AN ASSESSMENT OF FISH PREDATION ON THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA* (PALLAS 1771) AFTER RECENT COLONISATION OF TWO MANAGED BROWN TROUT LAKE FISHERIES IN IRELAND

M. Millane, M.F. O'Grady, K. Delanty and M. Kelly-Quinn

M. Millane (corresponding author; email: michael.millane@fisheriesireland.ie), M.F. O'Grady and K. Delanty, Inland Fisheries Ireland, Swords Business Campus, Swords, Co. Dublin; M. Kelly-Quinn, Freshwater Biodiversity, Ecology and Fisheries Research Group, School of Biology and Environmental Science, University College Dublin.

Cite as follows: Millane, M., O'Grady, M.F., Delanty, K. and Kelly-Quinn, M. 2012 An assessment of fish predation on the zebra mussel, *Dreissena polymorpha* (Pallas 1771) after recent colonisation of two managed brown trout lake fisheries in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **112**B, 1–9. DOI: 10.3318/BIOE.2011.18

Received 23 July 2009. Accepted 2 November 2010. Published 30 March 2012.

ABSTRACT

The zebra mussel (*Dreissena polymorpha*, Pallas 1771) invaded Lough Sheelin in the midlands of Ireland in 2001, providing a novel potential food resource for the resident fish species. This paper assesses fish predation on the mussel after the recent colonisation of the lake (with supplementary data from Lough Arrow). In addition, implications for the resident fish community are considered. Roach (*Rutilus rutilus* L.), and roach–bream hybrids (*R. rutilus* × *Abramis brama* L.) were found to consume zebra mussels in all sampling seasons. For other fish species (European perch [*Perca fluviatilis* L.], northern pike [*Esox lucius* L.] and the brown trout [*Salmo trutta* L.]) the occurrence of zebra mussels in the diet was low, in addition to being seasonal, and possibly consumed as incidental by-catch in some cases. The incorporation of mussels into the diet represents the most important change to the feeding habits of cyprinids. Adult roach populations have not increased despite feeding on zebra mussels and appear to be the most negatively impacted fish taxa since the establishment of the mussel in the lake. Brown trout and perch may be advantaged in the long-term, most likely due to reductions in chlorophyll *a*, habitat changes and altered food resources. The extent of fish predation on zebra mussels does not appear to be sufficient to suppress the mussel population in the lake.

INTRODUCTION

The addition of a new species to a food-web can have important implications for the community structure of an ecosystem that has been invaded, through both direct and indirect biotic interactions (MacIsaac 1996; Madenjian *et al*. 2002; Maguire *et al*. 2005; Munawar *et al*. 2005). As well as representing a novel potential food source for the resident fish population, the recent colonisation of Lough Sheelin by zebra mussel (*Dreissena polymorpha*, Pallas 1771) has the potential to affect changes to the dynamics of the pre-invasion food-web structure. In turn, this may have consequences for the long-term structure of the fish population in the lake. The introduction of the zebra mussel to Lough Sheelin most likely occurred in late 2001 (Minchin *et al*. 2002; Kerins *et al*. 2007).

Thirty-eight fish species have been documented to consume attached zebra mussels and fifteen species the planktonic veliger larval stage (Molloy *et al*. 1997). In Ireland, three fish taxa, common bream *Abramis brama* (L.), roach *Rutilus rutilus* (L.), and hybrids of roach and bream, have been reported in the literature to consume attached zebra mussels (Maguire *et al*. 2005). Anecdotal information suggests that species such as the northern pike *Esox lucius* (L.) and the brown trout *Salmo trutta* (L.) may also do so. Other freshwater fish species present in Ireland, which have been reported elsewhere in field studies to consume attached zebra mussels, include the common carp *Cyprinus carpio* (L.), the European eel *Angullia anguilla* (L.), the European perch *Perca fluviatilis* (L.), and tench *Tinca tinca* (L.) (Molloy *et al*. 1997). No Irish data are available concerning the consumption of zebra mussel veliger larvae. Common bream, perch, rudd *Scardinius erythrophthalmus* (L.) and roach have, however, been documented to consume this food source (Molloy *et al*. 1997).

The principal aim of this study was to assess predation on zebra mussels by the resident fish taxa of Lough Sheelin. It was hypothesised that zebra mussels would be a major component in the diet of cyprinid fish (bream, roach and roach–bream hybrids) and to a lesser extent be commonly represented in the diet of brown trout, but that no other species would use mussels as a food source. In addition, long-term implications for the resident fish community of the lake associated with predation on zebra mussels were considered.

MATERIALS AND METHODS

STUDY SITES

Lough Sheelin (53°48'N, 7°20'W) was the principal study site for this research. In addition, Lough Arrow (54°3'N, 8°19'W) was used to supplement fish diet data in spring 2006. Preliminary fieldwork indicated that the lakes were extensively colonised by the zebra mussel, with the initial introductions most likely occurring between late 2001 and 2003 (Minchin *et al.* 2002; Shannon and North Western Regional Fisheries Board staff, pers. comm.). Information on the characteristics of the resident zebra mussel populations in each lake corresponding to each sampling period was only available in spring 2005 and 2006 for Lough Sheelin (Table 1; adapted from Millane *et al.* 2008). Since the establishment of the zebra mussel in Lough Sheelin, there has been a significant reduction in chlorophyll *a* and a significant increase in water transparency, however, the total phosphorus concentration remains high (Millane *et al.* 2008).

The principal fish taxa resident in Lough Sheelin are brown trout, roach, European perch, northern pike, common bream, and hybrids of roach and bream. All of these fish, with the exception of brown trout, are considered non-native to Ireland (Minchin 2007). In Lough Arrow brown trout, European perch and northern pike constitute the main resident fish species. The European eel is also found in both lakes, albeit as a catadromous species. These waterbodies are managed as brown trout fisheries by Inland Fisheries Ireland (IFI) and previously by the Shannon Regional Fisheries Board (Lough Sheelin) and the North Western Regional Fisheries Board (Lough Arrow).

SAMPLING

To obtain fish specimens for diet analyses, Lough Sheelin was sampled in spring, summer and autumn 2005, and in spring 2006. Lough Arrow was sampled in spring 2006. The spring surveys were conducted as part of the Central Fisheries Board's (now IFI) annual fish population monitoring work. All surveys used a combination of multi-mesh braided and monofilament gill nets. The multi-mesh braided gill nets ranged in mesh size from 5.0–12.5cm stretched mesh increasing at 1.25cm intervals. Each gang was composed of seven individual nets 27.5m in length and 2.0m in height, randomly joined end-to-end to create a single unit (O'Grady 1981). The monofilament nylon gill nets were 30.0m in length and 1.5m deep. These were made up of twelve, different sized, 2.5m long mesh panels, with stretched mesh size ranging from 5.0mm to 55mm.

Approximately 30 braided gill net gangs were randomly set for the spring surveys in each lake. In Lough Sheelin these were supplemented by six of the monofilament nets. Five of these were set in locations proximal to zebra mussel quadrat sampling sites from a previous study (Millane *et al.* 2008), with the other net set in a random near shore area. For the summer and autumn samplings, six braided nets and six monofilament nets were used, one of each type set in locations corresponding to the above. In all surveys, nets were bottom-fished overnight (over approximately a 24-hour period). The angle of each net in relation to the shoreline was randomised.

SAMPLE PROCESSING

All fish caught were identified, measured (fork length) and weighed on calibrated electronic scales.

Table 1—Population characteristics of zebra mussels in Lough Sheelin in spring 2005 and 2006 (adapted from Millane *et al*. 2008).

Parameter		*2005*		*2006*	
		Stony substrate	*Soft substrate*	*Stony substrate*	*Soft substrate*
Density (no.s m^{-2})	Mean	2157.0 (416)	703.0 (196)	3016.0 (434)	587.7 (154)
	Range	32–20,288	44.4–11,144.0	96–13,936	44.4–9679.0
Shell length (mm)	Mean	14.7 (2.3)	9.7 (1.2)	16.2 (2.7)	11.5 (0.95)
	Range	3–28	1–26	3–31	2–27

Standard error in brackets; minimum value in range is minimum non-zero value.

In Lough Sheelin, fish gut contents from the six major fish taxa resident in the lake (bream, perch, pike, roach, roach–bream hybrids, wild brown trout and stocked trout) were examined for the presence of zebra mussels. In Lough Arrow, perch, pike and trout were examined (bream, roach and roach–bream hybrids are not known to occur in this lake). Fish diet analyses followed the methods employed by Gargan and O'Grady (1992). For trout and perch, the standard stomach (Ball 1961) was taken. As Cyprinidae lack a distinct stomach (Kapoor *et al.* 1975, as cited in Gargan and O'Grady 1992), the entire alimentary canal was removed from bream, roach and roach–bream hybrids. Pike stomach contents were generally examined in the field. For the other fish taxa, the gut contents removed were stored in 70% alcohol. In the laboratory, contents were examined under a binocular microscope.

The numbers of zebra mussel specimens found in each gut were recorded. In addition, mussel length was measured along the longest axis of the shell to the nearest mm. As Cyprinidae possess pharyngeal teeth that can fragment whole shells, intact mussels are not often present in the gut contents. Despite this, the septa (acute corners of the valves), commonly referred to as *beaks*, are usually preserved (Stein *et al.* 1975; Prejs *et al.* 1990). The left and right septa can be distinguished by orienting the shell fragment with the flat edge on the bottom. A linear relationship can be derived from the internal umbonal length of the septum to predict whole mussel length (Fig. 1; and see data analyses below for further details). Therefore, the numbers of fragmented mussels present can be estimated by pairing the left and right beaks together (Olszewski 1978; Prejs *et al.* 1990; Hamilton 1992).

DATA ANALYSES

The percentage occurrences of zebra mussels in non-empty stomachs were recorded for each fish taxon per lake and season as follows (Ball 1961; Hyslop 1980):

$$\%\text{ occurrence} = \frac{\text{number of stomachs in which zebra mussels occurred}}{\text{number of non-empty stomachs examined}}$$

A linear regression model was developed to predict whole zebra mussel length from the internal umbonal length of the left and right septa. The septal lengths of ten randomly selected mussels were measured and averaged per mm mussel size class (5–25mm) under a binocular microscope. STATISTICA 8.0 (Statsoft, Inc 2008) was employed for data analyses. In general, sample sizes prohibited the analyses of fish diet within specific length classes.

RESULTS

The diets of over 560 fish were examined during the course of this research. These consisted of a range of sizes of the major fish taxa resident in Lough Sheelin and Lough Arrow.

REGRESSION MODEL TO PREDICT WHOLE ZEBRA MUSSEL LENGTH FROM UMBONAL LENGTH

A strongly significant relationship was found between whole zebra mussel length and the respective internal umbonal lengths of the left septa ($r^2 = 0.989$, $y = 8.26x - 1.241$) and right septa ($r^2 = 0.987$, $y = 8.087x - 1.16$) (Fig. 2). This allowed the accurate reconstruction of whole zebra mussel lengths from the beak fragments found in the gut contents.

FISH PREDATION ON ZEBRA MUSSELS IN LOUGH SHEELIN

A detailed breakdown of the occurrence of zebra mussels in the diet of the major fish taxa examined in Lough Sheelin (with supplementary information from Lough Arrow), is provided in Table 2.

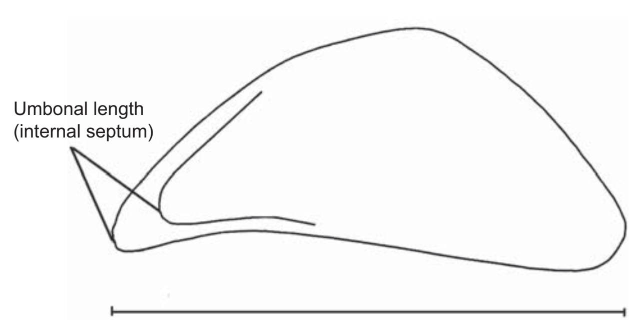

Fig. 1—Internal view of the right side of a zebra mussel shell with umbonal length indicated (adapted from Hamilton 1992).

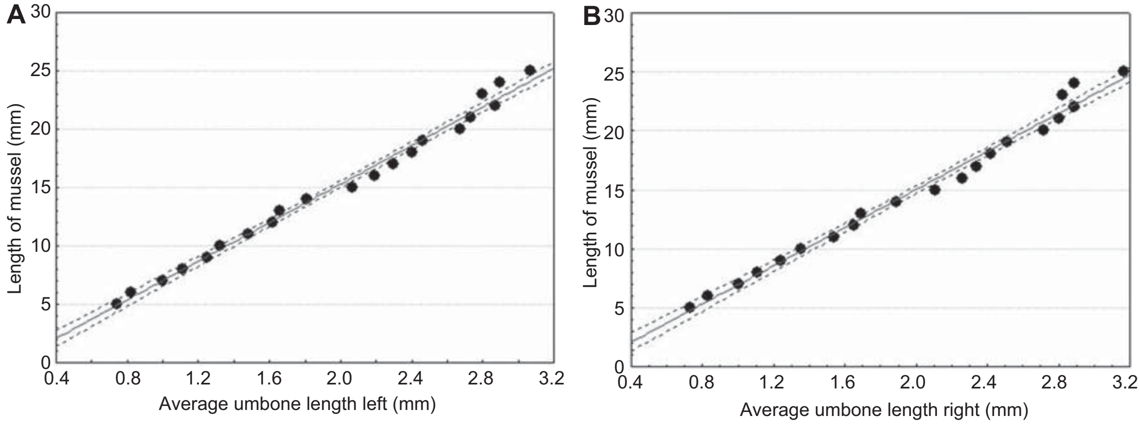

Fig. 2—Relationship between zebra mussel umbone length and whole mussel length for (A) left umbone; and (B) right umbone (dashed lines indicate 95% confidence intervals).

Table 2—Details of zebra mussels in the diet of the major fish taxa examined in Lough Sheelin with additional data from Lough Arrow (indicated by †).

Fish taxa	*Season[1]*	*No. of fish**	*No. of fish with mussels*	*% O[ψ]*	*No. of mussels in gut contents per fish*		*Size of zebra mussel shells consumed (mm)*		*Size of fish consuming mussels (fork length in cm)*	
					Mean	*Range*	*Mean*	*Range*	*Mean*	*Range*
Roach	*Sp 05*	21	6	28.6	4.8 (1.8)	1–11	8.9 (0.8)	1.3–16.6	25.4 (1.2)	20.2–28.5
	Su 05	22	14	63.6	11.1 (3.2)	1–32	11.5 (0.2)	2.4–16.9	25.6 (1.3)	17.2–31.3
	Au 05	27	4	14.8	*n/a - only beak-free shell fragments found*				27.6 (2.1)	20.4–31.5
	Sp 06	12	1	8.3	1	n/a	12.7	n/a	28.5	n/a
Roach–bream hybrids	*Sp 05*	18	9	50.0	5.5 (2.2)	1–17	6.3 (0.7)	0.3–16.6	32.8 (2.5)	23.8–41.7
	Su 05	10	8	80.0	7.0 (4.0)	1–26	12.3 (0.5)	5.3–18.6	36.8 (3.2)	17.7–44.3
	Au 05	8	2	25.0	2.0 (1.0)	1–3	13.5 (0.9)	11.0–15.1	35.4 (2.7)	32.7–38.0
	Sp 06	17	3	17.6	1.3 (0.3)	1–2	11.8 (0.4)	11.1–12.6	34.0 (2)	30.0–36.0
Trout[$]	*Sp 05*	29	3	10.3	1.0 (0.0)	n/a	7.0 (0.8)	6.0–8.0	33.4 (7.3)	25.1–48.0
	Su 05	9	0	0	-	-	-	-	-	-
	Au 05	3	0	0	-	-	-	-	-	-
	Sp 06	26	3	11.5	1.3 (0.3)	1–2	7.4 (1.4)	7.0–11.0	42.6 (4.6)	34.0–48.8
	Sp 06†	23	2	8.7	2.0 (0.0)	n/a	8.7 (0.2)	8.0–9.3	42.3 (2.3)	40.0–44.6
Perch	*Sp 05*	12	1	8.3	1	-	3.1	-	31.6	-
	Su 05	22	0	0	-	-	-	-	-	-
	Au 05	18	0	0	-	-	-	-	-	-
	Sp 06	11	0	0	-	-	-	-	-	-
	Sp 06†	25	0	0	-	-	-	-	-	-
Pike	*Sp 05*	23	0	0	-	-	-	-	-	-
	Su 05	10	3	30.0	1.0 (0.0)	n/a	7.8	n/a	54.6 (9.9)	35.2–67.6
	Au 05	4	0	0	-	-	-	-	-	-
	Sp 06	20	0	0	-	-	-	-	-	-
	Sp 06†	6	0	0	-	-	-	-	-	-

Standard error in brackets. *Fish with non-empty stomachs; [1]sp = spring, su = summer, au = autumn; [$]Does not include stocked trout; [ψ]Percentage occurrence; n/a = not applicable.

Roach and roach–bream hybrids were found to be the principal fish taxa to use zebra mussels as a prey item. The occurrence of zebra mussels in the other fish species investigated was restricted to a particular season (trout) or was evident in isolated instances. No fish were found to consume mussels greater than 18.6mm in length. No zebra mussel veliger larval stages were encountered in the gut contents of any of the fish taxa examined during the study.

ROACH, ROACH–BREAM HYBRIDS AND BREAM

Roach and roach–bream hybrids were found to consume zebra mussels in each season sampled. For both groups, percentage occurrence was highest in summer 2005 (63.6% and 80.0%, respectively) and lowest in spring 2006 (8.3% and 17.6%, respectively). Both fish consumed the highest numbers of mussels in summer 2005 (11.1 ± 3.2 mussels/fish and 7 ± 4 mussels/fish, respectively). Only one roach contained mussels in spring 2006. The mean size of roach consuming mussels was similar in all seasons (from 25.4 ± 1.2cm to 28.5 ± 0.0cm length). The smallest roach found preying on zebra mussels was 17.2cm in length in summer 2005. In all seasons, roach–bream hybrids had larger size distributions than roach. This is reflected in the greater mean size of hybrid fish preying on zebra mussels (32.8 ± 2.5cm to 36.8 ± 3.2 cm). The largest sized mussel consumed by any fish taxa (18.6mm shell length) was found in the gut contents of a hybrid fish.

Bream specimens were examined for zebra mussels in summer 2005. Of the nine non-empty guts, four contained mussel fragments, albeit in quite low abundances. As beaks were not conserved, in the main, the numbers and lengths of whole mussels could not be assessed. Only a single mussel length could be determined, which had a shell length of 14.3mm. The size of bream preying on mussels ranged from 28.7cm to 41.1cm length.

TROUT

In Lough Sheelin, wild brown trout were only found to consume zebra mussels in the spring of each year. In this case, the sample sizes in summer ($n=9$) and particularly autumn ($n=3$), were relatively small. Trout in Lough Arrow (spring 2006) were also found to be preying on mussels. No stocked trout examined contained mussels. Overall the level of predation (8.7–10.3%) was quite low, albeit within a narrow but consistent range. The numbers of mussels found per gut was low, with season means ranging only from one to two mussels per fish. The size of zebra mussel consumed ranged from 6–11mm shell length, with only the larger trout ingesting mussels (mean fish lengths from 33.4 ± 7.3cm to 42.6 ± 4.6cm).

OTHER FISH TAXA

Only a single perch was found to have consumed zebra mussels (Lough Sheelin, spring 2005) out of 88 non-empty stomachs examined during the whole study. This specimen 31.6cm in length contained a single mussel with a 3.1mm shell length. Pike were only found to contain zebra mussels in summer 2005 in Lough Sheelin, averaging a single mussel per stomach. This represented a 30% occurrence. A single tench was encountered during the sampling, again in summer 2005, in Lough Sheelin. This had one mussel present with a 9.4mm shell length.

GENERAL DESCRIPTION OF OTHER COMPONENTS OF FISH DIETS IN LOUGH SHEELIN

Wild brown trout were found to have a broad diet, predominantly feeding on fish fry, asellids, amphipods, corixids, cased Trichoptera, ephemopteran nymphs, non-dreissenid bivalves and gastropods. Chironomid and megalopteran larvae were present in spring of each year. Plankton (all Cladocera) were found in most seasons, albeit with a relatively low percentage occurrence. The few stocked trout encountered had a similar feeding pattern, but no plankton were evident in the gut contents.

Although zebra mussels were a large constituent of the roach diet, non-dreissenid bivalves, gastropods, plant remains, trichopteran and chironomid larvae commonly occurred. Corixids and ephemeropteran nymphs of *Ephemera danica* Müller were consumed in summer 2005. The major components of the roach–bream hybrid diet were similar to the above, with the exception of the additional occurrence of amphipods in the spring of each year. Bream were only examined in summer 2005. Here, the dietary items were similar to those recorded for roach.

Perch diet mainly consisted of fish fry, asellids, amphipods and chironomid larvae. In addition, Coleoptera, *E. danica* nymphs and trichopteran larvae had a low representation in the diet in some seasons. Pike fed primarily on small roach and perch, as well as on trout and sticklebacks. Asellids and amphipods also commonly occurred in the gut contents, but to a lesser extent. Gastropods were present in a small number of specimens.

DISCUSSION

The addition of the zebra mussel to Lough Sheelin represents a novel and abundant, potential food source for the resident fish population. Not all of the fish taxa examined, however, were found to be consistently exploiting this resource. Roach and roach–bream hybrids were found to consume zebra mussels in all sampling seasons. For other fish species (perch, pike and trout), the occurrence of zebra mussels in the diet was found to be low, in addition to being seasonal, and possibly consumed as incidental by-catch in some cases.

Out of the main fish taxa resident in the lake, predation on zebra mussels by roach has been the most comprehensively studied (Molloy *et al.* 1997). In fact this species has been reported to be the most aggressive fish predator of zebra mussels in Europe (Molloy *et al.* 1997). In Lough Sheelin, the percentage occurrence (mean 28.8 ± 12.3) and the numbers (range 1–32 mussels/fish) of zebra mussels consumed by roach appear to be relatively low compared to previous studies in waterbodies with well-established zebra mussel populations (Pliszka 1953; Stańczykowska 1987, as cited in Prejs *et al.* 1990; Molloy *et al.* 1997). For example, Pliszka (1953) found that roach 18–32cm in length fed almost exclusively on zebra mussels in a Polish lake (as cited in Molloy *et al.* 1997). In some other Polish lake studies, Stańczykowska (1987) found that zebra mussels represented 97% of roach food for fish 28–32cm in length. In common with this, Prejs *et al.* (1990) reported that zebra mussels represented ≥75% of food in roach from 23cm length and 95% in fish >28cm in length. Larger size classes of roach from some Eastern European-based studies have been documented to use zebra mussels as a principal food source, sometimes almost exclusively feeding on mussels during certain time periods (reviewed in Molloy *et al.* 1997). The highest percentage occurrence of zebra mussels in the diet of roach (63.6%) was in the summer (July 2005). This was also the case for roach–bream hybrids (80%). In one Polish-based lake study, roach were found to use zebra mussels as their main food source in July. This was attributed to an increase in the energy requirements necessary to maintain the high rate of growth that occurs during this time of year (Budzynska *et al.* 1956, as cited in Molloy *et al.* 1997).

Overall, the results are more comparable to the level of fish predation experienced by zebra mussels in some relatively recently colonised systems (e.g. Maguire *et al.* 2005). In Lough Erne in Ireland, medium to large sized roach with >13cm fork length were found to commonly consume zebra mussels (Maguire *et al.* 2005). Here, the percentage occurrence in the diet ranged from 18.2–37.0%. A similar pattern was evident for medium to large sized roach–bream hybrids (>15cm fork length) as well as for medium-sized bream (15–30cm fork length) with recorded occurrences of 11.1–55.0% and 20.0%, respectively. In the present study, bream diet was only examined in summer 2005 in Lough Sheelin (with a 44% occurrence of zebra mussels). Budzynska *et al.* (1956) found that although zebra mussels were found in 18% of bream in Goplo Lake, Poland, this made up an insignificant part (<1%) of their diet (reviewed in Molloy *et al.* 1997). For Lough Sheelin, when mussels were present in the bream gut contents, generally only a few fragments were found.

In contrast to Loughs Sheelin and Arrow, no zebra mussels were found in the gut contents of trout in Lough Erne. This was also the case for perch (Maguire *et al.* 2005). Brown trout or pike have previously not been documented to consume zebra mussels (reviewed in Molloy *et al.* 1997). As the numbers of actual mussels found in the gut contents were very low for these three fish species (≤2 mussels per fish), it is likely that these occurrences may be mainly incidental, arising from by-catch. It could be expected, though, that trout should have the ability to consume zebra mussels, as molluscs such as gastropods and small bivalves are known to be common in the diet of this species (Kennedy and Fitzmaurice 1971; Gargan and O'Grady 1992). One interesting point to note concerning this is that molluscs are known to constitute a greater proportion of the diet of brown trout in some of the large western lakes of Ireland (Loughs Corrib, Mask and Conn) than in the midland lakes, such as Lough Sheelin (Kennedy and Fitzmaurice 1971). Therefore, it is considered likely that brown trout may more frequently access zebra mussels as a food resource in these lakes (zebra mussels have only invaded Loughs Corrib and Conn in the past four to five years).

The size of roach preying on zebra mussels is broadly consistent with previous studies (Prejs *et al.* 1990; reviewed in Molloy *et al.* 1997). The lower size limit recorded for roach and hybrids consuming mussels was 17.2cm and 17.7cm, respectively. Roach and roach–bream hybrids, as cyprinids, characteristically possess pharyngeal teeth, a main function of which is in the crushing of mollusc shells (Jobling 1995). The possession of these may therefore confer an advantage over other fish species that do not have them in successfully accessing zebra mussels as prey (French 1993). The lower fish size threshold described above likely corresponds to the age when pharyngeal teeth become well developed (French 1993). In any case, small-sized fish are morphologically restricted by a smaller mouth, thus limiting the size of mussel that can potentially be consumed (Prejs *et al.* 1990). Moreover, it has been demonstrated that it is not worthwhile for small fish to prey on small zebra mussels, as the net energy benefit derived is relatively low compared to other less energy-consuming sources (Prejs *et al.* 1990). In general, roach under a minimum length range of 14–16cm do not use the attached stages of the zebra mussel as a food source (Prejs *et al.* 1990; reviewed in Molloy *et al.* 1997). Moreover, roach have been documented to progressively feed on zebra mussels in greater proportions as fish size increases (Prejs *et al.* 1990). There is limited evidence to suggest that this may be the case for roach and roach–bream hybrids in this study. However, sample sizes were inadequate to allow for a detailed statistical analysis.

It is interesting to note that no fish were found to consume zebra mussels greater than 18.6mm in length, even though mussels greater than this size were abundant and readily accessible in the environment (Millane *et al.* 2008). Fish may have difficulty ingesting and processing larger mussels. Prejs *et al.* (1990) found that there was a higher cost-to-benefit ratio for roach between the energy required to crush larger mussels and the resultant energy derived. As a result, the selection of the largest sized mussels present in the environment was limited.

As zebra mussels constitute an abundant and readily accessible food resource, particularly for roach, it should be expected that at least the adult population in Lough Sheelin should be advantaged. In some waterbodies, roach have seen an increase in growth rates and productivity following a zebra mussel invasion (Molloy *et al.* 1997 and references therein). In contrast, the roach population in Lough Sheelin has seen a dramatic decline in abundance since the lake has apparently reverted to a mesotrophic state (Millane *et al.* 2008; O'Grady *et al.* 2009). This is believed to be principally associated with the decline in pelagic primary and secondary production (i.e. phytoplankton and zooplankton) in response to the establishment of zebra mussels (Millane *et al.* 2008; O'Grady *et al.* 2009). Similar declines in roach populations have previously been observed when productivity was reduced (O'Grady and Delanty 2000; Horppila *et al.* 2000). Although there is no evidence available to examine whether there has been a post-zebra mussel reduction in zooplankton abundance in Lough Sheelin, a large significant decline in the phytoplankton population has been documented using chlorophyll *a* as a proxy measure (Millane *et al.* 2008). Zooplankton populations have been reported to be suppressed by zebra mussels elsewhere (Jack and Thorp 2000; Maguire *et al.* 2005). Therefore, as roach fry are known to feed almost exclusively on plankton (Persson and Greenberg 1990), the suppression of pelagic production may severely hinder the development of large juvenile roach populations. Indeed, perch fry, who also consume zooplankton, are known to be more adaptable in their diet than roach fry when plankton resources become scarce (Persson 1983; Persson and Greenberg 1990).

Perch have been found to compete better with roach after zebra mussel establishment in Lough Erne (Maguire *et al.* 2005). In Lough Sheelin, perch are now at a comparable abundance to roach (O'Grady *et al.* 2009). Although not examined, it is reasonable to assume the increase in water transparency post-establishment has resulted in the expansion of submerged vegetation. This is a common characteristic in response to zebra mussel colonisation (Skubinna *et al.* 1995; Mayer *et al.* 2002; Zhu *et al.* 2006). Previous research in the lake has shown that the Characeae beds have retracted in years of low water transparency and with a reduction in water quality, only to eventually become re-established after conditions improve (Champ 1993). Submerged macrophyte growth should favour perch over roach as it is a superior forager in this habitat (Winfield 1986). Indeed, charophytes provide a stable habitat for many macroinvertebrates that are important food items for brown trout (Kennedy and Fitzmaurice 1971; Champ 1993). Therefore, the re-expansion of the charophyte beds may eventually benefit trout numbers through an associated increase in the food resources necessary to sustain a large trout population in the lake (Champ 1993). Despite the apparent improvement in water quality conditions in Lough Sheelin that should favour brown trout (Champ 1998; O'Grady and Delanty 2000), the lake population has not yet recovered as has been expected (Martin O'Grady pers. comm.). It must be noted that dissolved phosphorus levels in the lake have not dropped since the establishment of the zebra mussel population (Millane *et al.* 2008). In addition, zebra mussels can suppress zooplankton populations, which are a common prey item for small-sized trout (Kennedy and Fitzmaurice 1971; Jack and Thorp 2000; Maguire *et al.* 2005; O'Grady *et al.* 2009).

Interestingly, a large decline in the cyprinid population has the potential to enhance the abundance of zebra mussel populations, as the physical disturbance and resuspension of the bottom sediments from the foraging of these fish is reduced (Lammens *et al.* 2002). This decline may also limit any overall impact that fish could exert on suppressing the zebra mussel population in the lake through direct predation.

One further point to consider is that small roach fry are known to extensively prey on the planktonic stages of zebra mussel veliger larvae. These may be abundant in the waterbody during certain periods in the summer months (Maguire 2002; Lucy *et al.* 2005). Bream and perch have also been documented as consuming this food (reviewed in Molloy *et al.* 1997). No veliger larvae were identified in the gut contents of fish examined in this study, but small fry were not sampled. The fact that brown trout are not known to consume zebra mussel larvae (Molloy *et al.* 1997) is probably more a function of the limited research in this area.

Overall, the results suggest it is highly unlikely that the current level of fish predation experienced by zebra mussels would be sufficient to act as a control on the mussel population. Furthermore, the potential effects on fish communities resulting from a zebra mussel invasion through the influence on the food-webs pose challenges to the characterisation and monitoring of fish communities as required under the Water Framework Directive (2000). The long-term trends in fish populations may be more reflective of the dynamics of an invasive species, rather than being a good measure of status alone.

ACKNOWLEDGEMENTS

For field support in Lough Sheelin, thanks to the staff of the Shannon Regional Fisheries Board, including Sean Gurhy and Martin Moffatt; and Brian Hayden and Derek Ryan of the Freshwater Biodiversity, Ecology and Fisheries Research Group UCD. In Lough Arrow, thanks Jimmy Fraser and the other North Western Regional Fisheries Board staff based at the lake. In addition, thanks to Frances Lucy for some helpful comments during the preparation of this manuscript. This research was supported by the Central and Shannon Regional Fisheries Boards, Lough Sheelin Trout Protection Association and the Irish Research Council for Science, Engineering and Technology.

REFERENCES

Ball, J.N. 1961 On the food of the brown trout of Llyn Tegid. *Proceedings of the Zoological Society of London* **137**, 599–622.

Budzynska, H., Romaniszyn, W., Romanski, J., Rubisz, A., Stangenberg, M. and Stangenberg, W. 1956 The growth and the summer food of the economically most important fishes of the Goplo Lake. *Zoologica Poloniae* **7**, 63–120.

Champ, W.S.T. 1993. Lough Sheelin – a 'success' story. In C. Mollan (ed), *Water of life*, 154–162. The proceedings of a Conference on the Inland Waters of Ireland held in the Royal Dublin Society from October 7–9, 1992.

Champ, W.S.T. 1998 Phosphorous/chlorophyll relationships in selected Irish lakes: ecological consequences and suggested criteria for ecosystem management. In J.G. Wilson (ed), *Eutrophication in Irish waters*, 91–105. Dublin: Royal Irish Academy.

French, J.R.P. III 1993 How well can fishes prey on zebra mussels in eastern North America. *Fisheries* **18**, 13–9.

Gargan, P.G. and O'Grady, M.F. 1992 Feeding relationships of trout *Salmo trutta* (L.), perch *Perca fluviatilis* (L.) and roach *Rutilus rutilus* (L.) in Lough Sheelin, Ireland. *Irish Fisheries Investigations* A **35**, 1–22.

Hamilton, D.J. 1992 A method for reconstruction of zebra mussel (*Dreissena polymorpha*) length from shell fragments. *Canadian Journal of Zoology* **70**, 2486–90.

Horppila, J., Ruuhijarvi, J., Rask, M., Karppinen, C., Nyberg, K. and Olin, M. 2000 Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a large lake. *Journal of Fish Biology* **56**, 51–72.

Hyslop, E.J. 1980 Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* **17**, 411–29.

Jack, J.D. and Thorp, J.H. 2000 Effects of the benthic suspension feeder *Dreissena polymorpha* on zooplankton in a large river. *Freshwater Biology* **44**, 569–79.

Jobling, M. 1995 *Environmental biology of fishes. Fish and fisheries series 16*. London: Chapman and Hall.

Kapoor, B.G., Evans, H.E. and Pevzner, R.A. 1975 The gustatory system in fish. *Advances in Marine Biology* **13**, 53–108.

Kennedy, G.J.A. and Fitzmaurice, P. 1971 The growth and food of brown trout (*Salmo trutta* L.) in Irish waters. *Proceedings of the Royal Irish Academy* **71B**, 269–352.

Kerins, C., Monahan, K. and Champ, T. 2007 *Lough Sheelin and its catchment: water quality status and nutrient loadings 1998–2005*. Shannon Regional Fisheries Board, Limerick, Ireland.

Lammens, E.H.R.R., Van Nes, E.H. and Mooij, W.M. 2002 Differences in the exploitation of bream in three shallow lake systems and their relation to water quality. *Freshwater Biology* **74**, 2435–42.

Lucy, F., Sullivan, M. and Minchin, D. 2005 *Nutrient levels and the zebra mussel population in Lough Key*. Environmental Research, Technological, Development and Innovation Report Series No. 34. Environmental Protection Agency, Wexford, Ireland.

MacIsaac, H.J. 1996 Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist* **36**, 287–99.

Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Banjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, E.S., Lavis, D.S., Robertson, D.M., Jude, D.J. and Ebener, M.P. 2002 Dynamics of the Lake Michigan food web, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 736–53.

Maguire, C.M. 2002 *The zebra mussel Dreissena polymorpha in the Erne system: Invasion, population dynamics and early ecological impacts*. PhD thesis. The Queens University of Belfast.

Maguire, C.M., Rosell, R.S. and Roberts, D. 2005 *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. Aquatic Systems Group, Queens University Belfast.

Mayer, C.M., Keats, R.A., Mills, E.L. and Rudstam, L.G. 2002 Scale-dependent effects on benthic invertebrates in a large eutrophic lake. *Journal of the North American Benthological Society* **21**, 616–33.

Millane, M., Kelly-Quinn, M. and Champ, T. 2008 Impact of the zebra mussel on the ecological integrity of Lough Sheelin: distribution, population characteristics and water quality changes in the lake. *Aquatic Invasions* **3**, 271–81.

Minchin, D. 2007 A checklist of alien and cryptogenic aquatic species in Ireland. *Aquatic Invasions* **2**, 341–66.

Minchin, D., Lucy, F. and Sullivan, M. 2002 *Monitoring of zebra mussels in the Shannon-Boyle navigation, other navigable regions and principal Irish lakes, 2001 and 2002*. Marine Institute, Dublin, Marine Environment and Health Series No. 5.

Molloy, D.P., Karatayev, A.Y., Burlakova, L.E., Kurandina, D.P. and Laruelle, F. 1997 Natural enemies of zebra mussels: predators, parasites, and ecological competitors. *Reviews in Fisheries Science* **5**, 27–97.

Munawar, M., Munawar, I.F., Mandrak, N.E., Fitzpatrick, M., Dermott, R. and Leach, J. 2005 An overview of the impact of non-indigenous species on the food-web integrity of North American Great Lakes: Lake Erie example. *Aquatic Ecosystem Health and Management* **8**, 375–95.

O'Grady, M.F. 1981 Some direct gillnet selectivity tests for brown trout populations. *Irish Fisheries Investigations, Series A (Freshwater) No.* 22.

O'Grady, M.F. and Delanty, K. 2000 *Central Fisheries Board Report on the status of Lough Sheelin's fish stocks*. Central Fisheries Board, Dublin, Ireland.

O'Grady, M.F., Kelly, M. and O'Reilly, S. 2009 *Brown trout in Ireland*. Irish Freshwater Fisheries Ecology and Management Series: Number 6. Central Fisheries Board, Dublin, Ireland.

Olszewski, Z. 1978 Reconstruction of the size of mollusc shells in studies on the food of fish. *Bulletin of the Polish Academy of Sciences II* **26**, 87–91.

Persson, L. 1983 Effects of intra- and interspecifc competition on dynamics and size structure of a perch *Perca fluviatilis* and roach *Rutilus rutilus* population. *Oikos* **41**, 126–32.

Persson, L. and Greenberg, L.A. 1990 Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*) – roach (*Rutilus rutilus*) interaction. *Ecology* **71**, 44–56.

Pliszka, F. 1953 Dynamics of feeding relations of the Lake Harsz. *Polish Archives of Hydrobiology* **1**, 270–300 (in Polish).

Prejs, A., Lewandowski, K. and Stańczykowska-Piotrowska, A. 1990 Size-selective predation by roach (*Rutilus rutilus*) on zebra mussel (*Dreissena polymorpha*): field studies. *Oecologia* **83**, 378–84.

Skubinna, J.P., Coon, T.G. and Batterson, T.R. 1995 Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* **21**, 476–88.

Stańczykowska, A. 1987 The place of mussel *Dreissena polymorpha* (Pallas) in the food-web of lake ecosystems. *Haliotis* **16**, 129–35.

StatSoft, Inc. 2008 STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

Stein, R.A., Kitchell, J.F. and Knežević, B. 1975 Selective predation by carp (*Cyprinus carpio* L.) on benthic molluscs in Skadar Lake, Yugoslavia. *Journal of Fish Biology* **7**, 391–9.

Water Framework Directive 2000 Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities* **43**, 1–72.

Winfield, I.J. 1986 The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, Perca fluviatilis. *Journal of Fish Biology* **29A**, 37–48.

Zhu, B., Fitzgearld, D.G., Mayer, C.M., Rudstam, L.G. and Mills, E.L. 2006 Alteration of ecosystem function by zebra mussels in Oneida Lake, NY: impacts on submerged macrophytes. *Ecosystems* **9**, 1017–28.