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# Possible competitive interactions between overwintering tufted duck (*Aythya fuligula* (L.)) and fish populations of Lough Neagh, Northern Ireland: evidence from diet studies

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## Abstract

The overwintering population of tufted duck (*Aythya fuligula*) on Lough Neagh, Northern Ireland, has varied over the last three decades, with numbers declining in the early 1980s but then increasing to former levels in the late 1980s. Population fluctuations of recently introduced roach (*Rutilus rutilus*) mirrored these trends. The present study explores the possibility that competition for benthic food resources is responsible for these changes by examining the diets of tufted duck, roach and other major fish species of the lake. Diet overlaps were generally high due to the common consumption of chironomid larvae. The diet of tufted duck overlapped most with that of roach because these two species were the only significant consumers of molluscs. This evidence provides further support for a tufted duck – roach competition hypothesis.

## Introduction

The important role played by fish in the functioning of some freshwater ecosystems is widely acknowledged in limnology (see for example Persson *et al.*, 1988), particularly the effects of fish predation on zooplankton dynamics (see reviews by Zaret, 1980 & Lazzaro, 1987). Other studies have shown a direct effect of fish on benthic macroinvertebrates (Andersson *et al.*, 1978; Post & Cucin, 1984; Lammens *et al.*, 1985), which indicates that distant competition (defined by Hurlbert *et al.*, 1986 as competition between taxonomically remote species) may occur between fish and waterfowl. There is increasing evidence that such competitive interactions do occur, at least during the waterfowl breeding season when their protein requirements are high. Eriksson (1979) found that the distribution of fledged goldeneye (*Bucephala clangula* (L.)) was negatively associated with the presence of fish, mainly roach (*Rutilus rutilus* (L.)) and perch (*Perca fluviatilis* L.), and increased their use of an experimental lake after the fish were removed. Eadie & Keast (1982) reported dietary evidence to support the competition hypothesis for goldeneye and *Perca* spp., and Giles *et al.* (1990) suggested that significant diet overlap exists between perch and the ducklings of mallard (*Anas platyrhynchos* (L.)) and tufted duck (*Aythya fuligula* (L.)). In addition, Pehrsson (1984) and Hill *et al.* (1987) have found experimental evidence of competitive interactions between fish and breeding mallard.

In all of the above interactions, the observed or postulated competition was asymmetrical with waterfowl being out-competed by fish. The effects of such competition on long-term population dynamics of waterfowl have not yet been clearly demonstrated and we know of only one study which has addressed this issue. Andersson (1981) suggested that declines in waterfowl, including tufted duck, on increasingly eutrophic lakes in southern Sweden have been caused at least in part by competition for benthic food resources with increasing cyprinid populations, principally roach and bream (*Abramis brama* (L.)). A similar decline occurred in the numbers of tufted duck overwintering on Lough Neagh in Northern Ireland during the early 1980s, although it was followed by an increase to former levels (Winfield *et al.*, 1989). Winfield *et al.*, (*op. cit.*) hypothesized that these fluctuations resulted from competition between tufted duck and recently introduced roach which has shown marked changes in abundance in recent years. In support of this hypothesis, the abundances of tufted duck and roach on Lough Neagh over the period from 1965–1989 have been shown to be negatively correlated (Winfield *et al.*, 1992).

Here, we investigate the potential for competitive interactions between adult tufted duck and roach on Lough Neagh by examining their diets and assessing the degree and nature of their overlap. The diets of the other major fish populations in the lake are also reported.

## Methods

### Study site

Lough Neagh is the largest lake in the British Isles (surface area *ca.* 387 km$^2$), although it is relatively shallow (mean depth of *ca.* 9 m). During this century, the lake has been severely enriched by inputs of nutrients such that in the early 1970s it was considered one of the most eutrophic lakes in the world with maximum nitrogen, phosphorus and chlorophyll *a* levels of 900, 60 and 93 mg m$^{-3}$ respectively (Wood & Gibson, 1973). Following the introduction of phosphate-stripping at the catchment's major sewage treatment works in 1981 (Gibson, 1986), water quality appears to be improving.

Primary production is dominated by phytoplankton and was estimated by Jewson (1976) to be 560 g C m$^{-2}$ y$^{-1}$. Due to a combination of depth, turbidity, and exposure, macrophytes are restricted to a relatively small number of sheltered inshore areas. The benthos has been extensively studied during the last twenty years and has been found to be dominated by chironomid larvae (particularly *Chironomus anthracinus* Zett.) and oligochaetes (Carter, 1976; Carter, 1978; Carter & Rippey, 1982), although sampling techniques are likely to have underestimated the density of molluscs. *Mysis relicta* Loven occurs both in the open water and at the sediment surface. Lough Neagh contains significant populations of roach, perch, pollan (*Coregonus autumnalis pollan* Thompson) and eel (*Anguilla anguilla* (L.)) which are all exploited by commercial fisheries (Winfield *et al.*, in press).

### Field sampling

During January 1988–March 1988, a total of 27 tufted ducks was obtained from Lough Neagh wildfowlers, although only five individuals had prey items present in the oesophagus/proventriculus region of the alimentary canal. In November 1988, a further six tufted duck were received from wildfowlers, but were all found to be devoid of food. During November 1989–March 1990, nine tufted ducks, all of which contained prey items in the first part of the gut, were obtained as accidental captures in commercial fishery and research gill nets. Of the 42 tufted duck examined, the present analysis is therefore restricted to a total of 14 individuals (five shot and nine netted) which contained large numbers of easily recognisable prey items in the oesophagus/proventriculus region of the gut.

Fish were obtained from monthly trawls on Lough Neagh during March 1989–March 1990 using a bottom trawl with a 6 mm mesh cod-end. Trawls were taken at four sites, at depths of 3, 5, 10 and 15 m, along a transect in the north-west part of the lake, running east from the sandy beach of Ballyronan Bay (Irish Grid Ref. H 956 869) out to the muddy sediments of the deeper waters (Irish Grid Ref. H 977 860). At each site a series of five 5 minute trawls was taken and all fish captured were counted and measured. Only those individuals greater than 70 mm fork length and with prey items present in the gut were included in the present analysis, which amounted to 155 pollan (size range 70 to 250 mm), 87 perch (70 to 194 mm), 69 roach (74 to 280 mm) and 25 eel (172 to 630 mm).

*Laboratory examination*

Following collection, all tufled duck were eviscerated following the method of Harrison (1960), either in the field immediately after they were shot or as soon as possible after they were received. The contents of the oesophagus/proventriculus region of the alimentary canal were then removed and preserved in 80% alcohol. Later, prey items were separated and counted under a binocular microscope, before being dried at 60 °C for 24 hours and weighed. Molluscs were weighed with their shells removed.

The contents of fish stomachs (or entire alimentary canal in the case of roach) were removed within minutes of capture and preserved in a solution of 4% formalin. Prey types for pollan, perch and eel were separated, counted and identified as far as possible before being dried at 60 °C for 24 hours and weighed. Again, molluscs were weighed with their shells removed. Diet analysis procedures are difficult for roach due to the mastication of macroinvertebrate prey by their pharyngeal teeth. As a result, our analysis of roach diet was restricted to prey frequency of occurrence.

*Assessment of diet overlap*

The overlaps in diet composition between the tufted duck and the four species of fish were ex-

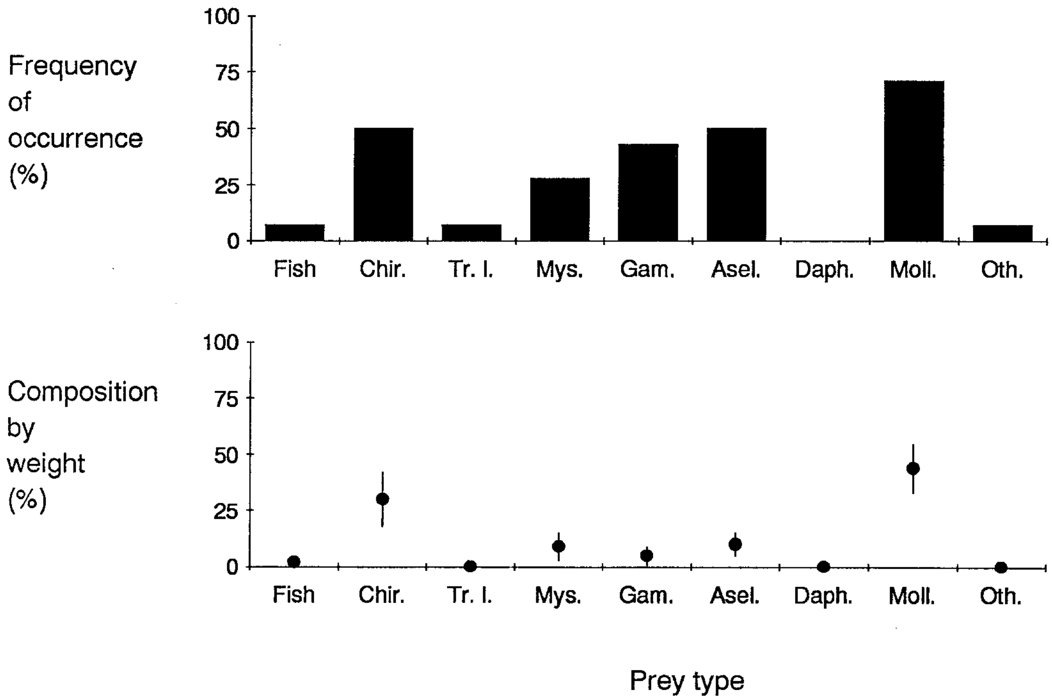


*Fig. 1.* The diet composition of tufted duck as assessed by prey frequency of occurrence, and prey weight (mean ± 1 S.E.). Abbreviations are as follows; Chir., chironomid larvae. Tr. l., Trichoptera larvae. Mys., *Mysis relicta*. Gam., *Gammarus* sp. Asel., *Asellus* sp. Daph., *Daphnia* sp. Moll., molluscs. Oth., other.

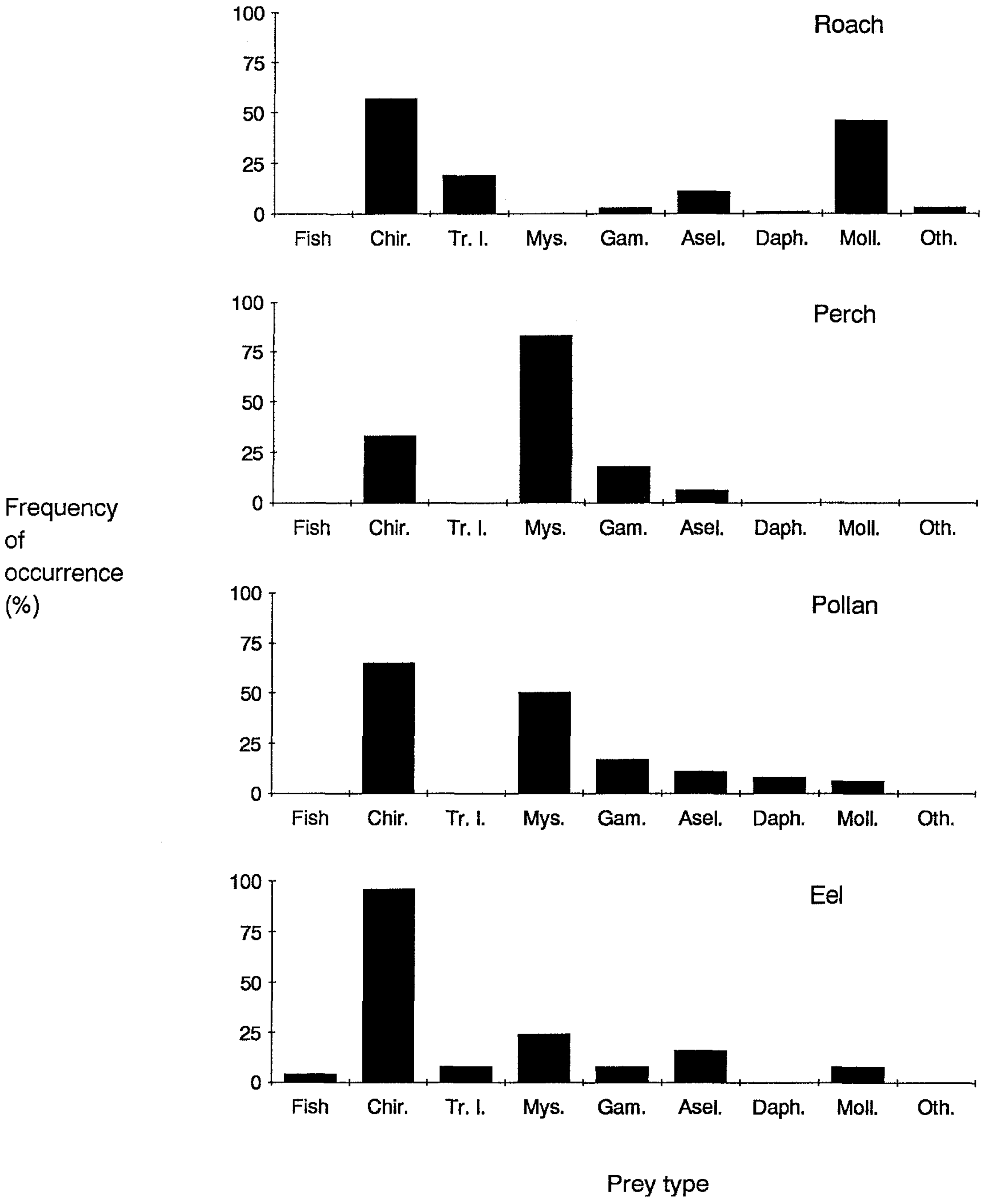


*Fig. 2.* The diet compositions of roach, perch, pollan and eel as assessed by prey frequency of occurrence. Abbreviations are as given in the legend of Fig. 1, except that Chir. also includes chironomid pupae and adults.

amined using the following formula proposed by Tokeshi (1986):

$$M = \Sigma_x \min\,[u_i(x), u_j(x)],$$

where $u_i(x)$ and $u_j(x)$ denote the proportional utilization of prey type $x$ by species $i$ and $j$ respectively. $M$ ranges between 0, which indicates no overlap, and 1, which indicates complete overlap.

Two sets of overlap values were calculated. Firstly, utilizations based on prey frequency of occurrence were used to assess overlaps between tufted duck and roach, perch, pollan and eel. Secondly, utilizations based on prey weights were used to assess overlaps between tufted duck and perch, pollan and eel.

## Results

### *Tufted duck diet*

The diet compositions of tufted duck in terms of prey frequency of occurrence and prey weight (based on a total of 2150 mg dry weight of prey) are shown in Fig. 1. Molluscs were the dominant prey in the diet of tufted duck in terms of both frequency of occurrence (71%) and weight (44 ± 11%, mean ± 1 S.E.). Four species of molluscs were found (*Hydrobia jenkinsi* Smith, *Lymnaea peregra* (Muller), *Planorbis albus* Muller and *Valvata piscinalis* (Muller)), but only *L. peregra* and *V. piscinalis* were important.

Chironomid larvae also formed a major component of the diet, occurring in 50% of individuals and comprising 30 ± 12% of the diet by weight. *Mysis relicta*, *Gammarus* sp. and *Asellus aquaticus* were common but only in small

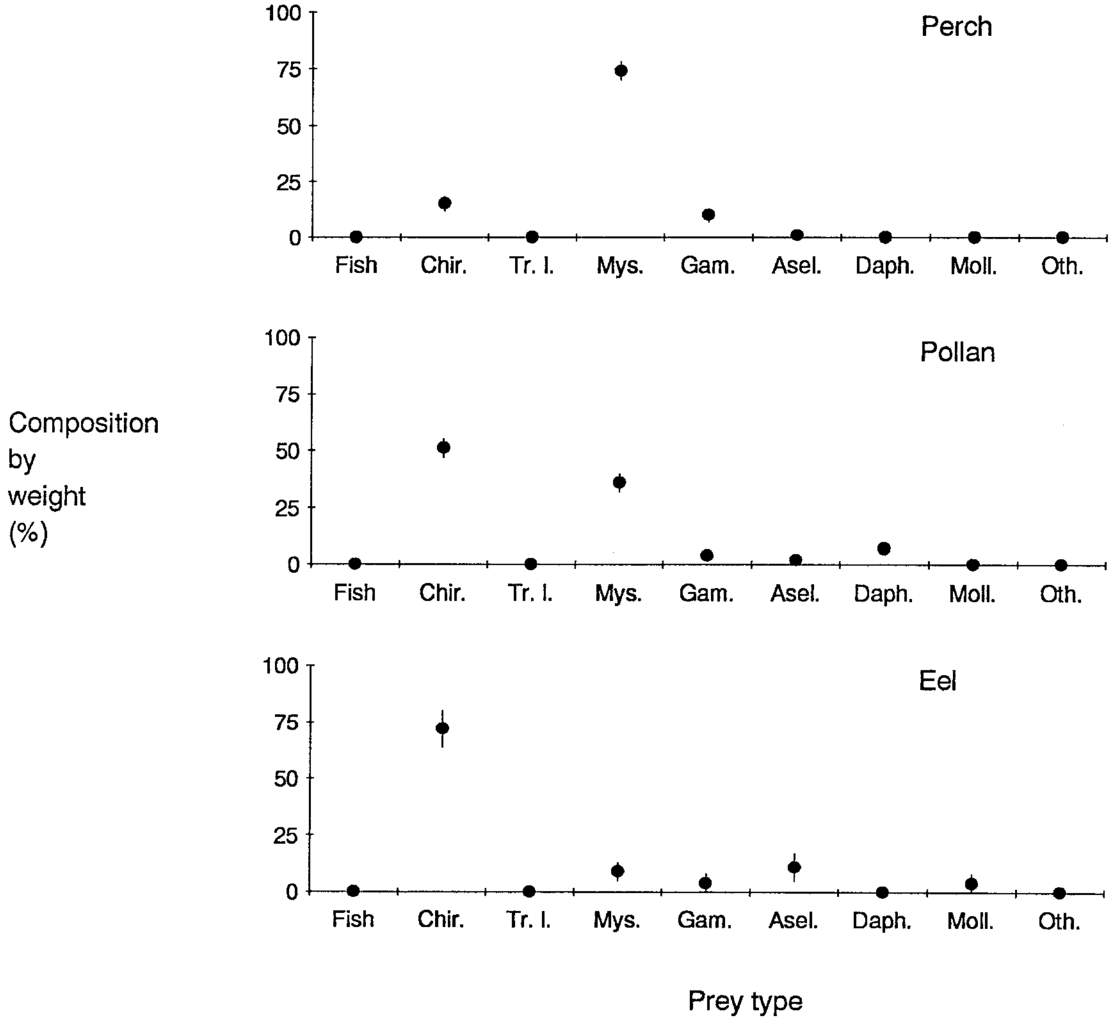


*Fig. 3.* The diet compositions of perch, pollan and eel as assessed by prey weight (mean ± 1 S.E.). Abbreviations are as given in the legend of Fig. 1, except that Chir. also includes chironomid pupae and adults.

amounts. Trichoptera larvae, *Potamogeton* sp. seeds (placed in the 'other' category of Fig. 1), and a single fish (a young eel of 90 mm in length) were each found in only one individual.

### *Fish diets*

The diet compositions of roach, perch, pollan and eel in terms of prey frequency of occurrence are presented in Fig. 2, while diet compositions by prey weight of perch, pollan and eel are shown in Fig. 3 (based on totals of 843 mg, 9858 mg and 5304 mg dry weight of prey for perch, pollan and eel respectively). Chironomidae and molluscs dominated in roach diets and were found in 57% and 46% respectively of all individuals, while Trichoptera larvae and *Asellus aquaticus* were taken by 19% and 11% respectively of all individuals. *Daphnia* sp., Corixidae and Ceratopogonidae (the latter two prey types placed in the 'other' category of Fig. 2) each occurred in only one individual, while *Gammarus* sp. were found in only two individuals.

Molluscs formed a major component of the diet of roach but fragmentation by the pharyngeal teeth precluded their gravimetric analysis and even consistent identification to species, although the majority were *Valvata piscinalis*. Another important aspect of molluscivory in roach is shown in Fig. 4. The frequency of mollusc consumption by roach in Lough Neagh is clearly dependent on fish size (*G* test on individuals pooled into 70–129, 130–189 and 190–309 mm size classes, $G = 38.06$, $p < 0.001$). Molluscs form a major dietary component only of roach greater than 160 mm in length.

The diet of perch was dominated by *Mysis relicta* which occurred in 83% of individuals and comprised 74 ± 4% of the diet by weight. Chironomidae and *Gammarus* sp. were the only other prey types important in the diet of this fish. The diet of pollan was similar, with Chironomidae constituting 65% of the diet by frequency of occurrence and 51 ± 4% by weight, while *Mysis relicta* was also of importance (frequency of occurrence 50%, contribution by weight 36 ± 4%). The diet of eel was overwhelmingly dominated by Chironomidae which were found in 96% of individuals and comprised 72 ± 8% of the diet by weight.

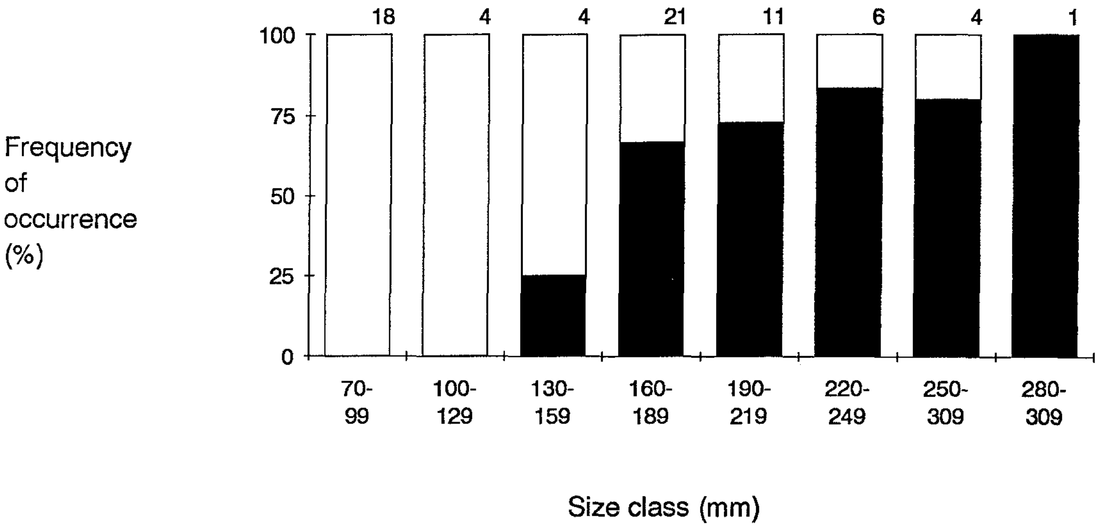


*Fig. 4.* The relationship between the size of roach and the consumption of molluscs. For each size class, the frequency of occurrence of molluscs is shown by the closed portion of the bar. The numbers of fish in each size class are given at the top of each bar.

*Table 1.* Overlap indices for the diets of tufted duck and roach, perch, pollan and eel (overlap based on diet composition by prey weight for tufted duck and roach could not be calculated).

| Overlap index | Roach | Perch | Pollan | Eel |
|---|---|---|---|---|
| By prey frequency of occurrence | 0.59 | 0.45 | 0.42 | 0.49 |
| By prey weight | – | 0.30 | 0.45 | 0.57 |

*Diet overlaps*

The diet overlap indices for tufted duck and the four species of fish are given in Table 1. In calculations based on prey frequency of occurrence, the highest overlap was between tufted duck and roach (0.59), largely due to their common consumption of molluscs. In calculations based on prey weight (for which roach data are unavailable) the highest overlap was between tufted duck and eel (0.57), in this instance due to their shared consumption of chironomid larvae rather than molluscs.

## Discussion

Competition is notoriously difficult to demonstrate unequivocally in natural communities (see for example Schoener, 1983), and is even more intractable when the studied species are as long-lived and mobile as waterfowl and fish. However, if such interactions do exist they are likely to have important implications for game and conservation management (Andersson, 1982; Wright & Street, 1985). This discussion is tendered as a part of a larger study of these potential interactions on Lough Neagh (Winfield, 1991; Winfield *et al.*, 1989; Winfield *et al.*, 1992) and is restricted to an assessment of diet overlaps between tufted duck and the major fish species.

Tufted ducks are primarily carnivorous with molluscs generally dominating the diet and chironomid larvae typically assuming primary importance only when the former are unavailable (see review by Cramp & Simmons, 1977). In mainland Europe the zebra mussel *Dreissena polymorpha* (Pallas) is the most preferred prey and the spread of this mollusc is thought to be at least partly responsible for observed increases in tufted ducks (Owen *et al.*, 1986). Despite the absence of this particular bivalve from Lough Neagh, molluscs are still very important in the local diet of tufted duck in contrast to those of the other diving duck species of this lake (Winfield, 1991). While the numbers of analysed ducks were small, diet compositions were consistent within a species and statistically significantly different between species (Winfield, *op. cit.*). More tufted ducks could have been obtained from Lough Neagh wildfowlers, but their gut contents are likely to have been of limited use because of the usual restriction of food to the gizzard region, reflecting the rapidity of digestion in wildfowl (Grandy, 1972). Analysis of diet composition based only on gizzard contents can result in severe bias because of differential digestion rates of hard and soft prey (Thompson, 1969; Swanson & Bartonek, 1970). As also noted by Bengston (1971) and Gardarsson (1979), we found that much better diet samples can be obtained from ducks taken in gill nets. However, given the small scale of winter gill net fisheries operating in the UK, only small sample sizes of overwintering ducks can be produced by this technique.

Within the Lough Neagh fish community, molluscs are consumed in appreciable amounts only by the roach population. In other localities, roach often feed predominantly on macrophytes or filamentous algae (see review by Lammens & Hoogenboezem, 1991) and such a plant-dominated diet was found by Giles *et al.* (1990) to minimise overlap between roach and waterfowl in a macrophyte-rich lake. However, roach can also feed extensively on animal food, especially zooplankton and molluscs, and this species is considered to be one of the most efficient molluscivores among European cyprinids (Nagelkerke *et al.*, 1991). While Giles *et al.* (1990) found that consumption of cladoceran zooplankton by adult roach minimised diet overlap between roach and waterfowl in a macrophyte-poor lake, such prolonged planktivory does not occur in Lough Neagh, probably because the zooplankton is dominated by less preferred copepods (A. G. Fitzsimons, F.B.I.U., Department of Agriculture N.I., pers. comm.). Our data indicate that molluscs were a major component of the diet of roach greater than 160 mm in length in Lough Neagh during 1989 and 1990. Small roach of age groups $0^+$ and $1^+$ in this lake thus have little overlap with tufted duck in terms of molluscan prey.

The rarity of macrophytes in Lough Neagh also has an important indirect effect on the diet of perch. In this lake, *Mysis relicta* largely replaces the macrophyte-associated macroinvertebrates such as Ephemeroptera and Trichoptera larvae which are normally common in the diets of perch (see review by Craig, 1987) and which have elsewhere led to high diet overlaps with waterfowl (Eadie & Keast, 1982). In contrast, the diets of benthivorous pollan and eel in Lough Neagh conform with the general patterns of diet compositions of these or closely related species observed in other lakes (see reviews by Jacobsen, 1982 and Sinha & Jones, 1975 respectively). The dominance of Chironomidae in the benthos of Lough Neagh and consequent importance in the diets of the tufted duck and fish results in generally high levels of diet overlap, although this is most marked for tufted duck and roach due to the selection for molluscs shown by these two species. The high overlap between tufted duck and eel is solely due to their joint consumption of chironomid larvae; eel do not feed extensively on molluscs in Lough Neagh and so are unlikely to be involved in competition for these prey.

Diet overlap is a pre-condition of exploitative competition for food resources, but it does not itself prove that competition is occurring as food resources must also be limited. In the eutrophic Lough Neagh, chironomid larvae have been very abundant for at least several decades (Carter, 1976; Carter, 1978; Carter & Rippey, 1982; Winfield, 1991) and so are probably not limiting to their vertebrate predators. For example, over the winter of 1989/1990 the density of chironomid larvae averaged over the lake as a whole was 6250 individuals $m^{-2}$ in September, declining to 3275 individuals $m^{-2}$ in March (Winfield, 1991). If competition does occur between tufted duck and the fish of Lough Neagh it is likely to be with the roach population for molluscs, and could result in a decline in the overwintering numbers of tufted duck as the benthivorous roach population increases. Similar reductions in overwintering numbers of waterfowl in response to reduced food resources have been recorded elsewhere, for example on the Firth of Forth in Scotland (Owen *et al.*, 1986), and are facilitated by the great mobility of this group of aquatic vertebrates.

Our analysis of the diets of tufted duck and roach was carried out following a marked decline in the abundance of the latter species and thus, we suggest, during a period of reduced competition. A further test of the competition hypothesis could be made by determining mollusc availability and contribution to the diets of tufted duck and benthivorous roach during any future period of high abundance of the latter, when we would predict that mollusc populations would be less abundant in the lake and reduced in importance in at least the diet of the tufted duck. Although good roach recruitment in the late 1980s (see Winfield *et al.*, 1992) has subsequently failed to result in an increase in the abundance of larger, benthivorous individuals (I.J.W., unpublished data), such a recovery may still occur in the future.

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