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Recent introductions of the ruffe (*Gymnocephalus cernuus*) to three United Kingdom lakes containing *Coregonus* species

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Although a native of the United Kingdom fish fauna, the distribution of the ruffe (*Gymnocephalus cernuus*) was, until recently, largely restricted to lowland England. However, it has now been introduced, probably by anglers fishing with ruffe as bait, to numerous localities elsewhere in the UK. This expansion has provoked concern because it has included introductions to lakes containing nationally-rare *Coregonus albula* or *C. lavaretus*. This paper documents the history of these introductions to Loch Lomond (Scotland), Llyn Tegid (Wales) and Bassenthwaite Lake (England), describes pertinent aspects of the local ecology of ruffe, and discusses implications for the continued survival of the coregonids.

1. Introduction

The ruffe *Gymnocephalus cernuus* (L.) is a small, bottom-dwelling and largely benthivorous member of the family Percidae found throughout most of Europe and northern Asia (Craig 1987). Although for many years, and in contrast to other percids, the ruffe has been considered to have little or no value for commercial or recreational fisheries, recent range expansions have raised concerns over potential negative effects that this species may have on other fisheries and on the conservation of rare fish species. In a recent bibliography of the ruffe, Winfield and McCulloch (1995) recorded 23 publications concerned with introductions of this species, of which one was published in the 1960s, six in the 1980s and 16 in the 1990s.

In mainland Europe, introductions have been reported from Lake Geneva (Matthey 1966), Italy (Chiara 1986), Norway (Kålås 1995) and Lake Constance (Rösch & Schmid 1996). The ruffe has also been accidentally transported across the Atlantic Ocean in the ballast water of freighters and introduced to Lake Superior in the Great Lakes of North America (Simon & Vondruska 1991). In most of these cases, the arrival of the ruffe has concerned those responsible for the management of local fisheries (e.g. Leach & Lewis 1991).

Although the ruffe is a member of the native UK fish fauna, it was until recently largely restricted to lowland England. However, within the last two decades it has been introduced, probably by anglers using live ruffe as bait, to numerous localities including other parts of England, Scotland and Wales. While the scarcity of lacustrine commercial fisheries in the UK has precluded significant fisheries concern, this expansion has provoked concern on wider conservation grounds because it has included introductions to three out of only nine lakes containing unexploited but nationally-rare vendace *Coregonus albula* (L.) or whitefish *C. lavaretus* (L.) (known locally in England, Scotland and Wales as schelly, powan and gwyniad, respectively). This paper documents three case histories of these introductions to Loch Lomond in Scotland and Llyn Tegid in Wales, which contain whitefish, and Bassenthwaite Lake in England, which is one of only two remaining UK lakes containing vendace. It also briefly describes the present local ecology of ruffe, and discusses implications for the continued survival of the coregonid populations in these lakes.

2. Threats potentially posed to *Coregonus* populations by ruffe introductions

The threats posed by ruffe introductions to native *Coregonus* populations include both predation and competition. However, predation by ruffe on free-swimming fish has rarely been documented. Although Huusko and Sutela (1992) reported some consumption of larval vendace by ruffe, they also found that it was not as great as that by minnows *Phoxinus phoxinus* (L.) or perch *Perca fluviatilis* L. Predation on the egg stage by ruffe, however, appears to be of much greater importance. Lacustrine *Coregonus* species are broadcast spawners, typically distributing eggs in the littoral zone during winter where they incubate, unprotected and vulnerable to predation for several weeks or months (e.g. Adams & Tippett 1991). Low water temperatures during the incubation period afford some protection from most poikilothermic predators through temperature-depressed feeding rates. However, this is not the case for ruffe which can maintain high activity at low temperatures (Bergman 1987), an ability which has been shown to translate into a higher predation rate on incubating whitefish eggs than that exacted by whitefish or trout *Salmo trutta* L. (Adams & Tippett 1991). Sterligova and Pavlovskiy (1985) and Sterligova *et al.* (1988) have both concluded that egg predation by ruffe can have a significant negative impact on adult whitefish abundance, although predation by other species and siltation of the spawning ground also were implicated in determining whitefish population size by Sterligova *et al.* (1988).

Introduced ruffe populations typically become a major feature of the fish community, potentially competing with other species for their major prey, benthic macroinvertebrates. In a series of experimental studies, Bergman (1991) and Bergman and Greenberg (1994) showed that ruffe can depress the abundance of benthic macroinvertebrates and so outcompete perch for this food resource. The ability of ruffe to remain active at low water temperatures mentioned above in a predation context may also confer on them a competitive advantage over other species and allow them to exploit all parts of thermally-stratified lakes (Bergman 1987). Although the ruffe is usually benthivorous, the work of Bergman and Greenberg (1994) has also shown that this species can feed efficiently on cladoceran zooplankton in the laboratory. In the context of introduced populations, it is relevant to note that Kålås (1995) found an introduced population of ruffe in Norway to feed largely on cladocerans, rather than on benthic macroinvertebrates as is more typical for the species. Such a diet clearly raises the possibility of competition with planktivorous vendace or whitefish populations.

3. The introduction of ruffe to Loch Lomond

Loch Lomond (Fig. 1) is the largest area (70.27 km^2) of fresh water in Scotland and has a maximum depth of 190 m. It is composed of three main basins, all of which are oligotrophic although its southern area verges on being mesotrophic. The ruffe was first recorded in the loch from the inshore zone of the middle basin in 1982 by Maitland *et al.* (1983). This constituted a first record of the species in Scotland and was attributed to discarded or escaped live bait of anglers fishing for pike *Esox lucius* L. Over the next five years, the ruffe population, monitored by recording the numbers of individuals entrapped by a local water abstraction system, increased dramatically (Maitland & East 1989). By 1989 (Fig. 2), ruffe accounted for 23% of 1 296 fish taken in survey gill nets (monofilament, approximately 1.8 m deep and 40 m long with 8 panels of equal length of bar mesh sizes 19, 22, 25, 30, 35, 40, 46 and 50 mm. For further sampling details see Adams, 1994).

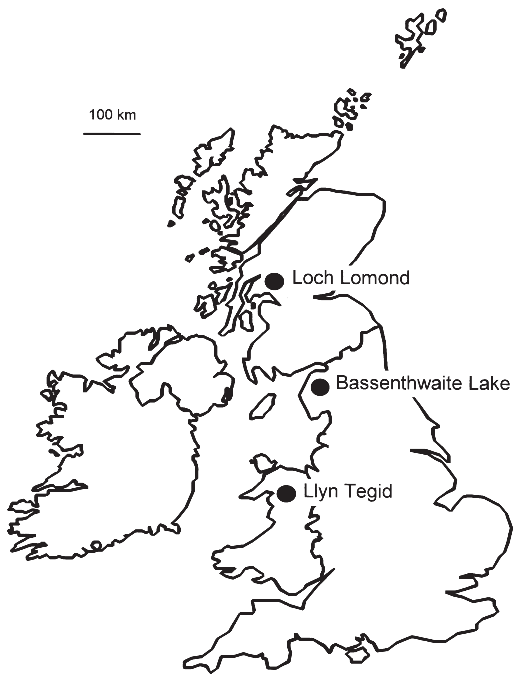


Fig. 1. Locations within the United Kingdom of Loch Lomond, Llyn Tegid and Bassenthwaite Lake.

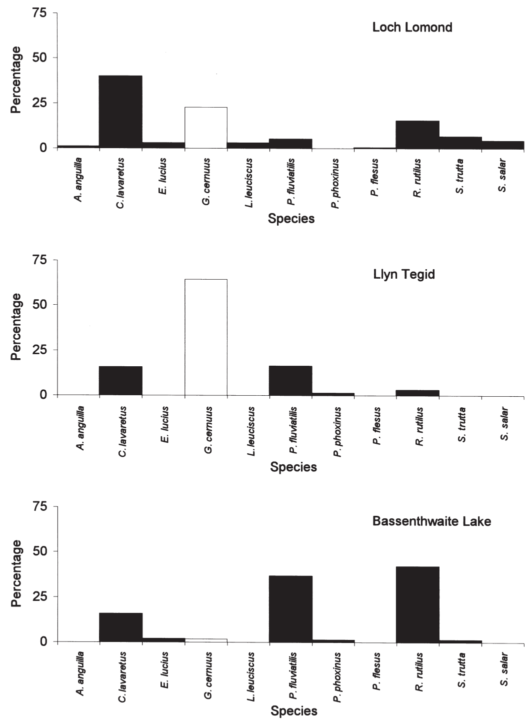
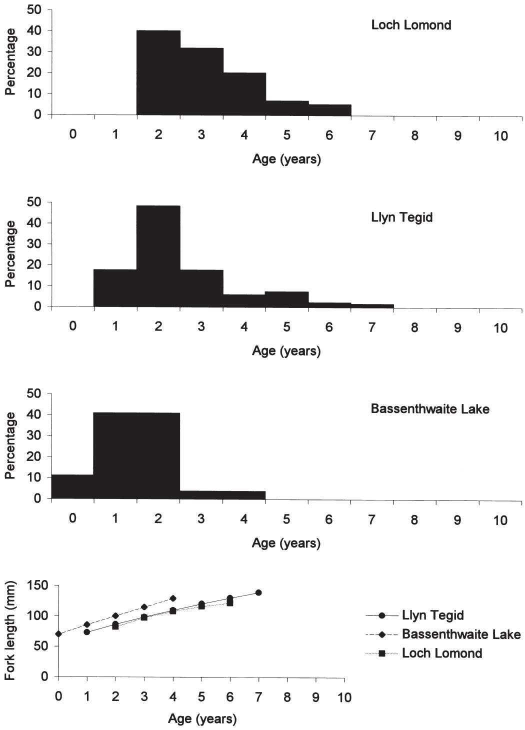


Fig. 2. Fish community compositions by number for Loch Lomond (N = 1 296), Llyn Tegid (N = 174) and Bassenthwaite Lake (N = 167) in 1988–89, 1991 and 1991, respectively. In each case, the introduced ruffe population is shown as an open bar. Full species names are *Anguilla anguilla*, *Coregonus albula*, *Coregonus lavaretus*, *Esox lucius*, *Gymnocephalus cernuus*, *Leuciscus leuciscus*, *Perca fluviatilis*, *Phoxinus phoxinus*, *Pleuronectes flesus*, *Rutilus rutilus*, *Salmo trutta* and *Salmo salar*.

A subsample of 60 ruffe from the above survey, which ranged from 75 to 125 mm in fork length and from 6 to 28 g in weight, was examined in detail. Individuals were aged by examination of otoliths, and their age frequency distribution and a fitted von Bertalanffy growth curve (L_∞ = 137 mm, K = 0.3319 and t_0 = – 0.7853. r^2 = 0.959) are given in Fig. 3. Fish ranged in age from 2 to 6 years and showed a smooth decline in abundance with age which is characteristic of a consistently-recruiting population. The diet composition of 15 ruffe (size range 30 to 122 mm) from the middle basin in July and August 1987 (Fig. 4) was dominated by Isopoda (46%, exclusively *Asellus* sp.) and Diptera (29%, largely chironomid larvae). The macroinvertebrate-dominated diet of ruffe showed little overlap with that of whitefish which was dominated by planktonic Cladocera, particularly *Bosmina* sp. (Pomeroy 1991). However, two predation-related effects of the ruffe introduction have been observed.

Firstly, examination of the diet of ruffe and other fish during the whitefish winter incubation period has shown that ruffe consume large numbers of eggs. Adams and Tippett (1991) found that ruffe consumed 64% of all whitefish eggs taken by the fish community and fed at a rate similar to that observed during summer months, although the overall effects of this new source of whitefish egg mortality were not determined. Secondly, a more indirect effect has also been recorded. Between 1989 and 1991, the diet was determined of the three most abundant piscivores in Loch Lomond, pike (Adams 1991), grey heron (*Ardea cinerea* (L.)) (Adams & Mitchell 1995) and cormorant (*Phalacrocorax carbo* (L.)) (Adams 1994). For the former two species, data were subsequently compared with equivalent data collected before the introduction of the ruffe. Ruffe were found to dominate the recent diets of all three species, which for pike represented a shift of predation pressure away from the whitefish which was formerly the most important prey of this piscivore.



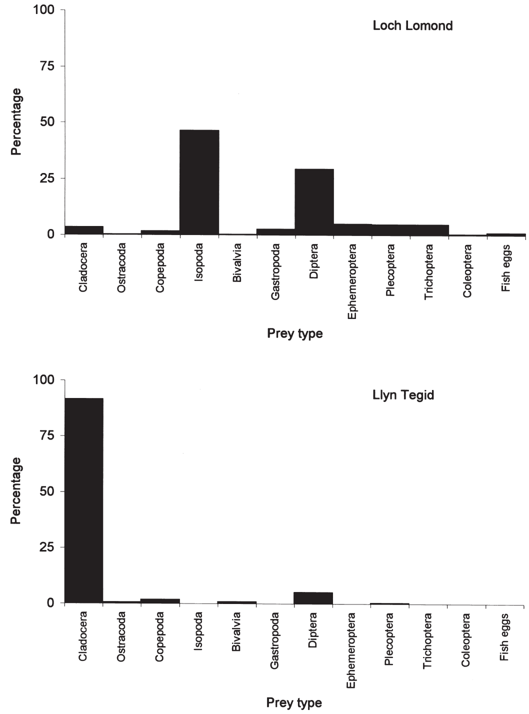


Fig. 4. Diet composition (percentage by prey numbers) of ruffe in the middle basin of Loch Lomond ($N = 15$) in July and August, 1987 and in Llyn Tegid ($N = 20$) in June, 1991.

Unfortunately, the status of the whitefish population in the 1990s has not been fully quantified. It was undoubtedly still abundant at the time of the above community study at the end of the 1980s, several years after the arrival of the ruffe, although the longevity of whitefish in Loch Lomond (up to 10 years, see Brown *et al.* (1991)) will tend to mask any immediate effects. In a static life-table analysis of Loch Lomond whitefish performed on data collected through the 1980s, Brown *et al.* (1991) concluded that adult mortality rates and fecundity had not changed since at least the 1960s, but admitted that their data were insufficient to assess the possible impact of the ruffe introduction and suggested that its effect on recruitment into the vulnerable 0 to 1 year-class may be critical.

4. The introduction of ruffe to Llyn Tegid (Lake Bala)

Llyn Tegid (Fig. 1), also known as Lake Bala, is the largest natural area (4.486 km^2) of fresh water in Wales and has a maximum depth of 40 m in its single mesotrophic basin. The ruffe was first recorded from this lake in June and July, 1991 during a multi-site gill net survey (monofilament, approximately 1.5 m deep and 40 m long with 14 panels of equal length of bar mesh sizes 6, 8, 10, 12, 16, 22, 25, 30, 33, 38, 43, 50, 60 and 75 mm) of the local whitefish population (Winfield *et al.* 1995, 1996). The gill net survey provided data on ruffe age and growth, diet, and relative abundance. Full sampling and processing details are given in Winfield *et al.* (1995). Either immediately on return to the laboratory or more usually after being partially thawed from storage at – 20°C, ruffe were measured (fork length, mm), the left opercular bones removed for ageing purposes with a nominal birthday of 1 May, and, for a sub-sample of fish, the stomach was dissected from the body cavity and placed in 4% formalin solution to await diet analysis.

Ruffe dominated the Llyn Tegid fish community (Fig. 2) where they accounted for 64% of 174 fish and were present in all inshore and offshore sites surveyed. With further sampling in December, 1991 and January and July, 1992, a total of 143 individuals was collected, which ranged in size from 49 to 142 mm *FL* and from 1 to 43 g. The age-frequency distribution and a fitted von Bertalanffy growth curve (L_∞ = 252 mm, K = 0.0774 and t_0 = – 3.4170. r^2 = 0.685) for 137 of these ruffe (six individuals could not be aged due to damage to their opercular bones) are presented in Fig. 3. Fish ranged in age from 1 to 7 years, with all intervening age groups represented in the population and 2 year-old fish being by far the most abundant. Analysis of diet composition of 20 ruffe (size range 72 to 139 mm) from June,1991 indicated that Cladocera, which were exclusively *Bosmina* sp., was by far the most important prey type and accounted for 91% by number (Fig. 4).

The ruffe has undoubtedly established itself with a diverse age structure and good growth in the fish community of Llyn Tegid, although it is difficult to determine just when the initial introduction occurred given the scarcity of previously published information. While quantitative accounts of past community composition are unavailable, the fact that Coles (1981) mentioned the presence of minnows, perch, trout and rudd *Scardinius erythrophthalmus* (L.) suggests that ruffe were not present in the mid 1970s, which is consistent with the observation of the present study of ruffe up to 7 years of age suggesting an introduction sometime in the 1980s. Although Coles (1981) also failed to mention roach *Rutilus rutilus* (L.), Jones (1953) did find this species, but not ruffe, in the lake in the 1950s.

The observed zooplankton-dominated diet of ruffe in June, 1991 can be compared with the diet of whitefish from July of the same year described by Winfield *et al.* (1995). Whitefish diet was divided almost equally into planktonic and non-planktonic prey types, the latter being largely the mollusc *Pisidium* sp. with a smaller component of chironomid larvae. Furthermore, the planktonic component of the whitefish diet contained *Daphnia* sp. but not *Bosmina* sp., in contrast to those of two other planktivorous whitefish populations in Red Tarn and Ullswater of the English Lake District (Winfield *et al.* 1995). In an investigation of the diet of whitefish in the early 1960s, Haram and Jones (1971) found the diet during July to be dominated by non-planktonic prey, particularly *Pisidium* spp. and chironomid larvae, although zooplankton were taken in this and subsequent summer months. Unfortunately, these authors did not subdivide the prey type 'Cladocera' so it is unknown whether or not *Bosmina* spp. were taken at that time. The finding of the present study of the importance of *Bosmina* sp. in the June diet of the recently-established ruffe population invites the hypothesis that the latter may be outcompeting the whitefish for this prey type.

However, coexistence between ruffe and whitefish is apparently occurring in Llyn Tegid where the latter remains abundant and shows consistent recruitment as evidenced by an equitable age structure of specimens collected in 1991 (Winfield *et al.* 1996). But, in view of the relatively long life cycles of both species, this conclusion of coexistence may yet prove to be premature.

5. The introduction of ruffe to Bassenthwaite Lake

Bassenthwaite Lake (Fig. 1) in the English Lake District has a surface area of 5 284 km^2 and a maximum depth of 19 m. It is composed of a single basin and has shown signs of increasing eutrophication in recent years, including intermittent deepwater hypoxia and the apparent siltation of inshore areas (see Winfield *et al.* 1996). The ruffe was first recorded from this lake in April 1991 during a multi-site, gill net survey (monofilament survey gill net as described above, with subsequent use of a multifilament survey net 1.5 m deep and 40 m long with seven panels of equal length of bar mesh sizes 16, 22, 25, 30, 33, 38 and 43 mm) of the local vendace population (Winfield *et al.* 1994, 1995, 1996). Sampling and processing details were as described above for the Llyn Tegid survey, although because of very small sample sizes, no ruffe were examined for diet composition.

Ruffe comprised only a minor component of the community in 1991 (Fig. 2) when they accounted for 2% of 167 fish. Because of their low numbers, catches of ruffe from April 1991 to November 1992 were pooled to give a total sample size of 27 individuals ranging in size from 66 to 153 mm *FL*, and from 4 to 50 g. The age-frequency distribution and a fitted von Bertalanffy growth curve (L_∞ = 843 mm, K = 0.0210 and t_0 = – 4.3430. r^2 = 0.450) are presented in Fig. 3. Fish ranged in age from 0 to 4 years, with a dominance by 1 and 2 year old fish. Clearly, the growth curve of the ruffe population has not yet approached an asymptote, resulting in a poor fit of the von Bertalanffy growth model.

The ruffe is probably a very recent addition to the Bassenthwaite Lake fish community and was probably introduced in the late 1980s. In a study of the Bassenthwaite Lake vendace population in 1986 and 1987, Mubamba (1989) failed to catch any ruffe, although he did record the first occurrence of roach which has subsequently established itself as a major component of the fish community (Winfield *et al.* 1996). Since 1991, the ruffe has been recorded from both shallow and deep areas of this lake (Winfield *et al.* 1994) and in May 1995 comprised 90% of 202 individuals taken in gill nets designed to sample yearling fish (mesh sizes of 6, 8 and 10 mm). Like the roach, this species is now an established component of the fish community.

In contrast to the whitefish of Llyn Tegid, the status of the vendace of Bassenthwaite Lake in the early 1990s is very poor. Although individuals of this almost exclusively planktivorous population show good condition and growth, the population as a whole shows extremely inconsistent recruitment (Winfield *et al.* 1996). While it may be postulated that the recent introduction of the ruffe is responsible for this situation, several factors suggest that this argument is seriously flawed. Firstly, similar patterns of good individual condition and growth, but poor population recruitment of vendace, were also observed by Mubamba (1989), several years before the apparent arrival of the ruffe and at the time of the first record of roach in this lake. As noted above, Bassenthwaite Lake has also apparently been affected in recent decades by increasing eutrophication, which may in itself be responsible for the observed inconsistent vendace recruitment of the 1980s and 1990s through the siltation of spawning grounds. It is notable that the only other UK vendace population in the nearby oligo-mesotrophic Derwentwater has not been subject to eutrophication and has displayed consistent recruitment through the 1980s (Mubamba 1989) and 1990s (Winfield *et al.* 1996).

6. Conclusions

The present study has brought together case histories of ruffe introductions to Loch Lomond, Llyn Tegid and Bassenthwaite Lake. In all three cases, the mode of introduction remains unproven, but anglers fishing for pike with live ruffe as bait are the most likely mechanism. Three of the four mainland UK lakes which hold *Coregonus* species and pike (Loch Lomond, Llyn Tegid, and Bassenthwaite Lake) have received ruffe introductions in recent years, while the remaining lakes which hold *Coregonus* species but not pike (Loch Eck, Brotherswater, Haweswater, Red Tarn and Ullswater) have remained free from introductions. The one lake which does not fit this pattern is Derwentwater which contains vendace and pike but not ruffe. However, even without a specific introduction, this lake will probably receive ruffe in the near future by their migration along the River Derwent, which connects Derwentwaters to Bassenthwaite Lake only 5.5 km away and 5.7 m lower in altitude.

Whatever their means of introduction, all three ruffe populations have become established to form major components of their respective communities, even though the three lakes encompass contrasting oligotrophic (Loch Lomond), mesotrophic (Llyn Tegid) and eutrophic (Bassenthwaite Lake) conditions. Indeed, observed differences in age-freqency distributions and growth curves may simply reflect differences in the stage of colonisation, with the most-recently introduced population of Bassenthwaite Lake showing the least number of age classes and a near-linear growth curve. Ruffe were found in both inshore and offshore habitats down to a depth of approximately 20 m in Loch Lomond, Llyn Tegid and Bassenthwaite Lake during the present study, overlapping spatially with Loch Lomond whitefish in both areas (see also Adams 1994), and with adult Bassenthwaite Lake vendace and Llyn Tegid whitefish in offshore areas (see also Winfield *et al.* 1995). Such common spatial distributions raise the possibility of competitive interactions.

Conclusive evidence of competition between the introduced ruffe populations and native coregonids requires demonstrations of diet overlap, limited food supplies, effects of predation on prey abundances, and ideally an experimental manipulation. Results of the present study indicated no appreciable diet overlap between ruffe and whitefish or vendace, although it could be argued that the consumption of *Bosmina* sp. by ruffe in Llyn Tegid has influenced the whitefish population of this lake to consume only daphniid cladocerans, in contrast to the whitefish populations of Loch Lomond (Pomeroy 1991), Red Tarn and Ullswater (Winfield *et al.* 1995) which feed extensively on bosminids. It is pertinent to note that in Loch Eck and Haweswater, the only two UK lakes where whitefish coexist with planktivorous Arctic charr *Salvelinus alpinus* (L.), whitefish diets contain few Cladocera and are instead dominated by benthic macroinvertebrates (Pomerory 1991, Winfield *et al.* 1995, respectively). Although a cladoceran-dominated diet of ruffe is unusual, it has also been recorded for an introduced population in Norway (Kålås 1995) and adds a new dimension to the threats potentially posed by the arrival of this species.

The evidence for predation-based effects of ruffe introductions on whitefish is far stronger, although it is difficult to assess quantitatively the net effects of increased egg mortality and decreased adult mortality arising from shifts in predation pressure. Furthermore, quantification of the latter factor is complicated by a lack of information concerning the effect of ruffe establishment on piscivore local abundance. If predator populations increase, then predation pressure on whitefish may also increase, even if there is a partial diet shift of piscivores to ruffe.

Complete answers to the above questions require long-term data, which are very limited in the absence of coregonid fisheries in the UK, and experimental work. Nevertheless, the very absence of fisheries in these lakes means that any apparent effects of ruffe introductions cannot be erroneously attributed to such activities, as they may be in the large lakes of Europe and the Great Lakes of North America. In this context, studies in the UK can make a valuable contribution to an international understanding of the consequences of ruffe introductions.

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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.

— 1994: The fish community of Loch Lomond, Scotland – its history and rapidly changing status. — Hydrobiologia 290: 91–102.

Adams, C. E. & Mitchell, J. 1995: The response of a Grey Heron Ardea cinerea, breeding colony to rapid change in prey species. — Bird Study 42: 44–49.

Adams, C. E. & Tippett, R. 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.

Bergman, E. 1987: Temperature-dependent differences in foraging ability of two percids, Perca fluviatilis and Gymnocephalus cernuus. — Environmental Biology of Fishes 19: 45–53.

— 1991: Changes in abundance of two percids, Perca fluviatilis and Gymnocephalus cernuus, along a productivity gradient: Relations to feeding strategies and competitive abilities. — Canadian Journal of Fisheries and Aquatic Sciences 48: 536–545.

Bergman, E. & Greenberg, L. A. 1994: Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. — Ecology 75: 1233–1245.

Brown, E. A. R., Finnigan, N. & Scott, D. B. C. 1991: A life table for powan, Coregonus lavaretus (L.) in Loch Lomond, Scotland: a basis for conservation strategy. — Aquatic Conservation 1: 183–187.

Chiara, G. 1986: (First record of Acerina (Gymnocephalus) cernua L. (Osteichthyes Perciformes) in Italy). — Quaderni Ente Tutela Pesca, Udine 59–60. (In Italian.)

Coles, T. F. 1981: The distribution of perch, Perca fluviatilis L. throughout their first year of life in Llyn Tegid, North Wales. — Journal of Fish Biology 18: 15–30.

Craig, J. F. 1987: The Biology of Perch and Related Fish. — Croom Helm, London.

Haram, J. & Jones, J. W. 1971: Some observations on the food of the gwyniad Coregonus clupeoides pennantii Valenciennes of Llyn Tegid (Lake Bala) N Wales. — Journal of Fish Biology 3: 287–295.

Huusko, A. & Sutela, T. 1992: Fish predation on vendace (Coregonus albula L.) larvae in Lake Lentua, Northern Finland. — Pol. Arch. Hydrobiol. 39: 381–391.

Jones, J. W. 1953: Part I. The scales of roach. Part II. Age and growth of the trout, grayling, perch and roach of Llyn Tegid (Bala) and the roach of the River Birkett. — Fishery Investigations London Series I 5: 1–18.

Kålås, S. 1995: The ecology of ruffe, Gymnocephalus cernuus (Pisces: Percidae) introduced to Mildevatn, western Norway. — Environmental Biology of Fishes 42: 219–232.

Leach, J. H. & Lewis, C. A. 1991: Fish introductions in Canada – provincial views and regulations. — Canadian Journal of Fisheries and Aquatic Sciences 48: 156–161.

Maitland, P. S. & East, K. 1989: An increase in numbers of ruffe, Gymnocephalus cernua (L.), in a Scottish loch from 1982 to 1987. — Aquaculture and Fisheries Management 20: 227–228.

Maitland, P. S., East, K. & Morris, K. H. 1983: Ruffe, Gymnocephalus cernua (L.), new to Scotland, in Loch Lomond. — Scottish Naturalist 1983: 7–9.

Matthey, G. 1966: Deux especes nouvelles de la faune du Leman: Dreissena polymorpha Pallas (Mollusca, Dreissenidae) Acerina cernua (L), (Pisces, Percidae). — Bulletin de la Societé Vaudoise des Sciences Naturelles 69: 229–232.

Mubamba, R. 1989: The ecology of the coregonid fishes in the English Lake District. — Ph.D.-thesis, University of Wales.

Pomeroy, P. P. 1991: A comparative assessment of temporal variation in diet of powan, Coregonus lavaretus (L.), from Loch Lomond and Loch Eck, Scotland, UK. — Journal of Fish Biology 38: 457–478.

Rösch, R. & Schmid, W. 1996: Ruffe (Gymnocephalus cernuus L.), newly introduced into Lake Constance: preliminary data on population biology and possible effects on whitefish (Coregonus lavaretus L.). — Ann. Zool. Fennici 33: 467–471.

Simon, T. P. & Vondruska, J. T. 1991: Larval identification of the ruffe, Gymnocephalus cernuus (Linnaeus) (Percidae: Percini), in the St. Louis River Estuary, Lake Superior drainage basin, Minnesota. — Canadian Journal of Zoology 69: 436–442.

Sterligova, O. P. & Pavlovskiy, S. A. 1985: Consumption of whitefish, Coregonus lavaretus, eggs by ruffe, Gymnocephalus cernua, and invertebrates. — Journal of Ichthyology 25: 166–169.

Sterligova, O. P., Pavlovskij, S. A. & Komulainen, S. F. 1988: Reproduction of coregonids in the eutrophicated Lake Sjamozero, Karelian ASSR. — Finnish Fisheries Research 1988: 485–488.

Winfield, I. J. & McCulloch, I. D. 1995: An indexed bibliography of the ruffe Gymnocephalus cernuus (L.) (Percidae): a carnivorous freshwater fish threatening rare fishes following recent introductions in Britain, Europe and North America. — Freshwater Biological Association Occasional Publication No. 31.

Winfield, I. J., Fletcher, J. M. & Cubby, P. R. 1994: Ecology of the vendace, Coregonus albula, in Bassenthwaite Lake. — Institute of Freshwater Ecology Report to North West Water Limited.

Winfield, I. J., Fletcher, J. M., Cubby, P. R. & Cragg-Hine, D. 1995: The fish communities of the Coregonus albula and C. lavaretus lakes of England and Wales. — National Rivers Authority R & D Note 423.

Winfield, I. J., Cragg-Hine, D., Fletcher, J. M. & Cubby, P. R. 1996: The conservation ecology of Coregonus albula and C. lavaretus in England and Wales, UK. — Aquatic Sciences. (In press.)