ECOLOGICAL CHANGE IN LOUGH ERNE: INFLUENCE OF CATCHMENT CHANGES AND SPECIES INVASIONS

CATHY MAGUIRE AND CHRIS GIBSON

**Dr C.M. Maguire, Aquatic Systems Group, Queens University Belfast, Newforge Lane, Belfast BT9 5PX, Northern Ireland*

Prof. C.E. Gibson, Department of Agriculture and Rural Development, Agricultural and Environmental Science Division, Newforge Lane, Belfast BT9 5PX, Northern Ireland

Introduction

Lough Erne in Northern Ireland has been the subject of much research over the last 30 years by, amongst others, the Department of Agriculture and Rural Development (DARD) (Gibson 1998). In this article, we provide a summary of a workshop held on the 16–17th October 2003 at the Manor House Country Hotel in Enniskillen, on the shores of Lough Erne, which gave an opportunity to step back and take a holistic look at the Erne lakes. Ecological change has been driven by many factors, including land use changes and species invasions. Much of the research in the last few years has focused on the impact of the zebra mussel (*Dreissena polymorpha*) invasion. The workshop enabled us to put these recent changes into a longer-term perspective and attempts were made to differentiate between natural change and change driven by anthropogenic influences. 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.

The workshop consisted of five sessions over one and a half days. Each session began with three or four short presentations, followed by discussion. A short summary of the presentations are given below, followed by a summary of the discussion and some conclusions.

* Corresponding author. Current address: Envirocentre, 27 College Gardens, Belfast, BT9 6BS, Northern Ireland. Email: cmaguire@envirocentre.co.uk

Session 1 – Invasive species, nutrients, phytoplankton and macrophytes

Trends in chlorophyll a *concentration, phytoplankton community composition, water clarity and silica in Lough Erne before and after the zebra mussel invasion* (Chris Gibson – Aquatic Systems Group, DARD)

Lough Erne consists of two connected lakes, Upper and Lower Lough Erne, and its water chemistry reflects the underlying geology, with a mixture of carbonate rich water from the limestone and soft acid water from the sandstones.

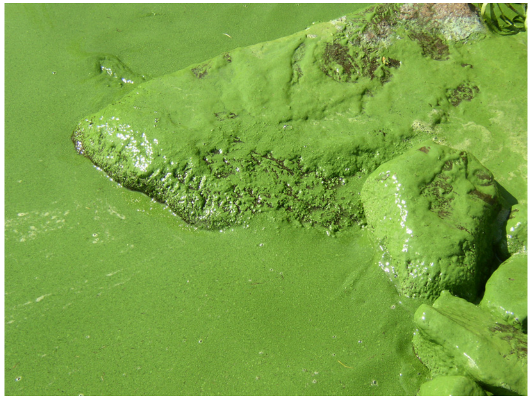
The first map of chlorophyll *a* concentration measured by towed fluorometer in Lower Lough Erne (LLE) was produced in 1973 (Gibson et al. 1980). It revealed greater production in the narrows and margins than in the large basin, known as the Broad Lough. One of the signature impacts of a zebra mussel invasion on water quality is a decrease in chlorophyll *a* concentration. Since the zebra mussel invasion, there has been a significant decline in chlorophyll *a* concentration throughout the Erne lakes.

Data available on phytoplankton community composition is not sufficiently precise to make quantitative comparisons among years, however qualitative information suggests that there has been little selectivity in zebra mussel feeding as the abundance of all phytoplankton species has declined. Although zebra mussels do not appear to have altered phytoplankton community composition, a monospecific bloom of *Microcystis* sp. occurred in LLE in 2003. This was a new occurrence: blue-green algal blooms do occur in Lough Erne but usually they consist primarily of *Anabaena* spp. and *Aphanizomenon* with some *Microcystis*.

Water clarity has also increased significantly, with water clarity in 2000 and 2001 significantly higher than during 1992–99 ($F_{3,30}=13.76$, $p < 0.0001$; least square means test, $p < 0.0001$). The peak summer measurement of water clarity in 2000 was the greatest since records began. Silica concentration in the Broad Lough was also significantly higher in 2001 than all other years (1991–2000) ($F_{3,30}=37.38$, $p < 0.0001$). This may reflect reduced uptake by a less abundant phytoplankton population. However, these changes in aspects of water quality have occurred in the short term and it is important to place these changes in perspective by looking at a longer time period reflected in the sediment record, as Lough Erne has undergone significant changes in the past as well.

Lower Lough Erne, showing drowned drumlin landscape

Zebra mussels



Microcystis bloom on Lower Lough Erne, August 2003

How have zebra mussels altered nutrient concentrations in Lough Erne?
(Bob Foy – Agricultural and Environmental Sciences Division, DARD)

Upper and Lower Lough Erne are both eutrophic with the second and third highest lake phosphorus (P) concentrations of the large lakes of Ireland, after Lough Neagh. Zebra mussels first invaded Lough Erne in 1996 but it was not until 1999–2000 that they reached sufficient numbers to have a noticeable effect on water quality.

Since monitoring began in 1973, P concentration in the Erne lakes and inflowing rivers has been increasing at rates of 1.5–2 μg P L^{-1} $year^{-1}$ (Hayward et al. 1993; Zhou et al. 2000). The increase in P concentration has been most noticeable in the SRP (soluble reactive phosphorus) fraction, and within the lakes there has been no increase in chlorophyll concentrations, an indication that the phytoplankton growth in Lough Erne has been P-saturated since the mid 1970s.

Analysis of P concentrations reveals a large reduction in particulate phosphorus (PP) since 1999; this decrease has been proportionate to the decrease in chlorophyll *a* and there is no evidence for a decrease in non-algal PP. It is likely that zebra mussels have impacted PP concentrations and during the winter months the impact of zebra mussel filtering can still be seen on both chlorophyll and PP concentrations. Concentrations of SRP have continued to increase but this increase is in line with the historic trends and may not reflect an increase in SOP (soluble organic phosphorus) compounds. The decrease in PP is greater than the increase in SRP, however, so it appears that the establishment of zebra mussels has resulted in a decline in lake TP (total phosphorus) concentration. For other nutrients such as nitrogen and ammonium, there is little evidence of striking change in the context of the large decrease in chlorophyll.

Impacts of alien invasive weeds on lakes and implications for management
(Max Wade – RPS Ecoscope Applied Ecologists)

Lough Erne has a diverse aquatic flora and experience of invasion is a natural element of its limnology. An alien invasive species that has negatively impacted on other lakes, Canadian pondweed (*Elodea canadensis*), is now a well established part of the aquatic flora of Lough Erne and there is no evidence that it has been responsible for extirpating other species from the lake.

Alien species may be present in an ecosystem for many years before they become invasive and start causing problems (lag phase). Regular surveillance for alien invasive species is needed so control or eradication attempts may be made at an early stage. Surveillance needs to occur at different spatial scales from the international to the local. Human activities such as boating and fishing act as vectors and facilitate invasions, and so surveillance of Lough Erne should focus on key parts of the lakes that have high levels of these activities.

A lake surveillance programme should monitor characteristic and/or novel species, truly aquatic plants, marginal plants, tree planting and land use changes. A surveillance programme will involve collation and co-ordination of records, 5–10 yearly surveys of lake, focused opportunistic surveys and focused site surveys at inflow bays/streams and launching ramps. Surveillance for invasive species should involve all water users, so it is necessary to raise awareness of the issues associated with invasive weeds.

Once an invasive species has become established control programmes can be time consuming and expensive. Precautions and preventative measures must also be taken. These include identifying and dealing with potential sources of invasive species; establishing the authority and the ability to eradicate a species from a site should an invasion occur; and adoption of lake management practises that minimise risks such as controlling weed around boat slips by mechanical harvesting.

Alien species and the Water Framework Directive
(Phil Boon – Scottish Natural Heritage)

The issue of invasive species has implications for assessing water bodies under the Water Framework Directive (WFD). The WFD is a complex directive in which all types of surface water are classified according to their ecological and chemical status. Whilst the text of the Directive does not explicitly mention alien species, Annex II lists specific pressures to which water bodies may be subjected, including '*…other significant anthropogenic impacts on the status of surface water bodies*'. In the knowledge that many alien species have been deliberately or accidentally introduced, it seems reasonable, therefore, to consider them as a potential 'anthropogenic impact' on the biological elements listed in Annex V.

The UK Technical Advisory Group (TAG) has drafted guidance on alien species pressures which is currently under discussion within TAG and with associated government departments. A three-tiered list of alien species with a high, low and unknown impact has been suggested.

For water bodies at risk of failing their environmental objectives because of the presence of alien species the aim should be eradication and restoration, where feasible, and prevention of further spread where not. If restoration is impracticable, the question may arise of whether the water body should be classified below the level of good ecological status. This issue, and the possible use of derogations under article 4 where member states may aim to achieve 'less stringent environmental objectives', are still under discussion.

Session 2 – Zooplankton, benthic macroinvertebrates and fish

The zebra mussel invasion of Lough Erne and impacts on zooplankton and benthic macroinvertebrate communities
(Cathy Maguire – Aquatic Systems Group, Queen's University Belfast)

After becoming established in Lower Lough Erne (LLE) in 1996, zebra mussels colonised the whole Erne system within three years, including the River Erne and Woodford Rivers that flow into Upper Lough Erne (ULE).

The zebra mussel population has continued to increase in the Erne lakes and ULE now supports a higher density of zebra mussels than LLE. Zebra mussel density varied with substrata and ranged from 0.08 to 2441.6 m^{-2} in 2002, but consistently remained low in some areas such as inflowing rivers. The total numbers and biomass of the zebra mussel population in the Erne lakes was estimated in 2003, with approximately 1.35×10^9 individuals (1914 tonnes) in LLE and 9.5×10^9 individuals (2238 tonnes) in ULE. The filtering capacity of the population was estimated using published data for filtration rates (Kryger & Riisgard 1998). Zebra mussels are capable of filtering the whole water mass of ULE every 2.35 days, LLE every 26.9 days, the Erne lakes every 16 days. This level of planktivory makes zebra mussels strong resource competitors with unionids, larval and some older fish.

Since the zebra mussel invasion there has been a decline in the total zooplankton density in L. Erne. 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; Jack & Thorp 2000). In L. Erne, although rotifers, copepods and cladocerans were all affected, there were apparent differences in impact on different species.

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. There were few data on benthic invertebrates in the Erne prior to the zebra mussel invasion. One of the most visible impacts was the colonisation of the native unionid mussels, the swan mussel *Anodonta cygnea* and the duck mussel *Anodonta anatina*.

The colonisation of the *Anodonta* population was rapid. One indicator of mortality is the percentage of live specimens collected in a sample. In June 1998 in ULE 96.8 % of specimens were live, average density was 0.3 m^{-2} and biomass was 8.7 g m^{-2}; by June 2003 no live *Anodonta* were found in ULE. In June 1998 in LLE 69.2 % of specimens were live, average density was 0.2 m^{-2} and biomass was 6.4 g m^{-2}; by June 2003 these values had decreased to 1.23 %, 0.007 m^{-2} and 0.04 g m^{-2} respectively. A comparison between L. Erne and other European and North American waterbodies revealed that in L. Erne there was a higher infestation density of unionids at lower zebra mussel densities than in other European waterbodies. It is likely that *Anodonta* will be extirpated from the Erne system.

A grab survey for other benthic macroinvertebrate species was carried out in August 2003. Zebra mussels and gammarids dominated samples. A more indepth survey is needed, but seven years after zebra mussels first arrived in the Erne system, it may be too late to detect an effect on benthic invertebrates (with the exception of unionids). These changes in the food web in L. Erne will have implications for the fish population.

Changes in fish communities of Lower Lough Erne following zebra mussel invasion (Robert Rosell – Aquatic Systems Group, DARD)

Lower Lough Erne (LLE) has a simple fish assemblage. Since the 1970s the fish community has been dominated by roach (*Rutilus rutilus*) and perch (*Perca fluviatilus*) which make up 61 % and 21 % of the total fish biomass respectively (based on average 1992–2002). Other major species include pike (*Esox lucius*) (5 %), bream (*Abramis brama*) (3 %), roach × bream hybrids (5 % – outnumbering the bream parent stock) brown trout (*Salmo trutta*)(2 %), pollan (*Coregonus autumnalis*) (< 1 %) and eels (*Anguilla anguilla*).

Zebra mussels can affect fish species by direct colonisation of spawning grounds, modifying habitat and by changing the populations of fish prey species. Since the 1970s roach has outnumbered perch 2:1 (Rosell 1994). However, surveys carried out in 2000 and 2002, after the zebra mussel invasion, showed that the balance of these two species had started to change. The number of perch has increased and the abundance ratio has shifted from 2:1 to 1:1. However roach still dominate the fish community by biomass. Roach have naturally variable recruitment and it is still possible that these changes are a short-term consequence of poor roach recruitment, and purely coincident with the establishment of zebra mussels. However, at the same time as there has been poor recruitment of roach, there has been an increase in recruitment of perch on a scale not recorded since studies began in 1991.

There are no apparent trends in trout populations post zebra mussel introduction. Concern has been expressed about the possible impact of the zebra mussel invasion on pollan (Harrod et al. 2001). Pollan, already endangered before the arrival of zebra mussels, requires shallow clean gravel or stony substrate to spawn – areas most likely to be colonised by zebra mussels. Recent sampling indicates that pollan have successfully recruited since zebra mussels became established in the Erne lakes.

Three years after the first major effects, the initial response of the fish community has been a decline in roach recruitment and an increase in perch recruitment. The fish populations would therefore appear to be

responding to the zebra mussel invasion as if to an effective reduction of trophic status.

Overview of the Erne eel and salmon enhancement programmes
(Milton Matthews – Northern Regional Fisheries Board)

There have been two major European funded programmes on the Erne – the Salmon Enhancement Programme and the Eel Enhancement Programme (Mathers & Crowley 2001; Matthews et al. 2001). The Erne system once supported a substantial wild salmon fishery. After the major modification of the river channel between Lower Lough Erne (LLE) and the estuary in the 1940s and early 1950s to create a series of hydroelectric dams, the salmon population persisted in a viable state but failed to recover after a major decline in the late 1960s and early 1970s. The aim of the Salmon Programme was to re-introduce a self-sustaining population of salmon to the Erne system. This required a major investigation into the causes of the lack of a self-sustaining population.

The main findings of the Salmon Enhancement Programme were that:

- there are large areas of suitable habitat in rivers in the Erne catchment and the genetic composition of the stock is not a constraint
- there is high coastal exploitation of returning adults (70–90 %)
- there are high adult mortalities as they pass into fresh water (12 % in 2001, 3 % in 2002), with a two-year study showing that mortality was due to stress rather than primary disease
- significant mortalities of smolts occur during the downstream migration, particularly between Belleek and the sea
- there has been deterioration of water quality.

Some of these problems are common to all Irish stocks but some are specific to the Erne. ESB (Electricity Supply Board) Fisheries Conservation are implementing some of the recommendations of the Programme report and further research is being carried out.

The Erne Eel Enhancement Programme was a major cross-border programme to maximise recruitment of juvenile eel to the system, to determine the current status of the eel fishery and to provide for an integrated management plan for future expansion of the Erne eel fishery. Elvers captured in traps at Cathaleen's Fall are also released into the Erne catchment above the hydroelectric stations.

Session 3 – An ecosystem approach – relating the previous sessions

Conceptual limitations of ecosystem modelling
(Colin Reynolds – Centre for Ecology and Hydrology)

The key issues in ecosystem models are:
- Can simple models represent inherently complex structures?
- Are we sure about even our basic knowledge of the systems we want to model?
- What do we want the model to tell us?

Ecosystems are highly complex with an enormous number of components, large number of drivers and possible responses. In developing an ecosystem model we seek reproducible patterns and propose explanatory hypotheses. Once these hypotheses have been developed the aim is to reject them.

By modelling an ecosystem we seek system overviews on the basis of simple inputs and we try to model processes. Ecosystem structure is emergent from the collective model of the behaviour of the constituents, but do we have any way of relating emergent phenomena from components? Can we predict the ecosystem structure (or its governing constraints) from first principles without modelling every intermediate process? Using phytoplankton as a model we can look at the resource constraints of an ecosystem and the processing constraints of species.

The role of energy and resource limitation in regulating the dynamics of population development is explored by means of a model. A matrix with axes of increasing energy and resource limitation can be used to define the primary strategies of phytoplankton with respect to the major sources of environmental characterisation and variability. The contingency of low resources and energy-limited mixing can be excluded as untenable for phytoplankton. The three remaining contingencies correspond to the provinces of C, S and R groups of phytoplankton:
- Conditions with increasing resources and increasing energy: C-species are primarily invasive strategists (competitor). They typically show fast growth and reproduction and have small cells. Success here goes to the species arriving first, or in the greatest numbers and by growing the fastest.
- Increasing resources, decreasing energy: S-species are primarily acquisitive (stress-tolerant) typically large, motile with slow growth. Success here depends on the ability to exploit the partitioning of its resources.
- Decreasing resources, increasing energy: R-species are primarily acclimating (ruderal) species, tolerant or dependent upon near-continuous entrainment within actively circulating water layers. Selection will eventually favour those that get the greatest return of new biomass for the available energy.

Many phytoplankton do not sit easily within these categories, many show characters intermediate between them.

We can develop a habitat template, with axes of fundamental selection to which we may now attempt to fit species traits. This approach works quite well for phytoplankton. What we see is that the characteristics of the key species are ‘filtered’ by the habitat constraints. The more exacting the resource constraints, the fewer tolerant species and the more predictable is the make up of the key components. Similarly, the more exacting are the processing opportunities the more predictable is the make up of the key components. The weaker the resource and processing constraints are, the wider the filter and the greater the number of species that may participate. The most successful species of these will be the fastest growing, with highest-exergy traits (r-selected).

On the basis that ecosystems involve the similar roles – primary producer, consumer webs, microbial recycles, systems stores, and they seem to show the same process of filtration, then it should be possible to predict emergence of each level – types of producer, most efficient consumer and most appropriate stores. With this approach, we have a new approach to modelling whole ecosystems, to a level where we can gauge sensitivity to axes of changing environmental drivers, vulnerability to climate change, alien species and exploitation.

Session 4 – How does Lough Erne fit into lake classifications? Implications of the Water Framework Directive

Use of biological characteristics to classify lakes (Brian Rippey, Shelley Doe, Yvonne McElarney & Martin Neale – University of Ulster)

The Water Framework Directive requires classification of the ecological status of a water body based on the structure and functioning of the aquatic ecosystem. The quality of the structure and functioning of the ecosystem is assessed using biological elements and supporting hydromorphological and physio-chemical elements.

Species-environment relationships were examined during 2000–2 in 29 of the least impacted lakes in Northern Ireland. Canonical correspondence analysis (CCA) was used to produce a Minimum Adequate Model for phytoplankton, aquatic macrophytes and littoral macroinvertebrates and two species-environment models were investigated – Multiple Discriminant Analysis (MDA, identical to RIVPACS) and CCA.

Alkalinity and area were the significant environmental variables for littoral macroinvertebrates. The lakes were classified into three invertebrate assemblages and MDA, using alkalinity and area, correctly classified 85.7 % of lakes. Alkalinity and pH were the significant environmental variables for aquatic macrophytes and a RIVPACS model, based on five macrophyte assemblages, was unsuccessful. A CCA model, based on alkalinity, pH, altitude and colour, was developed and used for bio-assessment. Only maximum lake depth was strictly a significant environmental variable for phytoplankton, but pH was also included. A RIVPACS model, based on five phytoplankton assemblages, was unsuccessful and a CCA model, based on maximum depth and pH, was developed. The model was used for lake bio-assessment in an identical way to that used for macrophytes.

In conclusion, the development of species-environment models (CCA and MDA) for reference conditions was found to be successful for phytoplankton, macrophytes and invertebrates in lakes. However, there is a need to refine, evaluate and validate the models and establish the errors. Other modelling approaches, such as constrained ordination with more ecologically relevant similarity coefficients and artificial intelligence, also need to be evaluated.

Ecological characteristics of lakes (David Griffiths – University of Ulster)

The Water Framework Directive (WFD) aims to protect and enhance the status of aquatic ecosystems. A key component of overall status is ecological status determined from a set of ecological quality elements (biological groups). This is essentially an indicator approach, i.e. species Y occurs with a certain probability when physical and chemical conditions 1, 2, 3 etc occur. According to the WFD, ecological status measures the structure and functioning of aquatic ecosystems, but the WFD makes no attempt to look at the interactions between ecological quality elements. The relationships between the biological elements – the ecological structure – will contribute to ecological function.

At any one trophic, i.e. functional, level there are major differences in ecological properties: primary producers (macrophytes and phytoplankton); primary consumers (benthos, zooplankton, fish); secondary consumers (benthos, zooplankton, fish). In addition the WFD ignores a key functional group, the zooplankton.

The productivity gradient is measured as total phosphorus (TP) and phytoplankton biomass (chlorophyll *a* concentration). Phytoplankton biomass is not a linear function of TP or total nitrogen (TN) concentration. Along the productivity gradient there are corresponding changes in algal composition, cell size and palatability. Nutrients concentrations and biological structure change with water depth. Shallow lakes are more likely to be N limited rather than P limited. When TP concentration reaches 100 $\mu g\ L^{-1}$ structural changes occur, with the biomass of zooplankton and fish levelling off. Structural changes also occur in the relative importance and composition of other variables.

These structural changes are consistent with trophic effects and may be a result of both bottom-up and top-down processes. Changes in algal biomass, palatability and size (and in bacterial abundance) along the productivity gradient will limit zooplankton biomass. This may be reflected in declining zooplankton–phytoplankton biomass ratios, which may also be due to increased predation pressure by zooplanktivorous fish. Consistent with this, there are changes in zooplankton community composition.

Ecosystem structure can be used to illuminate function. Estimation of the contribution by fish to nutrient recycling usually involves direct measurement or bioenergetic models, both of which are very time-consuming processes. The data suggest that, at least to a crude approximation, fish biomass is a reasonable predictor of P-recycling rate.

The implications of the Water Framework Directive (WFD) for Lough Erne and Natura 2000 sites
(Peter Hale – Environment and Heritage Service)

The Erne lakes should be looked at on a catchment basis, including the inflowing rivers and minor watercourses. Macrophyte classes in these watercourses range from oligotrophic to eutrophic. Implication 1 – the catchment influences the ecology of the lake downstream.

There are two key pieces of European legislation, the Water Framework Directive (WFD) and the Habitats Directive, which have different data requirements. The common feature of the two directives is to maintain the good and improve the ‘not so good’. Implication 2 – monitoring; the opportunity exists for mutually supportive biological/chemical monitoring for both directives, reducing duplication, allowing more to be done within current resources, delivering the required data for the two directives while expanding the knowledge of the ecosystem allowing sound management decisions.

The WFD outlines the required monitoring frequency and Lough Erne is in the > 50 ha class that has to be reported. Will the WFD monitoring frequency tell us enough about change? Implication 3 – we need to develop sensible and cost effective monitoring programmes suited to purpose. There is a need to develop and standardise lake assessment methods as a priority. Implication 4 – method development.

In catchment management it is important to take into account zonation in the Erne system. Invertebrate assemblages, macrophyte communities and distribution of fish species differ over the system. Paleobotanical records indicate zonation. Implication 5 – future management strategies should be based on ecologically different waterbodies and not the whole lake.

Implication 6 – future efforts to improve water quality may conflict with Habitats Directive aspirations.

Session 5 – Using new techniques to examine food webs and species invasions. Identifying a future research programme for Lough Erne

New developments in plankton monitoring
(Ivan Heaney – Aquatic Systems Group, DARD)

New techniques have been developed to improve spatial and temporal resolution in the monitoring of plankton by DARD.

The development of the undulating plankton sampler, U-Tow, by a consortium of the Sir Alister Hardy Foundation for Ocean Science, CEFAS, W.S. Oceans Ltd and DARD has allowed a large number of plankton measurements and associated variables to be determined simultaneously. This equipment has been used in transects across the Irish Sea for continuous sampling of the water column between about five and fifty metres. Measurements include temperature, salinity, depth, chlorophyll fluorescence, light, zooplankton and water samples for phytoplankton, bacteria, viruses and water chemistry. The results illustrate the complexity of the Irish Sea in terms of stratification, nutrients and plankton abundance.

Increased temporal resolution of plankton abundance has been achieved through the development of moorings in estuarine coastal waters of Northern Ireland and in the Irish Sea.

Improved sampling capability for plankton samples has allowed large numbers of samples to be collected which need to be identified and analysed. This is very laborious work and has led to the investigation of using computer-aided image analysis for identifying and counting phytoplankton samples.

Future developments include an underwater profiling system for operation off the north Atlantic shelf for interactive biogeochemical measurements. The possibility of imaging phytoplankton *in situ* and transmitting quantitative information on species abundance in near-real time is of interest to many, including those concerned with harmful algal blooms. Recent technological advances may soon turn this into reality.

Use of stable isotopes to study lake food webs
(Iwan Jones –Queen Mary, University of London)

Stable isotopes are naturally occurring forms of elements that, compared to their more abundant counterpart, have extra neutrons. The main isotopes used are carbon (C) and nitrogen (N) but hydrogen (H), oxygen (O) and sulphur (S) can also be used. When investigating aquatic food webs,

establishing diet from direct observation of gut contents is not always easy as prey can be digested or liquefied and remains can be unidentifiable. Gut content analysis gives a snap shot of ingestion, is invasive and short term, whereas stable isotope analysis (SIA) is an indicator of food that has been assimilated rather than just ingested. SIA reflects natural abundance and gives a longer-term perspective, but food sources are not observed directly, rather they are determined by inference.

Stable isotope analysis is more robust when multiple isotopes are used. Carbon is a good indicator of food source and nitrogen a good indicator of trophic level as the ^{13}C ratio differs between different food sources and ^{15}N ratio increases up the food web. A biplot of $\delta^{13}C$ and $\delta^{15}N$ will separate out components of the food web.

When applying SI techniques to freshwater studies it is also important to consider time and fractionation. $\delta^{13}C$ can change depending on how long an organism has been ingesting a particular food source. If the food sources have different $\delta^{13}C$ signatures and there is a change in diet then there may be a quick switch or a more gradual process of change in the isotopic signature, dependent on how rapidly the tissue sampled is turned over. $\delta^{13}C$ signature of sources may also change (e.g. seasonally – Yoshioka et al. 1994). Use of stable isotope techniques to quantify food web relationships also requires *a priori* estimates of the enrichment or depletion in $\delta^{13}C$ and $\delta^{15}N$ values between predator and prey – known as trophic fractionation. Although this is often assumed to be $\delta^{13}C$ -1.1 ‰ and $\delta^{15}N$ -3.3 ‰, the range can be much wider $\delta^{13}C$ -2.1 ‰ to +2.8 ‰ and $\delta^{15}N$ -0.7 ‰ to +9.2 ‰ (DeNiro & Epstein 1978; Vander Zanden & Rasmussen 2001).

Are stable isotopes any use? Sometimes species don't separate out along the expected food chain, indicating a high degree of omnivory, which in turn can be quantified. How useful stable isotopes are in investigating aquatic food webs will depend on the degree of omnivory, generalism and diet shifts (e.g. Jones & Waldron 2003).

Case studies involving stable isotopes
(Jon Grey – Max Planck Institute of Limnology)

The $\delta^{15}N$ of a primary consumer may be used to represent the isotopic base of the food web in preference to actual basal resources (Cabana & Rasmussen 1996). This gives better time integration, unaffected by small temporal fluctuations, and is often much easier to sample.

Different primary consumers have been used as isotopic baseline indicators. Mussels (pelagic) and snails (littoral) both are relatively long-lived with slow turnover of tissues so they integrate isotopes over a long temporal scale (Post 2002). Herbivorous copepods have been used as a baseline for omnivorous copepods as they are biologically related and have similar temporal or spatial integration of food source isotopes (Kling et al. 1992). *Daphnia* have been used as a fine scale temporal integrator (Matthews & Mazumder 2003). However stoichiometry of algal food potentially effects $\Delta^{15}N$ and thus the use of zooplankton as a baseline indicator (Adams & Sterner 2000). Bulk zooplankton should definitely not be used (Grey & Jones 1999). Chironominae and Orthocladinae have been used as baselines in saline wetlands. They are assumed to integrate the most available algal and detrital foods (Hart & Lovvorn 2003). *Chironomus plumosus* has been 'averaged' with mussel signatures to determine $\delta^{13}C_{base}$, however this assumes *C. plumosus* is a filter feeder (Vadeboncoeur et al. 2003).

How can we use stable isotopes to look at invasive species? Vander Zanden et al. (1999) studied the effect of a bass invasion in Canadian lakes: bass invaded the littoral and prey fish stocks declined. Lake trout $\delta^{13}C$ and $\delta^{15}N$ signatures decreased reflecting a shift to pelagic feeding at the same level as the prey fish. Mitchell et al. (1996) carried out a post-invasion study and found that zebra mussels and *Daphnia* occupied similar trophic positions in Oneida Lake, USA, although zebra mussels were using the entire seston resource whereas *Daphnia* were using a distinct prey source.

How will isotopic signatures reflect a zebra mussel invasion? The decline in phytoplankton could lead to a zooplankton food shift to the microbial loop and a shift in zooplankton composition. There has been a decline in zooplankton that may lead to a 0+ fish food-shift to the benthos. The increase in water clarity and light availability will have an effect on photosynthetic rate and kinetic discrimination against ^{13}C. Intraspecific isotopic variability may reflect changes in feeding pattern as a response to the zebra mussel invasion. An artificial stream study (Greenwood et al. 2001) found that when zebra mussels were present, fine benthic organic matter (FBOM) quality was higher, FBOM $\delta^{13}C$ lower and FBOM $\delta^{15}N$ higher. This reflected the input of planktonic material into the benthos and was detectable in some species such as *Gammarus* but not others such as *Lithasia*. This reflected likely turnover rates.

Historical specimens in museums and samples of zooplankton are chemically preserved through necessity. These can be used for SIA with knowledge of the procedures involved and care with interpretation (Feuchtmayr & Grey 2003). Different tissues have different rates of isotopic turnover – a spectrum of temporal information. In mussels, soft tissues reflect the isotopic signature of the diet while shell (biologically mediated C-based precipitate) reflects the inorganic environment. Seasonal changes in metabolism also result in changes in isotopic composition unrelated to changes in diet. All these factors should be taken into account when using SIA to investigate food webs and species invasions.

Summary of the discussion

Recent ecological change in Lough Erne: influence of catchment changes and species invasions

Both catchment changes and species invasions have driven recent ecological change in Lough Erne. Concentrations of nutrients are primarily determined by catchment activity and even though there has been a reduction in phosphorus after the establishment of zebra mussels, catchment activity is still the primary influence on nutrient concentrations, not biology. If P is not being taken up by a much less abundant phytoplankton community and is instead being taken up by more abundant macrophyte and phytobenthic communities, there may have been no net change in production in the Erne lakes. However, the recent changes in the plankton, benthic invertebrate and fish populations are likely to be a result of the establishment of zebra mussels. The recent blooms of *Microcystis* spp. which may be related to selective filtration by zebra mussels raise concerns about human health as Lough Erne and Lough Neagh both provide a substantial contribution to drinking water in Northern Ireland.

Management

It is clear from the various presentations and discussion sessions that the Water Framework Directive (WFD) will have a big impact on how Lough Erne is managed and that the establishment of invasive species and the response of the ecosystem presents a challenge in classifying the status of the Erne lakes. Even after the establishment of zebra mussels, Lough Erne remains a nutrient rich system with a large capacity for algal growth. Consideration must be given to assessment of the trophic status of a lake such as Lough Erne that has high P and low chlorophyll *a* concentrations. Zebra mussels can decouple the nutrient–chlorophyll relationship. Eutrophication and water quality models that are based on pelagic systems, with phytoplankton the dominant primary producers and crustacean zooplankton the dominant herbivores, may no longer be valid in water bodies with large populations of zebra mussels. Changes in nutrient loading may now be reflected more in changes in benthic algae. However, the overriding management objective is still to reduce nutrient input into the Erne lakes. Management of nutrients needs to occur at catchment level. While requirements of the WFD and Habitats Directive may provide an opportunity to carry out mutually supportive monitoring, reducing duplication, any conflict arising from the markedly different goals should be tackled so that management of the lake is not driven in two different directions.

Efforts to control zebra mussel spread need to continue as one concern is the incorrect perception that zebra mussels clean up the water. The public and anglers view zebra mussels favourably, seeing them as a controller of nutrient inputs. This undermines scientific advice to reduce nutrients as zebra mussels are viewed as a quick fix to the problem of eutrophication. There are economic as well as ecological reasons for wanting to control zebra mussels. The increased water clarity and macrophyte growth may impact on recreational tourism in the lakes as a result of macrophyte growth choking marinas and hindering boating. Additional mechanical control is now needed. The water treatment plant at Killyhevlin was easily modified to exclude zebra mussels because of the plant design. However, if zebra mussels spread to L. Neagh it will be much more complicated and expensive to exclude the mussel from water treatment facilities.

Developing ecosystem models

Discussion focused around the difficulties with ecosystem modelling and avoiding self-validation. The phytoplankton modelling approach described is based on laboratory experiments. Equations were derived and different variables for the organisms in laboratory experiments were input to give results. Conditions in the field are more complex, the weather plays a big part in any aquatic ecosystem and model, and the weather still cannot be predicted accurately. Ecological modelling is useful for managing water bodies such as reservoirs where a model can be used to inform management advice on mixing to reduce phytoplankton blooms, however it is more difficult to model lakes. Managers may need advice before scientists have sufficient understanding of an ecosystem to model it. Fisheries models are an example of this. Salmon models are relatively well developed but there isn't sufficient information from models to determine returns on quotas. A conceptual model of Lough Erne could be developed and this would need to take into account the different areas and the different responses of the margins compared to Broad Lough.

Research

The workshop demonstrated the value of long term monitoring and research. The Lough Erne dataset is one of the most comprehensive for an Irish lake. Although some research will require sampling programmes with greater spatial resolution in the Erne, the long-term dataset has proved invaluable in looking at ecological change and different drivers such as increasing nutrient inputs and species invasions. Maintenance of the dataset is vital and should not be compromised by the organisational changes that will occur in Government departments involved in the research in the next few years.

Climate change will be an important factor driving ecological change in the Erne and should be a part of any future research programme. There was a lot of emphasis in the workshop on species invasions and this was a reflection of the research interests of the organisers. It was apparent that to put the ecological changes that have occurred in response to the zebra mussel invasion into perspective, there is a need to carry out research into change in communities over a much longer timeframe as reflected in the sediment record. Macrofossil analysis would enable an assessment of how communities responded to the roach invasion as no research was carried out at the time, and this will put zebra mussel induced changes into perspective.

The role of macrophytes remains one of the least studied aspects of the Erne system, along with the phytobenthos. It is important to address this as macrophyte abundance is increasing in response to the increased water clarity in the Erne system. Of particular importance is the role macrophytes may be playing in the changes in abundance and community composition of zooplankton and fish populations.

Stable isotope analysis (SIA) could be an invaluable tool if used in conjunction with the current monitoring and research programmes in the Erne. It could be used to examine the dependence of the Erne system on inwashed C to support production. SIA could be used to further understanding of the food web in L. Erne. This should include examining the diets of zooplankton species and whether they have increased their dependence on allochthonous sources of carbon as a response to the depletion of phytoplankton and the role of zebra mussel veligers in the zooplankton and in diets of other species. Further research is also needed on fish populations – the method used for sampling does not sample 0+ fish or all 1+ fry. Although broad scale change such as altered biomass ratios between species can be determined with current monitoring levels, further research involving early life history studies will be required before the mechanisms of change in fish populations can be fully understood.

Outreach

The range of attitudes and misperceptions in both water users and the public about the zebra mussel invasion highlights the need for better communication between scientists and the public about ecological research. The Erne lakes are an important and highly valued natural resource to the communities living around them and public understanding of scientific research on the lakes is an important issue for local people and their representatives. This was demonstrated by the support of Fermanagh District Council for the workshop.

Final remarks

The standard of presentations was high, with discussion sessions which were lively and benefited from the different perspectives of the participants. We came away with some valuable ideas for future research and had an opportunity to explore future collaborations. The workshop demonstrated the value of long-term datasets to look at ecological change. The L. Erne dataset is one of the most comprehensive in Ireland and should be maintained.

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