

FEEDING SELECTIVITY OF BROWN TROUT (*SALMO TRUTTA*) IN LOCH NESS, SCOTLAND

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Introduction

Loch Ness (Fig. 1) lies in the Great Glen, a glacially-deepened rift which was originally tectonic in origin. Hence the loch has a very regular trench-like morphometry, with steeply shelving sides sloping down to a flat bed. This produces a restricted littoral zone, where powerful wave action on the steep, rocky shores permits growth of few macrophytes (Burgis & Morris 1987). The loch has the greatest mean depth of any lake in Britain and Ireland (ca. 132 metres) and comprises two basins, the north reaching a maximum depth of 227 metres and the south a maximum of 221 metres (Young & Shine 1993). Consequently, Loch Ness contains the largest volume of water for any lake in the British Isles ($74.52 \text{ m}^3 \times 10^8$). The loch drains eastwards via the River Ness and has been connected to the west coast by the Caledonian canal since 1822. It is oligotrophic and the water is extensively stained with peat (Burgis & Morris 1987), so that light attenuates rapidly in the Loch Ness water column.

Martin & Shine (1988) found that most of the pelagic fish in Loch Ness inhabited the top 30 metres of the water column, with Arctic charr *Salvelinus alpinus* dominating much of this stratum. Brown trout *Salmo trutta* occurred in the surface waters, with the exception of the larger ferox trout found within and below the charr layer. The loch's trout are a natural population, dating from the Pleistocene retreat some 8 to 10 thousand years ago (Campbell 1979). The pelagic food web in Loch Ness can be simplified thus: autochthonous and allochthonous production, linked with the microbial loop, is grazed by the crustacean zooplankton genera *Bosmina*, *Daphnia*, *Eudiaptomus* and *Holopedium*. The former three are themselves food for *Cyclops* which, along with the grazers it consumes, is thought to be predated by *Bythotrephes*, *Leptodora* and *Polyphemus*. Brown trout, Arctic charr and three-spined stickleback *Gasterosteus aculeatus* consume the zooplankton. Crustacean zooplankton abundance and species composition in Loch Ness is highly seasonal, with total numbers peaking in May 1998. Copepods, always numerically prominent, dominated the zooplankton assemblage in July and August 1998 when fish were taken for this study. By contrast, *Bythotrephes* and *Daphnia* constituted little of the zooplankton community.



FIG. 1. Loch Ness, Scotland. *Above*: Urquhart Castle and the bay where brown trout were caught on the north-western shore of the loch. *Below*: MV "Deepscan", the research vessel used for sampling zooplankton in Urquhart Bay. (Photographs by Jonathan Grey).

The aim of this study was to compare statistically the ingested zooplankton assemblage with that of the zooplankton in the water column. This would allow us to examine the apparent paradox that very few copepods appear to be consumed by trout at a time of year when they are numerous and readily available as food. Our investigation was limited to the crustacean zooplankters, since the rotifera are generally so small that they are only of interest to fish in the first few days of life (Brooks 1968).

Sampling

A total of 25 brown trout was obtained from anglers around the Urquhart Bay area on the north-western shore of Loch Ness (Fig. 1) in July & August 1998. Urquhart Bay is fed by the River Enrick and the River Coiltie. Often, only the digestive tract of each fish was received from the anglers, labelled with the length and weight of the fish from which it came and the date of capture. When whole fish were received, the stomachs were removed by dissection after recording weight and fork length. Trout stomachs were preserved by freezing until they could be analysed. The captured trout ranged from 27 g to 3856 g wet weight and 128 to 680 mm fork length. Some of the fish were carnivorous "ferox" trout, which feed extensively on smaller fish. The following analyses were limited to the non-ferox fish with discernible stomach contents.

Samples of pelagic zooplankton were obtained approximately monthly from 30-metre vertical net-hauls (mesh size 110 μm) in Urquhart Bay, working from the MV "Deepscan" (Fig. 1).

In the laboratory, dissected stomach contents were manually separated into crustacean zooplankton and macroinvertebrate fractions. These were identified to species level when possible, using a stereozoom microscope. Where digestion was advanced, certain "indicator" parts of organisms were counted as whole individuals. The caudal spines of *Bythotrephes longimanus* were used in this way (Mills et al. 1992). Counts of the ingested individuals of each zooplankton species were converted into percent relative abundances of each species in the ingested zooplankton assemblage. The two dietary fractions were dried on preweighed filter papers, the mass of the ingested material alone being obtained by difference. This allowed us to calculate the gravimetric contribution of each fraction to the diet.

Numbers of zooplankters in lochwater

Total numbers of individual zooplankters per litre of lochwater were lowest in February, March and December 1998, increasing to a maximum in April-May (Fig. 2). In the samples, *Bythotrephes longimanus* was scarce (abundances were calculated to be 0.01, 0.013 and 0.008 individuals per litre on 6 and 27 July and 24 August respectively) and *Daphnia hyalina* was found only in late

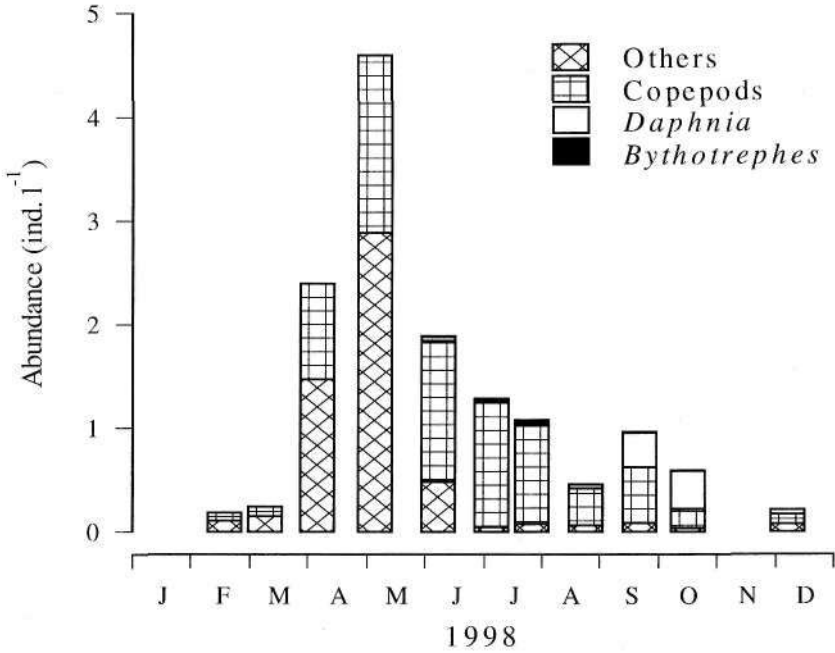


FIG. 2. Seasonality in the abundance and composition of zooplankton in Urquhart Bay, Loch Ness.

Table 1. The range in numbers of crustacean zooplankters (per litre of lake water) in six lakes, selected from a synoptic survey of UK lakes in the summer of 1997 (Grey, unpublished data).

Lake	Numbers per litre
Loch Ness	1.4
Ullswater	2.5
Rostherne Mere	2.6
Coniston Water	2.9
White Mere	144
Alderfen Broad	183

summer (September-October). The copepods *Cyclops abyssorum* and *Eudiaptomus gracilis* were numerically dominant from June to September (1-2 individuals per litre) and equally numerous in April-May, when other zooplankters were most abundant. The total numbers of zooplankters per litre of water are very low in Loch Ness when compared with several lakes in England (Table 1).

Species composition of available and ingested prey

If trout were to feed non-selectively, consuming prey as they were encountered, then there would be no significant difference between the species composition of zooplankton in the loch (available prey) and the ingested prey. The species composition of pelagic zooplankton was compared with that of ingested zooplankton by calculating the relative abundances of different species in each, based on counts of individuals found in pelagic samples and stomach contents of fish caught in July and August. Basing the percent species compositions of pelagic and ingested zooplankton on numerical counts of available and ingested zooplanktonic prey is believed to be appropriate, as salmonids are thought to consume visually detected prey individually, rather than employing a filter-feeding mechanism (Eggers 1977; Allan 1995; Lampert & Sommer 1997). Hyslop (1980) criticised the use of individual counts, as they overestimate the contribution of small prey items to diet compared with that of larger prey items which may contribute more to dietary bulk. In our analysis, relative abundances were calculated separately for zooplankton and macroinvertebrates, thus producing two categories within which prey items were more comparable in terms of size.

A statistical comparison of percent species composition in the loch and trout was significant ($p < 0.001$) using the Chi-squared test; counts of zooplankters cannot be assumed to follow parametric distributions (Cotes 1997). The significant difference between available and ingested prey implied that trout were feeding selectively.

Preferential prey selection by trout in Urquhart Bay: optimal foraging?

The selectivity shown for different prey species was quantified by two indicators of preference (Ivlev 1961; Chesson 1983):

Ivlev's Index $E = (r_i - p_i) / (r_i + p_i)$, and

Chesson's Index $a_i = (r_i \div n_i) / (\sum r_j \div n_j)$

where n_i and p_i correspond to the relative abundance of a prey item in the environment and r_i is its relative abundance in the diet. Ivlev's index has values ranging from +1 to -1, with a value of +1 indicating that a prey item is eaten more than proportionally, given its abundance in the water column, and thus is strongly selected for by the planktivore. A value of -1 indicates strong

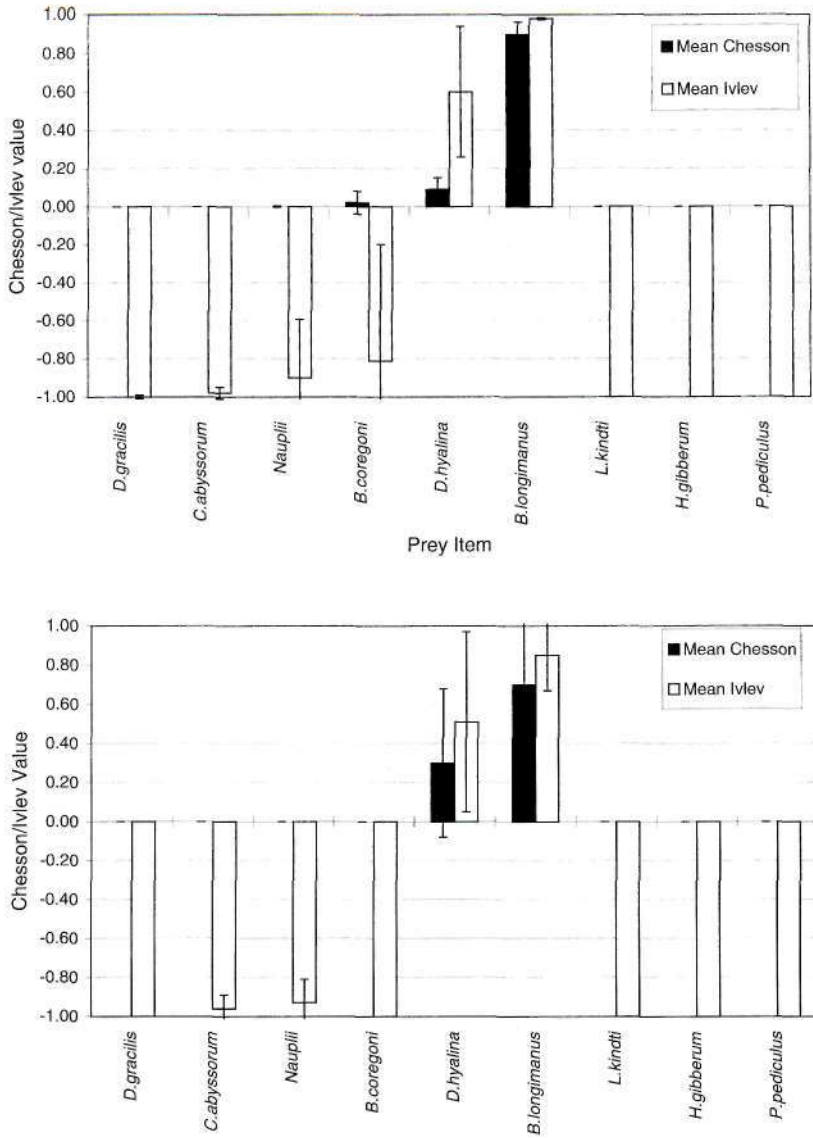


FIG. 3. Preferences of brown trout for zooplankton prey species in Urquhart Bay during July 1998 (above) and August 1998 (below), as measured by the Chesson and Ivlev indices of feeding selectivity.

negative selection for a prey item, in that it is eaten less than proportionally, given its abundance in the water column. A value of zero therefore indicates that a prey item is eaten as encountered and is the subject of no selection. Chesson's index has values ranging between 0 and +1, indicating the proportion of the diet that would be comprised of a particular prey item if all prey were equally abundant in the environment.

In both July and August (Fig. 3) consumption was more than proportionate for the predatory cladoceran *Bythotrephes longimanus* and (to a lesser extent) for the herbivorous *Daphnia hyalina*. By contrast the copepods *Cyclops abyssorum* and *Eudiaptomus gracilis* were consumed less than proportionately. This is particularly striking given the scarcity of the two cladocerans and the numerical dominance of the two copepods during the months of study (Fig. 2). This pattern of selection was consistent between the individual trout analysed. Such a pattern of preferential consumption of cladocerans rather than copepods has been observed by other authors (Derivo et al. 1991; Hegge et al. 1993; Martin & Shine 1993). More specifically, the alewife *Alosa pseudoharengus* feeds extensively on *Bythotrephes cederstroemi* at a time when this species was not detected in zooplankton (Mills et al. 1992). Given the particulate feeding mode of planktivorous fish, it seems that the selection process may actually occur before ingestion. Selective feeding of this form is often explained within the framework of optimal foraging theory. It is interesting, therefore, that such marked feeding selectivity by trout occurred in an oligotrophic and unproductive system, where zooplankton numbers per unit volume of water are very low. Werner & Hall (1974) showed that the degree of feeding selectivity in bluegill sunfish *Lepomis macrochirus* depends on the density of available prey items: large individuals of *Daphnia magna* were preferentially consumed at high prey densities, but there was no feeding selectivity at low prey densities. It is perhaps less energetically favourable to feed selectively under such conditions of low prey density, due to the large search time associated with finding preferred prey items. Therefore, it seems unlikely that the pattern of feeding selectivity demonstrated by brown trout in Loch Ness can be attributed to some form of optimal foraging, where the planktivores actually choose which prey to consume. Where zooplankton densities are low, perhaps it would be uneconomic to ignore less favoured prey items.

Feeding selectivity of trout in Urquhart Bay

The observed selectivity in the feeding of trout may be the product of planktivore perceptual bias and differences in capture efficiency between prey. The different prey species in Loch Ness may differ in their conspicuousness to visual predators and in their ability to evade capture. The copepods characteristically have a more "jerky" mode of swimming than the

cladocerans and are capable of making powerful swimming jumps against the water current which flows into a planktivore's mouth during the process of ingestion (Lampert & Sommer 1997). Copepods also possess sensory hairs on their antennae that are sensitive to microturbulence in the surrounding water (Lazzaro 1987). In this way they may detect the approach of a planktivore. Cladocerans lack the mechanoreception that copepods use to detect a planktivore attack and are not capable of such evasive swimming behaviour. Thus they may be more susceptible to predation. Eggers (1977) also believed that cladocerans would be more visible and more susceptible to predation since they have a greater surface area for their length than the copepods and so project a larger image onto the planktivore's retina. Within the cladoceran species present, *Bythotrephes* may be particularly susceptible due to its large size, coloration and the conspicuous large compound eye. Larger prey species are more visible and thus predators react to them at greater distances (Brooks 1968; Werner & Hall 1974). The large compound eye, in providing a contrast with the background, may also make *Bythotrephes* more noticeable to visual predators. Zaret & Kerfoot (1975) showed that the diameter of eye pigmentation in *Bosmina longirostris* greatly influenced its predation by the silverside *Melaniris chagresi*. Eggers (1977) places great importance on such contrasts in increasing the conspicuousness of prey species. The largest cladoceran in Loch Ness, *Leptodora kindti*, was actually the subject of strong negative selection by trout since, in this cladoceran, the visible body parts (the eye and gut) have been reduced, making *Leptodora* virtually transparent and therefore inconspicuous to visual predators despite its large size (Lampert & Sommer 1997).

The observed feeding selectivity may then be the result of differential efficiency of the trout at capturing different prey species. Some fish species can change their feeding mechanics to facilitate the capture of evasive prey (Lazzaro 1987). It is possible that the brown trout is not capable of such flexibility since this would require a small rounded mouth (typical of obligate planktivores) which is capable of generating greater suction speeds. Being a facultative planktivore, the brown trout has a large notched mouth to facilitate the capture of larger prey and so may not be capable of generating greater suction speeds.

Patchy distribution of zooplankton may affect selectivity by trout

The selectivity observed for some of the prey species may result from the patchy distribution of the prey relative to their predators. The great depth of Loch Ness makes it possible that there could be vertical segregation of predators and potential prey. This may be the case for *Bosmina coregoni*. Shine & Martin (1988) found that brown trout were concentrated in the surface waters of the loch, whereas *B. coregoni* was in greatest numbers just

below the thermocline at a depth of around 32 metres (Shine et al. 1993). The 30-metre vertical hauls used to sample zooplankton in our study are therefore far more likely to catch this zooplankton than the trout are when confined to near-surface waters.

Consumption of macroinvertebrates by trout in Loch Ness

Aquatic, terrestrial and airborne macroinvertebrates were also consumed by the brown trout of Loch Ness. Macroinvertebrates are known to be important in the diets of salmonids (Derovo et al. 1991; Hegge et al. 1993; Bridcut & Giller 1995). Although a variety of taxa were consumed (including a number of aerially derived and terrestrial species), chironomid larvae and pupae dominated in terms of occurrence (Table 2). Macroinvertebrate gravimetric contribution to diet varied with fish size (Fig. 4), assumed to correspond to ontogeny. On average, macroinvertebrates comprised 41% by mass of the diet (range 4 to 100%). The contribution was markedly higher for small fish than for larger individuals. It is unclear whether this corresponds to a threshold weight (100-125 g) above which the importance of macroinvertebrates to diet sharply declines, or if there is a gradual change in the contribution to diet with increasing fish size (age). If the threshold model were to apply, two groups of fish could be distinguished with very different levels of macroinvertebrate consumption. The median gravimetric contribution for each group is significantly different ($U = 0.000$, $p = 0.006$, Mann Whitney U-Test). Alternatively, if the change in dietary composition is assumed to be gradual, a regression line can be fitted to the data, where the coefficient of determination $r^2 = 0.63$. Additional data would be needed to characterise more exactly the form of the relationship.

Table 2. The percentage occurrences of major macroinvertebrate taxa found in brown trout with discernible stomach contents during July 1998.

Prey taxa	Occurrence (%)
Chironomid larvae/pupae	72.7
Diptera (excluding above)	63.6
Coleoptera	54.5
Plecoptera	18.2
Trichoptera	9.1
Hymenoptera	9.1
Hemiptera	9.1
Acari	9.1

The wide variety of macroinvertebrates consumed, and the lack of consistency for consumption of taxa by individual trout, may be attributed to

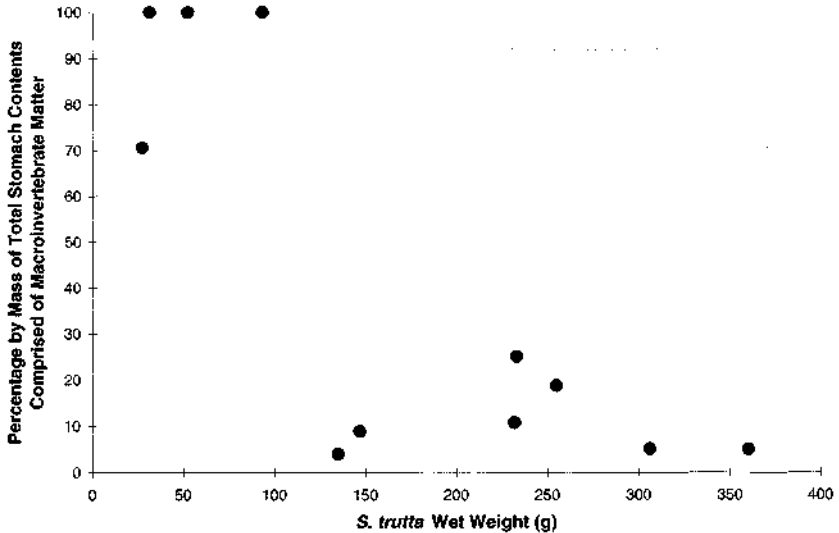


FIG. 4. The relationship between the wet weight of brown trout and the contribution by mass of macroinvertebrate matter to the total stomach contents of trout caught in July 1998.

the fact that a large proportion of the invertebrates were terrestrial or aerial in origin. Therefore the processes that brought these animals into the aquatic environment (falling from overhanging branches or being blown in by the wind) are not taxa-specific. The trout would therefore encounter a wide range of potential prey. A heterogeneous pattern of feeding on macroinvertebrate taxa may also occur if the trout switch their main prey, by feeding on zooplankton in the day and on more visible macroinvertebrates at night. Such prey switching has been observed in salmonids (Dervo et al. 1991) and under low light conditions it is unlikely that a distinction between taxa would be possible; hence individual trout would not be expected to show the same patterns of prey selection. The consumption of vegetative matter by some of the analysed fish may be cases of "mistaken identity" under such low light conditions. Consistent distinction between taxa also may not be possible, as macroinvertebrates are larger than zooplankters, so small differences in size and shape between taxa may be less critical in determining their relative visibilities. Chironomids occur widely in the diet as they migrate into the water column to emerge as adults or redistribute themselves horizontally. This would render them vulnerable to predation.

Changes in feeding of trout and habitat as they grow in size

The gravimetric contribution of macroinvertebrate matter in the diets of trout altered as they increased in weight (Fig. 4). This suggests that there is an ontogenetic shift in the habitat of fish as they increase in size (Haraldstad & Jonsson 1983; Hegge et al. 1993), when young trout move from the natal streams to the littoral zone and then to the pelagic of the loch. The littoral to pelagic areal ratio in Loch Ness is extremely low and as fish move into the pelagic zone the availability of airborne and terrestrial macroinvertebrate prey will decline. Jenkins (1969) reported a social hierarchy in brown trout that was based on success in agonistic interactions. The body weight of an individual correlated well with its success in such interactions, and therefore also correlated well with the hierarchical rank of the fish. Such a hierarchy might maintain the spatial segregation of differently sized fish in Loch Ness. Other authors report such spatial pattern in trout populations (Jenkins 1969; Hegge et al. 1993).

Conclusions

Feeding selectivity can be a misleading term, by implying that planktivores actively choose the prey consumed. Instead, differential consumption may occur because prey have different abilities to escape and different visibilities to their predators. Copepods can make powerful swimming jumps to avoid predation, but cladocerans lack the mechanoreception that copepods use to detect attacks by planktivores. *Bythotrephes* may be particularly favoured by trout due to its large size, coloration, and the conspicuous large compound eye. However, considering the low densities of zooplankton in Loch Ness, it is unlikely that this selectivity demonstrates optimal foraging by trout. At low prey densities it is energetically uneconomic to ignore less favoured prey; the search time for preferred prey would be too high.

The observed consumption of *Bythotrephes*, along with stable isotopic data suggesting that *Bythotrephes* feeds on copepods (Jones et al. 1998), implicates *Bythotrephes* as an important trophic link between copepods and fish in the Loch Ness food web.

Small trout may rely heavily on terrestrial macroinvertebrates for food, but this dependence declines markedly in larger trout. The variation in dietary composition with trout wet weight indicates an ontogenetic habitat shift producing spatial separation of young and older individuals.

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References

- Allan, J. D. (1995). *Stream Ecology: structure and function of running waters*. Chapman and Hall.
- Bridcut, E. E. & Giller, P. S. (1995). Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. *Canadian Journal of Fisheries and Aquatic Sciences* 52, 2543-2552.
- Brooks, J. L. (1968). The effects of prey size selection by lake planktivores. *Systematic Zoology* 17, 273-291.
- Burgis, M. J. & Morris, P. (1987). *The natural history of lakes*. University Press, Cambridge.
- Campbell, R. N. (1979). Ferox trout, *Salmo trutta* L., and charr, *Salvelinus alpinus* L., in Scottish Lochs. *Journal of Fish Biology* 14, 1-29.
- Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64, 1297-1304.
- Cortes, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 726-738.
- Dervo, B. K., Hegge, O., Hessen, D. O. & Skurdal, J. (1991). Diel food selection of pelagic arctic charr, *Salvelinus alpinus* (L.), and brown trout, *Salmo trutta* (L.), in Lake Atnsjø, SE Norway. *Journal of Fish Biology* 38, 199-209.
- Eggers, D. M. (1977). The nature of prey selection by planktivorous fish. *Ecology* 58, 46-59.
- Haraldstad, O. & Jonsson, B. (1983). Age and sex segregation in habitat utilisation by brown trout in a Norwegian Lake. *Transactions of the American Fisheries Society* 112, 21-31.
- Hegge, O., Hesthagen, T. & Skurdal, J. (1993). Vertical distribution and substrate preference of brown trout in the littoral zone. *Environmental Biology of Fishes* 36, 17-24.
- Hyslop, E. J. (1980). Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology* 17, 411-429.
- Ivlev, V. S. (1961). *Experimental ecology of the feeding of fishes*. Yale University Press.
- Jenkins, T. M. (1969). Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. *Animal Behaviour Monographs* 2, 57-123.
- Jones, R. I., Grey, J., Sleep, D. and Quarmby, C. (1998). An assessment, using

- stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in Loch Ness. *Proceedings of the Royal Society, London B* **265**, 105-111.
- Lampert, W. & Sommer, U. (1997). *Limnoecology: the ecology of lakes and streams*. Oxford University Press.
- Lazzaro, X. (1987). A review of planktivorous fishes: their evolution, feeding behaviours, selectivities and impacts. *Hydrobiologia* **146**, 97-167.
- Martin, D. S. and Shine, A. J. (1993). The food and feeding relationships of pelagic fish in Loch Ness. *The Scottish Naturalist* **105**, 149-174.
- Mills, E. L., O'Gorman, R., DeGisi, L., Heberger, R. F. & House, R. A. (1992). Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2009-2019.
- Shine, A. J. & Martin, D. S. (1988). Loch Ness habitats observed by sonar and underwater television. *The Scottish Naturalist* **100**, 111-119.
- Shine, A. J., Martin, D. S. & Marjoram, K. S. (1993). Spatial distribution and diurnal migration of pelagic fish and zooplankton in Loch Ness. *The Scottish Naturalist* **105**, 195-235.
- Werner, E. E. & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* **55**, 1042-1052
- Young, I. & Shine, A. J. (1993). Loch Ness bathymetric and seismic survey, December 1991. *The Scottish Naturalist* **105**, 23-43.
- Zaret, T. M. & Kerfoot, W. C. (1975). Fish predation on *Bosmina longirostris*: body size selection versus visibility selection. *Ecology* **56**, 232-237.