

The Ruffe Population of Loch Lomond, Scotland: Its Introduction, Population Expansion, and Interaction with Native Species

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ABSTRACT

The ruffe (*Gymnocephalus cernuus*), never before recorded in Scotland, was discovered in Loch Lomond in 1982. During the 1980s ruffe became well established and expanded its range throughout the loch and through the slow-flowing influent and effluent tributaries, only being excluded from tributaries with high flow rates. Recoveries of fish entrained at a pumping station, abstracting water for domestic supply, provide a measure of the rate of population expansion between 1982 and 1996 and the current status of ruffe in Loch Lomond. Between 1982 and 1992 the ruffe population grew exponentially. Since 1992 the population appears to have stabilized to some extent but at a very high level. Gill-netting surveys conducted throughout Loch Lomond have shown that the high abundance of ruffe recorded at this site is representative of a large population throughout the loch. The diet of ruffe feeding in Loch Lomond differed both spatially and seasonally. Although prey choice was diverse, it was primarily composed of benthic macro-invertebrates, but at times included underyearling fish (including ruffe) and eggs of other fish species. The most important of these is the powan (*Coregonus lavaretus*), a broadcast spawner of national conservation value. To examine the possibility of dietary overlap with perch (*Perca fluviatilis*) and brown trout (*Salmo trutta*), the diets of these three species were compared. The data showed very little evidence of overlap in diet, suggesting that feeding resource competition between ruffe and trout and ruffe and perch does not occur between adults of these species. Evidence for the disruption of predator-prey relations by introduced ruffe is reviewed. Ruffe are now the primary prey species for cormorants (*Phalacrocorax carbo*), herons (*Ardea cinerea*), and northern pike (*Esox lucius*) feeding in Loch Lomond. Calculations based on predator population sizes and consumption rates suggest that potentially up to 17 metric tons of ruffe, representing over 2 million individuals, may be being consumed annually by these predator species. The effects on native fish of this shift in diet in these predator species is discussed, as is the ability of ecologists to predict the impact of invasions of new species in aquatic communities.

Index words: Fish invasions, population expansion, resource competition.

INTRODUCTION

Loch Lomond (Fig. 1) is the largest area of water in Great Britain (71 km²) and also one of the deep est (190 m). The loch has a distinct dual character, the northern basin is long, narrow, and deep, whereas the southern basin is broad and shallow, with many islands. A small mid-basin, intermediate in physical character, separates these two larger basins. The catchment (781 km²) is mainly rough moorland to the north, whereas to the south the soils are richer and farmed more intensively (Smith *et al.* 1981). The nutrient status of the loch is regarded as oligotrophic, with total phosphorus loads ranging from 0 to around 50 µg/L, total oxidized nitrogen 100 to 660 µg/L, and Secchi depths of 2.3 to 7 m (Best and Trail 1994).

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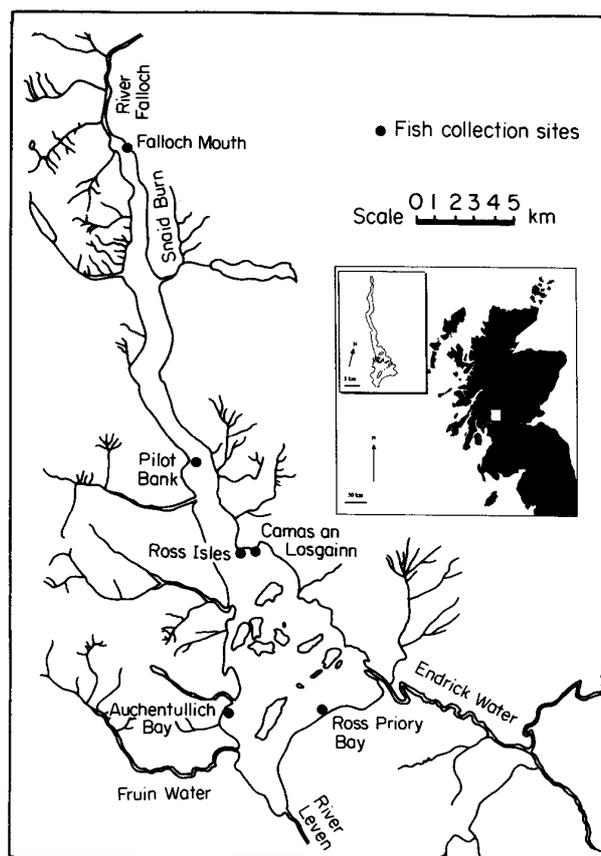


FIG. 1. Loch Lomond showing key sampling locations.

The species composition of the fish community of Loch Lomond appears to have been relatively stable in recent centuries and, up until the 1970s (Maitland 1972), was composed entirely of native species, 15 in total (Table 1). However, during the 1980s, 5 new species appeared in the loch and there are now 20 fish species established there (Adams *et al.* 1990, Adams and Maitland 1991, Adams and Mitchell 1992, Adams 1994, Grant *et al.* 1997). The first record of one of these, the ruffe (*Gymnocephalus cernuus*), was the first sighting of this species in Scotland (Maitland and East 1989). Although it is likely that the ruffe has been indigenous to south-east England since the last ice-age, historical evidence suggests that it was originally absent from northern England, Wales, and Scotland. Apparently using the canal systems, however, it gradually spread into the English Midlands and eastern parts of Wales during the 19th century (Maitland 1972). In the last two decades it has dispersed much further west and north, into north Wales, Cumbria, and Scotland (Loch Lomond), apparently being transported and then released by anglers who used it as live bait for fishing for northern pike (*Esox lucius*, Maitland 1991). Concern over the spread of ruffe in the U.K. has focused on the fact that it has now established populations in three lakes which are important for *Coregonus* species- Llyn Tegid (Wales), Bassenthwaite Lake (Cumbria, England), and Loch Lomond (Scotland) (Winfield *et al.* 1996). The goals of this paper are to: a) describe the introduction, establishment, growth, and current status of ruffe in Loch Lomond—data will be presented on captures of fish over 14 years from a pumping station on Loch Lomond and supplemented with netting data and a review of published (but inaccessible) records of fish collections for the catchment. b) examine the evidence for aquatic community change resulting from the introduction of ruffe to Loch Lomond—original data will be presented on the potential for feeding competition with two other common fish species and the evidence for other interactions within the ecosystem will be reviewed.

METHODS

Loch Lomond Ruffe Population Establishment, Growth, and Current Status

Systematic, continuous monitoring of fish populations from Loch Lomond began in 1981 utilizing information obtained from fish entrained at a pumping station at Ross Priory, on the south shore of Loch Lomond (Fig. 1). Water is drawn from Loch Lomond near Ross Priory (Fig. 1) through an intake placed 229 m from the edge of the

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loch and 2.6 m below the lowest recorded loch level. After passing through cowls, provided to prevent the formation of vortices, the water flows through twin 1.7 m diameter pipes to a coarse screening chamber. It then passes through mechanically operated, 8 mm mesh, band screens before being chlorinated and pumped to further treatment works elsewhere. A maximum yield of 455 megalitres is available from the loch, but the current level of pumping rarely takes this amount. Fish and other debris (mainly filamentous algae and loose macrophytes) are trapped on the band screens and washed into large baskets of the same mesh. Since late 1981, fish have been removed daily and placed in a bin of formalin nearby. They are collected from this on a monthly basis and subsequently washed, sorted, identified, and counted.

TABLE 1. A comprehensive list of native and introduced fish species with established populations in Loch Lomond and their representation in entrainment catches at the Ross Priory pumping station, expressed as a percentage of catches of all fish between January 1982 and December 1996. Total N = 81,870 fish, N/R = Not Represented.

Native Species	Scientific Name	Percentage of catch at pumping station 1982–1996
sea lamprey	<i>Petromyzon marinus</i>	N/R
river lamprey	<i>Lampetra fluviatilis</i>	0.004
brook lamprey	<i>Lampetra planeri</i>	0.001
atlantic salmon	<i>Salmo trutta</i>	0.02
brown/sea trout	<i>Salmo trutta</i>	0.10
powan	<i>Coregonus lavaretus</i>	0.07
northern pike	<i>Esox lucius</i>	0.004
minnow	<i>Phoxinus phoxinus</i>	0.02
roach	<i>Rutilus rutilus</i>	0.10
stone loach	<i>Barbatulus barbatulus</i>	N/R
eel	<i>Anguilla anguilla</i>	1.6
three-spined stickleback	<i>Gasterosteus aculeatus</i>	16.3
nine-spined stickleback	<i>Pungitius pungitius</i>	0.01
eurasian perch	<i>Perca fluviatilis</i>	2.3
flounder	<i>Platichthys flesus</i>	0.006
Introduced species		
crucian carp	<i>Carassius carassius</i>	N/R
gudgeon	<i>Gobio gobio</i>	0.002
chub	<i>Leuciscus cephalus</i>	N/R
dace	<i>Leuciscus leuciscus</i>	0.01
ruffe	<i>Gymnocephalus cernuus</i>	79.4

The fish caught on the screens at the pumping station do not accurately reflect their relative abundance within the community; for example one of the commonest fish collected in gill nets in Loch Lomond, the powan (*Coregonus lavaretus*), makes up only a very small proportion of the fish caught on screens. However, this method does provide a good within-species comparative index for some species that are represented in catches. Because of the comparative rarity of data relating to the changes which take place when a new species is introduced to an old established community (Maitland 1972), these data are considered in some detail here.

To examine the range expansion of ruffe within Loch Lomond, gill-netting was carried out at five littoral zone sites. Multi-panel, monofilament gill-nets (1.8 x 40 m, 19-50 mm half-mesh size) were set on the bottom on two occasions each month from November 1988 to October 1989 (full sampling details in Adams and Tippett 1991).

Interactions With Other Fish

To examine the diet of ruffe and to determine the potential for feeding competition between ruffe and other fish species with similar feeding habits, the stomach contents of ruffe from two sites and during two seasons was examined. Gill nets were set overnight to collect fish at Ross Priory (in the south basin of the loch) and 8 km away at the Ross Peninsula (in the mid-basin, see Fig. 1) during July and August 1987. To look for seasonal variation in diet, ruffe were also collected by gill-net at the Ross Peninsula site in January and February during the winters of 1989 and 1990. Ruffe caught were in the size range 31 to 118 mm fork-length. After collection, all fish were returned to the laboratory and initially frozen. Subsequently they were defrosted, the stomach contents removed, blotted dry, and weighed, and the number of each prey item counted under a low power stereo microscope.

TABLE 2. Numbers of fish caught on trash screens at the Ross Priory Pumping Station on Loch Lomond between 1982 and 1996.

Year	Ruffe	Three-spined stickleback	Perch	Eel	All other species	Total
1982	17	41	144	4	7	209
1983	47	82	98	2	14	243
1984	406	104	181	24	15	730
1985	1,551	797	270	19	14	2,651
1986	798	348	27	69	20	1,262
1987	1,280	58	20	27	13	1,398
1988	3,015	130	219	14	14	3,392
1989	835	82	45	6	20	988
1990	2,347	337	57	16	8	2,765
1991	5,547	165	37	115	18	5,882
1992	13,828	2,188	324	524	37	16,901
1993	9,428	3,400	128	210	47	13,213
1994	4,820	1,621	49	42	10	6,542
1995	9,803	2,489	102	129	33	12,556
1996	11,296	1,539	149	129	25	13,138

To attempt to assess the likelihood of competition between ruffe and perch (*Perca fluviatilis*) (see Bergman 1990) the summer diet of ruffe was compared with the diet of perch feeding at the same site, at the same time of year, in 1985 (perch size range 101 to 151 mm fork-length) and in 1977 (fork-length 130 to 180 mm) prior to the arrival of ruffe in Loch Lomond, (Giles and Tippett 1987). In addition, the diet of ruffe and brown trout (*Salmo trutta*) (brown trout size range 181 to 308 mm fork-length) caught at the same time, at the same site during the winters of 1989 and 1990 was compared.

To quantify the degree of resource overlap, Schoenherr's C_s index was calculated as:

$$C_{xy} = 1 - 0.5(\sum |p_{xi} - p_{yi}|) \quad (1)$$

(Schoenherr 1970).

Interactions With Fish Predators

To examine the possibility that the establishment of a large population of ruffe in Loch Lomond had influenced the relationship between predators of fish and their native prey, the diet of the three principal predators of fish feeding on Loch Lomond was examined between 1989 and 1991.

The diet of gray herons (*Ardea cinerea*) was determined during the 1990 breeding season by examining discards and regurgitations below nesting sites. This study repeated a study carried out in 1978, prior to the arrival of ruffe in Loch Lomond, and enabled a comparison of heron diet before and after the arrival of ruffe (Adams and Mitchell 1995).

The diet of northern pike was determined by stomach contents analysis of gill net captures in 1990. Data from this study were also compared with a similar study carried prior to the arrival of ruffe (Adams 1991).

Cormorant (*Phalacrocorax carbo*) diet was examined by an analysis of otoliths recovered from pellets deposited at a cormorant roost site between April 1990 and March 1991 (Adams *et al.* 1994). There had been no diet studies of this species carried out prior to the arrival of ruffe.

RESULTS

Ruffe Population and Range Expansion

Annual catches from 1982 to 1996 (Tables 1, 2) clearly show that four fish species (eel (*Anguilla anguilla*), three-spined stickleback (*Gasterosteus aculeatus*), perch, and ruffe) have consistently dominated catches of fish on the trash screens at the Ross Priory pumping station, making up over 99% of total catches over these years.

No ruffe had been seen in Loch Lomond prior to 1982 but 17 were entrained that year, followed by 47 in 1983 and 406 in 1984. With some variation from year to year, the general very rapid upward trend continued until 1992

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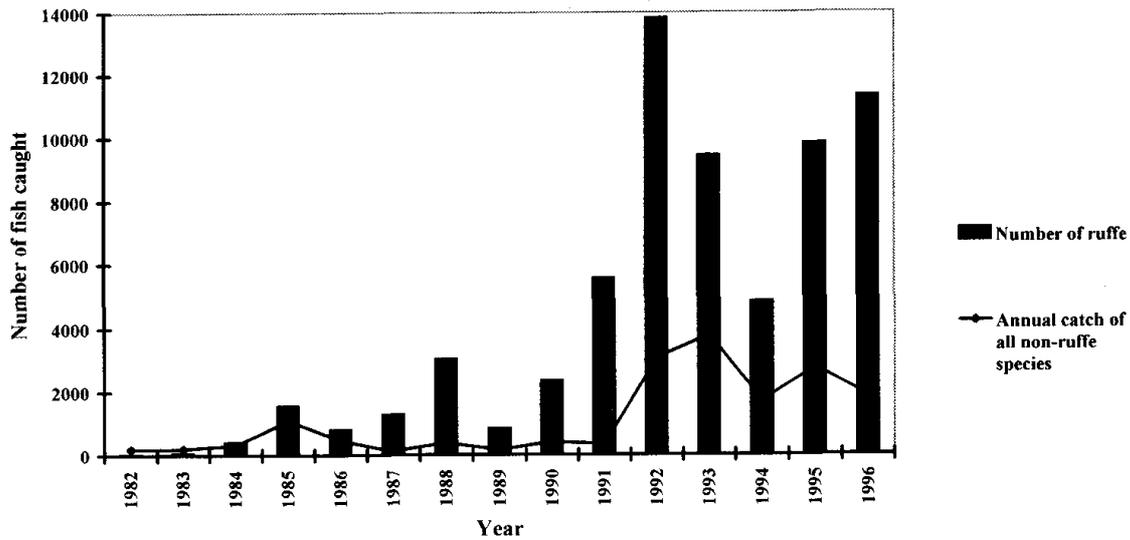


FIG. 2. Annual catches of ruffe and all other fish species combined, on trash screens at the Ross Priory Pumping Station, Loch Lomond between 1982 and 1996.

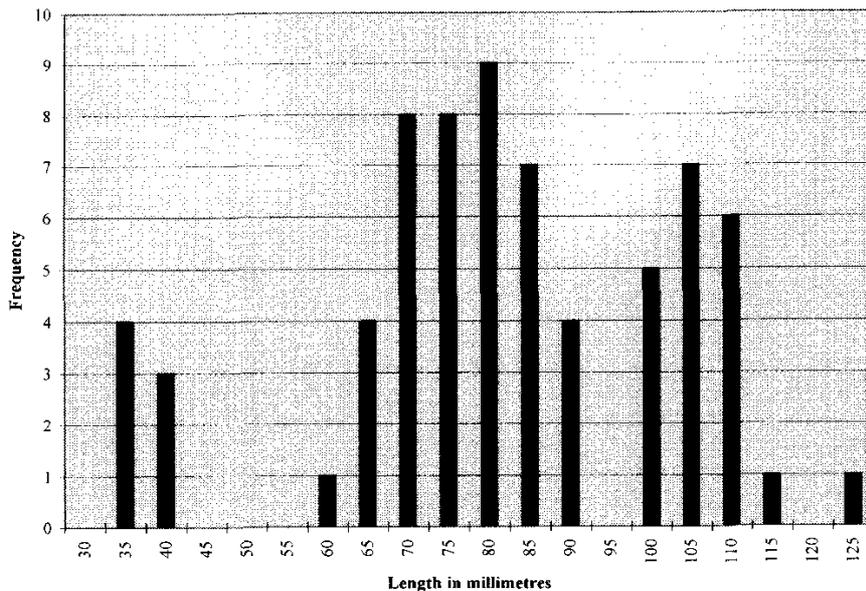


FIG. 3. Length-frequency histogram for ruffe collected from the Ross Priory Pumping Station in December 1985, Loch Lomond, Scotland.

when 13,828 ruffe were collected from the screens. Though numbers declined somewhat in the following years they have never fallen below 4,820 since 1991 and reached 11,296 in 1996 (Fig. 2).

Length-frequency data for ruffe caught on the trash screens at the Ross Priory pumping station in December 1985 show a tri-modal distribution (Fig. 3) indicating that only three year classes are represented in catches (although there may be a small number of older fish representing a fourth age class). Small (0+) ruffe are probably taken rarely on the screening system because of the coarse meshes on the drum screens and may only appear at the end of the year.

Other species are entrained at Ross Priory and, in addition to the four common fish discussed above, 12 species have been recorded during the study period 1982 to 96 (Table 1). However, none of these has ever been common. By 1989, gill net captures at five sites around Loch Lomond from the extreme north to the extreme south showed that ruffe was a very common species in the littoral zone (Table 3). At two sites ruffe was the commonest fish in gill net catches, at another site it was the second-most common species, and at a further two sites it was the third-most common species. There is a marked seasonality in the catches of ruffe, with most fish being entrained during spring

(Fig. 4). Catches peaked sharply in May, and rapidly decreased into mid-summer, rising again slightly in the winter. Entrainment catches at this site were mirrored by gill-net captures at the five littoral zone sites throughout the loch. Monthly catches of ruffe in gill nets during 1988 and 1989 at five locations each month across the loch showed a high degree of concordance in capture rate between sites (between site concordance in capture rate: Kendal coefficient of concordance for ruffe captures $W = 0.60$, d.f. = 7, $P < 0.01$). Thus it seems that seasonal inshore migrations are stable events occurring across the whole loch each year.

TABLE 3. Catches of fish from gill-nets (adjusted for catch-per-unit-effort) at five littoral zone sites around Loch Lomond expressed as a percentage of total catch. Introduced species in bold.

Falloch Mouth		Pilot Bank		Camas an Losgainn		Auchentullich Bay		Ross Priory Bay	
ruffe	30.3	powan	50.6	powan	68.4	powan	36.6	ruffe	31.3
powan	30.7	ruffe	29.4	brown trout	8.4	roach	27.9	roach	19.8
roach	14.1	trout	12.6	ruffe	7.4	ruffe	16.1	dace	14.8
northern pike	5.4	perch	3.4	perch	6.5	salmon	7.6	powan	14.1
brown trout	5.2	salmon	1.5	roach	5.5	pike	5.2	perch	9.8
perch	3.6	northern pike	0.7	salmon	3.4	perch	3.4	brown trout	3.7
salmon	1.5	eel	0.7	northern pike	0.5	trout	1.3	salmon	3.0
		roach	0.6			dace	0.4	pike	1.9
						flounder	0.4	eel	1.7
								flounder	0.5
N = 267		N = 210		N = 245		N = 319		N = 253	

The Diet of Ruffe in Loch Lomond and Its Overlap With Other Species

The diet of ruffe varied both seasonally and geographically within Loch Lomond. Table 4 shows the proportion of each prey item (% by prey number) in the stomachs of ruffe collected at Ross Priory (the south basin) and the Ross Peninsula (the mid basin) sites in summer and at the Ross Peninsula site in winter. The stomach contents of ruffe collected in summer at Ross Priory differed significantly from those of ruffe collected at the same time at the Ross Peninsula ($\chi^2 = 2214$, $N = 14$, $P < 0.001$). Stomach contents at Ross Priory were dominated by Diptera larvae, mostly Chironomidae although there were also some Ceratopogonidae (1.3%). The second most common prey group was Cladocera, making up 12% of prey items recorded. The isopod, *Asellus aquaticus*, constituted 4.8% of recorded prey items but all other taxa made up less than 3% of prey.

In contrast, the commonest prey item in stomachs of ruffe collected at the same time, at the Ross Peninsula, was *Asellus aquaticus* (46.3%). Diptera larvae were the secondmost abundant prey item recorded (29.3%). Nymphs of the insect orders Plecoptera and Ephemeroptera and Trichoptera larvae were also apparently relatively more important components of the diet ruffe at this site than at the Ross Priory site. Cladocera were much less abundant in stomachs of fish from the mid basin than the south basin, making up only 3.4% of prey items recorded (cf. 12% in the south).

As well as variation in stomach contents between sites within Loch Lomond, there was also evidence of seasonal variation in stomach contents. The frequency of prey items recorded from fish caught at the mid basin site in mid winter (January and February) was significantly different from those collected at the same mid basin site in summer ($\chi^2 = 1,247$, $N = 15$, $P < 0.001$). This difference was primarily the result of a high consumption of fish eggs recorded during winter. These were predominantly the eggs of the winter spawning powan, although a single egg of a brown trout was also recorded. As with the summer diet of ruffe at this site, *Asellus aquaticus* and Diptera larvae were important prey species in winter, making up 30.8% and 29.3% of the recorded prey items respectively. Insect nymphs and larvae made up small but significant proportions of the diet in both summer and winter. Cladocera were apparently less numerous in stomach contents in winter than in summer. The winter diet also included a small proportion of fish, including some juvenile (presumed 0+) ruffe.

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The frequency of ruffe with empty stomachs was significantly lower in winter (6.5%) than in summer (16.3% ($\chi^2 = 4.82$, $p < 0.05$). In addition, the median weight of prey items recovered from stomachs that did contain prey was significantly higher in winter than in summer (Mann Whitney $W = 532$, $p < 0.01$).

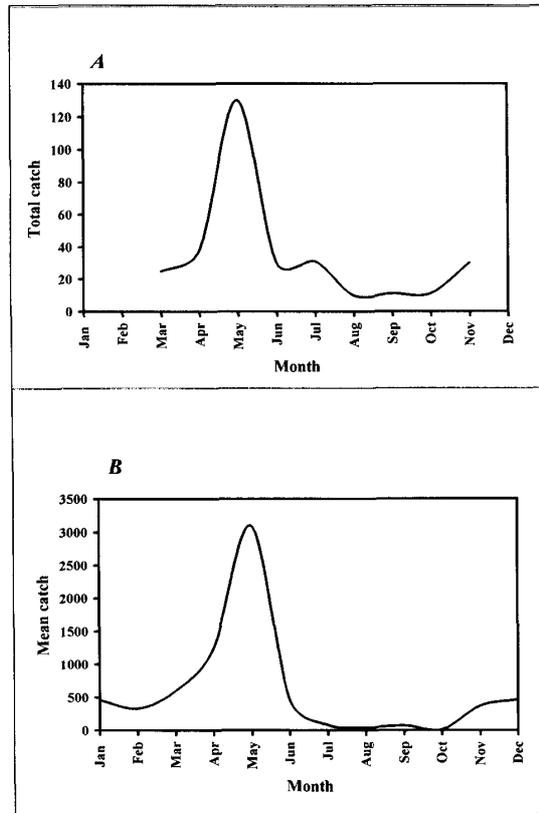


FIG. 4. Monthly changes in catches of ruffe A) in gill nets set in the littoral zone at five sites around Loch Lomond, Scotland in 1988 to 1989, and B) mean monthly catch at the Ross Priory Pumping Station between 1989 and 1996.

The stomach contents of ruffe collected at the Ross Peninsula in summer 1987 (July and August) and of perch collected at the same site, in the same season in 1977 before the arrival of ruffe (see Giles and Tippett 1987) showed that perch diet differed substantially from that of ruffe caught at the same site. Perch stomach contents were dominated by Cladocera, whilst *Asellus aquaticus* was the commonest prey item in ruffe stomachs; Cladocera

made up a relatively small proportion of prey items in the stomachs. Although perch fed on all the prey items recovered from the stomachs of ruffe, 7 of the 12 prey groups recorded from the stomachs of ruffe were not recorded in perch, indicating a greater breadth of prey consumption by ruffe. Thus Schoener's resource use overlap index for these two species is only 0.13, indicating a very low overlap in diet. Diet analysis of the small number of perch caught contemporaneously with ruffe in the mid and south basin sites in 1985 (Table 4) confirm that perch diet has not changed substantially since the arrival of a large ruffe population.

Stomach contents of ruffe and brown trout collected simultaneously during winter at one site showed that both brown trout and ruffe had been feeding extensively on the eggs of fish, predominantly those of powan which spawns in mid-winter. Because it is a broadcast spawner, its ova are abundant and particularly susceptible to predation. However, apart from this temporally highly abundant food source, the diet of ruffe and brown trout differs substantially. *Asellus aquaticus* was the second-most numerically abundant prey item in the stomachs of ruffe at this time (30.8%) but constituted only 1.9% of brown trout prey items. Tri-choptera and Cladocera were the first and third (after powan ova) most abundant prey items in the stomachs of trout. However, these made up only 7.7 and 0.1% of the prey items in ruffe. The calculated Schoener's resource overlap index for these two species was 0.34, indicating a relatively low rate of diet overlap.

Interactions With Fish Predators

All three piscivorous species studied (northern pike, herons and cormorants) were shown to feed predominantly upon the new and abundant ruffe population and showed a clear shift in diet away from native fish species (Fig. 5). Using published information on the daily ration of these three predators, data on predator population

size and diet, Adams (1996) attempted to quantify the possible magnitude of the effect of a shifting predation pressure by these predators from native species on to the ruffe population. Although provisional, estimates suggest that possibly between 18 and 20 metric tons of ruffe, representing between 2.2 and 2.6 million individuals, are now being consumed by these three predators that previously foraged upon native species (see Fig. 5 and Adams 1996).

TABLE 4. *The stomach contents (percentage prey by number) of: i) ruffe caught in the south and mid-basins during summer 1985 and in winter in the mid-basin in 1988-89; ii) perch from the mid-basin prior to the arrival of ruffe (in summer 1977) (Giles and Tippett 1987) and from the south and mid basins in summer 1985; iii) trout in winter 1988-89 in the mid-basin of Loch Lomond. Ruffe diet differed significantly between mid and south basins ($X^2 = 2214$, $df. = 13$, $P < 0.001$) and between summer and winter ($X^2 = 1,247$, $df. 14$, $P < 0.001$). Schoeners niche overlap index for perch and ruffe summer diets in the mid-basin $C_{xy}=0.13$ and for trout and ruffe diets in the mid-basin in winter $C_{xy}=0.34$*

Prey	Ruffe Summer Diet South basin 1985	Ruffe Summer Diet Mid-basin 1985	Ruffe Winter Diet Mid-basin 1989	Perch Summer Diet Mid-basin 1977	Perch Summer Diet 1985	Trout Winter Diet Mid-basin 1989
Gastropoda	1.3	2.6	0.1	0	0.03	7.8
Bivalvia	0.2	0.2	0.2	0	0	0.2
Oligochaeta	0	0	0.1	0	0	0.7
Cladocera	12.0	3.4	0.1	91.0	96.0	22.1
Ostracoda	0.6	0.2	0	0	0.05	0
Copepoda	1.2	1.7	3.5	4.0	3.2	0
Diplopoda	0	0	0	0	0	0.2
Asellus	4.8	46.3	30.8	3.3	0.05	1.9
Gammarus	0.4	0	0.1	0	0	0
Plecoptera	1.6	4.7	4.8	0	0.1	0.4
Ephemeroptera	2.3	4.9	2.0	0.9	0.02	0
Trichoptera	0.9	4.7	7.7	0	0.05	40.7
Hemiptera	0	0	0	0	0.02	0
Diptera	73.1	29.3	15.7	5.0	0.35	1.2
Coleoptera	0.4	0.4	0.5	0	0.02	0.6
Acari	0.1	0	0	0	0	0
Fish eggs	0	1.0	39.4=3	0	0	24.2
Fish	0	0	0.7	0	0.1	0
Total No. Prey	N = 1,411	N = 529	N = 1,423	N = 3,898	N = 6,250	N = 683
Total No. Fish	N = 53	N = 15	N = 93	N = 138	N = 7	N = 83

DISCUSSION

Invasion, Range, and Population Expansion and the Current Status of Ruffe in Loch Lomond

Prior to 1982, the nearest known population of ruffe to Loch Lomond was in the River Tees in England, some 100 km away. However, on 14 July 1982, during routine gill netting for other species, two specimens of ruffe (76 and 93 mm fork-length) were taken in the fine meshes of a mixed mesh survey gill net fished overnight in a bay east of Camas an Losgairn, Loch Lomond (Fig. 1) (Maitland *et al.* 1983). A third specimen (94 mm) was taken by gill net in Camas an Losgairn on 25 August 1982, and on the same date a fourth specimen (72 mm) was collected from the screening system at Ross Priory. Thereafter, ruffe became increasingly common in fish catches in different parts of the Loch Lomond system (Maitland and East 1989). Despite considerable, although sporadic, fish collecting effort, ruffe had never been recorded in Loch Lomond prior to 1982 (see Maitland *et al.* 1981 for summary).

It is not known exactly when ruffe were first introduced to Loch Lomond, but after their discovery in 1982, dispersal through the system seems to have been very rapid. By 1984, ruffe was already the dominant species in the catches at Ross Priory (see Table 2 and Maitland and East 1989). In the River Endrick, Loch

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Loch Lomond's largest inflow, regular trapping for lampreys in the lower reaches of the River Endrick was carried out between 1982 and 1984 (Maitland *et al.* 1994). In 1982 no ruffe were recorded, but in 1983, 18 ruffe were collected. By 1984 the catch had risen to 1,598 ruffe, representing 96% of the total fish catch by number. Similarly, though numbers are not available, ruffe were seen in the loch's outflow (the River Leven) on several occasions in 1983 and 1984, during electrofishing there.

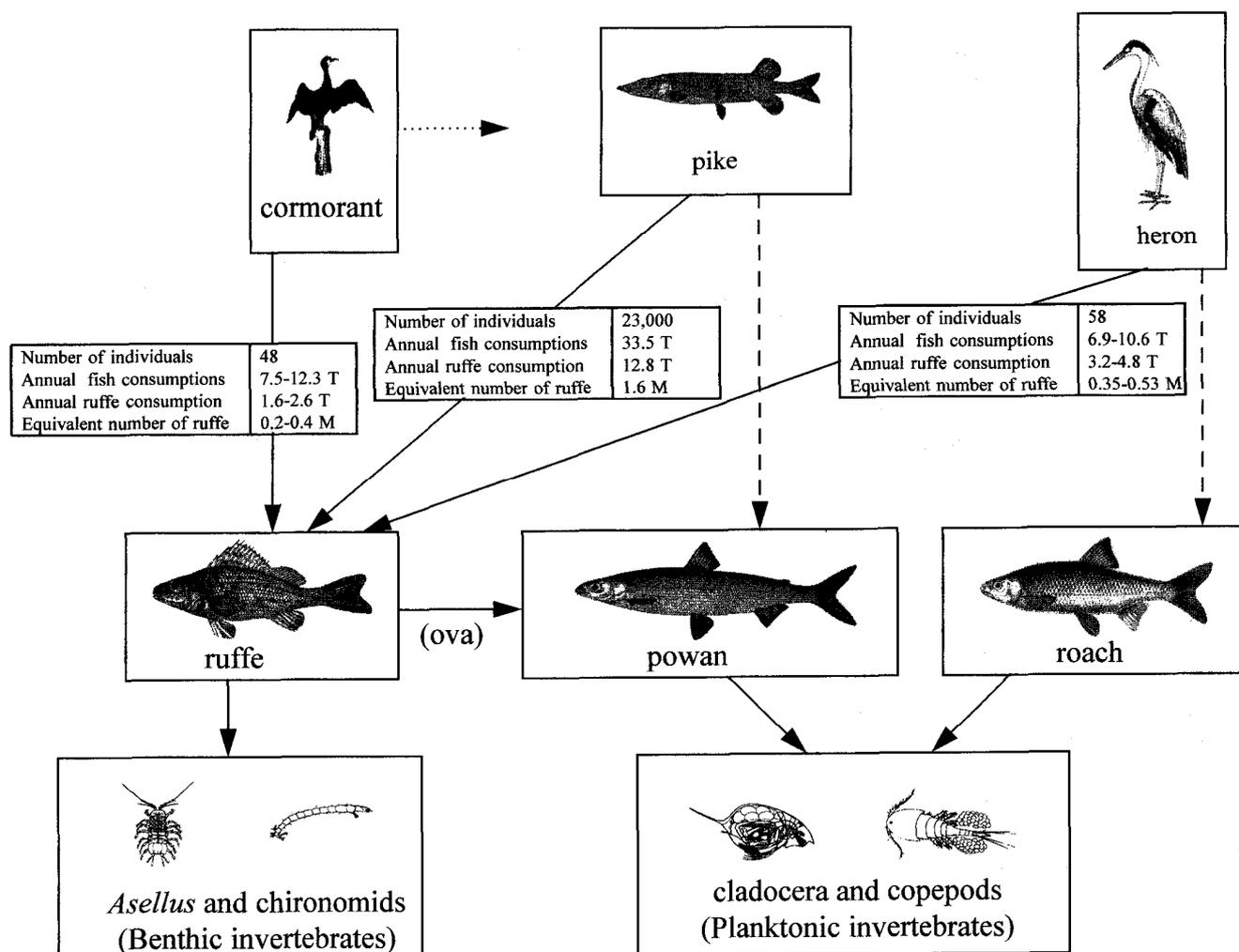


FIG. 5. Predator-prey relationships in Loch Lomond. Dashed lines indicate principal prey items prior to the establishment of ruffe, solid line indicate predator-prey relationships following the establishment of a large ruffe population. Inset boxes indicate estimates of predator population size, estimated annual fish consumption and estimated annual ruffe consumption by three 3 predators of fish. Note that the pathway to top predator now originates in the benthos whereas previously the route was planktonic. M = million, T= tonnes.

Gill-netting at Tarbet in 1984 and on MacDougal bank and at Ptarmigan in 1985 (Fig. 1) showed that ruffe were present at these sites by this time. By 1989, extensive gill-netting surveys at five points around the loch showed that ruffe were abundant in most parts of the loch and an important part of the fish community from the far north to the extreme south of the catchment (Table 3).

However, although ruffe were quick to invade most parts of the loch and upstream into the lower slow flowing reaches of the River Endrick and downstream into the River Leven, virtually none of the faster flowing tributaries of the loch were invaded. A survey of 17 of these tributaries in the summer of 1987 (D. Brown, personal communication) found no ruffe in any of them, though brown trout and eels were common and stone loach, *Barbatulus barbatulus*, brook lampreys, *Lampetra planeri*, river lampreys, *Lampetra fluviatilis*, minnows *Phoxinus phoxinus*, and three-spined sticklebacks occurred in a few places.

Thus there is no doubt that the ruffe is a new arrival to Loch Lomond and is now very well established there. Gill netting using a range of mesh sizes has been carried out by the authors for over 30 years and the first ruffe recorded (in 1982) were caught during the third year of a routine gill netting program using the same nets at the same localities. Thus, though the date of the original introduction is unknown, and was obviously prior to 1982, it may not have been too many years before that. The assumption is that a few fish were probably introduced around 1980 and started to breed successfully. The numbers rapidly increased during 1982 and by 1984, the species had colonized most suitable habitats in the loch and its associated rivers. By 1989 ruffe was the second-most common species in gill net captures (all sites combined) (see also Adams and Tippet 1991) but evidence from captures at one site, the Ross Priory pumping station, suggests that the ruffe population continued to expand until at least 1992, after which the population appears to have levelled off (Fig. 2).

Catches of fish using gill nets and at the Ross Priory pumping station showed seasonal inshore migrations of ruffe, peaking in May. Adams *et al.* (1994) showed that these inshore migrations resulted in increased predation upon ruffe by cormorants and suggested that as high numbers of ruffe in the littoral in early summer coincided with the occurrence of maturing adults, ruffe abundance in shallow water at this time was the result of a spawning migration.

Interactions With Other Species

According to Welcomme (1986) there are five possible routes through which an introduced fish species may interact with the existing fauna in a freshwater ecosystem. Here we examine the evidence for each of these impacts including competition being mediated through the introduction of ruffe to Loch Lomond.

Resource Competition

Competition between species for limited resources is widely believed to be one of the most important impacts of one species upon another and is therefore frequently suspected but rarely proven to be the mechanism of community change following invasion by new fish species (Schoenherr 1981). Studies that have demonstrated between-species competition following invasion are rare (Moyle 1987). This is mainly because the criteria necessary to demonstrate fully a competition effect between two species require it to be shown that both species exploit a common resource; that this resource is limiting; and usually also that one species is adversely affecting some aspect of the other (e.g., growth, survival or abundance) (Connel 1980).

Given the catholic nature of the diet of ruffe described both here and elsewhere (Aleksandrova 1974, Johnsen 1965, Boron and Kuklinska 1987, Ogle *et al.* 1995, Kalas 1995) the possibility of exploitative competition for food would seem to be great. The two native species with which, at least superficially, competition effects would be most likely are the perch, the phylogenetically closest relative of the ruffe in Loch Lomond, and the brown trout, another species with a highly catholic diet, but including a high proportion of benthic invertebrates.

Diet data presented here confirm that as with most other populations (see Aleksandrova 1974, Johnsen 1965, Boron and Kuklinska 1987, Ogle *et al.* 1995) ruffe in Loch Lomond are benthivorous (although see Kalas 1995), opportunistic, and highly flexible in their choice of prey. Prey items come from a wide range of benthic-living invertebrate taxa but also include the ova of other fish, such as coregonid and salmonid eggs. Ruffe also appeared to be cannibalistic at times. Here it has been shown that the diet of ruffe changes both geographically and seasonally in Loch Lomond. Winter diet of fish caught in the mid-basin of Loch Lomond differed significantly from the diet of ruffe collected at the same site in summer. The most significant change in diet was the heavy predation upon eggs of fish (povan), which spawn in this area during winter. More significant than seasonal differences in diet were geographic differences between ruffe collected from two sites, one in the south basin and the other 10 km distant in the mid-basin of Loch Lomond. In the summer in the south, ruffe diet was dominated by Diptera larvae, whereas in the mid-basin the most abundant prey item in stomachs was the isopod *Asellus aquaticus*.

Thus the potential for feeding competition between ruffe and other species would appear to be considerable. Despite this, the diet of both brown trout and ruffe and perch and ruffe caught at the same time, in the same place showed no significant overlap, indicating that these species do not share a common resource.

One potential effect resulting when new competitive relationships become established, however, is that one of the competing species switches its diet to feed on an alternative (and possibly sub-optimal) prey source.

Ruffe Invasion of Loch Lomond

Using published data for the diet of perch collected prior to the arrival and establishment of a large ruffe population in Loch Lomond, the diet of perch was compared prior to the possibility of any competitive interaction between perch and ruffe. The data very clearly indicate that, at least for the size ranges of the two species examined in this study, there is no resource overlap and thus it must be concluded that there is no feeding competition interaction between these species.

Hybridization Between Native and Introduced Fish

It is known that for freshwater fish species with poor powers of dispersal, genetic transfer between populations is limited and thus local adaptations to local conditions can arise. When the transfer of genetically dissimilar individuals between isolated populations occurs, followed by interbreeding of genetically locally adapted types, local adaptation may be lost. This can happen either when genetically dissimilar fish of the same species or of different species that are capable of interbreeding are introduced.

Natural hybridization between ruffe and perch has been recorded in the past. Regan (1911) cites a 1907 reference for perch and ruffe hybrids in the Danube, noting that "these hybrids are not fertile per se, but are quite fertile with either parent!" (see also Holcik and Hensel 1974). So far there is no evidence that ruffe have been interbreeding with native species. However, to date there have been no genetic, or detailed morphometric studies on either perch or ruffe in Loch Lomond to examine this possibility.

Concomitant Introduction of Parasites or Disease

For fish that are restricted to living in fresh water, land barriers between waters present a major obstacle to dispersal (Maitland 1987, 1989). This physical obstacle to fish movement also prevents movement of diseases and parasites of fish between unconnected waterways.

During extensive fish surveys in 1989 in Loch Lomond a parasite of fish, never detected previously there, was discovered. The crustacean, *Argulus folia-ceous*, is a branchiuran parasite of fish. It attaches externally to a fish host within 48 hours after hatching from the egg and feeds upon mucus and epidermis using a piercing stylet and rasping mandibles. Heavy infestations can cause substantial damage to fish (Fryer 1982). This parasite is now commonly recorded on fish collected from Loch Lomond and has also been recorded free-living (Adams 1994). Because this species is a conspicuous parasite, attaching externally and growing to relatively large size (8 to 9 mm) it is difficult to imagine that it has been previously overlooked by a range of fish biologists who have examined many thousands of fish since continuous fish research on Loch Lomond began in 1955. Thus, although it is impossible to provide definitive proof, as with other sites in Scotland (Northcott *et al.* 1997), circumstantial evidence strongly suggests that this parasite arrived in Loch Lomond recently. The most likely vector for its arrival is that it was introduced along with fish brought into the catchment.

New Species Induced Habitat Change

There is no evidence that the introduction of ruffe has induced habitat change in Loch Lomond.

Predation

The role of predation in reshaping freshwater communities following invasion by new fish species has recently been reviewed by Adams (1996). Direct predation by an introduced piscivorous species upon native species is undoubtedly the most clearly demonstrated mechanism through which one introduced fish species may have an impact on another (Barel *et al.* 1985, Barlow *et al.* 1987, Achieng 1990, Craig 1992). In Loch Lomond, both direct and more subtle indirect predation effects have been clearly demonstrated. As has been reported here and elsewhere (Adams and Tippett 1991), ruffe include both fish and fish eggs in their diet. Ruffe in winter ate an underyearling ruffe, ova of a brown trout, and powan ova. Powan are broadcast spawners, despite producing a relatively small number of large yolky eggs, but in the past have been to some extent protected from predation by poikilotherms by relatively cold water temperatures (usually less than 7°C) during the spawning period. As has been shown here the proportion of empty stomachs of winter feeding ruffe was lower than at the same site in summer despite a water temperature difference of around 8°C (7°C in winter; 15°C in summer). The temperature dependant stomach evacuation times for ruffe are unknown and although this undoubtedly has some effect on the rate of turnover of stomach contents, it is clear that ruffe, unlike other fish species (Adams and Tippett 1991), are feeding extensively in Loch Lomond in mid-winter. These data are concordant with high activity at low temperature in ruffe which has been demonstrated experimentally (Bergman 1988). Thus ruffe are capable

of maintaining food intake at temperatures previously affording protection for powan. The long-term effect of ruffe predation on the spawning success of powan is unclear as there has been no attempt to determine if ruffe predation represents an additional source of ova mortality in a species that, prior to the arrival of ruffe, had been shown to have exceptionally high natural mortality rates (Brown 1989). However, evidence from gill-netting since 1985 suggests that there has not yet been a catastrophic decline in the powan population.

Direct predation by piscivorous ruffe on other species is not the only ruffe-induced predation effect that has been demonstrated in Loch Lomond. Changes in the diet of piscivorous birds and northern pike would appear to amount to considerable predation relief for the native species that comprised the diet of fish predators before the arrival of ruffe (powan for northern pike and roach, *Rutilus rutilus*, for herons, (the diet of cormorants prior to the arrival of ruffe is unknown)). However, given our lack of understanding of the mechanisms regulating populations, it is unclear what will be the response of the predator population. If prey availability is limiting predator population size then predation pressure on native species could conceivably increase if the population expands.

A number of important points emerge from these studies. Firstly it is clear that it is through changes in relationships between predator and prey that the most significant changes to the freshwater community resulting from the introduction and establishment of a large ruffe population in Loch Lomond have occurred. Secondly, the changes that have occurred have been fundamental, with potential repercussions throughout the whole ecosystem. Thirdly, although the changes in species interactions and their consequences described here cannot be considered of positive benefit they may not all be, at least in the short term, deleterious and some changes that could have positive benefit to some members of the native community have been identified. Fourthly, from data presented here (Fig. 6) it is obvious that there has been a shift in the main energetic pathways in the food-chain in Loch Lomond. Top predators feeding on fish prior to the arrival of ruffe were consuming prey that fed primarily on plankton. Now, by consuming ruffe, they are feeding on a prey that consumes benthos. Fifthly, it is clear that it would have been very difficult to predict realistically the outcome of the invasion of Loch Lomond by ruffe. Our current knowledge of the factors controlling the population dynamics of freshwater fish species does not permit more than speculation at the constraints to population expansion that were missing in Loch Lomond, thus allowing the ruffe population to expand so rapidly. In addition, although theoretically the mechanisms of interaction between invading and native fish species are understood, it is not possible to predict with any accuracy exactly which will occur when an invader enters a new community.

It is clear that there is still great potential for further invasions of ruffe both in Scotland, where only two recently introduced populations are known (Loch Lomond and Loch Ken), and in North America where only Lake Superior and Lake Huron currently have populations (Winfield *et al.* 1998). In the British Isles in the past, it has been assumed that the success of fish invading from the south may be limited by lower temperatures in the north. However, although this may be true of some cyprinid species, this is certainly not true of ruffe. Almost 100 years ago, Maxwell (1904) indicated the potential for ruffe to invade more northerly habitats, pointing out that "its range is far more northerly than that of the perch, for the ruffe is not found in southern Europe, but abounds in Scandinavia, Russia and Siberia . . . may we not then consider the ruffe as hypothetically an Arctic perch, a survivor of more severe climatic conditions than now prevail in the regions which have been colonised by the more robust genus."

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REFERENCES

- Achieng A.P. 1990. The impact of the introduction of Nile perch, *Lates niloticus* (L.) on the fisheries of Lake Victoria. *Journal of Fish Biology* 37:17-23
- Adams C.E. 1991. Shift in pike, *Esox lucius* predation pressure following the introduction of Ruffe, *Gymnocephalus cernuus* 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* 290:91-103
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- _____. 1996. The impact of introductions of new fish species on predator-prey relationships in freshwater lakes. In *Aquatic predators and their prey*, eds. S.P.R. Greenstreet and M.L. Tasker, pp. 98-106. Oxford: Blackwell
- _____. and Maitland P.S. 1991. Evidence of further invasions of Loch Lomond by non-native fish species with the discovery of a roach X bream, *Rutilus rutilus* (L.) X *Abramis brama* (L.) hybrid. *Journal of Fish Biology* 38:961-963
- _____. and Mitchell J. 1992. Introduction of another non-native fish species to Loch Lomond: Crucian carp (*Carassius carassius* (L.)). *Glasgow Naturalist* 22:165-168
- _____. and Mitchell J. 1995. The response of a Grey Heron *Ardea cinerea* breeding colony to rapid change in prey species. *Bird Study* 42:44-49
- _____. and Tippett R. 1991. Powan *Coregonus lavaretus* ova predation by newly introduced ruffe, *Gymnocephalus cernuus* in Loch Lomond, Scotland. *Aqua-culture and Fisheries Management* 22:239-246
- _____. Brown D.W. and Keay L. 1994. Elevated predation risk associated with inshore migrations of fish in a large lake, Loch Lomond, Scotland. *Hydrobiologia* 290:135-139
- _____. Brown B.W. and Tippett R. 1990. Dace, *Leuciscus leuciscus* (L.), and Chub (*L. cephalus* (L.): new introductions to Loch Lomond. *Glasgow Naturalist* 22:165-168
- Aleksandrova A.I. 1974. A morphological and ecological description of the ruffe (*Acerina cernua*) of the middle reach of the Dnieper. *Journal of Ichthyology* 14:53-59
- Barel C.D.N., Dorit R., Greenwood P.H., Fryer G., Huges N., Jackson P.B.N., Kawanabe H., Lowe-McConnell R.H., Nagoshi M., Ribbink A.J., Tre-wavas E., Witte, F. and Yamaomk K. 1985. Destruction of fisheries in Africa's lakes. *Nature* 315:19-20
- Barlow G.C., Hogan A.E. and Rodgers L.J. 1987. Implications of translocated fishes on the apparent extinction in the wild of the Lake Eachan rainbowfish *Melanataenia eachamensi*. *Australian Journal of Marine and Freshwater Research* 37:897-902
- Bergman E. 1988. Foraging abilities and niche breadths of two percids *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. *Journal of Animal Ecology* 57:443-453
- _____. 1990. Effects of roach *Rutilus rutilus* on two percids *Perca fluviatilis* and *Gymnocephalus cernua*; importance of species interactions for diet shifts. *Oikos* 57:241-249
- Best G.A. and Trail I. 1994. The physico-chemical limnology of Loch Lomond. *Hydrobiologia* 290:29-39
- Boron S. and Kuklinska B. 1987. Food of ruffe (*Gymnocephalus cernuus* L.) and gudgeon (*Gobio gobio* (L.)) in Wloclawek Dam Reservoir. *Acta Ichthyologica et Piscatoria* 17:59-76
- Brown E.A.R. 1989. Growth processes in two Scottish populations of powan, *Coregonus lavaretus*. Ph.D. thesis, University of St Andrews
- Connel J.H. 1980. Diversity and co-evolution of competitors, or the ghost of competition past. *Oikos* 35:131-138
- Craig J.F. 1992. Human-induced changes in the composition of fish communities in African Great Lakes. *Reviews in Fish Biology and Fisheries* 2:93-124
- Fryer G. 1982. *The parasitic copepoda and branchiura of the British freshwater fishes*. F.B.A. Publication Number 46. Ambleside, F.B.A
- Giles, N., and Tippett, R. 1987. Annual migration and diet of perch *Perca fluviatilis* in Loch Lomond, Scotland. *Glasgow Naturalist* 21:287-285.
- Grant A., Duguid R.A. and Adams C.E. (1997). The rediscovery of Tench *Tinca tinca* in Loch Lomond. *Glasgow Naturalist* 23:59-61
- Holcik J. and Hensel K. 1974. A new species of *Gymnocephalus* from the Danube with remarks on the genus. *Copeia* 471-486
- Johnsen, P. 1965. Studies on the distribution and food of the ruffe (*Acerina cernua*) in Denmark, with notes on other aspects. *Medd. fra Danmarks Fiskeri- og Havundersogelser* 4:137-156.
- Kalas S. 1995. The ecology of ruffe *Gymnocephalus cernuus* (Pisces: Percidae) introduced to Mildevatn, western Norway. *Environmental Biology of Fishes* 42:219-232
- Maitland P.S., 1972. Loch Lomond: Man's effects on the salmonid community. *J. Fish. Res. Board Can.* 29:849-860
- _____. 1987. *Fish introductions and translocations - their impact in the British Isles*. Grange over sands, England, Institute of Terrestrial Ecology Symposium
- _____. 1989. Scientific management of temperate communities: Conservation of fish species. *Symposium of the British Ecological Society* 29:129-148

- _____. 1991. Ecology of the Ruffe *Gymnocephalus cernua* (Linnaeus 1758) in Europe. Saginaw: In *US EPA Introduced Species Workshop. 1990*, pp. 1-2
- _____. and East, K. 1989. An increase in the numbers of Ruffe, *Gymnocephalus cernua* (L.), in a Scottish loch from 1982 to 1987. *Aquaculture and Fisheries Management* 20:227-228
- _____. Smith, B.D., and Adair, S.M. 1981. The fish and fisheries, pp. 223-253. In *The Ecology of Scotland's Largest Lochs*, ed. P.S. Maitland, pp. 223-253. The Hague: Dr W. Junk Publishers
- _____. East, K., and Morris, K.H. 1983. Ruffe *Gymnocephalus cernua* (L.), new to Scotland, in Loch Lomond. *Scottish Naturalist* 7-9
- _____. Morris, K.H., and East K. 1994. The ecology of lampreys (Petromyzonidae) in the Loch Lomond area. *Hydrobiologia* 290:105-121
- Maxwell H. 1904. *British Freshwater Fishes*. London: Hutchinson
- Moyle P.B. 1987. Fish Introductions into North America: Patterns and Ecological Impact. In *Ecology of Biological Invasions of North America and Hawaii*, eds. H.A. Mooney and J.A. Drake Ecological Studies 58. New York: Springer-Verlag
- Northcott S.J., Lyndon A.R. and Cambell A.D. 1997. An outbreak of freshwater fish louse *Argulus foliaceus* L. seriously affecting a Scottish stillwater fishery. *Fishery Management and Ecology* 4:73-75
- Ogle D.H., Selgeby J.H., Newman R.M. and Henry M.G., 1995. Diet and feeding periodicity of ruffe in the St. Louis River estuary Lake Superior. *Trans. Am. Fish. Soc.* 124:356-369
- Regan C.T. 1911. *The freshwater fishes of the British Isles*. London: Methuen
- Schoenherr A.A. 1981. The role of competition in the replacement of native fishes by introduced species. In *Fishes in North American Deserts* eds. R.J. Naiman and D.L. Soltz. New York: Wiley
- Schoenherr T.W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408-418
- Smith I.R., Lyle A.A. and Rosie A.J. 1981. Comparative physical limnology. In *The Ecology of Scotland's Largest Lochs*, ed. P.S. Maitland, pp. 29-67. The Hague: Dr W. Junk Publishers
- Winfield I.J., Adams C.E. and Fletcher J.M. 1996. Recent introductions of the ruffe (*Gymnocephalus cernuus*) to three United Kingdom lakes containing *Coregonus* species. *Annals Zoologica Fennici* 33:459-466
- _____. Dodge, D.P., and Rosch, R. 1998. Introductions of the ruffe *Gymnocephalus cernuus*, to new areas of Europe and to North America: history, the present situation and management implications. In *Stocking and introduction of fish*, ed. I.G. Cowx, pp. 191-208. Oxford: Fishing News Books
- Welcomme R.L. 1986. International measures for the control of introductions of aquatic organisms. *Fisheries* 11:4-9

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