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Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen

Grey J. Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen.
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Abstract – The trophic ecology of many fish species in cold temperate lakes is often characterized by a generalist or opportunist strategy. In this study, the diets of polytrophic brown trout in Loch Ness, Scotland, have been examined using stable isotopes of carbon and nitrogen to complement gut content analyses and aging by otolith annuli counts. Using the stable isotope ratios, it was possible to trace trout ontogeny from parr development in a natal river to piscivory in the pelagic. Potential dilution of maternal isotope signatures from eggs to parr was also demonstrated. Despite the low productivity of the loch, intraspecific variability in isotope ratios suggested dietary specialization, rather than opportunism, in some individuals.

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Key words: *Salmo trutta*; ontogeny; gut contents, stable isotopes; Loch Ness

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The dietary intake of fish species usually alters during their lifespan, primarily due to morphological changes accompanying growth and age-specific habitat use or foraging tactics (Werner & Hall 1976). Shifts in diet and habitat may also be mediated by prey abundance and predation risk and consequently affect species interactions (Werner & Gilliam 1984; Holbrook & Schmitt 1988). Thus an understanding of these ontogenetic changes is essential in ecological studies of fish.

The brown trout (*Salmo trutta* L.) is a highly successful, polytypic species exhibiting a range of quantitatively complex life cycles (Elliott 1994). These can be simplified into four typical strategies. In the first and simplest, the trout remain in their natal stream for life, growing slowly and achieving only small size. The second involves migration of 1+ or 2+ parr from the natal stream to the parent river, and the mature adults do not return until they are ready to spawn. The third and fourth life cycles are exhibited by trout that migrate as smolts to a lake, or to the estuary or sea. A detailed review of the life cycle and its variability can be found in Elliott (1994). The first year of life is a period of rapid growth for the fish. Consequent associated changes in diet due to an increase in gape size and the ability to handle larger prey, and improved locomotory skills increasing potential for migration, account for considerable ontogenetic change early on in the trout life cycle.

Gut content analysis has been a standard technique to investigate diet and trophic relationships in fish species (Hyslop 1980). One major disadvantage of the technique is that it provides a mere "snapshot" of a diet that may vary substantially over differing temporal scales with regard to ontogeny. To remove temporal bias and obtain a more accurate representation of the assimilated intake from the diet, a different technique is required. Stable isotope analysis is being increasingly used by ecologists to assess food chain relationships, augmenting the more traditional gut content

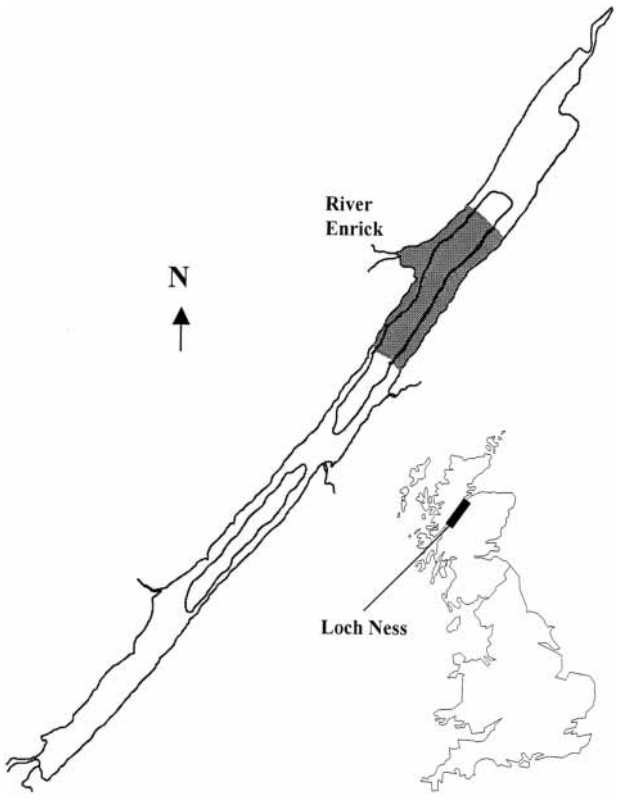

Fig. 1. Map of Loch Ness highlighting position of the R. Enrick and Urquhart Bay. Shading denotes area from which fish were collected.

analyses. The stable isotope technique relies on putative food sources exhibiting distinct and robust signatures. Since carbon and nitrogen stable isotope ratios in animals reflect those of the diet in a dependable manner, the relative importance of different food sources to the diet can be established (see Peterson & Fry 1987). Despite a wealth of marine studies that have shown organisms to exhibit intraspecific variability in stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$), in relation to body size (Rau et al. 1981, 1991; Fry 1983; Schell et al. 1989; Wada et al. 1993) there have been surprisingly few freshwater studies. Recent examples include the studies of France (1996 & 1997) relating ontogeny to crayfish and fish $\delta^{13}C$ as a measure of land-water ecotonal coupling, trophic studies of larval fish (Vander Zanden et al. 1998) and isotopic evidence for identifying anadromy in salvelinid populations (Doucett et al. 1999a, 1999b).

Trout behavioral ontogenesis has been studied in relation to swimming, aggressiveness, territoriality and habitat use, and feeding (e.g. Kreivi et al. 1999; Roussel & Bardonnet 1999). In the current study, the dietary ontogeny of brown trout has been investigated as part of a much larger study of the food web of Loch Ness, Scotland. Stable isotope analysis has previously been applied to assess the relative importance of allochthonous and autochthonous carbon sources to the pelagic inhabitants of Loch Ness (Jones et al. 1998; Grey et al. 2001a). Brown trout and Arctic charr (*Salvelinus alpinus*) are the predominant fish species in the loch, the charr occupying a more planktivorous role (Grey et al. 2001b). The putative food sources for brown trout have been characterized in terms of their carbon and nitrogen isotopic signatures as part of ongoing research. Thus, the first objective of this study was to complement the stable isotope technique with gut content analysis and otolith aging to examine any variability in isotopic ratios exhibited by the brown trout relative to ontogeny. If feeding plasticity (opportunism) is particularly advantageous in cold temperate lakes such as Loch Ness (as suggested by Keast 1979), then one might hypothesize that intraspecific variability in isotope ratios would be low. Therefore, the second objective was to investigate in further detail the potential diet specialization by brown trout in Loch Ness.

Study area

A detailed description of Loch Ness can be found in Jones et al. (1998). The River Enrick flows into Urquhart Bay on the north-west side of the loch (Fig. 1). It is the smallest of the four main subcatchments with an area of 177 km^2 and containing 87 lochs (Maitland 1981). Mean annual rainfall is 1185 mm and estimated mean annual flow in the river is 4.49 $m^3 \cdot s^{-1}$, contributing around 5% of total flow to L. Ness (Maitland 1981). The R. Enrick is of local importance as a spawning river for salmon (*Salmo salar*) and brown trout.

Material and methods

The trout used for this study were obtained by a number of methods. Fish in the 0+ age group were caught in kick samples from the River Enrick up to 12 km upstream from the loch. Fish from the river mouth and surrounding littoral zone were either sweep netted, gill netted (mesh size 10–48 mm) or caught by anglers. Pelagic fish were caught by trolling assorted lures between 2 and 15 m below the surface of the water. Eggs were removed from ovigerous females prior to spawning as sampling was not conducted during the actual spawning season, and it was not desirable to disturb salmon redds in the R. Enrick. Fish wet weight and length (snout to tail fork) were recorded upon capture (Table 1). In the laboratory, a small portion of muscle tissue (1–2 g wet weight) was taken from either side of the dorsal fin or from

Table 1. Ranges of brown trout length and wet weight, $\delta^{13}C$ and $\delta^{15}N$ of trout muscle, and number of fish samples recorded from different areas. Dominant prey identified from gut analyses and typical isotopic signatures of those prey are also tabulated. Sources: 1 – Grey, unpublished data; 2 – Grey et al. 2001a; 3 – Grey et al. 2001b; 4 – This study.

Site	*n*	Fish length (mm)	Fish weight (g)	Trout $\delta^{13}C$ (‰)	Trout $\delta^{15}N$ (‰)	Dominant gut content	Typical prey $\delta^{13}C$ (‰)	Typical prey $\delta^{15}N$ (‰)
Eggs samples from mature E	16			−28.6 to −25.3	7.9 to 13.5			
R. Enrick Parr	15	48–28	1.2–27	−26.0 to −22.5	7.5 to 9.9	Early to late instar lotic macroinverts.	−26.5 to −24.9	3.4 to 5.7[1]
Littoral & open water	41	102–350	13–360	−27.9 to −21.1	8.0 to 14.2	Benthic macroinverts., Aerial insects, Zooplankton	−26.5 -30.7 to −25.8	5.7[1] 7.8 to 17.7[2]
Piscivorous (Ferox)	28	290–750	263–5443	−27.7 to −23.2	11.3 to 15.2	Arctic charr, brown trout	−28.0 −27.9 to −21.1	11.7[3] 7.5 to 14.2[4]

the pair of pectoral muscles. One was treated to remove lipids according to the protocol of Bligh & Dyer (1959) and the other remained untreated. Tissues that contain large amounts of lipid tend to be more ^{13}C-depleted because the process of lipid synthesis favors the lighter isotope (DeNiro & Epstein 1977). However, the protocol used to remove the lipid fraction may have an adverse effect on the nitrogen isotope ratios and so nitrogen results were obtained from the untreated set (Pinnegar & Polunin 1999). Both samples were placed in pre-combusted glass vials, oven dried at 65°C, homogenized and stored frozen for isotope analysis. Egg samples were prepared in a similar manner to muscle tissue. Gut contents were examined using a stereozoom microscope and classified into four groups: crustacean zooplankton, aerial insects, lotic or benthic macroinvertebrates, and fish prey. An estimate was made of dietary dominance in the case of the first three groups. Otolith pairs (sagitta) were dissected from a sub-sample of fish, soaked in salicylic acid and annuli counted at ×25–40 magnification. In total, 84 individual fish were analyzed for their stable carbon and nitrogen isotope ratios (Table 1).

Carbon and nitrogen isotopic analysis was carried out using a Roboprep-CN continuous flow analyzer coupled to a Tracermass single-inlet triple-collector mass spectrometer (instruments by Europa Scientific). Samples were ground under liquid nitrogen in a freezer mill (Spex Industries Inc.). Results are given using the δ notation,

$$\delta R = [(R_{\text{sample}}/R_{\text{reference}}) - 1].1000$$

where $R = {}^{15}N/{}^{14}N$ or $^{13}C/^{12}C$ expressed in units of per mil (‰). The reference materials used were atmospheric nitrogen, and secondary standards of known relation to the international standard of Pee Dee belemnite for carbon. Precision and accuracy were generally in the order of 0.2‰ for both nitrogen and carbon.

Results

The data set comprised trout ranging in size from 1.2 to 5440 g wet weight and 48 to 750 mm in length and exhibiting a typical length-weight relationship (Fig. 2, Table 1). From gut content examination, trout parr from the R. Enrick contained only the early instars of typical lotic macroinvertebrates: *Ecdyonurus*, *Leuctra* and *Baetis* species. Aerially-derived winged insects and zooplankton were absent. Trout caught from the littoral zone or open water preyed upon a wider variety of organisms. Many fish were truly polytrophic, with gut compositions comprising benthic macroinvertebrates, zooplankton and winged insects. Two fish of ~300 mm contained not only

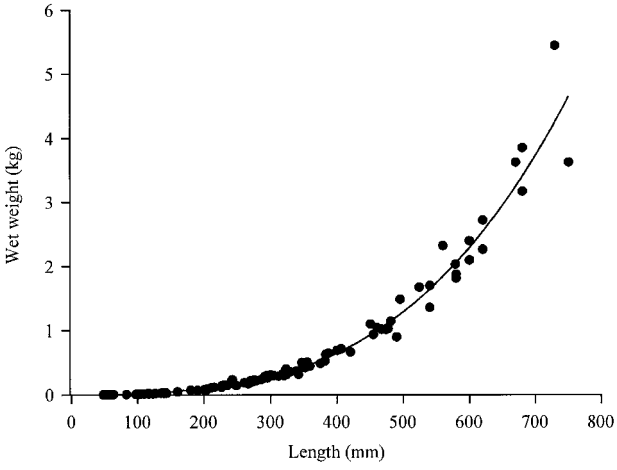

Fig. 2. The relationship between brown trout wet weight and length, from the River Enrick and Loch Ness: $y=(0.01x-3.74)x+273.8$, $r^2=0.96$.

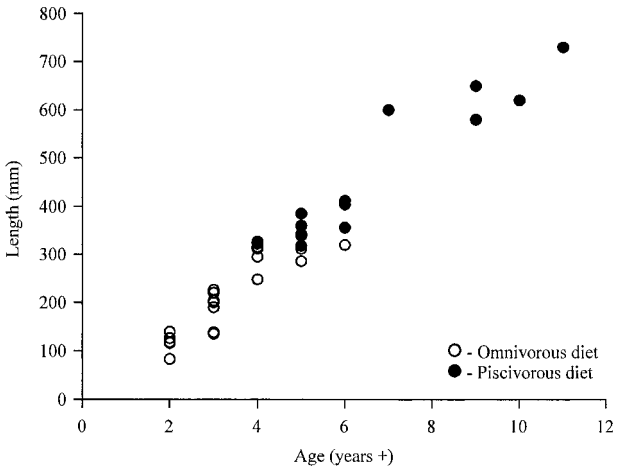

Fig. 3. The relationship between brown trout age calculated from otolith annuli, and length.

these groups but also small Arctic charr. Other individuals appeared to exhibit some specialization, with the gut dominated by one particular group. A number of fish in the 300 mm range had consumed only crustacean zooplankton prey, chiefly *Bythotrephes longimanus* and *Daphnia hyalina.* All of the trout of greater than 400 mm length either contained fish prey or had empty stomachs.

Otoliths were dissected from 37 fish, and the counted annuli revealed ages from 2+ to 11+ years. On the basis of this aging, length at age was plotted and the data-set sub-divided into trout with or without a contribution of prey-fish to the diet (Fig. 3). Some trout exhibited pure piscivory at age 4+ years when fish were greater than 300 mm in length (i.e. there was no evidence of other dietary sources revealed by gut analyses of these individuals). Other trout of 4–6+ years exhibited omnivory, but the omnivorous trait had disappeared above 6+ years. Piscivorous trout in year classes 4–6+ were generally larger individuals than omnivorous trout of the same age (Fig. 3).

Since the length-wet weight relationship was robust, length was used as the single variable against which to plot the fish muscle isotopic ratios (Fig. 4). The nitrogen isotope ratios of trout eggs ranged from 7.9‰ to 13.5‰ (Fig. 4a). The smallest parr in the river were generally ^{15}N-depleted relative to the eggs. Trout signatures became progressively more ^{15}N-enriched as fish length increased ($y=0.009x+8.7$, $r^2=0.68$, $t=13.5$, $P<0.01$). The range of nitrogen isotope values for the different classes of trout is shown in Table 1.

It is now established that the δ^{13}C of accumulated lipids in certain tissues can interfere with interpretation of isotopic results. Trout muscle samples used in the current study that were treated to remove lipids were consistently depleted in ^{13}C

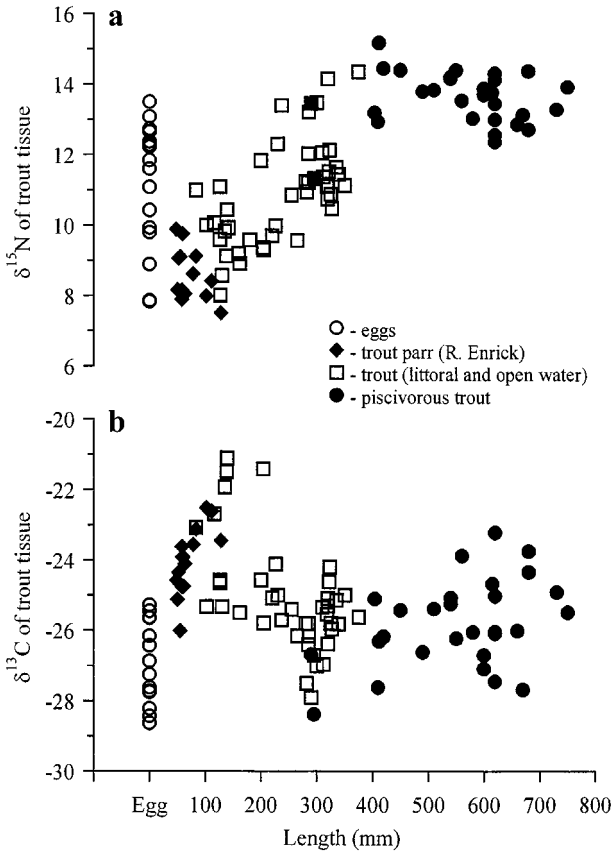

Fig. 4. Change in brown trout muscle: (**a**) δ^{15}N signature and (**b**) δ^{13}C signature with increasing fish length.

by only 0.6±0.4‰. Thus the data presented are not lipid corrected. Egg stable isotope ratios ranged in δ^{13}C from −28.6‰ to −25.3‰ (Fig. 4b). Trout carbon isotope ratios exhibited great variability, ranging from −27.9‰ to −21.1‰ and in contrast to the nitrogen ratios, did not show a particular pattern in relation to increasing fish length when all trout were considered. Trout parr of <150 mm length from the river were generally enriched in ^{13}C relative to the egg signatures and did exhibit a significant ^{13}C-enrichment with increasing length ($t=3.77$, $P<0.01$). Many of the trout caught in the littoral and open water zone (100–350 mm length) exhibited carbon isotope signatures of between −26.0‰ and −25.0‰. However, a small number were caught of similar lengths (280–300 mm) exhibiting more ^{13}C-depleted signatures (−28‰). The ferox trout (pure piscivores) exhibited considerable variability in carbon isotope ratios between −27.7‰ and −23.2‰.

The nitrogen and carbon isotopic relationships between the eggs and the muscle tissue of the female parent from which they were removed were also examined (Fig. 5). Eggs were generally associated to the female tissue signatures in a dependable

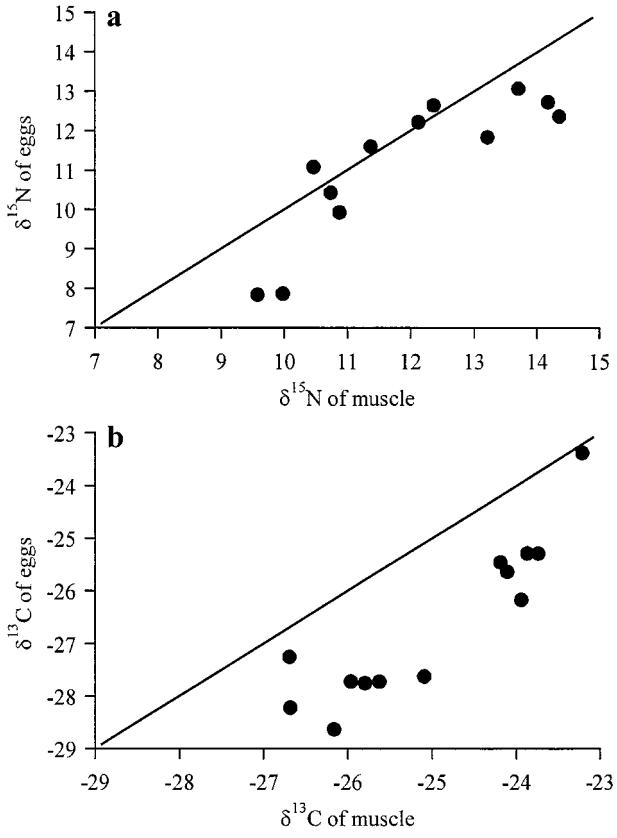

Fig. 5. Values for (**a**) δ^{15}N and (**b**) δ^{13}C of brown trout eggs relative to parental muscle tissue. Solid line: equality.

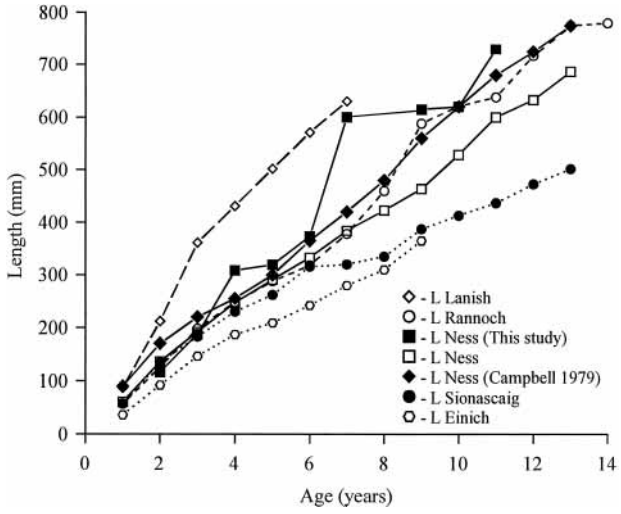

Fig. 6. The relationship between brown trout age and length from two studies of Loch Ness, compared with other Scottish lochs. Data from Campbell (1971, 1979).

manner: ^{13}C-depleted by 1.5±0.8‰ and ^{15}N-depleted by 0.8±0.4‰ (mean±1 SD), calculated from the difference between egg and muscle signature.

Discussion

The data discussed in this study were generated from a relatively small sample of fish compared to other studies which may include several thousand individuals (L'Abée-Lund et al. 1992). However, the length-weight relationship curve (when log-transformed) produced an equation: Log weight (W)=2.86 Log length (L)−4.66, comparable to the equation of J. Pope (Campbell 1979): Log W=2.57 Log L−4.12 for Scottish brown trout. Also, the length at age relationship for the initial six years, exhibited by trout from this study is comparable to previous work on Loch Ness trout (Fig. 6) (Martin & Shine 1993). The current study appears to have targeted fish of a larger size for their age (7+ years) compared with Campbell (1971) although sample size is small for older fish in both studies, and Campbell (1971, 1979) had back-calculated length from scales. Otoliths are generally thought to be a more accurate measure of age determination in salmonids (Kruse et al. 1997). Otoliths of the larger fish were difficult to obtain, as the fish were received as by-products from a local sport fishing venture and the carcasses were often retained as trophies. Nevertheless, despite the small sample size, the data generated are considered to be representative of the Loch Ness brown trout population.

In order to examine ontogenetic shifts throughout the life history of the Loch Ness trout, isotopic signatures were plotted for eggs and then against trout length (Fig. 4). Data from farmed salmon suggest that the egg signature does not change significantly at spawning (Grey unpublished data). Trout usually attain sexual maturity at the age of 2 or 3 years and are frequently iteroparous, thus the egg isotopic signature can vary considerably, depending on the age at which females spawn. Indeed, the egg stable isotope ratios did exhibit considerable variability but were consistently ^{13}C-depleted relative to their respective parent female muscle tissue signature. This is likely a function of discriminative fractionation during egg formation within the fish to produce abundant yolk lipids, since lipids are ^{13}C-depleted by 2–3‰ relative to most other body tissues (DeNiro & Epstein 1978). For the purposes of the current study, it was assumed that the range of egg signatures obtained were typical of those from which the examined R. Enrick trout parr hatched.

The isotopic signatures of the trout parr were considerably depleted in ^{15}N and enriched in ^{13}C relative to the eggs, and there was a subsequent substantial shift in isotopic signatures with increasing fish length. Although there are no data from

the current study for trout in the alevin stage, it is reasonable to suppose that both carbon and nitrogen isotopic signatures would not alter significantly from those of the eggs from which they hatched due to the yolk sac providing sustenance for the young fish until the "first feed" at ~25 mm length. Shifts in isotopic ratios in smallmouth bass (*Micropterus dolomieu*) commenced almost immediately after hatching, which led Vander Zanden et al. (1998) to postulate that either exogenous feeding was taking place earlier than anticipated or that the embryos were selectively utilizing light nitrogen (^{14}N) from the yolk sac nitrogen pool and excreting ^{15}N-enriched waste products. Certainly, when the trout fry begin to ingest and assimilate new food sources from their immediate environment, the incorporation of the dietary isotopic signature into the fish flesh should become readily apparent as a high percentage of assimilated material is laid down as growth. Empirical data from farmed salmon alevins suggest that an isotopic shift of ~2‰ and ~4‰ can occur in carbon and nitrogen isotope signatures respectively within 4 weeks of "first feed" (Grey unpublished data). Thus, the rapid accumulation of tissue during the initial growth period produces the peaks and troughs in the trout parr isotopic data (Fig. 4). Doucett et al. (1999a) described such a phenomenon as representing an isotope dilution factor in their study of anadromous and nonanadromous brook trout (*Salvelinus fontinalis*). Progeny of sea-run brook trout rapidly assimilated new food from the surrounding freshwaters of their natal streams and masked the marine-influenced signatures of their maternal parents. Later in the life cycle, when the trout are of greater body size, a shift in diet maybe be obscured by the slower turnover of isotopes as the percentage of new body mass laid down is lower. This has also been shown in broad whitefish (*Coregonus nasus*) and three-spined sticklebacks (*Gasterosteus aculeatus*) by Hesslein et al. (1993) and Grey (2001) respectively.

Limited prey handling capability due to the small gape-size of fish at the trout fry or parr stage restricts the diet to early instar macroinvertebrates which themselves feed upon the basal resources of periphyton and detrital material of allochthonous origin. The carbon and nitrogen isotopic signatures of periphyton were typically -22.1 ± 3.7‰ and 2.0 ± 1.9‰ respectively in the R. Enrick, although seasonal variability was high (Jones et al. 1998). Detrital particulate organic matter (POM) signatures for $\delta^{13}C$ were -26.7 ± 0.6‰ and 5.5 ± 2.1‰ for $\delta^{15}N$ (Grey et al. 2001a). Small bodied, low order consumers exhibited isotopic signatures consistent with feeding on a mixture of these basal food resources (e.g. *Leuctra* spp.: $\delta^{13}C$, -24.9‰; $\delta^{15}N$, 3.4‰) and thus the trout parr signatures reflected an additional trophic enrichment (Table 1). As trout parr increase in length and age, they are capable of handling larger prey items and ingest later instar lotic macroinvertebrates, and terrestrial and aerial insects that fall into the river. The isotopic signatures of these larger prey items are strongly influenced by terrestrial C3 vegetation (e.g. Hicks 1997). The common stream macroinvertebrate species *Gammarus*, *Isoperla*, *Ecdyonurus* and *Baetis* from the R. Enrick typically have mean $\delta^{13}C$ values of -26.5 and mean $\delta^{15}N$ of 5.7‰ (Table 1). Trout parr from near the river mouth exhibited signatures closely associated with these prey items (Fig 4b). In fact, six fish of ~ 100 mm length were considerably ^{13}C-enriched compared to the trout parr caught from the river, indicating that they had probably only recently migrated out from the river to forage in the loch littoral. Differing prey selectivity between age classes of juvenile brown trout has been directly observed in rivers. In the River Kuusinkijoki, Finland, age-0 trout preferred *Ephemerella* nymphs, whilst age-1 trout selected caddis larvae and both age classes ignored *Baetis* and aerial insects (Kreivi et al. 1999). However, it is unlikely that isotopic differentiation of diet can be discriminated at this level due to the dilution effects from the maternal signature. Fish of >150–250 mm in length were not caught from the R. Enrick, but were abundant in littoral samples. They also exhibited isotopic signatures closely related to those of macroinvertebrates and aerial insects. Crustacean zooplankton did not appear to contribute significantly to the isotopic signature of fish of this length, despite making a contribution to gut contents.

Trout of approximately 300 mm in length exhibited the greatest variability in both nitrogen and carbon stable isotope ratios. The $\delta^{15}N$ signature was elevated to between 10.5‰ and 13.5‰, whilst $\delta^{13}C$ ranged from -28.6‰ to -25.8‰. The extent of the variability can be explained by the truly polytrophic nature of trout of this size class. Not only is the individual fish of a size to allow locomotion across habitat boundaries (littoral, benthic, pelagic), but also the mouth morphology can incorporate organisms ranging in size from zooplankton to small fish. Gut analysis of a trout of 290 mm revealed the remains of four Arctic charr, macroinvertebrates and cladoceran zooplankton. However, Thackeray et al. (2000) reported a general decrease in the gravimetric contribution of macroinvertebrate matter to the diet of Loch Ness trout when they reached ~125 g wet weight (equivalent length ~225 mm). They suggested this reflected an ontogenetic shift in habitat. The extremely low littoral: pelagic areal ratio of Loch

Ness reduces the availability of aerially derived and terrestrial macroinvertebrate prey to fish in the pelagic.

It has been recognized that 300 mm is approximately the length when brown trout may "switch" to a purely piscivorous "ferox" mode of feeding (Greer 1995; Campbell 1979). Certainly, in Loch Ness the majority of fish > 300 mm exhibited a degree of piscivory (Fig. 3). Although their elevated nitrogen values may ultimately reflect a move up the food web, carbon as a source indicator may represent an amalgamation of a number of distinct sources. There is a variety of smaller fish species available as putative prey in Loch Ness, juvenile brown trout and Arctic charr, minnows (*Phoxinus phoxinus*) and three-spined sticklebacks, that could account for elevated $\delta^{15}N$.

Gut analyses and the heaviest $\delta^{15}N$ signatures suggested that the largest trout of >400 mm were pure piscivores or ferox trout, the top predators of the Loch Ness food web (Grey et al. 2001b). The high percentage (~50%) of completely empty stomachs of trout in this size range also indicates piscivory (Chapman et al. 1989). Although gut content analysis revealed nothing of the diet of these empty fish, the isotopic signature of the muscle tissue proved informative. The $\delta^{13}C$ values for ferox trout exhibited considerable range from −27.8‰ to −23.8‰. As large-bodied, powerful swimmers, ferox trout are the most capable of migration across habitat boundaries and thus potentially predate littoral brown trout and pelagic planktivores such as the Arctic charr, as well as salmon parr and smolts migrating from the river systems to the sea.

Perhaps the most intriguing trout carbon signatures were exhibited by the ^{13}C-depleted fish of approximately 300 mm, indicative of a zooplankton-biased diet similar to that reported for Arctic charr (Jones et al. 1998; Grey et al. 2001b). Indeed, gut analyses revealed that these trout had preyed selectively upon the larger cladocerans *Bythotrephes longimanus*, *Leptodora kindti* and *Daphnia hyalina*, although *Holopedium gibberum* was never identified within the gut contents (Grey 2000). Cladoceran carbon isotopic signatures fluctuate seasonally within Loch Ness, depending on the origin of the carbon source (autochthonous or allochthonous, Grey et al. 2001a), but generally range between −30‰ to −26‰. The selection of the largest predatory species (*Bythotrephes* and *Leptodora*) also accounts for the elevated $\delta^{15}N$ of the trout. Comparative feeding by charr and trout in Lake Atnsjø, southeastern Norway revealed that charr fed almost exclusively on zooplankton both day and night whereas the trout had a diurnal shift in diet from zooplankton during the day to surface insects and chironomid pupae during the night (Dervo et al. 1991). The pelagic of Loch Ness has a distinct paucity of these invertebrates and may thus potentially enforce resource competition between trout and Arctic charr. However, the well-mixed water column of Loch Ness is of considerable depth and vertical spatial separation of the two species may reduce conflict.

In order to exhibit such variable and distinct isotopic signatures, the trout must have been feeding on a particularly distinct food source for some considerable time; otherwise the turnover of differing dietary signatures within the tissues would cause masking and intraspecific variability would be negligible. Therefore, the carbon and nitrogen isotopic variability in these large, relatively slow growing fish suggests a degree of dietary specialization. Some trout appear to be planktivore specialists, while the range of carbon isotopes in the ferox trout suggests some may feed predominantly on smaller brown trout, some predominantly on Arctic charr, and some just opportunistically. In a similar study of pike (*Esox lucius*), Beaudoin et al. (1999) revealed that specialization on invertebrates or fish was a long-term trait of some individuals.

The length at age data (Fig. 3) also tentatively supports the hypothesis of diet specialization; some trout maintain an omnivorous diet and increase in age but do not show a corresponding increase in size, while other trout incorporate fish into the diet and exhibit extended life span and growth. Campbell (1971) suggested that in most Scottish lochs relatively few trout survive past 5 years, and it is only with a switch to pure piscivory, that ferox trout can go on to attain great size and age.

In Lough Melvin, western Ireland, three quite distinct forms of trout exist: sonaghen, an open-water planktivore; gillaroo, a littoral-benthic feeder; and ferox, a piscivore (Ferguson & Mason 1981; Ferguson 1989). Despite the isotopic evidence indicating trout of differing, and perhaps specialist feeding types in Loch Ness, similar to those of Lough Melvin, preliminary genetic studies of the Loch Ness trout suggest no evidence of polyphenism (A. Duguid, personal communication). Larger trout in lakes probably cease to be territorial and rather segregate according to size. Several studies have identified the use of littoral habitats by small-sized brown trout, while larger specimens occupy the pelagic zone (Hegge et al. 1993; Martin & Shine 1993; Hesthagen et al. 1997). Large individual trout and groups of up to eight large fish in Loch Ness are regularly located by sonar contact in distinct areas, usually at depths of 20–30 m from the surface, and 200–300 m from the shoreline (J. Minshull & B. Wynne, personal communications). Thus, the ferox trout appear to

be residing in the deeper waters of the pelagic below a layer of Arctic charr, and smaller trout are frequently encountered in the surface waters venturing out from the littoral (Martin & Shine 1993).

In summary then, following an initial dilution from the maternal signature, the nitrogen isotopic signatures of Loch Ness trout generally became heavier with increasing fish size, indicating a gradual move upwards through the trophic levels of the Loch Ness food web. This is comparable to other studies. In contrast, the carbon isotope signatures exhibited a much more complex pattern, reflecting ontogenetic shifts in habitat and associated dietary intake, from the natal river, through the littoral zone and out into the pelagic. The combination of both carbon and nitrogen isotope data for individual trout provided a more accurate appraisal of the assimilated diet and foraging location compared to the gut content analyses. The wide-ranging intraspecific variability in isotopic signatures of these relatively large, slow-growing fish (i.e. slow turnover of tissue signatures) suggests strong evidence for a spectrum of dietary specialization.

Resumen

La ecología trófica de muchas especies de peces en lagos de aguas frías de sistemas templados se caracteriza a menudo por una estrategia generalista o oportunista. En este estudio, se han examinado las dietas de la trucha marrón politrófica en el Lago Ness, Escocia, usando isótopos estables de carbón y nitrógeno como complemento a los análisis de contenido estomacal y recuentos de los anillos de los otolitos. Utilizando las proporciones de isótopos estables, fue posible seguir la ontogenia de la trucha desde la etapa juvenil en el río de nacimiento hasta la etapa de piscivoría en el sistema pelágico. También se demostró la dilución potencial de las señales isotópicas maternas desde los huevos hasta la etapa juvenil. A pesar de la baja productividad del lago, la variabilidad intraespecífica en los porcentajes isotópicos sugiere que existen individuos que no son oportunistas, sino que mantienen su especialización en la dieta.

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