

Invasive fish species in the largest lakes of Scotland, Northern Ireland, Wales and England: the collective U.K. experience

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Abstract

An invasive species is defined as an alien (or introduced or non-native) species whose establishment and spread threaten ecosystems, habitats or species with harm. Such threats to U.K. lake fish communities have long been appreciated and this review assembles case histories, including new data, from the largest lakes of Scotland, Northern Ireland, Wales and England to examine the hypothesis that at least some of these introductions have become invasive. Loch Lomond in Scotland has experienced six introductions (chub (*Leuciscus cephalus*), common bream (*Abramis brama*),

crucian carp (*Carassius carassius*), dace (*Leuciscus leuciscus*), gudgeon (*Gobio gobio*) and ruffe (*Gymnocephalus cernuus*)), of which the most significant has been that of the percid ruffe, which has been implicated in a recent decline of the native coregonid whitefish (*Coregonus lavaretus*). In Northern Ireland, the introduction of the cyprinid roach (*Rutilus rutilus*) to Lough Neagh has apparently had a negative impact on some overwintering waterfowl, although the native coregonid pollan (*Coregonus autumnalis*) remains abundant. Llyn Tegid in Wales has received three introductions (rudd (*Scardinius erythrophthalmus*), ruffe and silver bream (*Blicca bjoerkna*)), although no impacts on the native whitefish or other fish populations have been observed. In England, individuals of at least 12 native and non-native fish species have been brought to Windermere for the purpose of live-baiting, although only those of the cyprinids roach and common bream have established abundant populations. At the same time, the native salmonid Arctic charr (*Salvelinus alpinus*) has declined markedly while the native esocid pike (*Esox lucius*) has shown changes in abundance, distribution and individual condition, although these developments have not been shown to be causally linked. None of these introductions were sanctioned by appropriate fisheries or other regulatory bodies and almost all of them probably arose from the release or escape of live-bait used by pike anglers. Of the 10 species introductions documented here, four (common bream, gudgeon, roach and ruffe) have established abundant populations and two of these (roach and ruffe) have apparently caused or currently threaten harm, supporting the hypothesis that at least some of these introductions have become invasive.

Introduction

The Global Invasive Species Programme global strategy on invasive alien species (McNeely et al., 2001) defines alien species as ‘a species, subspecies, or lower taxon introduced outside its normal past or present distribution’ and invasive alien species as ‘an alien species whose establishment and spread threaten ecosystems, habitats or species with economic or environmental harm’. Alien species are also frequently referred to in the literature as introduced or non-native species with slightly varying accompanying definitions (see Colautti & MacIsaac, 2004), but for those species considered to be invasive there are two clear common defining elements of ‘introduced’ and ‘harm’.

Determining that a species has been introduced is relatively easy in theory, although in practise it is rather more complex given frequently limited historical data and complex conceptual issues as reviewed by Copp et al. (2005). Showing that an introduced species is threatening or actually causing harm is even more difficult, given that this can include both direct and indirect interactions which to be demonstrated require extensive and quantitative studies. For the fauna and flora of large lakes, such difficulties are usually further exacerbated by considerable sampling challenges.

Threats arising from species introductions to the depauperate lake fish communities within the collection of islands known as the U.K. have long been appreciated (Winfield, 1992) and have recently been shown to be due in large part to the use of live bait by anglers fishing for pike (*Esox lucius*) (Winfield et al., 2007). Recipient lakes include the largest standing water body of each of the four component countries of the U.K., which together present a diverse array of environmental conditions (e.g. altitude 4 to 158 m, surface area 415 to 38,179 ha, mean depth 9 to 37

m, and oligotrophic to eutrophic conditions (see below)) completely or largely free of fisheries impacts.

This review brings together the fish introduction histories of the largest lakes of Scotland (Loch Lomond), Northern Ireland (Lough Neagh), Wales (Llyn Tegid also known as Bala Lake) and England (Windermere), together with new data where available, in order to present the collective U.K. experience of this major environmental threat. Specifically, by analysing temporal trends in native and introduced fish species to look for decreases in the former coinciding with increases in the latter, the hypothesis is examined that at least some of these introductions have become invasive.

Loch Lomond

Loch Lomond is situated (56°7' N, 4°37' W; altitude 4 m) in the Loch Lomond & The Trossachs National Park of west-central Scotland (Fig. 1). It comprises an oligotrophic north basin (surface area: 2,280 ha, mean depth: 140 m), a mesotrophic mid basin (surface area: 1,410 ha, mean depth: 60 m) and a eutrophic south basin (surface area: 3,350 ha, mean depth: 27 m).

The fish community of Loch Lomond has been better documented than that of any other water body in Scotland, with many findings reviewed by Adams (1994) who noted a native fish community composed of 15 species including the nationally important whitefish (known locally as powan) (*Coregonus lavaretus*). This species number is higher than for any other loch and is due in part to the diverse nature of the loch's three basins. However, Adams (op. cit.) also reviewed a series of post-1970 fish species introductions, including the first records of gudgeon (*Gobio gobio*) in

1981, ruffe (*Gymnocephalus cernuus*) in 1982, dace (*Leuciscus leuciscus*) in 1987, chub (*Leuciscus cephalus*) in 1987, and crucian carp (*Carassius carassius*) in 1991. Adams (op. cit.) noted that gudgeon were deliberately introduced to a pond in the loch's catchment from which they made their way into the river system and thus the loch itself, whereas he considered that the other four introduced species probably arrived as discarded live-bait of pike anglers. Subsequently, Etheridge & Adams (2008) reported the first common bream (*Abramis brama*) in the loch in 2006.

Of all of the above introductions, that of the ruffe has been the most dramatic and the most concerning. Adams (1994) reported a survey of the fish community in 1988 and 1989 that found the native whitefish still dominating at 40% by numbers, but the ruffe comprising 24%. Adams & Tippett (1991) calculated that at that time ruffe accounted for 64% of whitefish egg predation, whereas its subsequent increased abundance has been reflected in changes in the diets of the loch's major piscivores pike (Adams, 1991), great cormorant (*Phalacrocorax carbo*) (Adams, 1994), grey heron (*Ardea cinerea*) (Adams & Mitchell, 1995) and Eurasian otter (*Lutra lutra*) (McCafferty, 2005). Changes in the reproductive strategy of the ruffe population with this increasing abundance, i.e. changes in size at maturity and size-related fecundity, suggest that food resources have become limiting (Devine et al., 2000). In turn, this situation increases the likelihood of significant harm occurring to the native fish community.

More recent and methodologically consistent surveys of Loch Lomond's fish community in inshore, offshore bottom and offshore surface habitats in 2004 (Winfield et al., 2006) and 2007 (Winfield et al., 2008a) found that the relative numerical contribution of whitefish to the fish community declined markedly ($\chi^2 = 12.110$, $df = 1$, $P < 0.001$) while that of the ruffe increased ($\chi^2 = 42.069$, $df = 1$, $P <$

0.001) (Fig. 2). In addition, the cyprinid roach (*Rutilus rutilus*) showed no significant change in relative abundance over the same time period ($\chi^2 = 0.054$, $df = 1$, $P > 0.10$). This latter finding is notable because although this species has been introduced to other large lakes in the U.K., Adams (op. cit.) considers it to be native to Loch Lomond.

Lough Neagh

Lough Neagh is situated (54°37' N, 6°25' W; altitude 10 m) in central Northern Ireland (Fig. 1). It comprises a single eutrophic basin (surface area: 38,179 ha, mean depth: 9 m) that has been strongly impacted by cultural eutrophication. Unique for the U.K., the lough supports commercial fisheries for European eel (*Anguilla anguilla*), Eurasian perch (*Perca fluviatilis*) (hereafter referred to as perch) and the nationally important pollan (*Coregonus autumnalis*).

In a review of the fish community, Kennedy & Vickers (1993) noted that although 21 species had been recorded, a paucity of historical data made the determination of their native or introduced status generally difficult. However, the roach is a notable exception because Went (1950) described its introduction to Ireland as live-bait in 1889 and Cragg-Hine (1973) reported its first record in the Lough Neagh catchment in 1970. In addition, in 1989 Winfield & Bean (1991) found a single common carp (*Cyprinus carpio*) in a small lake connected to Lough Neagh, although this species has not subsequently been recorded from the latter location (C. Harrod, Queen's University Belfast, pers. comm.).

In contrast, the roach population of Lough Neagh rapidly increased in distribution and abundance such that by the 1980s it had become a major component

of the lough's fish community (Winfield et al., 1993). During the same decade, the diets of the roach and nationally important overwintering tufted duck (*Aythya fuligula*) populations were found to show a high degree of overlap due to the common consumption of the mollusc *Valvata piscinalis* (Winfield & Winfield, 1994a; Winfield & Winfield, 1994b). Moreover, although the overwintering population of the piscivorous great crested grebe (*Podiceps cristatus*) had shown a positive relationship with increased roach abundance and Warke et al. (1994) considered that the increase in this cyprinid was causally related to an increase in cormorants in the area, roach abundance also showed a negative relationship with the numbers of overwintering tufted duck (Winfield et al., 1992). More recently, in a consideration of threats facing the pollan Harrod et al. (2001) noted possible food competition with roach. However, subsequent extensive sampling between 2006 and 2009 has shown that both species continue to form major components of the Lough Neagh fish community (C. Harrod, Queen's University Belfast, pers. comm.).

Llyn Tegid

Llyn Tegid is situated (52°53' N, 3°37' W; altitude 158 m) in the Snowdonia National Park of north Wales (Fig. 1). It comprises a single eutrophic basin (surface area: 415 ha, mean depth: 24 m) that has been impacted to some degree by cultural eutrophication.

In a review of studies on the fish community, Leah (2003) noted that a total of 16 fish species had been recorded including native populations of both salmonids and cyprinids and the nationally important whitefish (known locally as gwyniad) (*Coregonus lavaretus*). He also suggested a possible long-term decline in growth and

longevity of the whitefish, although early studies suffered from age determination problems, and he referred to unpublished semi-quantitative hydroacoustics data, which suggested no change in population density or distribution of this species between the 1960s and 1990s. Leah (op. cit.) also considered that introductions of rudd (*Scardinius erythrophthalmus*) and silver bream (*Blicca bjoerkna*), documented by Andrews (1977) and Grainger (1979) respectively, had probably arrived as live-bait in the 1970s. More notably, Leah (op. cit.) also reported that ruffe was first recorded in 1980 after which it increased rapidly in abundance between 1983 and 1992. At the same time, the native perch population declined, but this was considered probably to be due not to any interaction but to an ulcerative disease that had been responsible for perch declines elsewhere in the U.K. at that time. Leah (op. cit.) also referred to unpublished records and notes showing that roach have been present in significant numbers since at least the start of scientific studies in approximately 1939 and that perch and pike had both been culled by fishery managers in earlier decades.

Among the three species introductions described above, only that of ruffe has resulted in a significant change to the composition of the fish community in inshore and offshore habitats (Fig. 3). By 1991 (Winfield et al., 1996), this percid comprised a numerically substantial component and continued to do so in 2003 (Winfield et al., 2003) although its relative numerical contribution to the fish community had decreased over the intervening period ($\chi^2 = 63.643$, $df = 1$, $P < 0.001$). In contrast, neither whitefish ($\chi^2 = 0.060$, $df = 1$, $P > 0.10$) nor the at least long-established and possibly native roach ($\chi^2 = 0.576$, $df = 1$, $P > 0.10$) showed any significant relative change over the same period.

Windermere

Windermere is situated (54°21' N, 2°56' W; altitude 39 m) in the Lake District National Park of north-west England (Fig. 1). It comprises a mesotrophic north basin (surface area: 805 ha, mean depth: 25 m) and a eutrophic south basin (surface area: 672 ha, mean depth: 17 m), although nutrient levels in both basins have long histories of change as a result of cultural eutrophication and its management.

The fish community of Windermere, which comprises 16 species including the nationally important Arctic charr (*Salvelinus alpinus*), is undoubtedly the best studied lake fish community in the U.K. Much of the resulting extensive literature of the previous century was reviewed by Le Cren (2001), with many of the more recent studies being reviewed and extended by Winfield et al. (2008b) and Winfield et al. (2008c) which focussed on its Arctic charr and pike populations, respectively. In addition, Winfield & Durie (2004) reviewed the history of fish species introductions in Windermere and nearby lakes, to which individuals of a total of 12 native (brown trout (*Salmo trutta*), European minnow (*Phoxinus phoxinus*), perch, pike) and non-native (common bream, crucian carp, dace, grayling (*Thymallus thymallus*), rainbow trout (*Oncorhynchus mykiss*), roach, rudd and tench (*Tinca tinca*)) fish species are known to have been brought for the purpose of live-baiting. Given these recent extensive reviews, the present review will be largely restricted to the species introductions of roach and common bream.

Watson (1899) contains the first published reference to roach in Windermere, noting that the species was first seen in the late 1890s following its apparent introduction by visiting anglers live-baiting for pike. He also remarked that common bream was absent from the area. Roach subsequently remained a scarce and spatially restricted component of the fish community throughout almost all of the extensive

research reviewed by Le Cren (2001), which included a period of marked eutrophication in the lake's south basin. It was only in the 1990s, when the water temperature of Windermere showed a significant and sustained increase (Winfield et al., 2008b), that roach numbers started to increase. Periodic sampling of the fish communities of the two basins showed that by the early 2000s roach had become significant components of the fish communities of inshore and offshore surface habitats (Winfield et al., 2008b).

Additional and more consistent temporal information on roach, common bream and the native salmonids Arctic charr and brown trout in Windermere is available from long-term sampling of the lake's pike population conducted since the 1940s and described in detail by Winfield et al. (2008c). In addition to adult pike caught by the 64 mm bar mesh gill nets used in this programme, large roach, common bream, Arctic charr and brown trout in excess of 300 mm fork length are also sampled. For these two cyprinids and two salmonids, such size selection is very strongly biased to only the largest and oldest members of the populations. The first roach and common bream taken in this way were both recorded in 1999 in the lake's south basin, with the first records of roach and common bream in the north basin not occurring until 2005 and 2009, respectively. Temporal trends in these records expressed as catch-per-unit-effort (CPUE) from 1990 to 2009, together with corresponding patterns for Arctic charr and brown trout, are given in Fig. 4. In the north basin, neither roach (ANOVA, $F = 0.905$, $df = 19$, $P > 0.10$), common bream (ANOVA, $F = 3.000$, $df = 19$, $P > 0.10$), nor brown trout (ANOVA, $F = 0.021$, $df = 19$, $P > 0.10$) have shown any significant trend, but Arctic charr has shown a significant decline (ANOVA, $F = 16.078$, $df = 19$, $P < 0.001$). In contrast, significant changes have occurred for all species in the south basin where roach (ANOVA, $F = 4.612$, $df = 19$, $P < 0.05$),

common bream (ANOVA, $F = 11.312$, $df = 19$, $P < 0.01$) and brown trout (ANOVA, $F = 4.091$, $df = 19$, $P = 0.05822$) have increased and Arctic charr (ANOVA, $F = 8.808$, $df = 19$, $P < 0.01$) have decreased.

A correlation analysis for each permutation of native species, introduced species and lake basin is presented in Table 1, with data for native species augmented by time series for pike from the same gill-netting programme and for perch from a perch-specific trapping programme (see Winfield et al., 2008c). As expected from the temporal trends, no correlations were significant in the north basin. However, in the south basin there were three significant correlations; a positive correlation between common bream and perch, a negative correlation between roach and Arctic charr, and a positive correlation between roach and brown trout. In addition, over the same time period common bream and roach showed no correlation in the north basin (Kendall rank correlation, $\tau = -0.053$, $P > 0.10$) but a positive one in the south basin ($\tau = +0.416$, $P < 0.01$), Arctic charr and brown trout showed no correlation in the north basin ($\tau = +0.198$, $P > 0.10$) but a negative one in the south basin ($\tau = -0.318$, $p < 0.05$), and Arctic charr and pike showed no correlation in the north basin ($\tau = -0.097$, $P > 0.10$) but a negative one in the south basin ($\tau = -0.105$, $P > 0.10$).

The above trend and correlation analyses are necessarily simple and considerably restricted by available data. For example, they consider only changes in fish CPUE as a surrogate for abundance when in fact it is known that the pike population has also shown recent marked changes in distribution and individual condition (Winfield et al., 2008c). Other species may also have shown changes in these population features. In addition, the analyses do not take into account environmental factors such as the deoxygenation of Windermere's deep water (Jones et al., 2008) which is likely to have differential effects on different components of the

fish community. Perhaps most importantly, such analyses can only demonstrate association and not causality and so the construction of an elaborate interpretation of the observed relationships would be premature at this time. Nevertheless, they show that the recent marked expansion of roach and common bream in the south basin of Windermere has been accompanied by a decrease in the abundance of Arctic charr. Furthermore, they suggest that colonisation of the less eutrophic north basin is simply at an earlier stage and may develop in the same way as events in the south basin, although the ability of all of the major fish species to migrate between the basins further complicates the situation. The causalities of these marked population changes currently remain under study.

Cross-lake synthesis

This review has brought together case histories from the largest standing water body of each of the four component countries of the U.K., which together present a diverse array of environmental conditions (e.g. altitude 4 to 158 m, surface area 415 to 38,179 ha, mean depth 9 to 37 m, and oligotrophic to eutrophic conditions). Furthermore, and uniquely in a European context, each water body is completely or largely free from fisheries impacts which greatly simplifies the interpretation of observations in the context of invasive species.

The above sections of this review were presented using a simple lake-specific framework and with the exceptions of Winfield (1992), Winfield et al. (1996), Winfield & Durie (2004) and Winfield et al. (2007), cross-lake syntheses are largely absent from the U.K. lake fish introduction literature. This scarcity reflects both the historically and geographically limited nature of lake fish community monitoring in

the U.K. and the conceptual difficulty of drawing robust lessons from the study of one aspect of a number of diverse and complex lacustrine ecosystems. Nevertheless, some attempt will be made here to offer a cross-lake synthesis of the present findings.

The most striking observation from all four study lakes is that none of the recorded fish introductions were sanctioned by appropriate fisheries or other regulatory bodies and almost all of them probably arose from the release or escape of live-bait used by anglers fishing for pike. This common agency of introduction in turn probably contributed to the common taxonomic composition of the introductions, i.e. a strong dominance of cyprinids in general and roach in particular. The frequent introduction of the percid ruffe through live-baiting may be unexpected given that the highly spined and cryptic nature of this species presumably make it a relatively unattractive prey for pike, but it is extremely robust which facilitates its easy transport by anglers using just simple containers (Winfield & Durie, 2004). To some degree, all four study lakes also share a common taxonomy of their native communities in the form of substantial components of coregonids, i.e. whitefish, or salmonids, i.e. Arctic charr and brown trout. Consequently, in each lake a native salmonid-containing assemblage has met with an introduced cyprinid-containing assemblage.

This contrasting taxonomy of natives and invaders is accompanied by contrasting environmental requirements of the two groups, with the native salmonids thriving in oligotrophic and cold conditions and the invading cyprinids preferring more eutrophic and warmer surroundings. Thus, any movement towards the latter conditions as a result of cultural eutrophication and/or climate change is likely to accelerate the development and potentially ultimate dominance of introduced cyprinids. For example, had Lough Neagh not been subjected to extreme eutrophication and had instead retained its original conditions which once supported

Arctic charr (Kennedy & Vickers, 1993), then its waters may not have become dominated by introduced roach. However, eutrophication alone does not necessarily induce an expansion of introduced roach as shown by the case history of Windermere. In this lake, significant nutrient enrichment of its south basin and a more limited enrichment of its north basin during the middle part of the last century did not result in any significant population increase. Such expansion only occurred in the last decade of the previous century after water temperatures increased, although it has been both more pronounced and more rapid in the more eutrophic south basin. The history of Windermere also shows that an introduced population can withstand a prolonged period of relatively inhospitable conditions, before increasing dramatically when conditions become more suitable. Further increases in temperatures in the U.K. resulting from climate change (see Jenkins et al., 2008) may 'wake' more currently dormant introduced fish populations, particularly in northern parts of the country.

Conclusion

Introductions of fish species have now occurred in all of the largest lakes of Scotland (Loch Lomond), Northern Ireland (Lough Neagh), Wales (Llyn Tegid) and England (Windermere). None of these introductions were sanctioned by appropriate fisheries or other regulatory bodies and almost all of them probably arose from the release or escape of live-bait used by anglers fishing for pike. Although some have been historic, the rate of new introductions has accelerated markedly in recent decades. Of the 10 introduced (or alien or non-native) species documented above, four of them (common bream, gudgeon, roach and ruffe) have established abundant populations. Although causality has not been demonstrated, two of these species (roach and ruffe)

have apparently caused or currently threaten harm, supporting the hypothesis that at least some of these introductions have become invasive. Such apparently negative effects have been seen in three (Loch Lomond, Lough Neagh and Windermere) of the largest lakes of each of the four component countries of the U.K. As noted by Boon & Bean (in press), prevention is by far the most preferred management tool for invasive species and for fish in large lakes it is effectively the only feasible option. Consequently, formal consent is now required throughout the U.K. for fish species introductions and live-baiting is banned on many lakes (Winfield & Durie, 2004). However, such regulations need effective public support if they are to be successful and Bremner & Park (2007) observed that such help is greatest when individuals are well informed. Public awareness and education are crucial tools in the management of invasive species and environmental scientists must play their part in such activities.

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References

- Adams, C. E., 1991. Shift in pike, *Esox lucius* (L.), predation pressure following the introduction of ruffe, *Gymnocephalus cernuus* (L.) to Loch Lomond. *Journal of Fish Biology* 38: 663-667.
- Adams, C. E. & R. Tippet, 1991. Powan, *Coregonus lavaretus* (L.), ova predation by newly introduced ruffe, *Gymnocephalus cernuus* (L.), in Loch Lomond, Scotland. *Aquaculture and Fisheries Management* 22: 239-246.
- Adams, C. E., 1994. The fish community of Loch Lomond: its history and its rapidly changing status. *Hydrobiologia* 290: 91-103.
- Adams, C. E. & J. Mitchell, 1995. The Response of a Grey Heron *Ardea cinerea* Breeding Colony to Rapid Change in Prey Species. *Bird Study* 42: 44-49.
- Andrews, C. R., 1977. The occurrence of rudd (*Scardinius erythrophthalmus*) in Llyn Tegid. *Nature in Wales* 15: 31-50.
- Boon, P.J. & C. W. Bean, in press. Freshwater non-native species - prevention, control or eradication? In Baxter, J. M. & C. A. Galbraith (eds), *Species Management: Challenges and Solutions for the 21st Century*. TSO Scotland, Edinburgh.
- Bremner, A. & K. Park, 2007. Public attitudes to the management of invasive non-native species in Scotland. *Biological Conservation* 139: 306-314.
- Colautti, R. I. & H. J. MacIsaac, 2004. A neutral terminology to define 'invasive' species. *Diversity and Distributions* 10: 135-141.
- Copp, G. H., Bianco, P. G., Bogutskaya, N. G., Erős, T., Falka, I., Ferreira, M. T., Fox, M. G., Freyhof, J., Gozlan, R. E., Grabowska, J., Kováč, V., Moreno-Amich, R.,

- Naseka, A. M., Peňáz, M., Povž, M., Przybylski, M., Robillard, M., Russell, I. C., Stakėnas, S., Šumer, S., Vila-Gispert, A. & C. Wiesner, 2005. To be, or not to be, a non-native freshwater fish. *Journal of Applied Ichthyology* 21: 242-262.
- Cragg-Hine, D., 1973. Coarse fish and fishery management in Northern Ireland. *Proceedings of the 6th British Coarse Fish Conference*. University of Liverpool, Liverpool: 52-59.
- Devine, J. A., Adams, C. E. & P. S. Maitland, 2000. Changes in reproductive strategy in the ruffe during a period of establishment in a new habitat. *Journal of Fish Biology* 56: 1488-1496.
- Etheridge, E. C. & C. E. Adams, 2008. Bream (*Abramis brama*), a new fish species confirmed in Loch Lomond. *Glasgow Naturalist* 25: 93-94.
- Grainger, R. C., 1979. The occurrence of silver bream (*Blicca bjoerkna* (L.)) in Llyn Tegid. *Nature in Wales* 16: 250-251.
- Harrod, C., Griffiths, D., McCarthy, T. K. & R. Rosell, 2001. The Irish pollan, *Coregonus autumnnalis*: options for its conservation. *Journal of Fish Biology* 59 (Supplement A): 339-355.
- Jenkins, G. J., Perry, M. C. & M. J. Prior, 2008. The climate of the United Kingdom and recent trends. Met Office Hadley Centre, Exeter, U.K. 117 pp.
- Jones, I. D., Winfield, I. J. & F. Carse, 2008. Assessment of long-term changes in habitat availability for Arctic charr (*Salvelinus alpinus*) in a temperate lake using oxygen profiles and hydroacoustic surveys. *Freshwater Biology* 53: 393-402.
- Kennedy, G. J. A. & K. U. Vickers, 1993. The fish of Lough Neagh, Part A: A historical and taxonomic perspective of the fish fauna of Lough Neagh. In

- Wood, R. B. & R. V. Smith (eds), Lough Neagh. Kluwer Academic Publishers, Dordrecht: 381-395.
- Leah, R. T., 2003. The ecology and conservation of the fish of Llyn Tegid. In Gritten, R. H., Duigan, C. A. & H. Millband (eds), Llyn Tegid Symposium: The Ecology, Conservation and Environmental History of the Largest Natural Lake in Wales. University of Liverpool, Liverpool: 115-138.
- Le Cren, E. D., 2001. The Windermere perch and pike project. *Freshwater Forum* 15: 3-34.
- McCafferty, D. J., 2005. The dietary response of otters (*Lutra lutra*) to introduced ruffe (*Gymnocephalus cernuus*) in Loch Lomond, Scotland. *Journal of Zoology* 266: 255-260.
- McNeely, J. A., Mooney, H. A., Neville, L. E., Schei, P. & J. K. Waage (eds), 2001. A Global Strategy on Invasive Alien Species. International Union for Conservation of Nature and Natural Resources, Gland. 50 pp.
- Warke, G. M. A., Day, K. R., Greer, J. E. & R. D. Davidson, 1994. Cormorant (*Phalacrocorax carbo* [L]) populations and patterns of abundance at breeding and feeding sites in Northern Ireland, with particular reference to Lough Neagh. *Hydrobiologia* 279-280: 91-100.
- Watson, J., 1899. The English Lake District Fisheries. George Routledge and Sons Ltd, London.
- Went, A. E. J., 1950. Notes on the introduction of some freshwater fish into Ireland. *Journal of the Irish Department of Agriculture* 47: 1-8.
- Winfield, I. J. & C. W. Bean, 1991. First record of the carp, *Cyprinus carpio* L., in the Lough Neagh catchment (Northern Ireland). *Journal of Fish Biology* 38, 629-630.

- Winfield, I. J., 1992. Threats to the lake fish communities of the U.K. arising from eutrophication and species introductions. *Netherlands Journal of Zoology* 42: 233-242.
- Winfield, I. J., Winfield, D. K. & C. M. Tobin, 1992. Interactions between the roach, *Rutilus rutilus*, and waterfowl populations of Lough Neagh, Northern Ireland. *Environmental Biology of Fishes* 33: 207-214.
- Winfield, I. J., Tobin, C. M. & C. R. Montgomery, 1993. Ecological studies of the fish community. In Wood, R. B. & R. V. Smith (eds), *Lough Neagh*. Kluwer Academic Publishers, Dordrecht: 451-471.
- Winfield, D. K. & I. J. Winfield, 1994a. Possible competitive interactions between overwintering tufted duck (*Aythya fuligula* (L.)) and fish populations of Lough Neagh, Northern Ireland: evidence from diet studies. *Hydrobiologia* 279/280: 377-386.
- Winfield, I. J. & D. K. Winfield, 1994b. Feeding ecology of the diving ducks pochard (*Aythya ferina*), tufted duck (*A. fuligula*), scaup (*A. marila*) and goldeneye (*Bucephala clangula*) overwintering on Lough Neagh, Northern Ireland. *Freshwater Biology* 32: 467-477.
- Winfield, I. J., Fletcher, J. M. & P. R. Cubby, 1994. Status of Rare Fish, Project Record Volume 1. Unpublished report. National Rivers Authority, Bristol. 244 pp.
- Winfield, I. J., Adams, C. E. & J. M. Fletcher, 1996. Recent introductions of the ruffe (*Gymnocephalus cernuus*) to three United Kingdom lakes containing *Coregonus* species. *Annales Zoologici Fennici* 33: 459-466.
- Winfield, I. J., Fletcher, J. M. & J. B. James, 2003. Gwyniad translocation project: Phase One – A condition assessment of the potential donor population in Llyn

- Tegid. CCW Contract Science Report No. 597. Countryside Council for Wales, Bangor. 52 pp.
- Winfield, I. J. & N. C. Durie, 2004. Fish introductions and their management in the English Lake District. *Fisheries Management and Ecology* 11: 1-7.
- Winfield, I. J., Fletcher, J. M. & J. B. James, 2006. SCM of fish in standing waters (Phase II). Unpublished report. Scottish Natural Heritage, Clydebank. 40 pp.
- Winfield, I. J., Fletcher, J. M. James, J. B., Duigan, C., Bean, C. W. & N. C. Durie, 2007. Long-term case histories of ruffe (*Gymnocephalus cernuus*) introductions to four U.K. lakes containing native vendace (*Coregonus albula*) or whitefish (*C. lavaretus*) populations. *Advances in Limnology* 60: 301-309.
- Winfield, I. J., Fletcher, J. M. & J. B. James, 2008a. SCM of fish in standing waters 2007/2008 (Phase I). Unpublished report. Scottish Natural Heritage, Clydebank. 36 pp.
- Winfield, I. J., Fletcher, J. M. & J. B. James, 2008b. The Arctic charr (*Salvelinus alpinus*) populations of Windermere, U.K.: population trends associated with eutrophication, climate change and increased abundance of roach (*Rutilus rutilus*). *Environmental Biology of Fishes* 83: 25-35.
- Winfield, I. J., James, J. B. & J. M. Fletcher, 2008c. Northern pike (*Esox lucius*) in a warming lake: changes in population size and individual condition in relation to prey abundance. *Hydrobiologia* 601: 29-40.

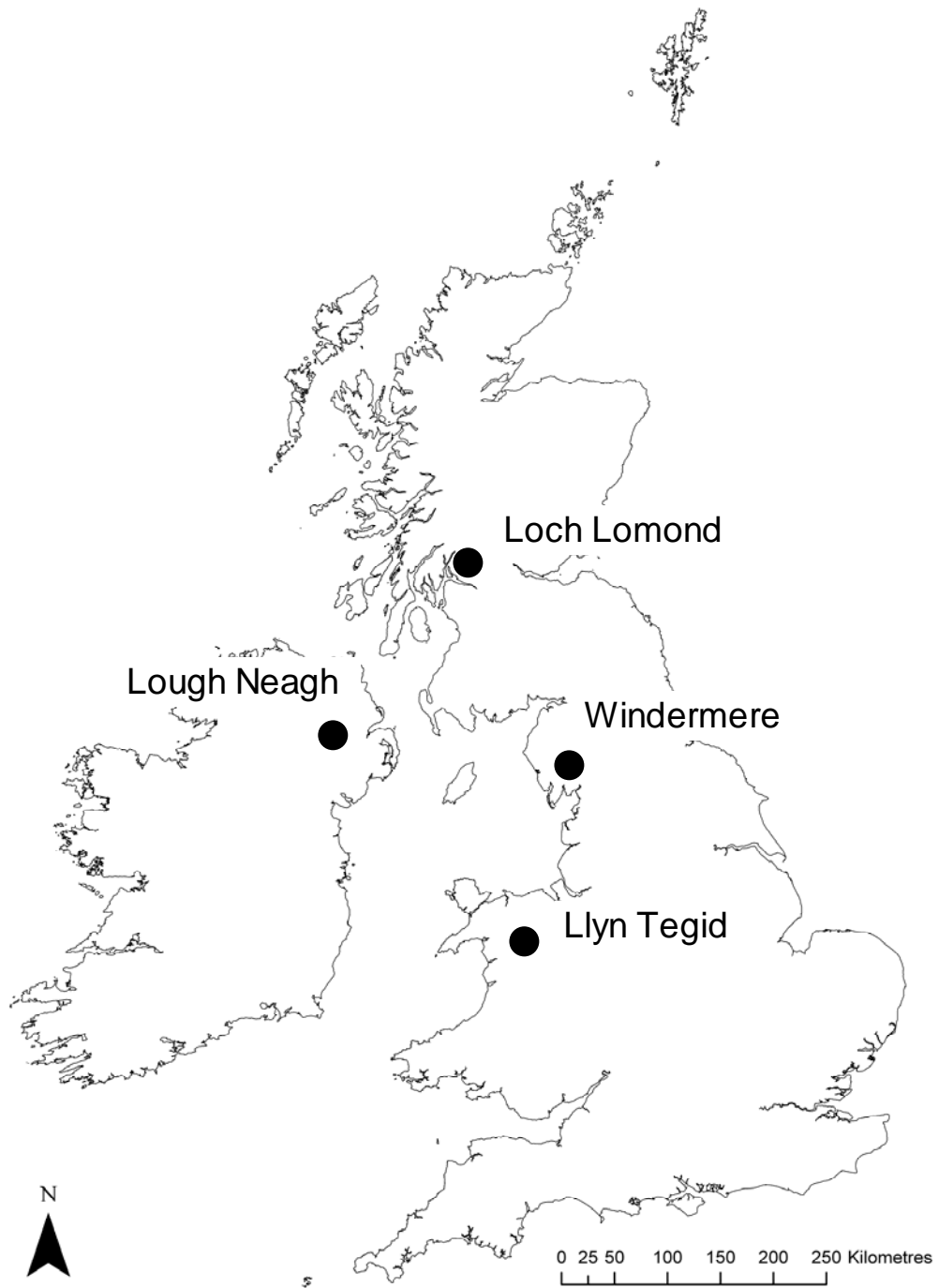
Figure Captions

Figure 1. The approximate locations of the study sites of Loch Lomond (Scotland), Lough Neagh (Northern Ireland), Llyn Tegid (Wales) and Windermere (England) within the U.K.

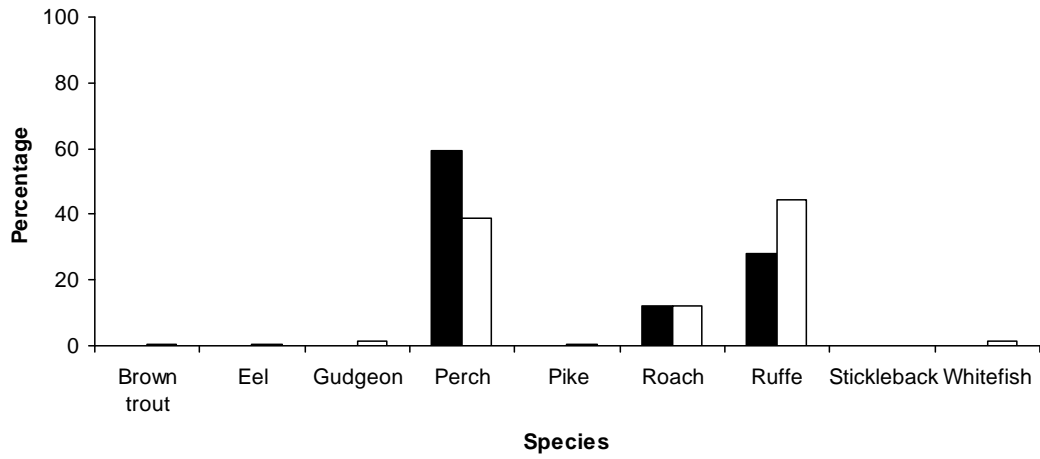
Figure 2. Fish community compositions for inshore, offshore bottom and offshore surface habitats of Loch Lomond in 2004 (N = 135 fish, closed bars) and 2007 (N = 321 fish, open bars). Redrawn from Winfield et al. (2006) and Winfield et al. (2008a). Scientific names of all fish species are given in the main text, with the exception of that of the three-spined stickleback (given as stickleback in the figure) which is *Gasterosteus aculeatus*.

Figure 3. Fish community compositions for inshore, offshore bottom and offshore surface habitats (2003 only) of Llyn Tegid in 1991 (N = 174 fish, closed bars) and 2003 (N = 179 fish, open bars). Redrawn from Winfield et al. (1994) and Winfield et al. (2003). Scientific names of all fish species are given in the main text.

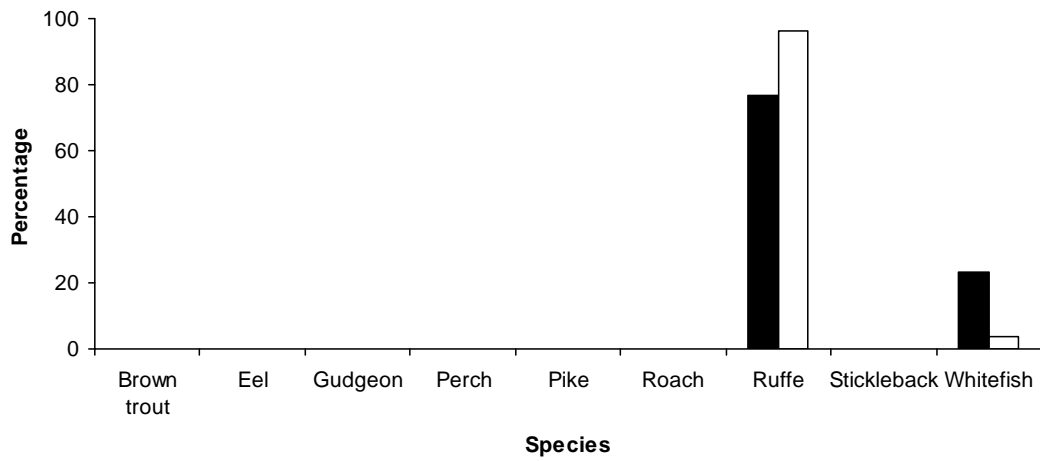
Figure 4. Catch-per-unit-effort (CPUE) for native Arctic charr and brown trout (closed symbols and continuous lines) and introduced common bream and roach (open symbols and broken lines) in the north and south basins of Windermere from 1990 to 2009. Scientific names of all fish species are given in the main text.



Inshore



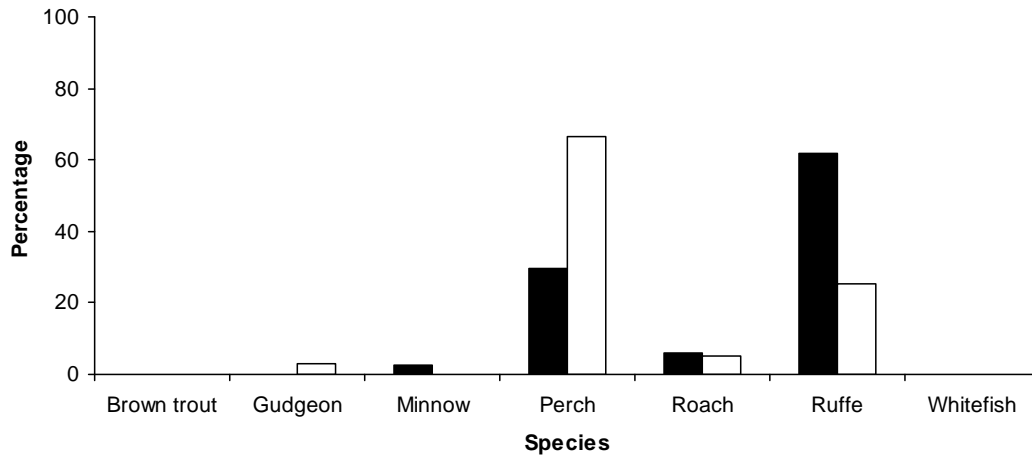
Offshore bottom



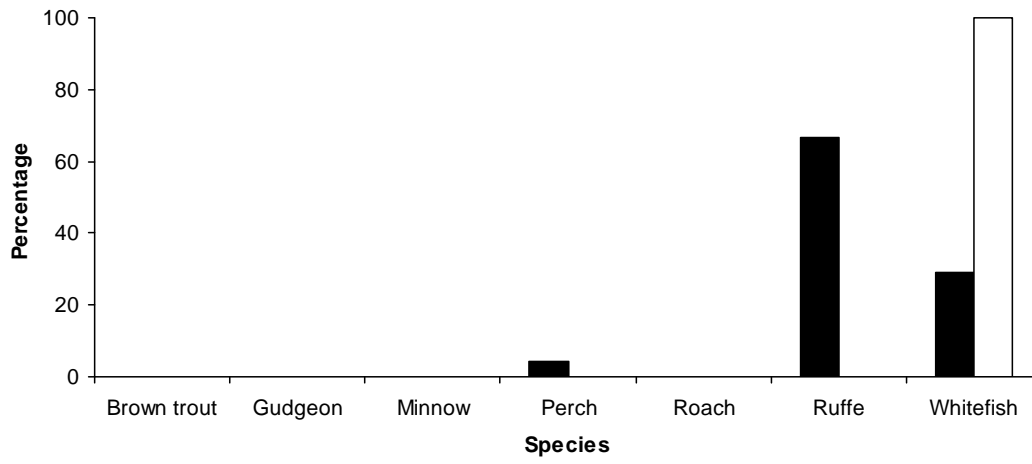
Offshore surface



Inshore



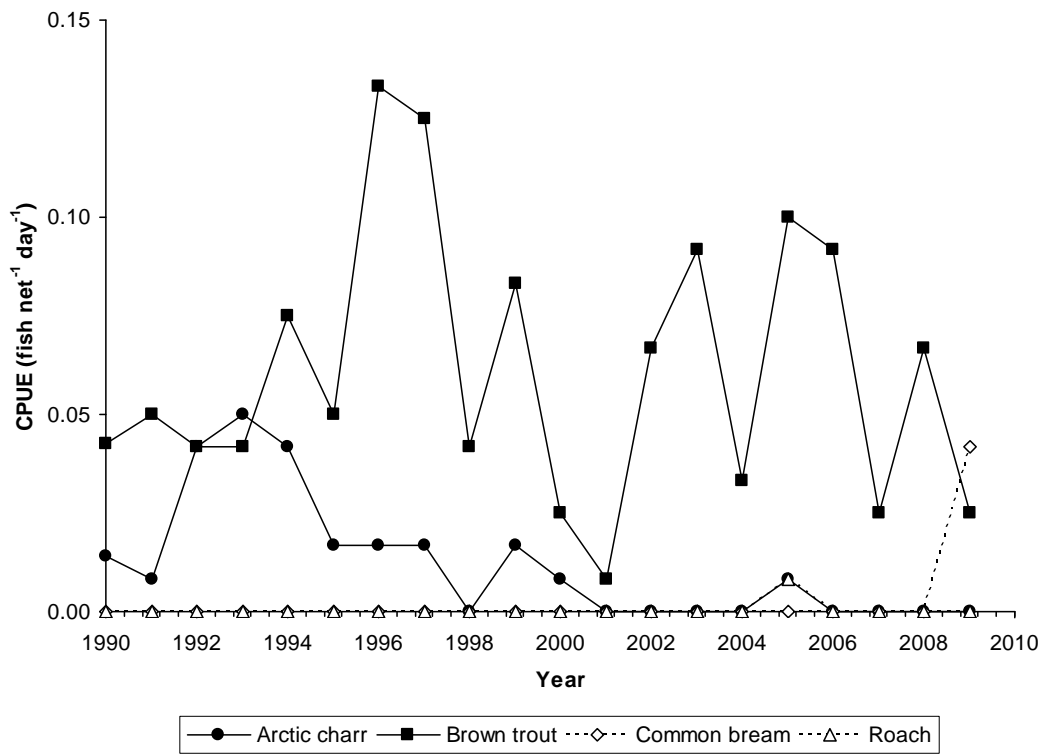
Offshore bottom



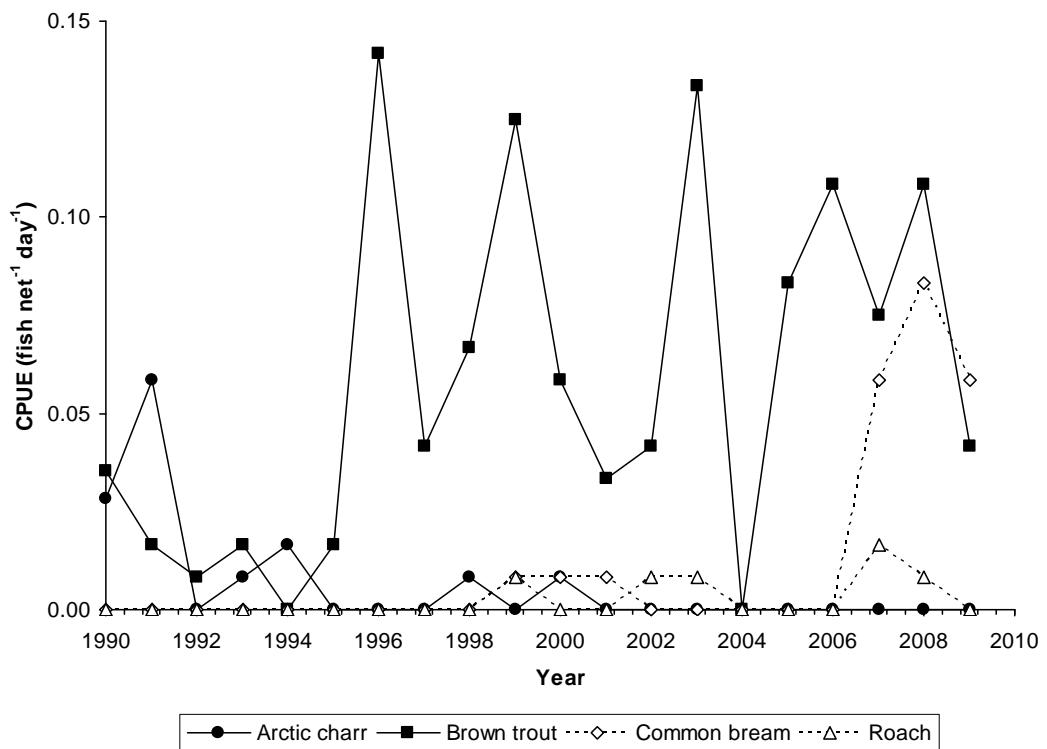
Offshore surface



North



South



Table

Table 1. Kendall rank correlation coefficients (τ , with their statistical significances P) between catch-per-unit-efforts of introduced common bream and roach and those of native Arctic charr, brown trout, perch and pike in the north and south basins of Windermere from 1990 to 2009. Scientific names of all fish species are given in the main text. Coefficients significant at the 0.05 level are indicated by *.

Species pair	Basin	τ	P
Common bream / Arctic charr	North	-0.210	0.195
Common bream / Brown trout	North	-0.256	0.115
Common bream / Perch	North	+0.150	0.356
Common bream / Pike	North	-0.283	0.081
Common bream / Arctic charr	South	-0.230	0.156
Common bream / Brown trout	South	+0.243	0.134
Common bream / Perch	South	+0.365	0.025*
Common bream / Pike	South	-0.045	0.780
Roach / Arctic charr	North	+0.019	0.906
Roach / Brown trout	North	+0.256	0.115
Roach / Perch	North	-0.316	0.051
Roach / Pike	North	+0.150	0.356
Roach / Arctic charr	South	-0.344	0.034*
Roach / Brown trout	South	+0.400	0.014*
Roach / Perch	South	+0.302	0.063
Roach / Pike	South	-0.235	0.160