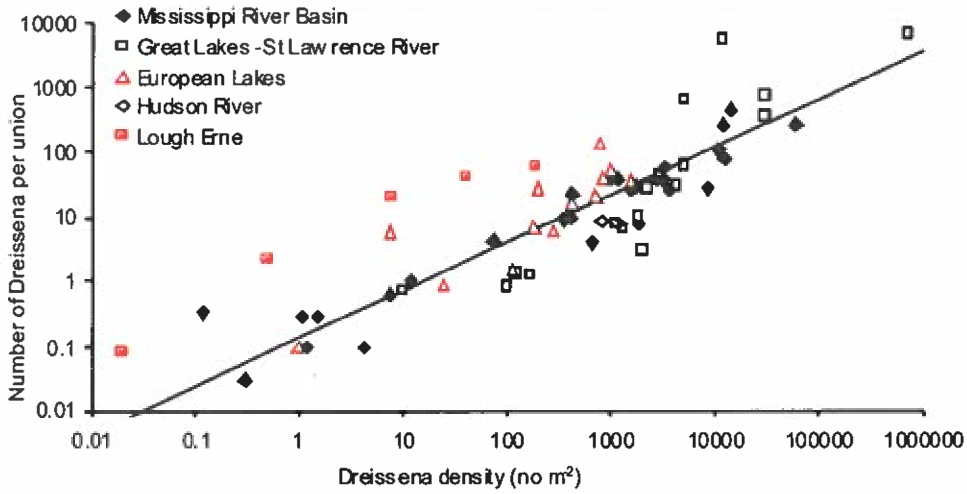


Figure 11. Infestation level of zebra mussels on unionids as a function of local Dreissena density in North American and European waterbodies (adapted from Ricciardi, 2003)

The extirpation of unionids from Lough Erne has implications for developing conservation strategies for unionids in Ireland because the majority of waterbodies in Northern Ireland are suitable for establishment of zebra mussels and reductions in chlorophyll *a* concentrations have been observed in all Irish lakes invaded by zebra mussels. Current conservation plans for unionids threatened by zebra mussels in North America focus on three alternative strategies: (1) captive care, propagation and reintroduction, (2) cleaning, quarantine and translocation, and (3) periodic cleaning and replacement in situ (Hallac & Marsden, 2001; Hart *et al.*, 2001). Unless such strategies are adopted in Ireland, long-term survival of unionid populations is unlikely in Irish lakes invaded by zebra mussels due to zebra mussel fouling impacts, competition for food and resulting decline in condition.

2.7 Fish diets.

The addition of a novel species to a food web can have important consequences for the community structure of an invaded ecosystem, both through direct and indirect biotic interactions. Mixing of faunal associations can lead to predators switching to prey which have never previously occurred in the system if indigenous prey are scarce or a new prey species is abundant or more accessible (Nikolksii, 1969).

Throughout their ontogeny, fish usually undergo several diet shifts by progressively consuming larger prey items that may require the use of different feeding habitats such as the pelagic and benthic environments, or as in anadromous fish, extensive migrations between fresh and salt water (Werner & Gilliam, 1984). As larvae, fish mainly feed on small zooplankton such as rotifers and nauplii, this can be followed to a transition to larger zooplankton, benthic invertebrates and ultimately to other fish depending on their size and preferred prey (Mittlebach & Persson, 1998). The addition of zebra mussels to the Lough Erne fauna represents a novel food source for fish and the introduction of a species affecting important components of fish diets.

The difficulty with assessing the effect of an altered food web structure on fish diets is the lack of pre invasion data. In the present study, samples were retained for gut content analysis from the 2000 and 2002 fish population surveys, both after the establishment of zebra mussels. Therefore an assessment of any change in diet of the main fish species as a result of the zebra mussel invasion was not possible. The main prey species of each fish species was identified and the implications of change in populations of these species are discussed (see Appendix 5 for further details). It was not possible to quantify the proportion of each prey category to the diet of the main fish species as prey species were crushed and fragmented in samples retained from roach, bream and roach/bream hybrids and some samples from 2000 had not preserved properly. Therefore it was only possible to record the presence of prey species. Samples were retained from three size categories of brown trout (*Salmo trutta*), roach (*Rutilus rutilis*), bream (*Abramis brama*), roach bream hybrids and perch (*Perca fluviatilis*) (Table 3).

Table 3. Size categories of fish

Species	Size category (cm)		
	Small	Medium	Large
Bream	<15	15-30	>30
Roach	<13	13-22	>22
Roach Bream Hybrid	<15	15-30	>30
Perch	<13	13-20	>20
Trout	<20	20-30	>30

There were no samples available from small bream and from small roach bream hybrids in 2002.

Table 4 to be inserted - problem with formatting in document so saved as separate file

The abundance of zebra mussels mean they now play a significant role in the feeding relationships of the fish of Lower Lough Erne. Zebra mussels are now a substantial component of the diet of all size classes of roach, bream and roach bream hybrids, but not perch or trout (Table 4).

A typical bream diet consists of chironomids, caddis-fly larvae, amphipods and other benthic invertebrates. Both medium and large bream had a diverse diet containing gastropods, zebra mussels, benthic invertebrates and plant material/detritus, although caddis-fly larvae were not recorded in any samples.

Perch normally undergo an ontogenetic niche shift, initially being plankton feeders as larvae and small juveniles, later becoming benthos-feeders, and from a certain body size, shifting to a piscivorous diet as yearlings and adults (Borcherding *et al.*, 2000). Small perch mainly preyed on zooplankton and benthic invertebrates and their diet in 2002 was more diverse than in 2000, though more fish were sampled which may explain the higher number of prey categories found. Medium and large perch were piscivorous and also preyed on zooplankton, benthic invertebrates and aquatic insects, with a more diverse diet recorded in 2002 than 2000 with a similar sample size. The greater variety of benthic invertebrates recorded in 2002 may be a reflection of the continued reduction in zooplankton abundance as a lack of zooplankton may cause juvenile perch to adopt a diet containing larger benthic macroinvertebrates (Persson, 1983).

Roach are omnivorous, feeding on zooplankton, zoobenthos, detritus, epiphytes, phytoplankton and macrophytes. Zooplankton remains a substantial component of small roach diets, along with zebra mussels and chironomids. Diets of medium and large roach were diverse incorporating zooplankton, benthic invertebrates, plant material/algae and detritus but dominated by zebra mussels. The % occurrence of zooplankton recorded in diets was lower in 2002 than 2000 and some individual fish were feeding exclusively on blue-green algae. The percentage of zooplankton in the diet of roach usually decreases and the percentage of benthos and plant material increases with the increasing size of fish (Horppila, 1994). The diet of roach bream hybrids consisted of various gastropods, chironomids, caddis-fly larvae and zebra mussels with little variation between size classes or years.

Trout diets can vary seasonally and in the present were fairly diverse incorporating zooplankton, chironomids, Gammarus, mayfly and stonefly nymphs, caddis-fly larvae and aerially derived insects. All size classes of trout were piscivorous, feeding mainly on perch fry.

There was interspecific diet overlap between perch and roach with both species feeding on zooplankton and chironomids. However, roach also fed on prey categories that were not utilised by perch such as zebra mussels, other gastropods and primary producers. Diet overlap is often assumed to be related inversely to competition intensity, since high competition tends to result in niche segregation between the competing groups, but positive relationships between competition and overlap have also been reported. However, the conclusions of the interactions between perch and roach have been derived mostly from studies conducted in enclosures and ponds, or in lakes of small surface area. In larger lakes perch and roach are able to effectively utilise the different habitats and diverse food resources (Horppila *et al*., 2000). In Lough Erne, roach has incorporated the novel food source provided by zebra mussels into its diet whereas perch has not.

2.8 Implications of these changes for fish populations.

Since zebra mussel have become established in Lough Erne there has been a significant increase in water clarity and an increase in macrophyte growth with more extensive littoral vegetation in shallow areas of the Erne lake system (EHS, 2004). There has been a reduction in phytoplankton abundance and a reduction in autochthonous resources available for zooplankton. This has led to a reduction in zooplankton abundance and more dependence on allochthonous resources. There may have also been a reduction in the diversity of the benthic invertebrate community, although there is no evidence of a reduction in abundance, with the exception of the extirpation of unionids. These changes have implications for fish in Lough Erne through modification of habitat, food webs and available resources.

The reduction in available zooplankton resources may increase competitive interactions and has the potential to impact on recruitment and growth of zooplanktivorous fish. Although the feeding habits of the larval stages of many fish species are not well understood, larvae are often the most visually orientated predators of zooplankton during the earliest life stage and larval fish also experience high mortality (Raikow, 2004). The reduction in zooplankton could result in diminished larval fish growth and survival. An abundant zebra mussel population will be beneficial to those species that can incorporate zebra mussels in their diet. Although zebra mussel colonies on soft substrates may reduce fish foraging success by blocking access to the benthos or by reducing the ability of fish to find and capture prey (Beekey *et al.*, 2004). Those species that require clean gravel to spawn may be affected by zebra mussel colonisation of hard substrata. The habitat provided by the zebra mussel colonies with abundant gammarids and chironomids will be beneficial to benthic feeding fish. Habitat provided by macrophyte growth will favour perch over roach as it is a superior forager within littoral vegetation (Winfield, 1986).

2.9 Changes in the abundance, population structure and biomass of the six main fish species.

Lough Erne has a relatively simple fish assemblage which is important for recreational use and associated tourism. The 5 main species present are roach *Rutilus rutilus* (L.), European perch *Perca fluviatilis* (L.), northern pike, *Esox lucius* (L.), common bream *Abramis brama* (L.), and brown trout, *Salmo trutta* (L.). These 5 species, along with hybrids between roach and bream, make up the majority of the fish populations and are the main species of importance for anglers. Other species present are eels *Anguilla anguilla* (L.) and very small species, such as gudgeon *Gobio gobio* (L.) and stickleback species. Since the 1970's the fish community has been dominated by roach and perch, which between them comprise 85% or more of fish abundance and biomass. Roach are themselves an introduction, arriving in the Erne system in the 1960's (Cragg Hine, 1973) and have been implicated in zooplankton depletion resulting in increased algal blooms since their introduction (Rosell & Gibson, 2000).

DARD and DCAL have monitored the fish populations in Lower Lough Erne since 1991 with sampling undertaken at a maximum interval of 4 years. Fish are sampled in multi-panel gill nets with a progression of mesh sizes set at 30 or more sites between July and September (see Appendix 5 for further details). Survey frequency was increased to every two years in the years after the introduction and establishment of zebra mussels to determine the impact of subsequent ecological change on fish populations.

Fish abundance is presented as Catch Per Unit Effort (CPUE) expressed as numbers per survey net or and because roach and perch were more abundant than other species the data was log transformed to show trends (if any) in the less abundant species (Figure 12). The relative abundance between species is shown in Figure 13. The biomass of the main fish species is presented in Figures 14 and 15.

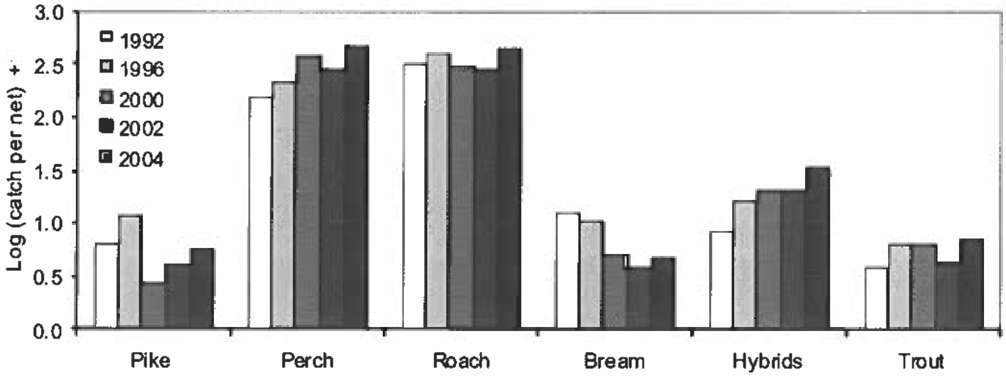


Figure 12. Survey net catch per unit effort (log transformed abundance) in Lower Lough Erne from 1992 to 2004.

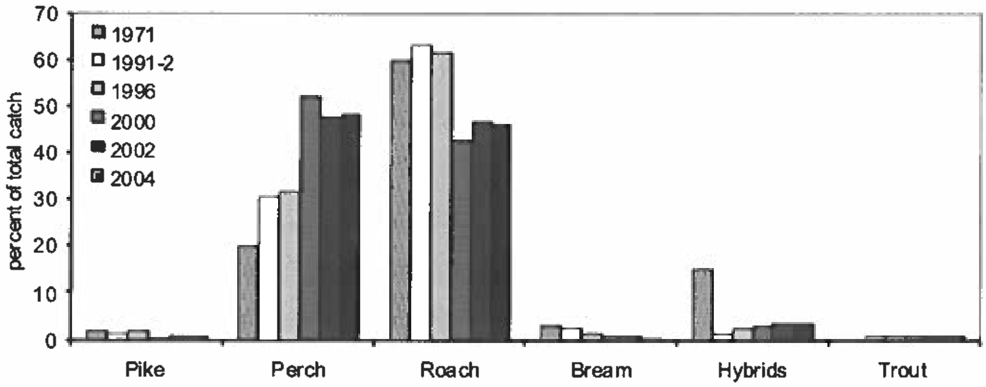


Figure 13. Relative abundance of fish species (% of total survey net catch by number) in Lower Lough Erne from 1971 to 2004.

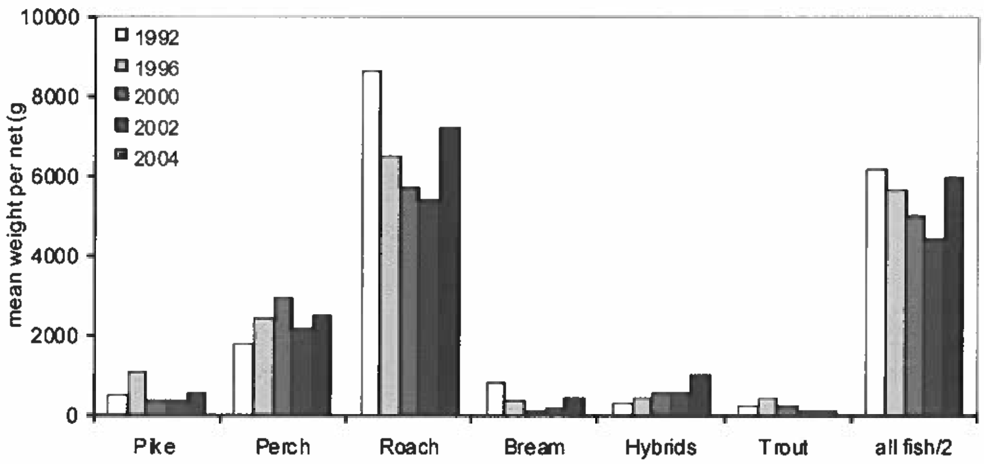


Figure 14. Catch per unit effort (biomass) of fish species in Lower Lough Erne from 1992 to 2004.

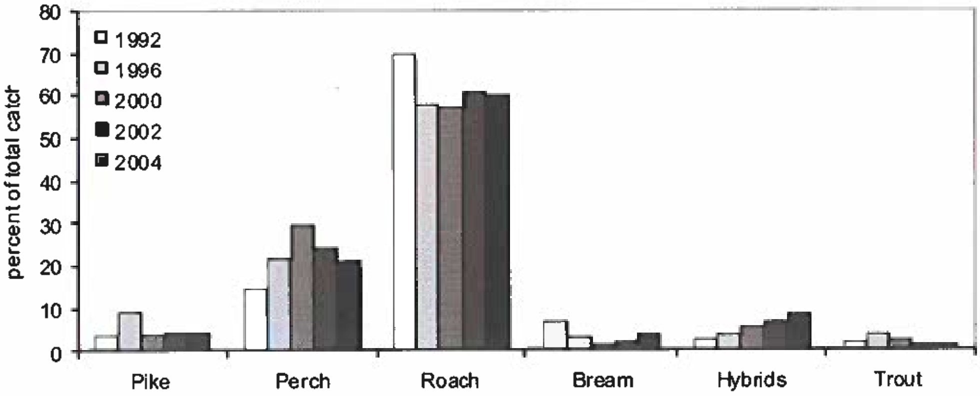


Figure 15. Relative biomass (% of total catch per weight) of fish species in Lower Lough Erne from 1992 to 2004.

There were no clear trends in abundance or biomass over time for pike, bream, roach bream hybrids and trout. This is at least in part due to small sample sizes, a drawback of the multimesh survey net method. Netting effort capable of showing anything other than very major changes in these less abundant species would take unmanageable samples of roach and perch. A typical summer survey catches few specimens (up to 1 per net) of pike, bream and trout resulting in low sample sizes and high inter sample variation. Given the increases in water clarity, and observations elsewhere, an increase in feeding success might be expected for pike, the largest piscivorous species, however, no population effect has been noted. There are many other factors unconnected with zebra mussels affecting pike numbers in the lough, including loss of spawn in spring water level fall, and continuing commercial fishing (Rosell & MacOscar, 2002).

Reports of increased trout catches were received after the establishment of zebra mussels, but this seems to have occurred without any significant population increase. Trout numbers are probably controlled mainly by factors in the feeder streams, unaffected by zebra mussels, where spawning and early life occurs, than in the lake itself. Being a visual feeder, increased catchability by lure and fly angling is perhaps to be expected with increased water clarity. Once recruited to lakes, trout are very adaptable in their feeding habits and it would seem unlikely that zebra mussels would have a negative impact on trout populations.

However there were changes in both abundance and biomass of the two dominant fish species roach and perch over time, in particular since the establishment of zebra mussels. The abundance and biomass ratios (Figures 16 and

17 respectively) show some change since 2000, the number of perch has increased and the abundance ratio has shifted from 2:1 to 1:1. This is reflected in the population structure (length-frequency distributions) of roach (Figure 18) and perch (Figure 19).

The three surveys undertaken after the establishment of zebra mussels (2000-) were characterised by high perch recruitment. The highest recorded recruitment was in 2003 with the year class showing as a major 1+ peak in the 2004 length frequency CPUE distribution (Fig 19), reaching twice the highest CPUE previously recorded for this year class of perch. Roach are known for their variable recruitment and the tendency for the population to be dominated by a small number of year classes (Maitland & Campbell, 1992). The present study shows this tendency clearly, with strong year classes emerging circa 1984/85, then in 1994/95 and again in 2002 and 2003 (Figure 18). These year classes can be seen tracking through the time series (Figure 18). Throughout the period of zebra mussel introduction roach recruitment remained low.

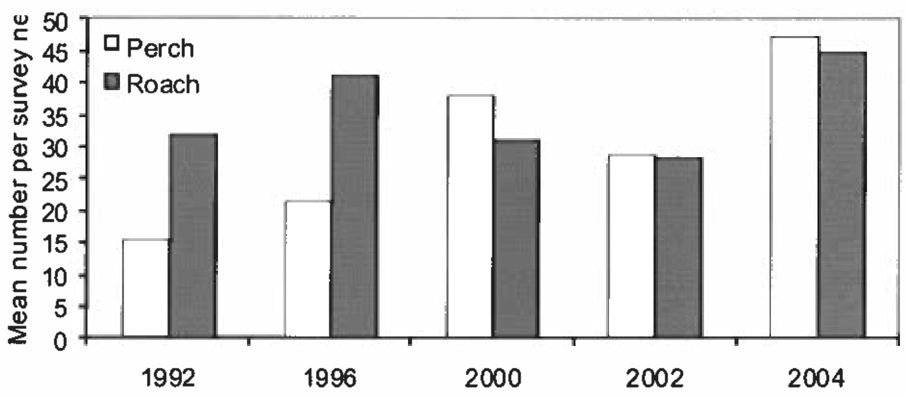


Figure 16. Abundance ratio of perch and roach in Lower Lough Erne from 1992-2004.

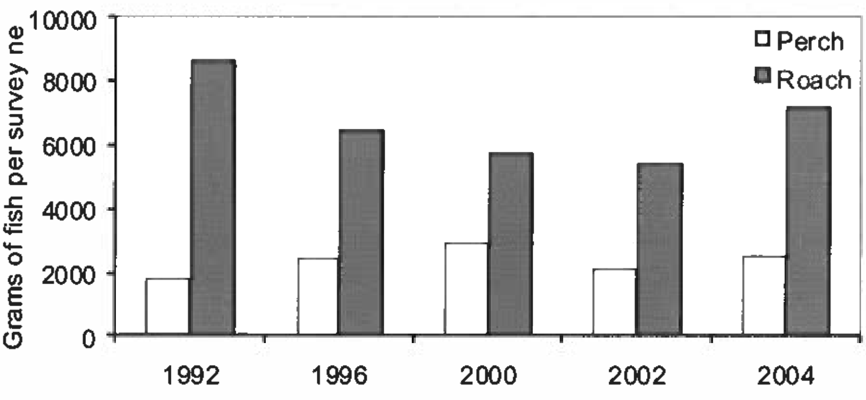


Figure 17. Biomass ratio of perch and roach in Lower Lough Erne from 1992-2004.

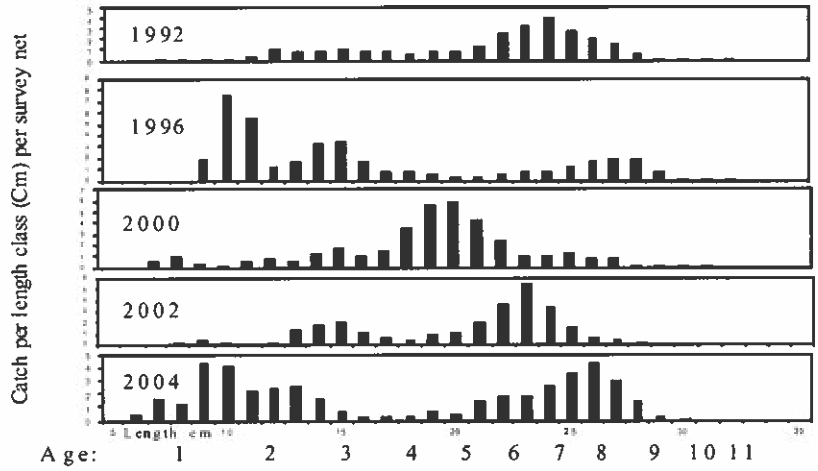


Figure 18. Population structure (length frequency as a surrogate of age, scaled to catch per unit effort) of roach in Lower Lough Erne from 1992-2004.

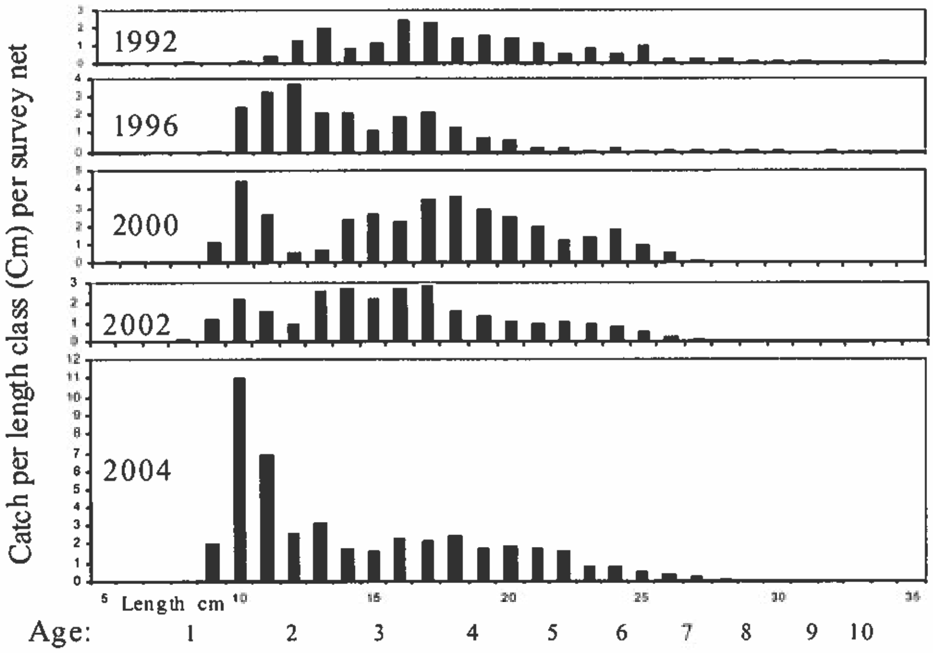


Figure 19. Population structure (length frequency as a surrogate for age scaled to catch per unit effort) of perch in Lower Lough Erne from 1992-2004.

The gill netting method used here is designed to give a picture of the general trends on the 5 species of greatest recreational angling importance. Some groups of fish may be missed, including gudgeon, sticklebacks and eels. It is not known if there have been changes in the populations of these species.

The only major change in the fish population concomitant with the establishment of zebra mussels is increased perch recruitment. Roach and perch pass through a juvenile competitive bottleneck, both feeding on small zooplankton and aquatic invertebrates, but with 0+ perch shifting to benthic invertebrates as roach pressure on zooplankton resources increases (Persson & Greenberg, 1990). In eutrophic, turbid water roach appear to emerge more successfully from this bottleneck, whereas in clear water with dense macrophytes cover or in cryptic habitats perch may be more able to compete with roach (Winfield 1986, Persson 1983). The competitive interactions between roach and perch have been explored in numerous studies with relatively consistent results. The abundance of roach and perch changes reciprocally with changing productivity of lakes (Horppila *et al.*, 2000).

Before the establishment of zebra mussels, Lough Erne was eutrophic and generally turbid and the abundance ratio of the fish species demonstrated that roach had an advantage over perch (Rosell, 1994). The increase in water clarity and littoral vegetation and the additional food source associated with the zebra mussel colonies on previously bare hard substrates have favoured perch. Young perch may under some circumstances directly prey on larval roach (Braband, 2001) and it is also possible that increased water clarity has enabled perch to feed more effectively on larval roach.

Low roach recruitment concomitant with the establishment of zebra mussels cannot categorically be attributed to the effects of zebra mussels. The intervals between strong year classes of roach are long, 8-10 years in the data presented here, and this is normal for the species in British waters (Maitland & Campbell, 1992). It is also common for roach populations to be dominated at any one time by a small number of year classes. Strong roach year classes may also limit the emergence of new year classes through prey depletion (Cryer *et al.*, 1986). There are other potential factors which may affect roach recruitment, such as variations in early summer temperature (Maitland & Campbell 1992).

The impact of zebra mussels on the fish population in Lower Lough Erne is unlike other documented impacts. Previously documented impacts from the North American experience include the decline of lake trout (*Salvelinus namaycush*) which require clean spawning substrates within a lake; and the decline of yellow perch (*Perca flavescens*), ecologically and physically very similar and closely related to European perch, possibly due to reduced zooplankton availability to larval fish, or increased competitive advantage of other visual feeders (Marsden & Robillard, 2004). However, there are also major ecological differences between North American and Irish waterbodies. The Great Lakes are larger, with much more diverse fish populations, generally lower trophic status and larger temperature ranges. The impact on perch depends on the outcome of a series of complex trade-offs between decreased zooplankton availability, increased benthic food availability associated with zebra mussel colonies, and increased ability of the prey items such as *Gammarus* and *Asellus* to find refuge in the new, more structurally complex benthic habitats (Mayer *et al.*, 2001; Cobb, 2002). Clearly perch have benefited post zebra mussel in Lough Erne whereas their close relatives did not in North American lakes. The different outcome is probably due to a combination of factors associated with the general situation that Irish lakes are smaller, shallower, have far fewer (generally less that 10) common fish species, are often enriched, and suffer less extreme temperature variation.

2.10 Summary of food web change.

The Lough Erne food web has undergone rapid and extensive ecological change since the establishment of zebra mussels. Concentrations of nutrients are primarily determined by catchment activity and continue to increase, although this is no longer reflected in pelagic measurements of phytoplankton abundance. Catchment activity is still the primary influence on nutrient concentrations. The reduction in phytoplankton and zooplankton abundance, reduction in diversity of benthic invertebrates and changes to recruitment patterns of the fish populations are likely to be a result of the establishment of zebra mussels, as there is no evidence of major confounding changes in external driving variables of the Erne ecosystem during the invasion period. Light appears to be a crucial factor in determining the impact of zebra mussels on the pelagic lower trophic levels. However, the long-term effects are yet to be determined. In a long-term study (40+ years) in Lake Lukomske, Belarus, the zebra mussel invasion caused an increase in water clarity and macrophyte and zoobenthos biomass and a decrease in phytoplankton and zooplankton biomass. After approximately ten years, zebra mussel impacts were less pronounced but the lake ecosystem did not return to a pre-invasion state (Karatayev *et al.*, 1997). Whether Lough Erne follows a pattern similar to that of Lake Lukomske will only be ascertained by continued study of the food web.

3.0 Implications for other waterbodies.

3.1 Potential impacts on the fish populations in the top ten list of vulnerable waterbodies

The top ten vulnerable waterbodies (or group of waterbodies) in Northern Ireland is comprised of 131 individual lakes. Some of these lakes, such as Lough Neagh and Lough Melvin have well described fish communities, whereas no data are available on the fish communities of many lakes vulnerable to zebra mussel invasion. While it is not possible to make specific predictions for each individual lake, some general implications for fish populations in different types of lakes can be outlined. Impacts of the establishment of zebra mussels can also be site specific and the complex web of direct and indirect effects make specific predictions of impact on individual species difficult as causal links are difficult to demonstrate. The influence of zebra mussels on fish should vary widely across ecosystems as a function of system morphology, factors that limit primary production and diets of the fish species (Strayer *et al.*, 2004). Several pathways link suspension feeding bivalves to fish and the strength of each of these pathways varies across ecosystems. The net effect of suspension-feeding bivalves on fish populations depends on the strength and balance among all the interaction pathways. In general, planktivorous fish should be negatively impacted and littoral zone fish should benefit but the size of these changes may vary widely. The response of fish species that feed on open water benthos, fish that are flexible enough to exploit various kinds of food, and the overall production or biomass of all fish species combined is difficult to predict (Strayer *et al.*, 2004).

Benthic filtering bivalves such as zebra mussels have the potential to sequester much of the pelagic primary production, thereby altering the balance between pelagic and benthic foodwebs (Johannsson *et al.*, 2000). The biomass and production of the benthic and pelagic fish communities will shift to reflect these changes. Borgmann (1982) argued that an ecosystem has a characteristic efficiency of biomass or transfer of energy from smaller to larger organisms, and that the amount of biomass or energy passed to predators by prey depends on their relative size. In this way, a fish obtains more energy from larger organisms, like amphipods, than from smaller organisms, like cladocerans. Thus, pelagic and benthic biomass are not equivalent in supporting fish production.

The present study has shown that in lakes with high colour zebra mussels can dramatically reduce both phytoplankton and zooplankton abundance decreasing the amount of pelagic resources available for fish. Zebra mussels have been shown to substantially reduce the growth of some fish species (*Lepomis macrochirus*) in mesocosm experiments during the critical larval stage (Raikow, 2004). In lakes with less peat staining the impact on zooplankton may not be as great. The establishment of zebra mussels in a water body may not reduce the amount of benthic resources available for fish, as such, and therefore there may not be a reduction in fish production in invaded waterbodies. However while zebra mussels colonies may facilitate macrozoobenthos, colonisation of soft sediments has the potential to affect the foraging success of a range of fish species (Beekey *et al.*, 2004). The fish populations in Lough Erne appear to have responded to the zebra mussel invasion as if to an effective reduction of trophic status. Fish populations in other vulnerable waterbodies may also do so, especially lakes where both perch and roach are present as zebra mussels appear to modify habitat and resources in a way that benefits perch in terms of competitive interactions with roach.

Loughs Neagh, Portmore and Beg and the rivers flowing into Lough Neagh contain much the same species mix as the Erne system, having pike, perch, roach, bream and dollaghan (the Lough Neagh brown trout), but with larger numbers of salmon, pollan and eels. Lough Neagh also represents the last remaining viable population of pollan (*Corregonus autumalis*) in Ireland (Harrod *et al.*, 2001). Pollan are now rare and endangered and the subject of an UK and Northern Ireland Species Action Plan. This species could be greatly affected by the invasion of zebra mussels through colonisation of spawning grounds and modifying zooplankton resources available to pollan. Pollan require clean gravel to spawn and zebra mussels may colonise these areas. In addition, pollan are largely zooplanktivorous and the abundance of zooplankton has decreased in other Irish lakes after the establishment of zebra mussels. It is important to note that pollan recruitment has been documented in Lough Erne after the zebra mussel invasion.

Lough Neagh supports a highly productive European eel (*Anguilla anguilla*) industry, and is one of the largest and most commercially important fisheries for this species in Europe (Kennedy & Vickers, 1993; Woodman & Mitchel, 1993). Approximately 95% of the Northern Ireland eel catch is taken in Lough Neagh (DARD, 1999). At the height of the eel season some 6 to 9 tonnes may be dispatched daily throughout the European Union, specifically to Germany and the Netherlands. In 1999, the industry had a total yield of 669 tonnes and a net profit of £2,089,264 (DARD, 1999). However to date the total yield has decreased by 20 -

25% and a zebra mussel invasion of Lough Neagh could have potential impacts on this industry. For example zebra mussels have been found in eel stomachs and can cause lacerations of the gut and zebra mussels may cause problems with hauling of draft nets (D. Evans, pers. comm.).

Lough Melvin is one of the few remaining examples in north-western Europe of a natural post-glacial salmonid lake which is typically very fragile and susceptible to disruption. Lough Melvin and its biological feature interest species are potentially extremely vulnerable to zebra mussel invasion and subsequent impacts. Lough Melvin supports a unique salmonid community with three genetically distinct populations of trout, the Sonaghen (*Salmo trutta nigripannis*), Gillaroo (*Salmo trutta stomachius*) and Ferox (*Salmo trutta ferox*) (Ferguson, 1986). As a result Lough Melvin is regarded as the best game fishery in Northern Ireland (Northern Ireland Tourist Board, 2002). Sonaghen spawn in the affluent streams which are unlikely to be colonised by zebra mussels, but are adapted to feeding in mid water on plankton making them vulnerable to a reduction in zooplankton resources. The Gillaroo spawn in the outflowing river which would be colonised by zebra mussels following invasion. The ferox trout spawn in lower reaches of the largest affluent river and are piscivorous and known to feed in deep water on char and other fish, therefore, the impact of a zebra mussel invasion is difficult to predict.

Lough Melvin also has stocks of Atlantic Salmon (*Salmo salar*) which is listed in Annex II of the EC Habitats and Species Directive, including a particularly important spring running to sea winter stock. Also present is the Arctic Charr (*Salvelinus alpinus*), an Irish Red Data species which spawns on shallow rocky areas of Lough Melvin (EHS, 2003c). Zebra mussel colonisation of these areas may have an adverse impact on this species. Any changes or perceived changes to the quality of fishing in Lough Melvin will have an economic impact on the tourist industry in the area.

The MacNean lakes contain much the same species mix as the Erne lakes with and dominance changes along a trophic gradient. Upper MacNean is mesotrophic and dominated by perch whereas Lower MacNean is more eutrophic and dominated by cyprinid species. The establishment of zebra mussels in the MacNean lakes would probably have a similar impact on the interactions between perch and roach as in the Erne lakes.

In addition to the predictable impacts on fish in particular lakes, there are also likely to be unpredictable impacts of zebra mussel spread on fish in other water bodies. As yet, no lakes containing either carp (*Cyprinus carpio*) or tench (*Tinca tinca*) have been colonised. Both these species are themselves potentially invasive with a documented ability to feed on molluscs and may spread with a water temperatures rise of one or two degrees. Another unknown is the potential effect of zebra mussel on rudd (*Scardinius erythrophthalmus*), a non native species introduced in mediaeval times and then ousted from much of its range by subsequent invasion of roach. Rudd would benefit from clear water and dense macrophyte beds in much the same way as perch and could conceivably recolonise zebra mussel affected lakes.

3.2 Implications for the conservation objectives of the Upper Lough Erne Special Area of Conservation (SAC) and Area of Special Scientific Interest (ASSI).

The Upper Lough Erne SAC comprises of the open waters of the main lough and smaller satellite loughs and contains a variety of aquatic communities typical of natural eutrophic lakes. The site also supports large numbers of over-wintering and breeding birds important in an all-Ireland context in addition to internationally important numbers of wintering whooper swan (*Cygnus cygnus*) which has been recognised by its SPA designation. The SAC boundary also includes 9 ASSIs, two of which, Mill Lough and Killymackan Lough, are highly vulnerable to zebra mussel invasion (Maguire & Sykes, 2005).

The overall conservation objective for the site is to maintain in favourable condition the features for which Upper Lough Erne was selected as a candidate SAC and designated as an ASSI. Zebra mussel can potentially impact several of these features such as classification as a natural eutrophic lake with *Magnopotamion* or *Hydrocharition* vegetation and notable water beetle, aquatic bug and dragonfly invertebrate assemblages. Zebra mussels appear to have increased the overall macrophyte abundance in ULE with the expansion of the range of larger, rooted species particularly the fine leaved *Potamogeton* sp, *P. obtusifolius* and *P. pectinatus*. Several other species including *Sparganium emersum*, *Nuphar lutea* and *Myriophyllum spicatum* have responded in a similar manner. The distribution of duckweeds, *Lemna minor* and *L. trisulca* appear to have been reduced along with the shoreweed *Littorella uniflora*, particularly on exposed shores (EHS, 2004). As the presence and distribution of *Potamogeton* sp is one of the attributes by which favourable condition is measured, zebra mussels do not appear to have impacted negatively on this attribute. It is not known whether zebra mussels have impacted on the notable water beetle, aquatic bug and dragonfly invertebrate assemblage as criteria have not been set for invertebrate assemblages. Further research is needed to ascertain potential impact.

3.3 Potential impacts on the conservation objectives in the top ten list of vulnerable waterbodies.

Lakes in Northern Ireland possess a number of conservation designations including Special Areas of Conservation (SACs), Special Protection Areas (SPAs), Areas of Special Scientific Interest (ASSIs), and these designations are based upon a number of features and species which may be affected by zebra mussels. The overall conservation objective is to maintain each of the features for which the lakes have been designated in favourable condition. Although some zebra mussel impacts consistently occur in lakes, they may differ in magnitude between individual waterbodies. Otherwise there is a complex set of direct and indirect interactions between zebra mussels and other ecosystem components making it difficult to predict accurately what will happen to any particular species or habitat after the establishment of zebra mussels. A range of potential impacts on features and species are outlined below. There may be negative and positive impacts on the features and conservation objectives.

Feature/Species	Potential impact
UK PRIORITY HABITAT	
Mesotrophic lakes	Zebra mussels have consistently increased water clarity, decreased abundance of phytoplankton and increased macrophyte growth in all Irish lakes after becoming established. They may potentially alter nutrient cycling by decreasing the particulate phosphorus concentrations and increasing concentrations of soluble phosphorus and soluble silica. They may also alter the food web resulting in changes in abundance and species composition of zooplankton, benthic invertebrate and fish populations.
Eutrophic standing waters	As above
Natural eutrophic lakes (*Magnapotamion* and *Hydrochariton* type Vegetation)	As above

Oligotrophic to mesotrophic standing waters (vegetation of the *Littorelletea uniflorae* and/ or *Isoeto-Nanojuncetea*)	Oligotrophic lakes may not support a large population of zebra mussel due to food limitation. Potential impacts are as above
Hard oligo-mesotrophic waters (benthic vegetation of stoneworts, *Chara* species)	As above
UK PRIORITY SPECIES	
Pollan (*Corregonus autumnalis*)	Colonisation of spawning grounds and reduction of the zooplankton resource may impact on pollan recruitment
Macrophytes (pondweed *Potamogeton perfoliatus*, and shoreweed *Littorella uniflora*)	An increase in water clarity may benefit *P. perfoliatus* but evidence from ULE indicates *L. uniflora* may be negatively impacted.

Lough Neagh and its satellite lakes (Portmore Lough and Lough Beg) have been designated as a National Nature Reserve (NNR) an Area of Special Scientific Interest (ASSI) and a Special Protection Area (SPA). Lough Neagh has had long-term problems with excess nutrients entering the lake from both point (sewage) and diffuse (agricultural) sources. The zebra mussel may mask increased nutrient input to the lake by reducing phytoplankton abundance.

Lough Neagh provides habitat for numerous species of wintering wildfowl. The site qualifies under Article 4.2 of the Birds Directive as a wetland of international importance by regularly supporting over 20,000 waterfowl in winter (EHS, 2003b). Zebra mussels may have an impact on a number of bird species present in Lough Neagh that are internationally important, such as Whooper Swans (*Cygnus cygnus*), Pochard (*Aythya ferina*), Tufted Duck (*Aythya fuligula*), Scaup (*Aythya marila*) and Goldeneye (*Bucephala clangula*). This is because the zebra mussel may become a novel food source for some species. The increase in water clarity that results from the presence of a large population of mussels will increase the photic depth and thus encourage increased growth of aquatic vegetation on which some species feed. Some species of wildfowl may be adversely affected because of the potential effect that zebra mussels exclude chironomids from the littoral zone. Unionds are also likely to be extirpated from Lough Neagh with the establishment of zebra mussels. Potential impacts on fish species, an ASSI feature are outlined in section 3.2.

The majority of the 2125 hectares of Lough Melvin lie in Leitrim in the Republic of Ireland. It is designated as an Area of Special Scientific Interest (ASSI) and has been proposed as a candidate Special Area of Conservation (SAC). Lough Melvin is the best example of a relatively unpolluted (mesotrophic) and undisturbed large lough in Northern Ireland (EHS, 2003c) but increases in nutrient input to the Lough have been recorded recently (J. Girvan, pers. comm.). In comparison Lough Erne and Lough Neagh have undergone eutrophication and been altered hydrographically. Increased nutrient loading to a lake normally results in increased algal blooms. The zebra mussel de-couples the nutrient-chlorophyll relationship so this normal response does not occur. Eutrophication models that link nutrient loadings and pelagic measures of water quality may not be valid in water bodies that have large zebra mussel populations (Maguire, 2002). In water bodies invaded by zebra mussels changes in nutrient loadings are better reflected in changes in benthic algae. If the zebra mussel spreads to Lough Melvin normal indicators of increased nutrient input to the lake will be masked. It is probable that the establishment of zebra mussels in Lough Melvin will lead to an increase in water clarity, decrease in phytoplankton and zooplankton abundance and an increase in macrophyte growth. Potential impacts on fish species are outlined in section 3.2.

Measures that should be taken to minimise the risk of the spread of zebra mussels to these vulnerable lakes to maintain their integrity and conservation value are outlined in the Zebra Mussel Management Strategy for Northern Ireland.

3.4 Implications of the impact of zebra mussels for the Water Framework Directive and the Habitats Directive.

The EC Water Framework Directive (WFD) (2000/60/EC) came into effect in December 2000. The purpose of the WFD is to establish an overall framework for the protection of surface and ground water throughout Europe. This will be delivered through the development of River Basin Management Plans (RBMPs). Under the WFD water bodies will be classified according to biological, hydromorphological and chemical status. The biological status of lakes will be determined by invertebrate, plant, phytoplankton and fish communities.

The WFD requires that water bodies that are already of high quality be maintained to "high status" level. It also requires the prevention of deterioration of current water bodies and aims to achieve a classification of at least "good status" for all water bodies by 2015 (Joint North / South Consultation Paper, 2003).

The WFD does not make explicit reference to non-indigenous species and the subject of the impact that invasive species may have on the definition of the status of water bodies has yet to receive full consideration (UK TAG Guidance, 2004). However, Annex II of the Directive refers to anthropogenic pressures to which water bodies may be subjected. As zebra mussels have been introduced via human activities, they can be considered an anthropogenic impact. The WFD classification of water bodies that have high ecological significance is based on the concept of naturalness. However, the presence of non-indigenous species will detract from this classification in numerous water bodies.

Zebra mussels in particular may have an extensive impact on the biological parameters that have been selected to determine the status of water bodies (Table 5). For example, to achieve "good status" with regard to biological quality only slight changes from reference conditions in the composition and abundance of phytoplankton, macrophytes, phytobenthos and benthic invertebrates can occur. Zebra mussels can potentially impact on all these parameters. For the purpose of a risk assessment of alien species under the WFD, UK TAG Guidance (2004) classified a number of alien species as having a 'high impact'. These are defined as species that are known to be invasive and have caused documented harm. The guidance recommends that their impacts are considered in future risk assessments for the WFD. Zebra mussels are included on this list.

UK TAG guidance also recommends a set of guidelines to ensure that alien species are taken into account in the classification of water bodies. For example, a water body should only receive a 'high status' classification if no alien species on the 'high impact' list are present. The guidance also states that if a water body is provisionally classified as of 'good status' but is suffering significant impacts from species on the 'high impact' list, it then is liable to fail achieving a classification of 'good status'. If the risk assessment guidance is applied, Ireland and numerous other countries will be at risk of failing to achieve at least 'good status' of all water bodies by 2015, due to the presence of zebra mussels and other alien species.

Table 5. Elements of the WFD classification of good status for lakes that may be affected by zebra mussels.

Parameter / (Status)	Definition	Effect of zebra mussel
General conditions (Good status)	"Temperature, oxygen balance, pH, acid neutralising capacity, transparency and salinity do not reach levels outside the range established so as to ensure the functioning of the ecosystem and the achievement of the values specified for the biological quality elements."	Transparency or water clarity can increase significantly
Phytoplankton (Good status)	"Slight changes in the composition and abundance of planktonic taxa compared to the type-specific communities."	Decrease in phytoplankton abundance and alteration of community composition
Macrophytes and phytobenthos (Good status)	"Slight changes in the composition and abundance of macrophytic and phytobenthic taxa compared to the type-specific communities. Such changes do not indicate any accelerated growth of phytobenthos or higher forms of plant life."	Increased abundance of macrophytes and phytobenthos
Benthic invertebrate fauna (Good status)	"Slight changes in the composition and abundance of invertebrate taxa compared to the type-specific communities."	Alteration in the abundance of particular taxa and change in community composition.

The Habitats Directive aims to promote the maintenance of biodiversity through the conservation of habitats and species that are important in a European context, taking account of economic, social and cultural requirements and regional and local characteristics. The potential impacts of zebra mussels on the sites and species designated under the Directive which are vulnerable to zebra mussels are outlined in section 3.3. The Habitats Directive also requires monitoring to be carried out on designated sites (SAC) with a condition assessment undertaken every six years. There is a need for surveillance for zebra mussels in the most vulnerable lakes, many of which are SACs or candidate SACs. This surveillance should be incorporated into current monitoring programmes. The spread of zebra mussels to lakes such as Lough Neagh and Lough Melvin will affect the condition assessment and may lead to sites being considered to no longer be in favourable condition.

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