An assessment, using stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in Loch Ness

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The natural abundance of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) was determined for components of the pelagic food web in Loch Ness, a deep oligotrophic lake in northern Scotland, and compared with values from the inflow rivers and the catchment vegetation. Phytoplankton $\delta^{13}\text{C}$ was low compared to values reported from other lakes, possibly reflecting a high use of ^{13}C -depleted CO_2 from respired organic matter before further isotopic fractionation during photosynthesis. Phytoplankton $\delta^{13}\text{C}$ was appreciably lower than that of dissolved and particulate organic matter (DOM and POM) in the loch. The DOM and POM were evidently overwhelmingly of allochthonous origin and ultimately derived from terrestrial plant detritus. The distinctive $\delta^{13}\text{C}$ values for phytoplankton and detritus in the loch allowed the use of food sources by grazing crustacean zooplankton to be assessed, and the contributions of phytoplankton carbon and detrital carbon to zooplankton total body carbon appeared to be about equal. Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for zooplankton and fish allowed assessment of trophic structure in the loch. The very high dependence of the pelagic food web in Loch Ness on allochthonous organic matter inputs from the catchment may be exceptional in a large lake, but has important implications for our understanding of lake ecosystem processes as well as for lake management.

Keywords: Loch Ness, stable isotopes, food web, pelagic, plankton

1. INTRODUCTION

The traditional view that planktonic food chains in lakes are dependent on carbon fixed *in situ* by the autotrophic phytoplankton is under serious challenge. Several studies of small humic lakes have indicated that allochthonous organic carbon inputs from the catchment are less refractory than had been previously assumed and can support bacterial metabolism (Jones & Salonen 1985; Hessen 1992; Tranvik 1992). In fact, bacterial respiration alone frequently exceeds phytoplankton production in unproductive lakes (Del Giorgio *et al.* 1997), consistent with observations that many such lakes are net heterotrophic systems (Del Giorgio & Peters 1994). This would explain earlier reports of widespread carbon dioxide supersaturation in the surface waters of lakes (Cole *et al.* 1994). A lake in which the plankton acts as a net heterotrophic system must receive external subsidies of metabolizable organic carbon into its plankton, although in theory these might originate either from the littoral zone of the lake or from its catchment. Jones (1992) hypothesized that the relative importance of allochthonous organic carbon inputs should generally decrease with increasing lake trophy and that allochthonous inputs should be more important in coloured, humic lakes than in clear-water lakes of comparable trophy. Although reported patterns of

planktonic production:respiration ratios in lakes largely support these hypotheses (Del Giorgio & Peters 1993, 1994), direct evidence of the origins of allochthonous sources of dissolved and particulate organic matter (DOM and POM), and of their contribution to carbon flux through plankton, has been elusive.

Stable isotope analysis is potentially a powerful tool for assessing food chain relationships. Carbon stable isotope ratios in animals are known to reflect quite closely those of their diet, whereas ^{15}N in animals often shows considerable enrichment compared to their diet (Peterson & Fry 1987; Michener & Schell 1994). This means that, provided different food sources have distinctive carbon isotope ratios, their relative importance in the diet of consumers can be established, while use of carbon and nitrogen stable isotope analysis together can often provide much more information about feeding relationships than either ratio alone. Although this approach has been applied with some success to trace the flow of organic matter through aquatic food webs (Fry & Sherr 1984; Michener & Schell 1994), to date a major problem in studies of plankton has been the separation of phytoplankton from other microbes and detritus to obtain values for phytoplankton stable isotope ratios. For example, in a study of 28 Canadian lakes, Del Giorgio & France (1996) showed that zooplankton in unproductive lakes were particularly depleted in ^{13}C relative to smaller planktonic size classes. They attributed this to the degree of POM dilution by

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nonalgal sources of organic carbon and inferred systematic differences in organic carbon flow pathways between lake types, although they had not been able to distinguish the carbon isotope signatures of total POM and phytoplankton.

Here, we present results from stable isotope analyses that show the pelagic food web in Loch Ness, Scotland, to be heavily dependent on detrital carbon derived from terrestrial vegetation in the catchment. Loch Ness is the largest volume of water in the British Isles and occupies a simple trench-like basin 39 km long and 1.5 km wide. The loch has a maximum depth of 230 m and a mean depth of 132 m, and the strong winds which frequently blow up the long axis mean that, even during summer stratification, the depth of mixing extends to 30–40 m. Together with poor light penetration into the moderately humic water, this means that the underwater light climate experienced by the phytoplankton in the loch is exceptionally unfavourable, and the maximum daily rates of areal phytoplankton photosynthesis achieved in Loch Ness are only around $100 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Jones *et al.* 1996a). A previous study (Laybourn-Parry *et al.* 1994) showed that this phytoplankton production was insufficient to support even the measured bacterial production, clearly implying that the plankton in Loch Ness depends on external inputs of organic carbon. In fact, the total organic carbon content of the loch is dominated by detrital carbon (Jones *et al.* 1996b) and, since the phytoplankton production is so low and the loch morphometry precludes significant inputs of organic carbon from the littoral region to the pelagial, this detrital carbon may be presumed to originate from the catchment. Loch Ness therefore provides an ideal site to assess the relative importance of autochthonous phytoplankton carbon and allochthonous terrestrial carbon in the pelagic food chain of a large lake.

2. METHODS

Samples were collected on 11 September 1996 and some additional sampling was carried out on 20 November 1996. Water samples for POM and DOM (POM, $>0.2 \mu\text{m}$; DOM, $<0.2 \mu\text{m}$) were collected from the upper water column of Loch Ness using an integrating tube sampler 30 m long, and from a depth of 100 m using a Friedinger sampler. Water samples were also collected from the main river inflows close to their point of discharge into the loch. All water samples were stored in acid-washed 10 l aspirators. POM was concentrated using a Minitan tangential flow ultrafiltration apparatus fitted with multiple $0.2 \mu\text{m}$ Durapore (polyvinylidene fluoride) filter plates. The concentrated POM was then collected on a precombusted Anodisc inorganic filter and dried at 60°C . The ultrafiltrate was collected and concentrated for DOM analysis by freeze drying.

Plankton from the loch was collected by vertical hauls from a depth of 30 m to the surface, with a plankton net of mesh $110 \mu\text{m}$ and stored without preservation. Crustacean zooplankton were later picked from the samples by hand using a fine pipette, with different species being separated when numbers permitted. Sufficient individuals of each species were collected on precombusted GF/F filters, rinsed with Milli-Q water and dried at 60°C . On 11 September, large diatoms, which make up most of the phytoplankton biomass in Loch Ness throughout the year (R. I. Jones, unpublished data), were separated from other particles by repeated sedimentation. Microscope examination of the resultant

concentrate confirmed that it consisted almost entirely of large diatoms (mainly *Aulacoseira subarctica* and *Asterionella formosa*), and that other particles were negligible. Subsamples of the diatom concentrate were then collected on precombusted GF/F filters, rinsed and dried at 60°C . Separation of diatoms was not achieved on 20 November when densities were much lower. Samples of epilithon from the river inflows were scraped from stones, collected on precombusted GF/F filters and dried at 60°C . Samples of leaf material from some common types of vegetation were collected from several locations around the catchment, rinsed and subsequently chopped and dried at 60°C . Two individuals of arctic charr (*Salvelinus alpinus*) and three individuals of three-spined sticklebacks (*Gasterosteus aculeatus*) which had been collected in pelagic trawl nets in November 1992 were also available for analysis. The charr had been frozen and samples of dorsal muscle tissue were taken and freeze dried. The sticklebacks had been preserved in alcohol and each entire individual was freeze dried. In addition, two individuals of migratory Atlantic salmon (*Salmo salar*) freshly caught from the loch were obtained from local anglers, and were used to provide samples of dorsal muscle tissue which were freeze dried.

Analysis for ^{13}C and ^{15}N was carried out using a Roboprep-CN continuous flow analyser coupled to a Tracermass single-inlet triple-collector mass spectrometer (both instruments by Europa Scientific, Crewe, UK). Samples for carbon were run directly, but those for nitrogen were first analysed for total per cent N. Sample weights in the second run, for the determination of $\delta^{15}\text{N}$, were then adjusted to provide $120 \mu\text{g N}$ in each case; this technique is essential for adequate precision when using a mass spectrometer where there is a non-linear relationship between the pressure in the source and the apparent $^{15}\text{N}/^{14}\text{N}$ ratio.

Treatment of samples prior to combustion varied. Those collected on GF/F papers and which remained firmly embedded in the fibres of the filter paper were cut into strips and the sample and glass fibre combusted together. In other cases, where the weight of sample was greater, the sample peeled away from the glass fibre on drying and could be combusted on its own. This was to be preferred, as molten glass from the GF papers soon blocks the oxidation tube and is difficult to remove. Where Anodisc filters (13 mm, no polypropylene support ring) were used to collect samples, the aluminium oxide was ground to a fine powder between two small watch glasses. Larger samples were ground under liquid nitrogen in a freezer mill (Spex Industries Inc., Edison, New Jersey). Results are given using the δ notation where $\delta = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 1000$, expressed in units of per mil (‰), and where $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The reference materials used were secondary standards of known relation to the international standards, Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen.

3. RESULTS

DOM in Loch Ness showed no significant difference (*t*-test, $p > 0.05$) in $\delta^{13}\text{C}$ between 0–30 m depth samples and those from 100 m depth on either date (table 1). By contrast, a small but significant difference (*t*-test, $p < 0.01$) was found between POM from the two depth zones on 11 September, with the POM from 0–30 m being slightly depleted in ^{13}C . This probably reflects a small but detectable contribution of phytoplankton to total POM in the 0–30 m samples but not in those from 100 m, since the separated phytoplankton samples were appreciably depleted in ^{13}C relative to the total POM (table 1). This

Table 1. *Isotopic composition (as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for components of the pelagic food web in Loch Ness and from the main river inflows*
(Values are means of n replicates $\pm$ s.d.)

sample type	$\delta^{13}\text{C}$	11 September 1996 $\delta^{15}\text{N}$	n	20 November 1996 $\delta^{13}\text{C}$	n
fish					
<i>Salmo salar</i>	-19.47 ± 1.01	10.72 ± 0.49	2	—	—
<i>Salvelinus alpinus</i>	-27.45 ± 0.98	11.94 ± 0.83	2	—	—
<i>Gasterosteus aculeatus</i>	-26.91 ± 0.14	11.49 ± 0.91	3	—	—
zooplankton					
<i>Bythotrephes longimanus</i>	-27.87 ± 0.66	10.21 ± 0.70	5	—	—
<i>Leptodora kindti</i>	-27.60 ± 0.25	9.02 ± 0.14	4	—	—
mixed copepods	-28.51 ± 0.63	7.83 ± 0.27	5	—	—
<i>Cyclops abyssorum</i>	—	—	—	-27.70 ± 0.63	3
<i>Diaptomus gracilis</i>	—	—	—	-27.80 ± 0.31	5
<i>Daphnia hyalina</i>	-28.54 ± 0.70	4.40 ± 0.56	5	-25.78 ± 0.23	6
phytoplankton	-31.15 ± 0.18	—			
POM					
Loch (0–30 m)	-27.75 ± 0.41	—	4	-25.30 ± 0.26	3
Loch (100 m)	-26.34 ± 0.46	—	4	-24.77 ± 0.38	3
River Enrick	-25.94 ± 0.80	—	2	-25.00 ± 0.99	2
River Moriston	-26.30 ± 0.51	—	3	-26.43 ± 0.31	3
River Oich	-27.10 ± 0.93	—	4	-26.00 ± 0.20	3
River Foyers	-26.44 ± 0.81	—	4	-26.10 ± 0.14	2
DOM					
Loch (0–30 m)	-27.33 ± 0.22	2.51 ± 0.57	4	-27.03 ± 0.24	3
Loch (100 m)	-27.40 ± 0.23	—	5	-27.06 ± 0.05	3
River Enrick	-26.83 ± 0.19	—	5	-27.85 ± 0.11	3
River Moriston	-27.29 ± 0.37	—	5	-28.44 ± 0.88	3
River Oich	-27.79 ± 0.43	—	5	-28.01 ± 0.06	3
River Foyers	-26.31 ± 0.30	3.92 ± 0.38	5	-28.02 ± 0.07	3
inflow epilithon					
River Enrick	-20.91	—	1	-28.17 ± 0.64	3
River Oich	-25.64	—	2	-25.90 ± 0.85	2
River Foyers	-23.80	—	1	-32.90 ± 0.53	3

interpretation is supported by results from 20 November, when phytoplankton biomass had declined markedly. The $\delta^{13}\text{C}$ for POM (0–30 m) was then significantly higher than on the earlier date (t -test, $p < 0.001$) and there was no significant difference in POM $\delta^{13}\text{C}$ between depths (t -test, $p > 0.05$). Therefore it appears that phytoplankton and detritus (POM and DOM) in Loch Ness have distinct $\delta^{13}\text{C}$ values, which should allow their relative contributions to zooplankton diets and body carbon to be traced.

A number of crustacean zooplankton types could be isolated manually from the plankton hauls on 11 September and analysed separately: the predatory cladocerans *Bythotrephes longimanus* and *Leptodora kindti*, the filter-feeding cladoceran *Daphnia hyalina*, and a mixture of the copepods *Diaptomus gracilis* and *Cyclops abyssorum*. Numbers of copepods were too small to permit separate analysis of the latter two species, which were analysed as a mixture containing *Diaptomus* and *Cyclops* in a numerical ratio of approximately 5:1. The only other crustacean zooplankters which can be important in Loch Ness (Maitland *et al.* 1981) are the cladocerans *Bosmina coregoni*, *Holopedium gibberum* and *Polyphemus pediculus*, none of which were present in sufficient numbers at the time of

sampling to permit separation. Comparison of $\delta^{13}\text{C}$ values for the crustacean zooplankton groups with those for phytoplankton and detritus (table 1, figure 1) shows clearly that an appreciable part of the body carbon of both *Daphnia* and copepods was derived from detritus. Animals typically show a slight (0.5–1.0‰) enrichment in ^{13}C relative to their diet (Michener & Schell 1994). Therefore, assuming the maximum enrichment level of 1‰, animals feeding exclusively on phytoplankton ($\delta^{13}\text{C}$, -31.2‰) or detritus (POM 0–30 m, $\delta^{13}\text{C}$, -27.8‰) would be expected to develop a ^{13}C signature of -30.2‰ and -26.8‰ , respectively. The average of these two values is -28.5‰ , which is actually the observed value for both *Daphnia* and the copepods. Applying a simple mass balance equation to these figures therefore suggests that 50% of the body carbon of these grazing zooplankton is likely to have been derived from phytoplankton and 50% from detritus. The two predatory cladocerans, *Bythotrephes* and *Leptodora*, showed $\delta^{13}\text{C}$ values enriched by 0.6–0.9‰ relative to *Daphnia* and copepods, which is consistent with their having preyed almost entirely on other zooplankton with little or no uptake of phytoplankton or detritus.

Figure 1. Carbon isotope composition of zooplankton, phytoplankton and POM and DOM from Loch Ness (11 September 1996). Values shown are means $\pm$ 95% confidence limits for n samples.

Figure 2. Carbon isotope composition of POM and DOM from 100 m depth in Loch Ness and from the main inflows (11 September 1996). Also shown is the isotopic composition of leaf samples from several types of vegetation in the catchment. Values shown are means $\pm$ 95% confidence limits for n samples.

The samples from 20 November contained too few of the predatory cladocerans to allow these to be separated. However, on this occasion separate samples of *Cyclops* and *Diaptomus* were obtained for analysis, as well as samples of *Daphnia*. Neither *Cyclops* nor *Diaptomus* showed a significant difference in $\delta^{13}\text{C}$ from that of the earlier value for mixed copepods (t -test, $p > 0.1$). By contrast, *Daphnia* $\delta^{13}\text{C}$ was significantly higher than on the previous date (t -test, $p < 0.001$), and was very close to the $\delta^{13}\text{C}$ value for POM. Therefore, it appears that on this second occasion a greater proportion of *Daphnia* body carbon was of detrital origin. The more rapid response of *Daphnia* than of the copepods to the changing $\delta^{13}\text{C}$ of potential food particles probably reflects the faster turnover of individuals in a population of parthenogenetic organisms with rapid reproduction but short life spans.

Carbon stable isotope analysis also allowed the source of the detritus to be traced with some confidence (figure 2). On 11 September, $\delta^{13}\text{C}$ values for DOM in Loch Ness (-27.3‰ for 0–30 m, and -27.4‰ for 100 m) were very similar to the mean value of -27.1‰ for the main river inflows. This mean value takes no account of the relative discharges of the inflows. However, differences in $\delta^{13}\text{C}$ values between the inflows were only slight (table 1). Similarly, the $\delta^{13}\text{C}$ value of -26.3‰ for POM from 100 m in the loch (which should be largely free from the influence of the ^{13}C -depleted phytoplankton) was very similar to the mean value of -26.5‰ for the inflows. On 20 November, loch POM and DOM again had values similar to those of the inflows (table 1). These results strongly indicate that the detrital DOM and POM in Loch Ness is derived from riverine inputs. Further, the mean $\delta^{13}\text{C}$ value for leaf material from several species of terrestrial plant around the catchment was -27.8‰ . Considering the degree of interspecific variability in the plant $\delta^{13}\text{C}$ values (table 2) and the fact that only leaf material was sampled, this mean value was remarkably close to those for the POM and DOM in the rivers. Samples of epilithon from three of the inflows on 11 September were appreciably more ^{13}C -enriched, with $\delta^{13}\text{C}$ values between -20.9 and -25.6‰ , although on 20 November the epilithon was more ^{13}C -depleted (table 1). These results indicate that riverine POM and DOM was predominantly terrestrial in origin and not produced within the rivers.

Sufficient material was available from the zooplankton from 11 September and from the fish samples for $\delta^{15}\text{N}$ analysis. Whereas animals show only a slight enrichment in ^{13}C compared with their diet, field studies show an average 3.2‰ enrichment in $\delta^{15}\text{N}$ per trophic level (Michener & Schell 1994). Plotting $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ values (figure 3) provided a clearer insight into the feeding relationships towards the top of the Loch Ness pelagic food web. *Daphnia* had the lowest $\delta^{15}\text{N}$ at 4.4‰. Unfortunately, the ^{15}N signature of phytoplankton and POM could not be determined due to insufficient sample, but we would predict a value in the region 1.5‰. The mixed copepods were ^{15}N -enriched by 3.4‰ relative to *Daphnia*, suggesting that their diet probably included a substantial proportion of small animals as well as phytoplankton and detritus. *Diaptomus gracilis* is generally considered to be herbivorous, but *Cyclops abyssorum* is known to be omnivorous, ingesting filamentous diatoms and other algae, rotifers, chironomid larvae and other crustacean zooplankton (Johnson & Walker 1974; Jewson *et al.* 1981). Although *Diaptomus* were numerically dominant in the mixed copepod sample, the larger *Cyclops* individuals may have contributed more to the total N in the sample and hence had greater influence on the $\delta^{15}\text{N}$ value. The predatory cladocerans, which are presumed to feed largely on smaller crustacean zooplankton, were further enriched in ^{15}N , *Bythotrephes* somewhat more so than *Leptodora*. This implies that both species included copepods and *Daphnia* in their diet but that *Leptodora* took a higher proportion of *Daphnia* than did *Bythotrephes*. The two types of fish collected in pelagic trawls, charr and sticklebacks, had very similar mean $\delta^{15}\text{N}$ values (11.9‰ and 11.5‰, respectively), indicating a similar dietary mix for both species. The degree of ^{15}N enrichment is consistent with these fish consuming a mixture of predatory and herbivorous cladocerans as well as copepods.

Table 2. Isotopic composition (as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for leaf samples from several types of vegetation from the Loch Ness catchment

(Values are means of three replicates $\pm$ s.d.)

vegetation type	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Pinus sylvestris</i>	-27.46 ± 0.08	0.59 ± 0.33
<i>Betula pendula</i>	-30.61 ± 0.07	1.09 ± 0.60
<i>Fraxinus excelsior</i>	-25.42 ± 0.05	4.17 ± 0.36
<i>Alnus glutinosa</i>	-27.99 ± 0.35	-1.77 ± 0.58
<i>Calluna vulgaris</i>	-28.78 ± 0.04	0.47 ± 0.30
<i>Pteridium aquilinum</i>	-26.37 ± 0.11	0.65 ± 0.39
<i>Sphagnum</i> spp.	-27.16 ± 0.76	-0.26 ± 0.30
mixed herbage	-28.52 ± 0.21	0.58 ± 0.48

However, the migratory salmon, which accumulate the bulk of their body tissue at sea, had very different $\delta^{13}\text{C}$ values reflecting their quite different food source, although showing similar, high $\delta^{15}\text{N}$ values to the charr and sticklebacks as a consequence of their equivalent position at the top of the food chain.

4. DISCUSSION

The total organic carbon in Loch Ness is known to be dominated by DOM and detrital POM, with living biomass contributing at most around 1% (Jones *et al.* 1996b). Given the very low phytoplankton production in the loch (Jones *et al.* 1996a) and the very restricted littoral zone relative to the great volume of the loch, the detrital DOM and POM must be presumed to originate in the catchment as partially decomposed terrestrial vegetation. The results from stable isotope analyses of terrestrial vegetation, riverine DOM and POM and river epilithon clearly support this presumption. Loch Ness therefore provides an example of a large lake in which potential organic carbon sources for pelagic consumers are overwhelmingly dominated by allochthonous inputs.

Attempts to assess pelagic food web structure using stable isotope analysis are generally hindered by the difficulty of physically separating the similarly sized components at the base of the food web: phytoplankton, bacteria, protozoa and detrital particles. In this study we were able to obtain $\delta^{13}\text{C}$ values for large diatoms and show that these were distinct from values for bulk POM. Our $\delta^{13}\text{C}$ value for large diatoms of -31.2‰ is lower than values reported by Zohary *et al.* (1994) of -17.9 to -23.2‰ for a dinoflagellate, *Peridinium gatunense*, and other phytoplankton in Lake Kinneret, although they did find a diatom, *Melosira granulata*, to have a very light isotopic composition (-32‰) in January. Yoshioka *et al.* (1994) also reported higher $\delta^{13}\text{C}$ values for various phytoplankton types in Lake Suwa.

Variations in phytoplankton $\delta^{13}\text{C}$ reflect both the degree of isotope fractionation during photosynthesis and the value of the inorganic carbon source. Phytoplankton are typically depleted in $\delta^{13}\text{C}$ by around -20 to -30‰ compared to their dissolved inorganic carbon (DIC) source (Goericke *et al.* 1994) although the degree of isotopic fractionation does vary between species and is dependent on factors such as growth rate and temperature.

Figure 3. Carbon and nitrogen isotope composition of zooplankton (11 September 1996) and pelagic fish (various dates, see §) from Loch Ness. AS, Atlantic salmon (*Salmo salar*); AC, arctic charr (*Salvelinus alpinus*); S, three-spined stickleback (*Gasterosteus aculeatus*); B, *Bythotrephes longimanus*; L, *Leptodora kindtii*; C, mixed copepods; D, *Daphnia hyalina*. Values shown are means $\pm$ 95% confidence limits.

When growth rate is determined by variations in light, P or N availability, ^{13}C depletion in organic C is generally greatest for cells with low growth rate, whereas when growth rate is determined by inorganic carbon supply, ^{13}C depletion in organic C is greatest for the fastest growing cells. However, in freshwaters the variability in $\delta^{13}\text{C}$ of the source DIC is likely to be more important in determining the $\delta^{13}\text{C}$ of phytoplankton. In particular, the balance between DIC originating from the atmosphere, from ^{13}C -enriched carbonate rocks or from metabolic release of CO_2 from ^{13}C -depleted terrestrial detritus will be critical. Unfortunately, at the time of this study we did not have a successful protocol established for determining the $\delta^{13}\text{C}$ of the low concentrations of DIC in Loch Ness. DIC in lakes often has a $\delta^{13}\text{C}$ value around -5‰ , although during stratification hypolimnetic DIC may be more ^{13}C -depleted (Quay *et al.* 1986; Keough *et al.* 1996). However, in lakes with a substantial input of allochthonous organic matter which may be metabolized to release ^{13}C -depleted DIC, lower $\delta^{13}\text{C}$ values of around -12‰ may be common (Meili *et al.* 1996). Since this is likely to be the case in Loch Ness, the low measured value of -31.2‰ for phytoplankton would then be consistent with the expected further ^{13}C depletion during photosynthesis.

Large diatoms dominate the phytoplankton carbon in Loch Ness throughout the year (R. I. Jones, unpublished data), although small diatoms (*Cyclotella* spp. and *Synedra* spp.) together with cryptomonads also make some contri-

bution. The faster growth rates and high edibility for zooplankton of the smaller species may give them a greater importance in the food web than is indicated by their biomass, but it was not technically possible to determine the $\delta^{13}\text{C}$ for these smaller phytoplankton separately. However, reported $\delta^{13}\text{C}$ values for larger phytoplankton types and nanoplankton generally show rather little difference, at least compared with seasonal variations (Yoshioka *et al.* 1994; Zohary *et al.* 1994; Keough *et al.* 1996), particularly when it is not certain how pure the phytoplankton samples were in all cases. Therefore, we must assume that our measured $\delta^{13}\text{C}$ value for large diatoms is a reasonable reflection of the value for the phytoplankton community as a whole in Loch Ness.

Our results suggest that in Loch Ness at most only about half the carbon flux through the pelagic food web derives from phytoplankton carbon fixation, with the remainder derived from detrital carbon of terrestrial origin. A strong dependence of zooplankton on detrital organic matter has been reported previously for small humic lakes. In small-scale laboratory experiments using a steady-state radiotracer technique, Salonen & Hammar (1986) found that as little as 5% of zooplankton carbon could be derived from phytoplankton photosynthesis. Hessen *et al.* (1990) reported results from long-term tracer studies in 2 m³ enclosures in a small humic lake in Norway, which showed that detritus supported 46–82% of body carbon in a range of zooplankton species. However, results from such laboratory or small-scale enclosure studies may not properly reflect carbon flow patterns in the whole lake. Stable isotope analyses have the great advantage of providing a picture of carbon flux through unmanipulated communities. Previous stable isotope studies of lake plankton have tended to confirm the importance of phytoplankton photosynthesis (Yoshioka *et al.* 1994; Zohary *et al.* 1994) except in small humic lakes where detritus has been shown to be important (Meili *et al.* 1996). Our study of Loch Ness appears to be the first in which allochthonous detrital carbon is shown to be a major source of carbon for the zooplankton in a large lake.

The humic staining and unusually deep mixing in Loch Ness combine to constrain phytoplankton production to exceptionally low levels (Jones *et al.* 1996a) so that the relative importance of allochthonous organic carbon in the pelagic food web may be higher than in other lakes with similar loadings of terrestrial detritus, leading to zooplankton $\delta^{13}\text{C}$ values unusually close to those of the bulk POM for a lake of that trophic state. Moreover, most of our results were obtained from samples collected in September when the phytoplankton biomass in Loch Ness is around its maximum development (Jones *et al.* 1996a). The limited samples collected in November actually suggested an even greater dependence of zooplankton on detrital carbon at that time. Further studies are required to establish the extent to which the relative importance of phytoplankton and detrital carbon alters through the year leading to seasonal fluctuations in zooplankton $\delta^{13}\text{C}$.

It is possible that the zooplankton use detrital POM directly, albeit with low assimilation efficiency (Hessen *et al.* 1990). Alternatively, detrital organic matter may be channelled to the crustacean zooplankton via a 'microbial link' consisting of bacteria and protozoa (Jones 1992). The

relative importance of these processes cannot yet be assessed since it is impossible to separate the microbial and detrital components for determination of isotopic signatures. Our measurements were of bulk POM, which would include both detrital particles and living bacteria and protozoa. Such bulk measurements undoubtedly mask a degree of variability in $\delta^{13}\text{C}$ in the constituents of POM, and at present little is known about how the $\delta^{13}\text{C}$ signal may change along a microbial link from DOM to protozoa. Del Giorgio & France (1996) analysed available literature data and showed that lake zooplankton are generally depleted in ^{13}C relative to microplankton (>20 µm). They attributed this to selective feeding by zooplankton on isotopically light phytoplankton, and even suggested that, in the absence of an isotopic signature for pure algal carbon, herbivorous zooplankton might provide the best representation of the isotopic signature of autochthonous algal carbon in lakes. Our results clearly suggest that such a practice would not be justified since, at least in some circumstances, non-phytoplankton material can contribute significantly to zooplankton carbon stable isotope signatures.

Combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed that the organisms higher up the pelagic food web in Loch Ness were probably largely dependent on grazing cladocerans and copepods as a food source. Analysis of the gut contents of pelagic charr and brown trout caught in Loch Ness at a mid-loch location (Martin & Shine 1993) showed that cladocerans (*Daphnia* and *Bythotrephes*, and to a lesser extent *Leptodora* and *Bosmina*) were the preferred prey; although often numerically dominant in the loch, copepods were rarely recorded in fish gut contents. If the copepods are not exploited directly by the fish, they may be mainly used by the predatory cladocerans; certainly the $\delta^{15}\text{N}$ values of the latter appeared to be too enriched for them to have been feeding only on *Daphnia*. The presence of small numbers of benthic organisms in the charr guts (Martin & Shine 1993) suggested that these fish could occasionally forage in the littoral zone but that their diet consisted largely of pelagic zooplankton. Chironomid larvae were also recorded in the guts of charr at certain times of the year, and in Loch Ness late instar chironomid larvae can be taken in plankton hauls (A. Shine, personal communication), but were not available from our samples for stable isotope analysis.

Since the predominant pelagic fish in Loch Ness depend largely on a food chain stemming from the grazing zooplankton, whose body carbon is about half derived from terrestrial detritus, it follows that fish production in the loch must be highly dependent on the input and use of terrestrial organic matter. This linkage between fish production and allochthonous organic matter revealed by stable isotope analysis must have real implications for fisheries management in some lake types, particularly if the loading of allochthonous organic matter from catchments alters with changes in land use or climate (Schindler *et al.* 1992; Forsberg 1992).

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