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RELATIONSHIPS BETWEEN THE POPULATION AND FEEDING ECOLOGIES OF THE DIVING DUCKS AND FISH OF LOUGH NEAGH, NORTHERN IRELAND: A SYNTHESIS

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ABSTRACT

Lough Neagh is a large (surface area 387 km^2), eutrophic (long-term annual mean total phosphorus 107 mg l^{-1}) lake in Northern Ireland, U.K., which supports large overwintering populations of the diving ducks Common Pochard (*Aythya ferina*), Tufted Duck (*Aythya fuligula*), Greater Scaup (*Aythya marila*) and Common Goldeneye (*Bucephala clangula*) (approximate densities of up to 100, 90, 6 and 26 individuals km^{-2}, respectively). An examination of long-term population trends between 1965 and 1988 revealed that the abundance of Common Pochard and scaup had been relatively stable and Goldeneye had shown a recent increase. In contrast, the numbers of overwintering Tufted Duck had declined markedly during the early 1980s, but recovered to former levels in the winter of 1987/1988. These latter changes were subsequently found to mirror those in the abundance of roach (*Rutilus rutilus*), a cyprinid fish which was first recorded in the Lough Neagh system in 1970. After its introduction, the roach rapidly increased in abundance before declining in the late 1980s, probably due to heavy infestation by the cestode tapeworm *Ligula intestinalis*.

Studies carried out in the late 1980s, when the roach population was in a state of relative decline, showed that the diets of the above diving ducks and the major fish of the lough (i.e. roach, perch *Perca fluviatilis*, pollan *Coregonus autumnalis* (Pallas) and eel *Anguilla anguilla*) showed relatively high overlaps due to the common consumption of chironomid larvae. However, three major groupings were apparent. Common Pochard, Greater Scaup, Common Goldeneye and eel formed a group with diets dominated by chironomid larvae, while perch and pollan formed a smaller group in which the crustacean *Mysis relicta* Loven was an important dietary component. Tufted Duck and roach formed a third and distinct group in which molluscs, particularly *Valvata piscinalis* (Muller), were important in the diet.

It is suggested that the feeding ecology of Tufted Duck and roach in Lough Neagh forms an example of distant competition which may be responsible for the observed fluctuations in the numbers of overwintering Tufted Duck. Consistent with this hypothesis, during the early to mid 1990s the roach population has remained low in abundance and the numbers of Tufted Duck have remained high. The strengths and weaknesses of this interpretation, and those likely to be met in any study of competition between ducks and fish, are discussed.

INTRODUCTION

Limnology has always involved a multi-disciplinary approach to the study of fresh waters, with even its earliest studies involving physics, chemistry and biology (see Persson *et al.*, 1988). However, it was not until the 1960s, following the pioneering studies of Hrbacek *et al.* (1961) and Brooks and Dodson (1965), that limnological investigations truly expanded to include vertebrate animals in the form of teleost fishes. By the 1980s and early 1990s, expansion had continued to include the remaining major group of temperate zone aquatic vertebrates, the waterfowl. While such investigations of birds in freshwater ecosystems are still in their infancy, they have already contributed greatly to our understanding of their role in the trophic webs of lakes, with implications for both fundamental and applied ecology (see collected papers in Kerekes and Pollard, 1994).

Although studies of fish and waterfowl in a limnological context have only a short history, investigations in a fisheries context have a much longer standing. However, such studies, which may be traced back to Beach (1937) and earlier, have been concerned largely with the predatory impact of piscivorous waterfowl on fish populations of commercial importance (see review by Suter, 1991). In contrast, few studies have considered possible competitive interactions between these two major groups of aquatic vertebrates. Notable exceptions have been a study by Hurlbert *et al.* (1986) of competition for zooplankton by Chilean flamingos (*Phoenicopterus chilensis*) and cyprinodont fish (*Orestias* spp.), and work by several European authors including Eriksson (1979), Pehrsson (1984), Hill *et al.* (1987) and Giles (1994) addressing competition between young dabbling (e.g. *Anas* sp.) or diving (e.g. *Bucephala* sp.) ducks and fish (e.g. *Perca* sp., *Rutilus* sp., *Abramis* sp.) for macroinvertebrates, particularly emerging chironomid larvae.

The present paper provides a synthesis of our work (Winfield *et al.*, 1989; Winfield, 1991; Winfield *et al.*, 1992; Winfield *et al.*, 1993; Winfield and Winfield, 1994a; Winfield and Winfield, 1994b) on the waterfowl and fish populations of Lough Neagh, Northern Ireland, where competition for macroinvertebrate prey appears to be an important factor in determining the overwintering population dynamics of at least one species of diving duck. The study is unique among investigations of competition between waterfowl and fish because it incorporates both long-term population data and information on resource (i.e. food) utilisation and availability. Moreover, the system has been subject to major perturbations which, while not being purposefully designed or controlled, have been particularly illuminating.

THE STUDY SITE

With a surface area of approximately 387 km^2, Lough Neagh is the largest expanse of fresh water in the British Isles, even though its mean depth is only *c.* 9 m. This eutrophic (long-term annual mean total phosphorus 107 mg l^{-1}, R. H. Foy, Department of Agriculture for Northern Ireland, unpublished data) lough has been extensively studied over the last three decades and an authoritative review is provided by Wood and Smith (1993). Macrophytes are limited to a few sheltered bays, but the offshore benthos is abundant and dominated by oligochaetes and chironomid larvae. Molluscs are also present, although not the zebra mussel (*Dreissena polymorpha* (Pallas)) which is an important component of the diets of some waterfowl in mainland Europe (Cramp and Simmons, 1977).

The fish community of Lough Neagh contains significant populations of perch (*Perca fluviatilis*), pollan (*Coregonus autumnalis*) and eel (*Anguilla anguilla*), all of which are exploited by commercial fisheries (see Winfield *et al.*, 1993). In addition, following an introduction in 1970 (see below), the lough now also supports a fluctuating population of roach (*Rutilus rutilus*), a cyprinid fish which although not fished commercially became a major target of recreational angling on the lough's larger tributaries.

Within the lough's waterfowl community (see Winfield *et al.*, 1989), numbers of the overwintering diving ducks Common Pochard (*Aythya ferina*), Tufted Duck (*Aythya fuligula*), Greater Scaup (*Aythya marila*) and Common Goldeneye (*Bucephala clangula*) are all of international importance, and approximate densities of up to 100, 90, 6 and 26 individuals km^{-2}, respectively, have been recorded over the last three decades.

DIVING DUCK POPULATION TRENDS, 1965-1988

Our study began with an analysis of long-term trends in the numbers of waterfowl overwintering on Lough Neagh between 1965 and 1988 (Winfield *et al.*, 1989). **Figure 1** presents the trends observed in the four most abundant species of diving ducks, i.e. Common Pochard, Tufted Duck, Greater Scaup and Common Goldeneye.

The numbers of Common Pochard showed considerable short-term variation which made it difficult to discern any long-term changes, while Greater Scaup remained relatively stable although with occasional very large peaks. Common Goldeneye numbers also showed little long-term change up to the last two winters of the dataset, which saw considerable increases.

The long-term trend which generated most interest and concern among conservationists, however, was that displayed by Tufted Duck. A dramatic decline occurred during the early 1980s following a period of stability through the 1960s and probably the 1970s (note that counting was intermittent during the latter decade), although it was apparently reversed in the last winter of the dataset with a peak of over 19,000 birds in January 1988. Moreover, the facts that the Tufted Duck overwintering on Lough Neagh originate from a number of discrete European breeding grounds (see ringing returns given in Winfield, 1991) and European overwintering numbers have been consistently increasing (Owen *et al.*, 1986) suggest that local trends in numbers are the result of local rather than distant environmental conditions.

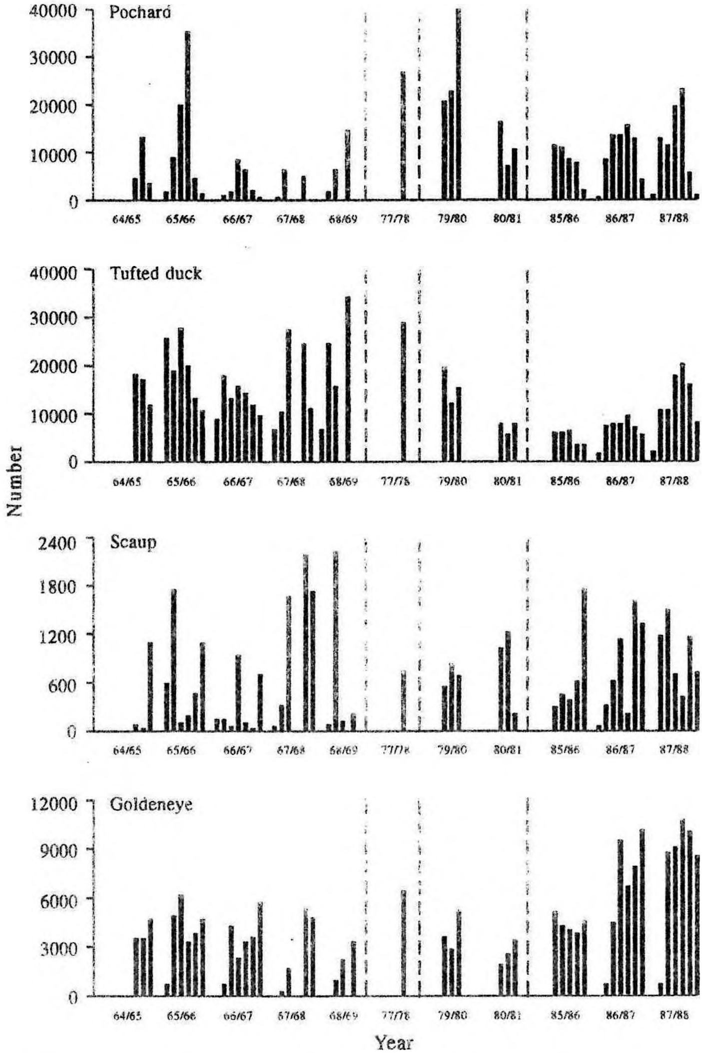

Figure 1: Trends in the numbers of Common Pochard, Tufted Duck, Greater Scaup and Common Goldeneye overwintering on Lough Neagh between 1965 and 1988. The horizontal axis plots all of the seasons for which data are available with one division for each month (seven per winter) and one division space between each year. The broken lines indicate breaks in the count coverage of one year or greater. Redrawn from Winfield *et al.* (1989) with permission from the Irish Wildbird Conservancy.

The population increase of Tufted Duck in Europe as a whole has been attributed to an increase in suitable man-made habitat and the continental spread of the zebra mussel, a preferred food item, (Owen *et al.*, 1986), but neither of these factors are applicable to the Lough Neagh situation. Furthermore, while Lough Neagh has been subject to changes in both lake levels and eutrophication, neither have occurred with a magnitude or timescale likely to have been responsible for the observed changes in the numbers of Tufted Duck (for a fuller argument see Winfield *et al.*, 1989).

By a process of elimination, interactions with the fish community were left as a possible agency of the fluctuations in the numbers of Tufted Duck overwintering on Lough Neagh. In particular, given the earlier findings of workers such as Pehrsson (1984) and Hill *et al.* (1987), competition for macroinvertebrate prey appeared to be a plausible hypothesis. However, in contrast to the situations studied by the above authors, such interactions on Lough Neagh would have to be occurring between fish and adult, rather than duckling, waterfowl. Furthermore, for the hypothesis to be correct, significant changes would have had to have occurred in the Lough Neagh fish community during the time period of the observed changes in the abundance of Tufted Duck.

THE FISH COMMUNITY AND INTRODUCTION OF THE ROACH

Like the fish communities of many lakes in Ireland, that of Lough Neagh is relatively species-poor when compared with similar lakes elsewhere in Europe, even though the native fauna has been augmented by anthropogenic introductions of new species over historical time. A brief description of the mid 1980s fish community of Lough Neagh is given by Winfield *et al.* (1993), who recorded bream (*Abramis brama*), eel, gudgeon (*Gobio gobio*), perch, pike (*Esox lucius*), pollan, river lamprey (*Lampetra fluviatilis*), roach, rudd (*Scardinius erythrophthalmus*), salmon (*Salmo salar*), stone loach (*Barbatula barbatula*), tench (*Tinca tinca*), three-spined stickleback (*Gasterosteus aculeatus*), and trout (*Salmo trutta*).

Even though complex patterns of spatial distributions (see upper part of **Figure 2**) and sampling biases make the calculation of an overall numerical composition of the Lough Neagh fish community a difficult and arguably misleading exercise, it is beyond doubt that eel, perch, pollan and roach are the four most abundant species and dominate the community in terms of both numbers and biomass. Moreover, during the mid 1980s the roach was the dominant fish in the inshore region of the lough during the summer, and was also important in the deepwater community during the cooler parts of the year when shallow habitats had been vacated (see lower part of **Figure 2**).

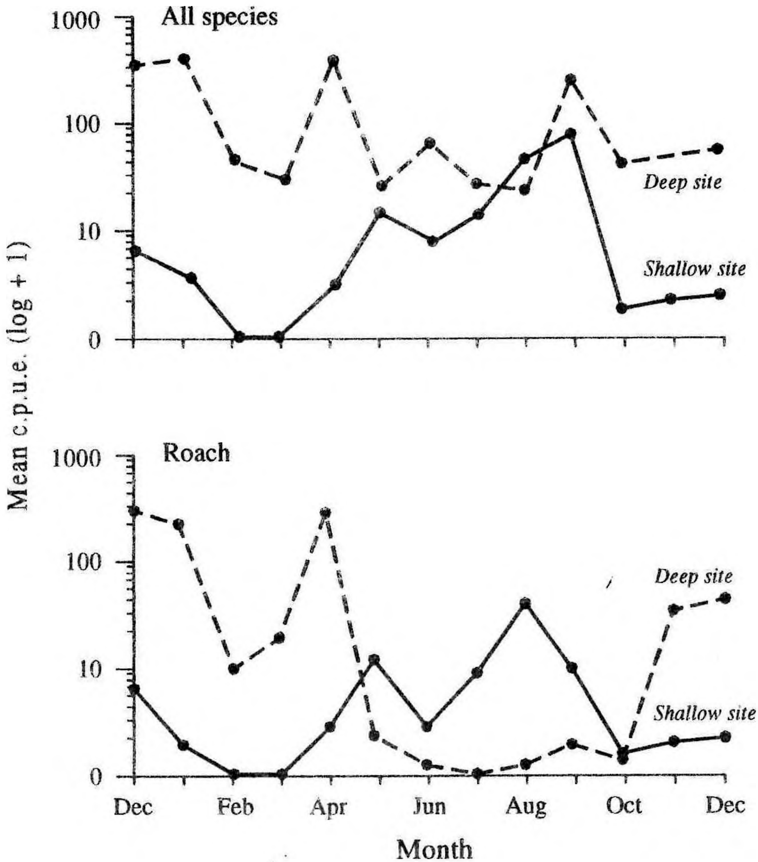

Figure 2: Seasonal changes in the abundance of all fish species and roach alone at shallow (Ballyronan Bay) and deep (Toome Bay) sites in Lough Neagh sampled by scientific trawling from December 1985 to December 1986. Redrawn from Winfield *et al.* (1993) with permission from Kluwer Academic Publishers.

This importance of roach in the Lough Neagh fish community was particularly remarkable because the species was only first recorded in a backwater of the catchment in 1970, presumably as a result of introduction by anglers (Cragg-Hine, 1973). While anecdotal evidence suggested a rapid subsequent increase in abundance and distribution during the 1970s (Cragg-Hine, *op. cit.*; Winfield *et al.*, 1993), quantitative data on the population dynamics of the roach in Lough Neagh are only available for the mid to late 1980s. Nevertheless, the introduction and establishment of the roach has undoubtedly been the major feature of the recent ecology of the Lough Neagh fish community.

DIVING DUCK AND FISH POPULATION CHANGES, 1985-1989

Although roach had become established as the dominant inshore fish of Lough Neagh by 1985, it subsequently underwent a dramatic decline in abundance as recorded by catch-per-unit-effort (c.p.u.e.) of scientific trawling (see insert of **Figure 3**) and the bycatch of the commercial fisheries (I.J.W., personal observations). Between 1985 and 1988, the declining roach population showed significant changes in individual size (main body of **Figure 3**) and age distributions. In 1985 the population was dominated by fish of approximately 90 mm in length and 2 years of age. This year class continued to dominate through to 1988, and thus the modal size class of the population reflected the growth of these fish. As a result, in 1988 the much reduced roach population was composed largely of fish approximately 150 mm in length and 5 years of age. There was very little recruitment of young roach until 1989 when a new strong year class appeared and the now declined population became dominated by fish approximately 40 mm in length and 1 year of age. The mechanism of the decrease in roach is difficult to determine, although a heavy infestation by the tapeworm *Ligula intestinalis* was recorded at the time (Tobin, 1986) and the observed repeated recruitment failure is a typical effect of this parasite.

It was notable that the increase in abundance of roach during the late 1970s and early 1980s coincided with the decrease in Tufted Duck presented in Fig. 1. Furthermore, the decline of roach during the mid to late 1980s occurred over a time period similar to that in which the overwintering Tufted Duck population recovered to its former levels of the 1960s. As a result, the c.p.u.e. of roach in a given summer was significantly negatively correlated with the average number of Tufted

Duck present during the following winter (Spearman's Rank Correlation r_s = -8.86, N = 9, p < 0.01). Thus, when roach were abundant, Tufted Duck were present in lower numbers (**Figure 4**).

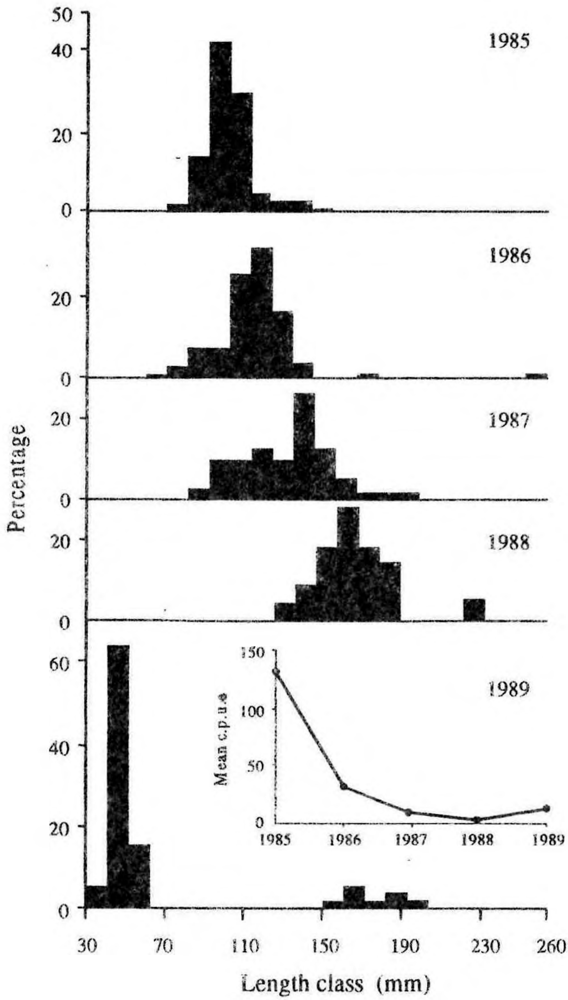

Figure 3: Changes in the size structure of the roach population during the period 1985 to 1989, with the corresponding trend in mean catch-per-unit-effort shown as an insert. Redrawn from Winfield *et al.* (1992) with permission from Kluwer Academic Publishers.

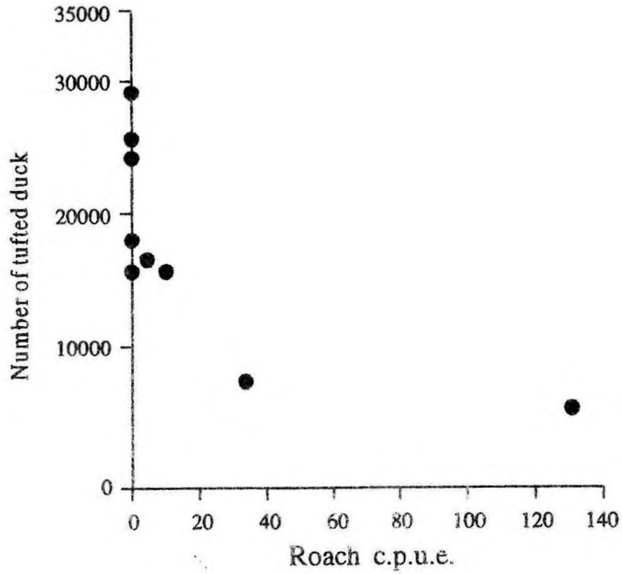

Figure 4: The relationship between the mean catch-per-unit-effort of roach from scientific trawling in a given summer and the mean number of Tufted Duck present during the following winter from 1965 to 1989. Points from the pre-1973 period assume that the catch-per-unit-effort of roach was zero. Redrawn from Winfield *et al.* (1992) with permission from Kluwer Academic Publishers.

When considering the possible mechanisms behind this apparent negative effect of roach on overwintering Tufted Duck, the agency of direct predation can be confidently discarded because even though the diet of the roach has been studied extensively (e.g. see review by Lammens and Hoogenboezem, 1991), predation on ducks or any other large vertebrates has never been recorded. On a more subtle level, Andersson (1981) has suggested three ways in which cyprinids such as roach may influence duck populations, i.e. by an indirect reduction of macrophytes, by an increase in eutrophication resulting from cascading effects through the zooplankton, or by direct competition for invertebrate food supplies. As macrophytes have been rare and the level of eutrophication has been relatively steady over the period of the observed interactions, only the latter mechanism can be operative on Lough Neagh. Further exploration of a competition hypothesis requires information on the feeding ecology of the waterfowl and fish of Lough Neagh.

DIVING DUCK AND FISH DIETS

Figure 5 shows the diet compositions of Common Pochard, Tufted Duck, Greater Scaup and Common Goldeneye, based on birds taken by shooting or accidental capture in gill nets between 1988 and 1990 (for further details see Winfield and Winfield, 1994b), in terms of both prey frequency of occurrence and composition by weight. The diets of Common Pochard, Greater Scaup and Common Goldeneye were dominated by chironomid larvae (100, 100 and 91 % by frequency of occurrence, respectively), although that of Common Goldeneye included a greater range of less important prey types. In contrast, the main prey of Tufted Duck was molluscs (71 %), with *Lymnaea peregra* (Muller) and *Valvata piscinalis* (Muller) being particularly important, and chironomid larvae being the second most frequently taken prey type (50 %).

The diet compositions of roach, perch, pollan and eel, based on fish over 70 mm in fork length collected by monthly trawling between 1989 and 1990 (for further details see Winfield and Winfield, 1994a) are given in **Figure 6**, although only data on prey frequency of occurrence could be consistently presented because of extensive prey mastication by the pharyngeal teeth of roach (diet descriptions for perch, pollan and eel based on prey weight may be found in Winfield and Winfield, *op. cit.*). Chironomid larvae were important in the diets of all four fish species, and dominated those of roach, pollan and eel (57, 65 and 96 % by frequency of occurrence, respectively). However, with the exception of eel, other prey types were also of considerable importance in the diets. For perch and pollan, the malacostracan *Mysis relicta* Loven was particularly important (83 and 50 %, respectively). Most notably, however, the second most frequently taken prey type of roach was molluscs (46 %), particularly *Valvata piscinalis*. Moreover, data presented in detail in Winfield and Winfield (*op. cit.*) showed that molluscs were only a major dietary component of roach greater than 160 mm in length.

A summary of overlaps among the above waterfowl and fish diets is presented as a dendrogram in **Figure 7** (for full methodological details see Winfield and Winfield, 1994b). Three distinct groupings were apparent. Common Pochard, Greater Scaup and eel formed a close group with diets overwhelmingly dominated by chironomid larvae, with which Common Goldeneye was also associated. Tufted Duck and roach formed a second group in which molluscs were also important in the diet. Finally, pollan and perch constituted a third and very isolated group in which *Mysis relicta* was an important dietary component.

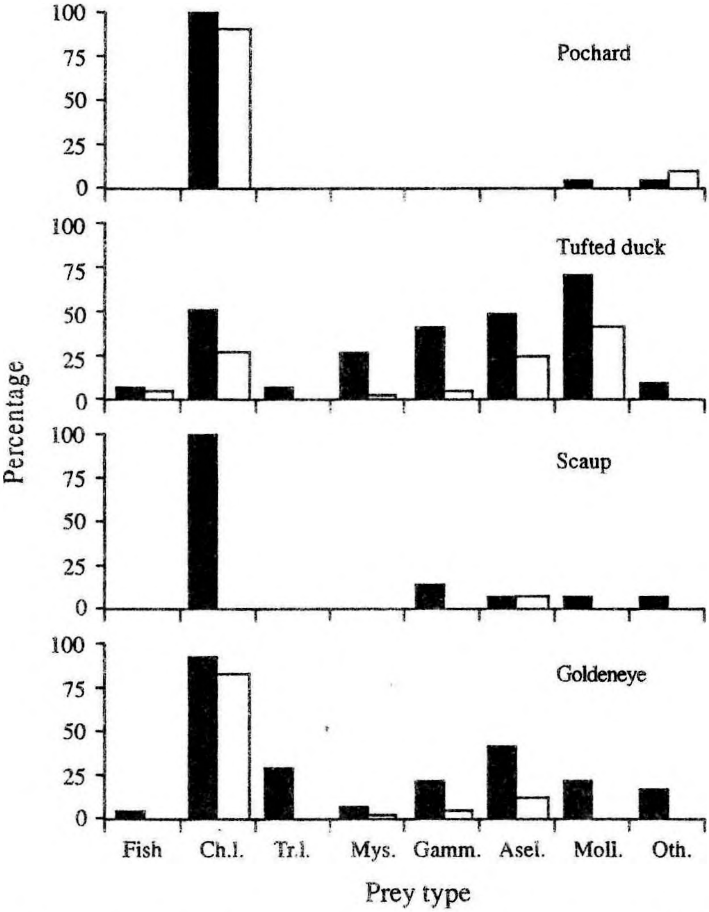

Figure 5: The diet compositions of 25 Pochard, 14 Tufted Duck, 14 scaup and 23 Common Goldeneye presented as prey frequency of occurrence (closed bars) and percentage by weight (open bars) during 1988 to 1990. Abbreviations are as follows; Ch. l., chironomid larvae. Tr. l., Trichoptera larvae. Mys., *Mysis relicta*. Gam., *Gammarus* sp. Asel., *Asellus* sp. Moll., molluscs. Oth., other. Redrawn from Winfield and Winfield (1994b) with permission from Blackwell Scientific Ltd.

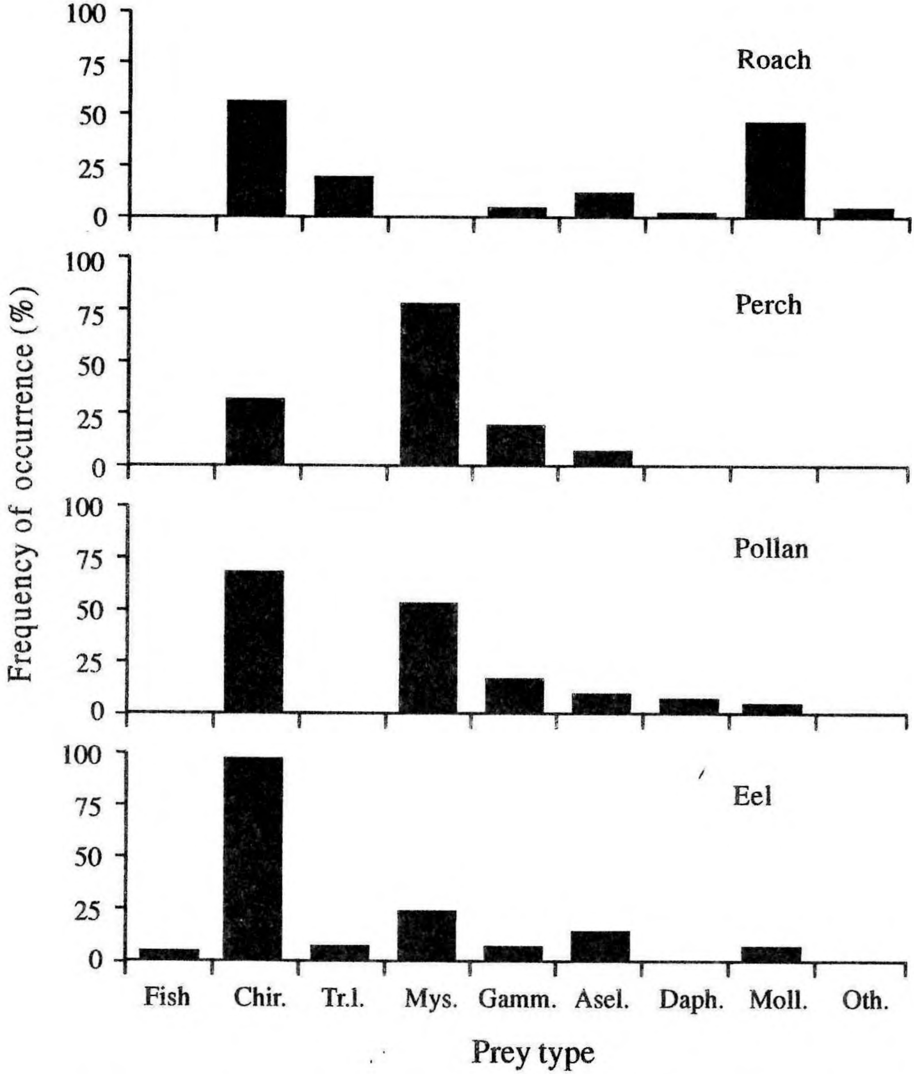

Figure 6: The diet compositions of 69 roach, 87 perch, 155 pollan and 25 eel greater than 70 mm in fork length as assessed by prey frequency of occurrence during 1989 and 1990. Abbreviations are as follows; Chir., chironomid larvae, pupae and adults. Tr. l., Trichoptera larvae. Mys., *Mysis relicta*. Gam., *Gammarus* sp. Asel., *Asellus* sp. Daph., *Daphnia* sp. Moll., molluscs. Oth., other. Redrawn from Winfield and Winfield (1994a) with permission from Kluwer Academic Publishers.

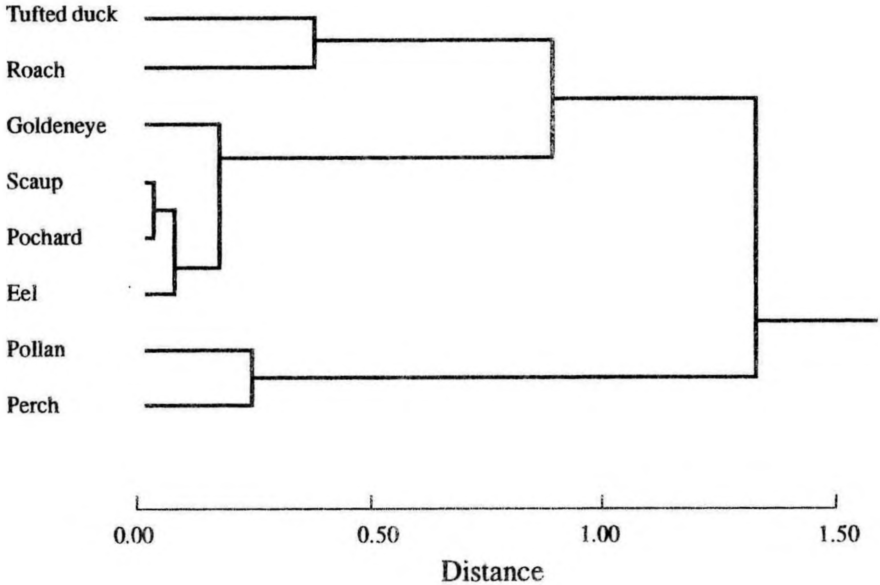

Figure 7: Dendrogram showing the diet similarities based on prey frequency of occurrence among the major diving duck and fish populations of Lough Neagh. Redrawn from Winfield and Winfield (1994b) with permission from Blackwell Scientific Ltd.

Although the above analyses revealed a high dietary overlap between Tufted Duck and roach consistent with a competition hypothesis, they do not in themselves show that competition is actually occurring. In order to demonstrate such an interaction unequivocally, the commonly-exploited food resources must also be shown to be limiting and, ideally, the system should be manipulated experimentally. While information on the abundance and distribution of the Lough Neagh benthos was obtained during 1989 to 1990 (for details see Winfield and Winfield, 1994b), it was not possible to determine if the absolute densities observed were effectively limiting in the context of the foraging requirements of Tufted Duck s and roach. Nevertheless, it did appear that the inshore areas of the lough offered poor feeding conditions for diving ducks because chironomid larvae and molluscs were of small individual body size or low abundance. This led to Tufted Duck s foraging at least in part at depths greater than those usually exploited, which in turn may have made them more likely to be outcompeted by a truly aquatic benthivore such as roach.

Unfortunately, the experimental manipulation of a system involving a very large lake, tens of thousands of waterfowl and probably hundreds of thousands of fish is clearly impossible. However, given the 'natural experiments' produced by the introduction of the roach in the 1970s and its subsequent demise in the 1980s, it is possible that a third natural experiment may occur in the 1990s in the form of a recovery of the roach population. In such circumstances, the continued monitoring of the overwintering Tufted Duck population and a repetition of the diet and benthos studies described above would produce information pertinent to the competition hypothesis.

THE SITUATION IN THE 1990s

While the consistent scientific monitoring of the roach population described above has been discontinued in the 1990s, other scientific sampling (R. C. Kirkwood, University of Ulster Freshwater Laboratory, unpublished data) and anecdotal information from the commercial fisheries of Lough Neagh have shown that, unfortunately in the context of this study, the roach population has not yet shown any signs of recovery. This situation is also indicated by the trend between 1985 and 1994 in the winning weight of angling matches held on the Upper Bann, one of the lough's major tributaries to which fish freely migrate (see Winfield *et al.*, 1993) and where roach formed a major component of the catch at the beginning of this period (**Figure 8**). Winning weights usually exceeded 50 kg in the mid 1980s, but since 1990 they have not exceeded 20 kg and other species such as bream are now of more importance.

Although the lack of a roach recovery is frustrating in that it does not allow further 'experimental' testing of the competition hypothesis, it is relevant to note that following the recovery of Tufted Duck in the late 1980s, the numbers of overwintering birds in the 1990s have remained remarkably stable (**Figure 8**), as would be predicted by the competition hypothesis.

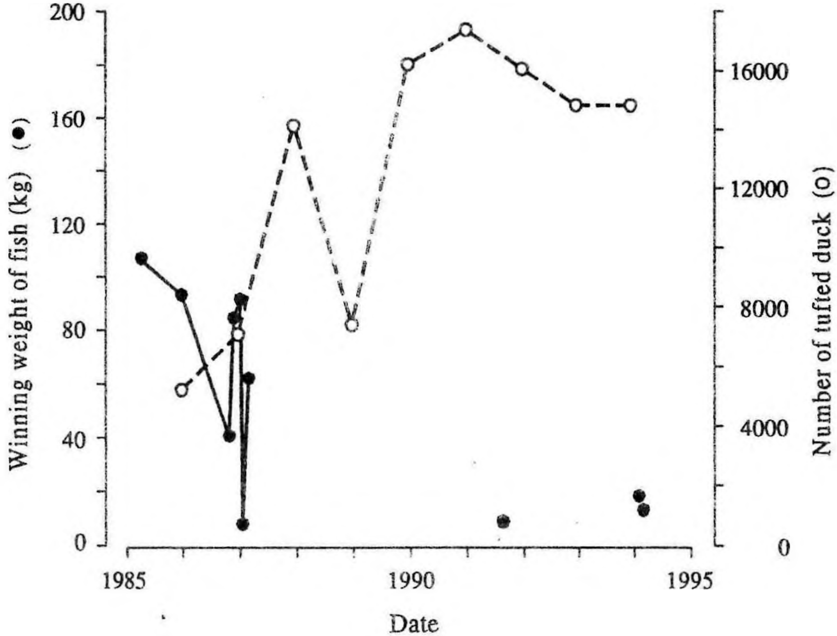

Figure 8: Trends between 1985 and 1994 in the winning weight of angling competitions (closed circles) held on the Upper Bann, a major tributary of Lough Neagh, and the mean numbers of overwintering Tufted Duck (open circles).

CLOSING REMARKS

The present synthesis of our study of the overwintering waterfowl and fish of Lough Neagh is presented not as a completed investigation, but as the story so far in a project which by its very nature must be both long-term and broad. The study contains both strengths and weaknesses, some of which are likely to be found in any investigation of interactions between waterfowl and fish, which will be briefly considered in this closing section.

Firstly, while waterfowl, fish and limnology are still sometimes investigated by workers residing in discrete research bodies, arguably the greatest strength of our study is that it has combined the expertise of workers from these three areas and as a consequence has allowed the combination of long-term population data with detailed information on feeding ecology. However, this collaboration only arose through largely fortuitous circumstances. Although communication and collaboration between relevant disciplines are improving through workshops such as that reported in the present volume and that of Kerekes and Pollard (1994), much remains to be done to bring researchers into full contact with each other. Expertise transfer and increased accessibility should remain a fundamental goal of the research community.

Studies of competition between any organisms can be conducted either by simple correlative analyses, which may reveal apparent manifestations of competition but are in themselves inconclusive and indicate nothing of the responsible mechanisms, or by experimental manipulations of varying scale, which are more robust. Examples of waterfowl-fish correlation analyses in space and time are provided by Eriksson (1979) and Andersson (1981), respectively, while Pehrson (1984), Hill *et al.* (1987) and Giles (1994) described experimental studies of increasing scale and complexity. In particular, the study of Giles (*op. cit.*) involved an entire-lake manipulation in which the abundance of a cyprinid-dominated fish community of a medium-sized flooded gravel pit was greatly reduced. Such an ambitious approach is to be applauded and highly recommended for future research projects, although in practice the difficulties inherent in such work are likely to remain a major restriction on the common use of this powerful technique. Moreover, fish removal is usually impossible on larger or natural water bodies such as Lough Neagh, where researchers are likely to have to continue to wait patiently for 'natural experiments' such as those described in this review.

Another difficulty in any study of competition lies in translating prey abundance as measured by the researcher into prey abundance as perceived or assessed by a foraging animal, e.g. what densities of molluscs expressed as a number of individuals per square metre of substratum may be foraged profitably (in energetics terms) by a diving duck? Studies on other predators suggest that what may appear to be a relatively high absolute abundance may in fact be too low for the predator to exploit. For example, young roach switch from feeding on planktonic cladocerans to taking benthic species when the density of the former falls to *c.* 40 individuals per litre (Townsend *et al.*, 1986), which would otherwise probably be interpreted as still a relatively high density. For diving predators such as many waterfowl, additional factors including water depth will also be critical in the energetics of benthivory. A full understanding of this aspect of the feeding ecology of adult Tufted Duck would require laboratory-based experimental observations similar to those carried out by Giles

(1990) for Tufted Ducklings. As with the technique of entire-lake manipulation, such an approach is certainly to be recommended but is unlikely to become commonplace.

Finally, and perhaps most importantly, some comment must be made on the role of long-term investigations in the study of interactions between waterfowl and fish. Most members of both of these animal groups are relatively long-lived and so a long-term component is essential in any programme of research into their population dynamics. Fortunately, the long-standing popularity of birdwatching as a recreation has resulted in the accumulation of decades of waterfowl population data which are now available for many lakes in Europe and elsewhere. Unfortunately, the rarity of such studies on other components of lake biota, including fish (see Elliott, 1990), means that most of these counts cannot be exploited in the study of interactions between waterfowl communities and other aspects of lake ecosystems. In the frequent absence of long-term fish data, the study of competitive and other interactions between these two major groups of freshwater vertebrates will be regrettably slow, but their importance is such that their investigation must not fall into neglect.

ACKNOWLEDGEMENTS

Many people and organisations too numerous to mention here, but already acknowledged in our earlier publications, made invaluable contributions to our work. However, we would like to record again our particular thanks to the many who have counted the waterfowl of Lough Neagh over the last 30 years, to the staff and students of the University of Ulster's Freshwater Laboratory, and to Bob Foy for the total phosphorus data. Robert Buick of the Ulster Coarse Fishing Federation kindly made available the match angling records, while the figures were ably and swiftly produced by Trevor Furnass.

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