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Continuous variation in the pattern of marine *v.* freshwater foraging in brown trout *Salmo trutta* L. from Loch Lomond, Scotland

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Carbon stable-isotope analysis showed that individual brown trout *Salmo trutta* in Loch Lomond adopted strategies intermediate to that of freshwater residency or anadromy, suggesting either repeated movement between freshwater and marine environments, or estuarine residency. Carbon stable-isotope ($\delta^{13}C$) values from Loch Lomond brown trout muscle tissue ranged from those indicative of assimilation of purely freshwater-derived carbon to those reflecting significant utilization of marine-derived carbon. A single isotope, two-source mixing model indicated that, on average, marine C made a 33% contribution to the muscle tissue C of Loch Lomond brown trout. Nitrogen stable isotope, $\delta^{15}N$, but not $\delta^{13}C$ was correlated with fork length suggesting that larger fish were feeding at a higher trophic level but that marine feeding was not indicated by larger body size. These results are discussed with reference to migration patterns in other species.

Key words: $\delta^{13}C$; $\delta^{15}N$; anadromy; mixing model; *Salmo trutta*; stable-isotope analysis.

INTRODUCTION

The brown trout *Salmo trutta* L. is a highly polytypic salmonid. Individual fish within a population show considerable variation in life history characteristics and are facultatively anadromous (Elliott, 1994; Klemetsen *et al.*, 2003; Cucherousset *et al.*, 2005). Spawning occurs in natal streams; in open systems, a variable proportion of the total population, but rarely the whole population, undergoes a metamorphosis (smolting), that adapt individuals to life in salt water and these fish subsequently migrate to sea to feed. Other individuals within the population remain in fresh water as residents (McDowell, 1988; Jonsson & Jonsson, 1993; Elliott, 1994). Therefore, a binary choice of life history trajectories for individuals is conventionally described in *S. trutta* (Eek & Bohlin,

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1997; Bagliniere *et al.*, 2001; Charles *et al.*, 2004), namely: (1) freshwater residency or (2) anadromy, migration to sea to feed before returning to natal streams to spawn.

Anadromy in salmonids is well studied, particularly in Atlantic salmon *Salmo salar* L. (McDowell, 1988; Fleming, 1996; Garcia-Vazquez *et al.*, 2001). The benefits of migration to sea include access to more profitable food resources and so increased growth (Berg & Jonsson, 1990; Olsson *et al.*, 2006), while the costs include increased predation by marine predators and an energetically costly migration (Bohlin *et al.*, 2001; Dieperink *et al.*, 2002). Females have a significantly higher energy requirement than males and thus are more likely to adopt an anadromous pathway (Elliott, 1994; Klemetsen *et al.*, 2003). The benefits of anadromy are thus less obvious for males. Large anadromous males compete for females directly, while small resident males can adopt 'sneaking' reproductive tactics in which they do not compete directly for access to the female. These 'sneaking' males can have substantial reproductive success, without the costs of migration (Myers & Hutchings, 1987; Garcia-Vazquez *et al.*, 2001). Despite the life history differences between them, however, migrant and resident brown trout can spawn together successfully. The prevalent view, therefore, is that where resident and anadromous brown trout spawn or occur together they are freely interbreeding fractions of a single spawning stock (Elliott, 1994; Klemetsen *et al.*, 2003).

A number of laboratory techniques have been used to identify resident and anadromous fishes, including: carotenoid pigment profiling (Youngson *et al.*, 1997), measurement of the strontium content of scales and bony tissue (Kalish, 1990; Eek & Bohlin, 1997; Veinott *et al.*, 1999) and analysis of stable isotope ratios (McCarthy & Waldron, 2000; Jardine *et al.*, 2005). Stable isotopes of nitrogen and carbon are widely used in the study of animal movements and trophic interactions (Grey, 2001; Grey *et al.*, 2002; Harrod *et al.*, 2005). Naturally occurring stable isotopes are assimilated by animals and fractionation by biochemical processes causes the heavier isotope to be accumulated in animal tissue. $\delta^{15}N$ (the change in the ratio of ^{15}N to ^{14}N compared with a standard) is typically enriched by *c.* 3–5‰, allowing the long-term trophic position of consumers to be estimated (Peterson & Fry, 1987; Post, 2002; Sweeting *et al.*, 2007). In contrast, trophic enrichment in $\delta^{13}C$ (the change in the ratio of ^{13}C to ^{12}C compared with a standard) is typically minor (*c.* <1‰) and $\delta^{13}C$ is used as a robust and consistent indicator of the carbon source the organism has been assimilating (Peterson & Fry, 1987; Hobson, 1999). $\delta^{13}C$ has specifically been used to distinguish between freshwater and marine carbon sources in a range of mobile consumers in a number of studies (Hobson, 1999; Harrod *et al.*, 2005; Guelinckx *et al.*, 2006). $\delta^{13}C$ values are relatively ^{13}C depleted (more negative) in fresh water compared to marine habitats, with a gradient between the two extremes that correlates with salinity (Fry & Sherr, 1984; Riera & Richard, 1996).

Different tissues vary in the rate at which their isotopic values reflect that of their food source, with high turnover tissues such as liver changing quickly and thus responding to a change in diet rapidly, while low turnover tissues such as bone changes slowly (Bearhop *et al.*, 2004). The turnover of muscle depends on growth rate and falls somewhere in between these two extremes, being measured in months (Perga & Gerdeaux, 2005; Phillips & Eldridge, 2006).

A general anecdotal observation from earlier studies of fish in Loch Lomond has been that many of the brown trout caught in Loch Lomond were small in size, consistent with freshwater residency, but also silver in colouration consistent with anadromy. Here, analysis of the stable isotopes of carbon and nitrogen in muscle tissue is used to test the null hypothesis that *S. trutta* exhibit a typical binary sea migration pattern in Loch Lomond, Scotland.

METHODS

In total 75 multi panel Nordic-pattern gillnets, which comprise 12 panels, ranging from 5 to 55 mm, knot-to-knot mesh, were set overnight at sites in the north, mid and south basins of Loch Lomond over the winter of 2005–2006 (from 9 November 2005 to 24 January 2006) as part of a broader fish survey. These nets are non-selective for salmonids within the modal size range 45–495 mm fork length (L_F) (Jensen & Hesthagen, 1996). During this period, 44 brown trout were caught. Fish were frozen within 4 h of capture. In the laboratory, fish were defrosted, scales were removed below the dorsal fin for ageing, and a small piece of white muscle posterior to the head and above the lateral line was removed for stable isotope analysis. Tissue was dried at constant temperature (50° C for at least 48 h), ground to a fine powder using a grinder (Revel Ltd, Pribram, Czech Republic) and 0·5 mg of dried ground muscle was packed into pressed 10 × 10 mm tin weighing pans and used in simultaneous analysis of stable C and N isotopes. Stable isotope ratios were determined by continuous flow isotope ratio mass spectrometry at the Max Planck Institute for Limnology, Germany. Stable isotope ratios are given using the δ notation expressed in units per mil where $\delta(‰) = 1000\,[(R_{sample} R_{standard}^{-1}) - 1]$ and $R = {}^{13}C{:}{}^{12}C$ or ${}^{15}N{:}{}^{14}N$. The reference materials used were secondary standards of known relation to the international standards of Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen. Typical precision for a single analysis was ±0·1‰ for $\delta^{13}C$ and ±0·3‰ for $\delta^{15}N$. All $\delta^{13}C$ values were subsequently adjusted for lipid concentration variation (Kiljunen *et al.*, 2006).

To determine the relative contribution of energy derived from freshwater and marine sources, a single isotope, two source mixing model was applied to the brown trout $\delta^{13}C$ data (Phillips & Gregg, 2001). This approach assumes that marine and fresh water represent the only two sources of available carbon and that the $\delta^{13}C$ values of the tissue are representative of the diet of the fish. It was also assumed that the brown trout with the most depleted $\delta^{13}C$ values represented individuals assimilating only fresh water derived carbon, *i.e.* 100% freshwater feeding, and the brown trout with most enriched $\delta^{13}C$ values were wholly deriving their energy from marine sources, *i.e.* 100% marine feeding. A mean freshwater $\delta^{13}C$ value was also derived for two freshwater fish species from Loch Lomond, namely bream *Abramis brama* (L.) and powan *Coregonus lavaretus* (L.). A cross-species mean marine $\delta^{13}C$ value for 11 north-east Atlantic species was also derived from the literature. Species included were albacore tuna *Thunnus alalunga* (Bonnaterre), whiting *Merlangius merlangus* (L.), flounder *Platichthys flesus* (L.), monkfish *Lophius budegassa* Spinola, hake *Merluccius merluccius* (L.), red mullet *Mullus barbatus* L., tope *Galeorhinus galeus* (L.), black-mouth catshark *Galeus melastomus* Rafinesque, starry smooth hound *Mustelus asterias* Cloquet, spiny dogfish *Squalus acanthias* L. and lesser-spotted dogfish *Scyliorhinus canicula* (L.) (Das *et al.*, 2000; Pinnegar *et al.*, 2001; Badalamenti *et al.*, 2002; Domi *et al.*, 2005).

RESULTS

Of the 44 brown trout sampled in winter 2005–2006 from fresh water in Loch Lomond, muscle tissue $\delta^{13}C$ values ranged between −27·7 and −17·8‰. The most depleted (negative) $\delta^{13}C$ values recorded were consistent with those derived

from obligate freshwater fishes (powan and bream), $-27{\cdot}2 \pm 0{\cdot}9$ (mean ± S.E.). At the other extreme the most enriched (positive) $\delta^{13}C$ values from brown trout were consistent with mean ± S.E. values calculated from north-east Atlantic marine fishes ($-17{\cdot}8 \pm 0{\cdot}3$). Between these extremes, the brown trout showed a wide range of $\delta^{13}C$ values (Fig. 1). The nitrogen isotope analysis of brown trout tissue samples showed signatures ranging from 8·4 to 14·4‰. There was a weak, but statistically significant positive relationship between $\delta^{13}C$ and $\delta^{15}N$ ($F_{1,43}$, $R^2_{(adj)} = 0{\cdot}07$, $P < 0{\cdot}05$).

A two source linear mixing model was used to determine the contribution of freshwater and marine carbon sources to brown trout muscle tissue collected in Loch Lomond at this time using the $\delta^{13}C$ values adjusted for lipid variation. The relative frequency distribution of calculated marine source C contribution in muscle tissue is shown in Fig. 2. The modal marine contribution to muscle tissue from this sample was 30%, with the lower and upper and lower inter-quartiles being 19 and 42%, respectively.

Regression analysis was used to explore any factors that might be affecting the stable isotope results. Date of capture was not correlated with $\delta^{13}C$ ($F_{1,43}$, $R^2_{(adj)} = -0{\cdot}01$, $P > 0{\cdot}05$) or with $\delta^{15}N$ ($F_{1,43}$, $R^2_{(adj)} = -0{\cdot}02$, $P > 0{\cdot}05$). Ln L_F was not correlated with $\delta^{13}C$ ($F_{1,43}$, $R^2_{(adj)} = 0{\cdot}02$, $P > 0{\cdot}05$), however, there was a significant correlation between L_F and $\delta^{15}N$ of Loch Lomond brown trout (Fig. 3) ($F_{1,43}$, $R^2_{(adj)} = 0{\cdot}47$, $P < 0{\cdot}001$). The L_F and age are not affected by the $\delta^{13}C$ signature of Loch Lomond brown trout muscle tissue (MANCOVA, $F_{1,43}$, $P > 0{\cdot}05$).

DISCUSSION

Stable isotope analysis of muscle tissue of brown trout caught in Loch Lomond revealed an unexpectedly broad range of values for both $\delta^{13}C$ and

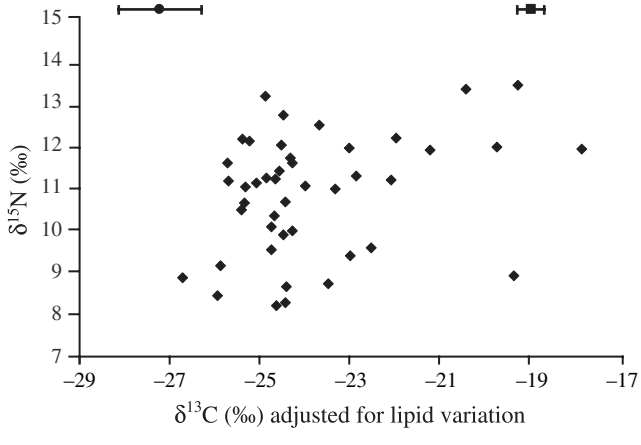

FIG. 1. $\delta^{13}C$ adjusted for lipid variation and $\delta^{15}N$ of muscle from brown trout from Loch Lomond. Mean ± S.E. freshwater $\delta^{13}C$ for non-migratory fish from Loch Lomond, $-27{\cdot}2 \pm 0{\cdot}9$ (●), and mean marine $\delta^{13}C$ for north-east Atlantic species, $-17{\cdot}8 \pm 0{\cdot}3$ (■) (Das *et al.*, 2000; Pinnegar *et al.*, 2001; Badalamenti *et al.*, 2002; Domi *et al.*, 2005) are shown.

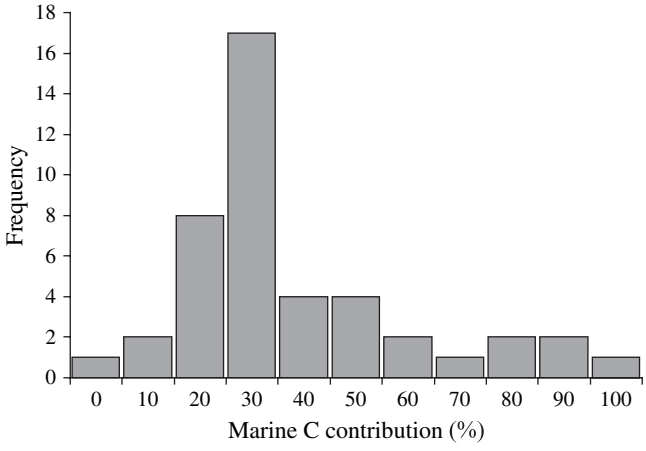

FIG. 2. The percentage estimated marine C contribution to tissue of brown trout from Loch Lomond calculated using a single isotope, two-source linear mixing model applied to the data (Phillips & Gregg, 2001). The simple mixing model assumes that brown trout with the most depleted $\delta^{13}C$ value (−27·7‰) represents a wholly freshwater foraging history, and the brown trout with most enriched $\delta^{13}C$ value (−17·8‰) represents a wholly marine foraging history.

$\delta^{15}N$. The range of $\delta^{13}C$ is consistent with the brown trout population in Loch Lomond feeding and assimilating C from both freshwater and marine systems. The distribution of $\delta^{13}C$ values is not, however, consistent with a dichotomous marine and freshwater foraging strategy, where anadromous fish migrate to sea to feed and residents remain in fresh water to feed. Rather these data show more continuous variation between freshwater and sea feeding (and consequently migration extremes) in this population.

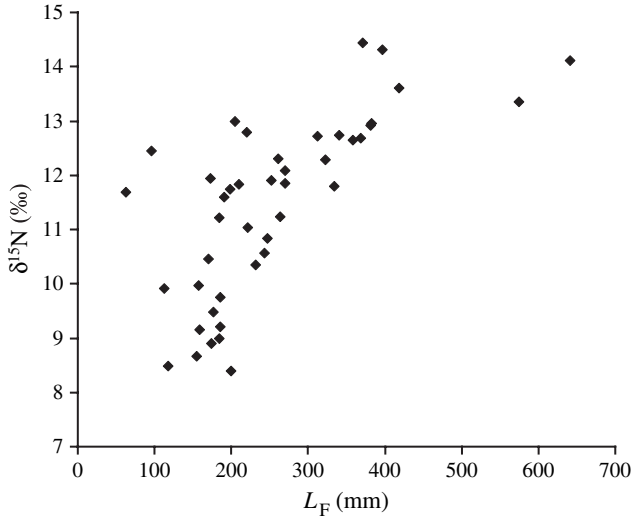

FIG. 3. Fork length (L_F) and $\delta^{15}N$ of muscle from brown trout from Loch Lomond. There is a significant positive correlation ($F_{1,43}$, $R^2_{(adj)} = 0{\cdot}47$, $P < 0{\cdot}001$).

Both $\delta^{13}C$ and $\delta^{15}N$ are enriched in marine environments in comparison to fresh water (Mizutani & Wada, 1988; Post, 2002), and this is supported in the positive relationship between $\delta^{13}C$ and $\delta^{15}N$ from brown trout in this study. The strong positive relationship between L_F and $\delta^{15}N$ (Fig. 3) is indicative of larger fish feeding at higher trophic levels than smaller individuals. The individual with the lowest $\delta^{15}N$ value was smaller (200 mm) and had a depleted $\delta^{13}C$ value (−24·6‰) indicating freshwater residency, in comparison to the individual with the greatest $\delta^{15}N$ value which was larger (371 mm) and had an enriched $\delta^{13}C$ value (−19·2‰) indicating a more marine signature. Due to the weak relationship between $\delta^{13}C$ and $\delta^{15}N$, the variation in $\delta^{15}N$ is probably due to larger brown trout feeding at a higher trophic level, rather than differences in the baseline $\delta^{15}N$ values between fresh water and marine habitats. The MANCOVA results indicate that growth does not appear to be significantly affected by $\delta^{13}C$ value, which suggests there is no growth benefit in migration for these brown trout. This also reflects that by chance, no larger and older fish were caught that had a large proportion of marine C contributing to muscle tissue; alternatively, it is possible that these fish may over winter in the marine environment (Olsen *et al.*, 2006).

The results of the linear mixing model show frequencies of estimated marine C contribution to muscle $\delta^{13}C$ that are consistent with individuals having variable proportions of the assimilated diet coming from freshwater and saltwater sources. The mean foraging strategy of the brown trout sampled here suggests that 33% of muscle tissue in winter is derived from marine sources. The most likely explanation is that many brown trout in this population either spend most of their time in fresh water, but move into sea water for a short period in the months previous to capture, or they spend a significant proportion of their time in an intermediate area between fresh water and oceanic salt water. There are three alternative, but less probable situations. One is that the diet of large resident brown trout is partially reliant on small anadromous fish, resulting in partially marine isotope values. There is no significant size difference, however, between brown trout with a more marine $\delta^{13}C$ value and those with a more freshwater $\delta^{13}C$ values suggesting predation would be problematic, and brown trout with intermediate isotope values are not noticeably larger. The second is that resident brown trout have been feeding primarily on $\delta^{13}C$ enriched invertebrate prey such as freshwater snails or other epilithic microalgal scrapers (Finlay *et al.*, 1999). Since brown trout have been shown to be opportunistic feeders it seems unlikely they would specialize enough on prey species of the same trophic guild to affect the diet to such an extent. The third is that anadromous brown trout are feeding in fresh water on their return migration and so are diluting the marine signature of their muscle tissue. If this were the case a correlation between date of capture and marine C signal would be expected, however, there was no evidence for such a relationship. Furthermore, depressed feeding and growth in late autumn and winter leads to slow tissue turnover rates in winter, and the bulk of the carbon assimilated into muscle tissues reflects summer feeding (Perga & Gerdeaux, 2005).

Movement at sea in *S. trutta* is known to be more geographically restricted and shorter in duration than *S. salar* (McDowell, 1988). Subcategories within resident and anadromous brown trout groups have been previously described.

Resident brown trout may (1) spend their entire life in their natal stream, (2) migrate from their natal stream to the parent river and (3) migrate from their natal streams to a lake; anadromous brown trout can be sub-categorized into (1) short distance migrants (estuarine or slob brown trout) that migrate into estuaries to feed and (2) long distance migrants that migrate to coastal waters (Elliott, 1994). Migration can also be restricted in time. Most anadromous brown trout spend at least 18 months at sea, but some returning fish spend only *c.* 6 months away from fresh water, these individuals are commonly referred to as 'finnock' in Scotland. The proportion of finnock among returning fish varies considerably between rivers and years. In many populations most finnock are males, since these are small they follow a sneaking reproductive strategy (Elliott, 1994).

It is likely that there are benefits to following a life history intermediate between that of fully resident and anadromous fishes. Estuaries are often used as nurseries by juvenile marine fishes (Brown, 2006; Guelinckx *et al.*, 2006) hence the most productive feeding areas for these brown trout may be in estuarine areas and not the sea (Elliott, 1986). It is also possible that some marine predators are avoided if the brown trout do not move into coastal waters. Other advantages of migration may include avoidance of intraspecific competition (Bult *et al.*, 1999; Landergren, 2004; Olsson *et al.*, 2006). It is possible that Loch Lomond brown trout move only far enough towards sea to take advantage of the benefits without undertaking a strenuous and potentially hazardous migration to fully marine habitats.

Individual life history variation have been identified using element analysis in a number of species: white-spotted charr *Salvelinus leucomaenis* (Pallas) (Arai & Morita, 2005), pond smelt *Hypomesus nipponensis* McAllister (Arai *et al.*, 2006), European eel *Anguilla anguilla* (L.) (Harrod *et al.*, 2005) and Japanese eel *Anguilla japonica* Temminck & Schlegel (Tzeng *et al.*, 2002, 2003). This is the first time, however, stable isotope analysis has been used to elucidate the complex migration of individuals in a brown trout population. These findings suggest that Loch Lomond brown trout have a flexible migration strategy with a high degree of behavioural plasticity with an ability to utilize the full range of salinities available.

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