Strand 4 Carbon Isotope Analysis Technical Report

Lough Melvin Nutrient Reduction Programme

Carbon dynamics and food web reliance on allochthonous carbon in Lough Melvin

C. D. Barry, School of Biological Sciences, Queens University Belfast. Newforge Lane, Belfast BT9 5PX, Northern Ireland.
c.barry@qub.ac.uk

R. H. Foy, Agri-Food & Biosciences Institute, Newforge Lane, Belfast BT9 5PX Northern Ireland.
Bob.Foy@afbini.gov.uk

Preface

Humic lakes such as Lough Melvin receive large subsidies of organic carbon from their catchments, readily observed by the deep peat staining of the waters. This catchment-derived organic matter has the potential to fuel production by biota while simultaneously restricting photosynthetic production by plants and algae. Catchment-derived organic matter can therefore be an important determinant of lake ecosystem functioning.

Several recent studies from a number of geographical regions have documented increasing losses of organic matter from the landscape, but with no consensus yet as to the causative factors. These studies have highlighted the need for a better understanding of the potential impacts of catchment-derived organic matter upon aquatic ecosystems and the need to expand upon existing datasets. Furthermore, in spite of the significant stores of soil carbon in the form of peatlands, no high resolution temporal data of drainage water dissolved organic carbon has been recorded for Ireland.

This report details the sources and quantities of organic matter exported to Lough Melvin and presents the results of a food web study where stable isotope analysis was employed to determine the importance of catchment derived organic matter to consumers.

Acknowledgements

This project was possible due to the financial support provided to the Lough Melvin Nutrient Reduction Programme by Interreg IIIA. It benefited greatly from the help and assistance given by the following:
The Lough Melvin Nutrient Reduction Programme team for logistical and technical support
The Northern Regional Fisheries Board for regular use of their boat.
The Fisheries Officers of the Northern Regional Fisheries Board for their extensive help during sampling, which is greatly appreciated.
The officers and members of the Garrison and Lough Melvin Anglers Association for their co-operation in sampling trout from the lake for stable isotope analysis.
Special thanks to Neil Armour of Queen's University Belfast for assistance in the field and laboratory.

Executive Summary

Catchment derived organic carbon inputs to Lough Melvin represent a flux of carbon from the landscape that exceeds 4000 tonnes annually. The magnitude of this can be readily appreciated from the deeply peat stained waters of the lake. This strongly coloured water exerts among the most significant of the effects of catchment derived material upon Lough Melvin, where it has limited the light climate sufficiently to cap the responses of algae to the considerable nutrient enrichment that has taken place since 1995. Catchment derived organic matter therefore limits production occurring within the lake by plants and algae thus limiting the energy available for lake consumers.

Parts of Lough Melvin catchment were shown to exhibit export rates for dissolved organic carbon that are amongst the highest observed globally. Of the organic carbon delivered to the lake, retention is approximately 20%. Stable isotope analysis of the food webs showed that consumers rely upon this catchment-derived organic matter for a significant proportion of their production and that heterotrophic bacteria are an important trophic link between dissolved organic matter and higher trophic levels. The importance of catchment-derived organic matter could be traced to top consumers such as fish, where stable isotope analysis identified their different feeding niches and showed the absence of a dietary overlap between salmonids and more recently introduced species such as rudd and perch.

Lough Melvin is designated as a Special Area of Conservation (SAC) on the basis of its low to moderate trophic status and associated high quality aquatic vascular plant and salmonid fish communities. Increasing productivity or trophy tends to result in pronounced changes to animal and plant communities and therefore threatens the conservation status of the lake. Although phosphorus is the nutrient that usually limits primary production in lakes catchment-derived coloured dissolved organic matter is also a key determinant of lake productivity in Lough Melvin by reducing the amount of light available for photosynthetic production, potentially capping photosynthetic responses to nutrient enrichment. Thus algal production in Lough Melvin has remained at low levels despite a ~35% increase in phosphorus concentration.

Catchment-derived organic matter was significantly utilised as a food source by lake biota in Lough Melvin and the evidence for increasing of organic matter loading may be shifting the balance between food web reliance upon algal production and catchment-derived organic matter, potentially altering community structure. As in-lake photosynthetic production and catchment-derived organic matter vary markedly in their nutritional quality, reductions in photosynthetic production caused by increasing organic matter loading should theoretically result in lower overall productivity of the system.

Introduction

Lakes receive organic carbon from two principal sources: primary production occurring within the lake and catchment derived terrestrial production (autochthonous and allochthonous organic carbon[1]). Despite early recognition of the importance of allochthonous organic carbon (Birge & Juday, 1927) lakes were traditionally viewed as isolated ecosystems in which mobilization of solar energy by phytoplankton, benthic algae and macrophytes formed the base for production by aquatic consumers. Consequently much research emphasis on lakes has been on the responses of primary producers to nutrient availability (Vollenweider, 1968; Nat. Acad. Sci., 1969). The strong empirical relationship of chlorophyll and phosphorus (McCauley et al., 1989) and remediation of eutrophication through nutrient reduction and grazer community manipulation (Schindler, 1974) justify the use of lake trophic status as the primary interpretive paradigm in the study of lake ecosystems. Its ease of utility for lake assessment is undeniable, however it is limited to one of many characteristics of lake ecosystems: nutrient limitation of productivity.

Allochthonous organic carbon can be considered as major determinant of lake-ecosystem functioning as it affects several key processes including primary production and microbial metabolism. Indeed, recent increases in the flux of organic carbon from the landscape highlight the need for a better understanding of its dynamics and influence of upon lakes.

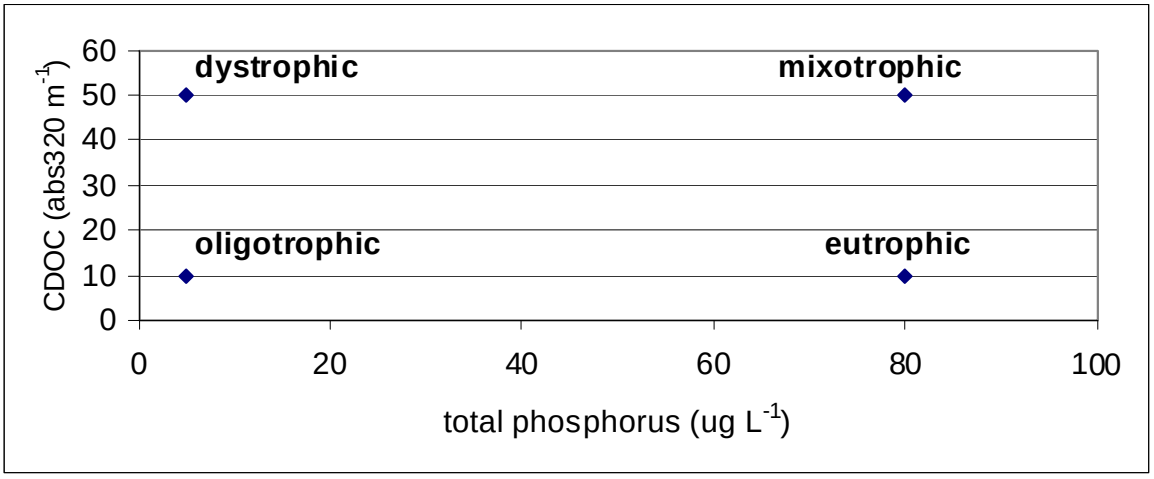

Figure 1. Lake types based upon the supply of allochthonous and autochthonous matter using coloured dissolved organic carbon (absorbance at 320nm m^{-1}) and total phosphorus (µg L^{-1}) as proxies respectively. Adapted from Williamson et al. (1999) based upon Rodhe (1969).

Incorporating allochthonous organic carbon into the trophic paradigm for lake study is not a new concept. Rodhe (1969) categorized four basic lakes types based along two axes: the rate of supply of allochthonous organic matter and the rate of supply of autochthonous organic matter (Figure 1). The term mesotrophic has been adopted for lakes exhibiting moderate levels of nutrients and productivity but currently there is no similar term available for moderately enriched lakes with high

[1] The terms autochthonous and allochthonous mean, 'originating where found' and 'not originating where found' respectively

allochthonous carbon loading. Subsequent studies and an increasing understanding of the role of microbial cycling of detrital organic matter (Pomeroy, 1974; Azam *et al*., 1983; Scavia & Laird, 1987) helped to resurrect interest in defining how allochthonous organic carbon supports both the microbial and metazoan wood webs in lakes (Figure 2).

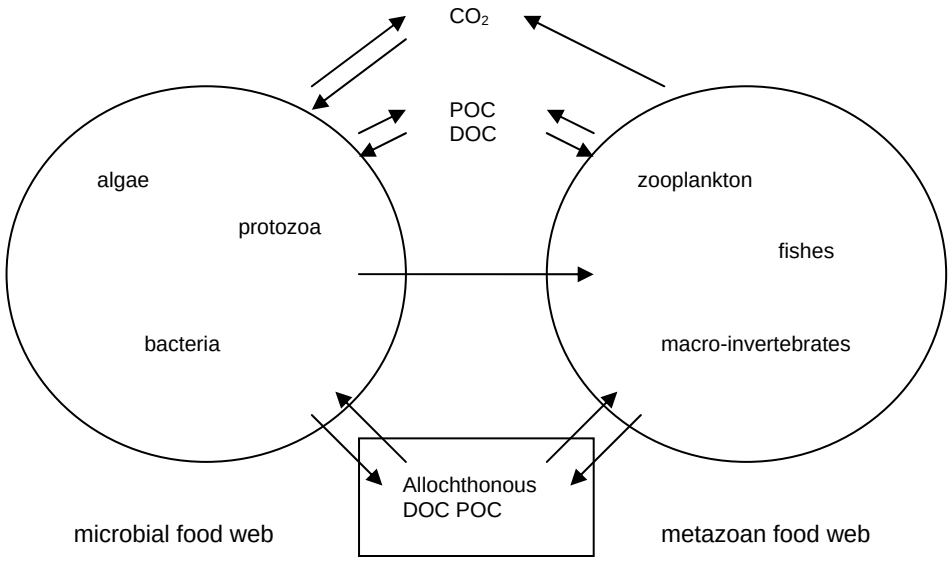

Figure 2. Simplified model of pelagic food webs in which microbial production based upon allochthonous and autochthonous organic carbon supports the metazoan food web. Adapted from Sherr & Sherr (1988).

Characterisation of organic carbon

The term, 'organic carbon' covers a vast array of substances. The foremost division is into particulate and dissolved fractions (POC & DOC), defined by filtration between 0.2 - 0.7µm. Although this is an arbitrary division within a continuum of large particles to small molecules it has a significant bearing upon biogeochemical aspects that determine the fate of organic carbon.

Organic carbon consists of a mixture of microbial, plant and animal products at various stages of decomposition. For simplification, Aiken *et al.* (1985) categorised non-humic and humic substances. Non-humics are low molecular weight compounds such as carbohydrates, fats, peptides and amino acids that are colourless in solution. They are relatively labile and low concentrations are found in natural waters due to preferential and rapid degradation by microorganisms. Humic substances are formed largely as a result of microbial activity upon plant material. In sharp contrast to non-humics they have high molecular weight and absorb light strongly in the low end of the visible spectrum and in the ultra-violet, resulting in the characteristic yellow-red to brown-black colouration of waters with high organic matter content. Autochthonous organic carbon, being of more recent origin, consists of a greater proportion of non-humic compounds compared to allochthonous organic carbon. Terrestrial bio-chemical degradation that precedes the arrival of allochthonous organic carbon in watercourses results in a lower nutritional value relative to its 'fresher' autochthonous counterpart. Molar C:N ratios in the region of 12:1 and 50:1 for allochthonous organic carbon and autochthonous organic carbon respectively provide a measure of their relative nutritional quality (Wetzel, 2001).

The ability to distinguish between carbon sources is a fundamental criterion for understanding how each affects lake processes, particularly the extent to which they are utilised by biota. Carbon stable isotope analysis is increasingly used to differentiate between terrestrial and aquatic organic matter. The proportions of the elements that constitute molecules of autochthonous organic carbon and allochthonous organic carbon, particularly nitrogen, phosphorus and carbon, determine its quality or bio-availablity and are therefore important characteristics. However precise determinations of organic matter quality are frequently prohibited by the analytically complex procedures required and other means of assessing quality have been investigated. The spectral characteristics of water differ according to DOC composition, allowing the use of optical analytical methods to provide measures of the quality and origin of the DOC (Stedmon & Markager, 2001; Anderson & Stedmon, 2007). Since allochthonous DOC tends to absorb light strongly at the low end of the visible spectrum (Hessen & Tranvik, 1998) absorption coefficients within these wavelengths have been used as proxies for DOC concentration in humic waters due to the analytical ease involved (Meili, 1992; SNV, 1986).

Export of terrestrial organic carbon

On average >95% of terrestrial primary production remains at the site of production and for the most part is decomposed there (Dosskey & Bertsh, 1994). Export of non-decomposed organic matter is mostly in the form of dissolved compounds and is largely dependent on climate, hydrological regime and soil and vegetation type (Engstrom, 1987). Fluxes of DOC from peatlands and swamp forests are particularly high (Table.1); the anoxic conditions prevent a degree of microbial degradation that results in photosynthetic production exceeding decomposition and a net accumulation of carbon and consequently more DOC is leached to groundwaters and surface runoff. The flux of POC is hydrologically more variable with peak exports occurring during spate and flood events when more surface material is washed into watercourses.

Table 1. Annual riverine DOC flux from different soils and vegetation habitats. Adapted from Wetzel (2001). * x 10 = kg C ha^{-1} yr^{-1}

Biome	Observed DOC flux (g C m^{-2} yr^{-1})*
Cool grasslands	0.386
Tropical savannah	1.090
Warm deciduous forests	1.410
Cool deciduous forests	1.927
Warm conifer forests	3.684
Cool conifer forests	4.226
Heath / Moorlands	5.650
Tropical forests	6.336
Peatlands	8.567
Swamp forests	9.913

Recent rises in allochthonous organic carbon export

On a global scale peatlands hold a vast pool of organic carbon that is estimated to represent near to one third of the global soil stock (Jenkinson *et al.*, 1991; Gorham, 1991). Observations of increasing DOC concentrations in waters draining peatlands from a variety of geographical areas over the last 30-40 years have lead to concerns that these stores are destabilising (Forsberg, 1992; Freeman *et al.*, 2001; Tranvik & Jansson, 2002; Worrall *et al.* 2004). The possible causes are under debate with increased precipitation, warming, increased nitrogen deposition, decreased sulphur deposition and higher CO_2 concentrations suggested. Warming is implicated because increased decomposition might be expected at higher temperatures, however observed rises in temperature alone (~1°C) are insufficient to account for observed rises in DOC flux. Increased nitrogen deposition and atmospheric CO_2 levels have been suggested as they might stimulate typically nitrogen limited forests and ground flora and give rise to increased primary production, more litter and thus more humic material.

Precipitation has been shown to account for a significant portion of the increases in riverine DOC export in some studies (Forsberg, 1992) whereas others have found significant flow-independent increases (Worrall *et al.*, 2003). More recently DOC release from a variety of vegetation types has been shown to increase under conditions of elevated CO_2 and was greatest from vegetation with the highest nutrient availability (Freeman *et al.*, 2004). Declining anthropogenic sulphur deposition has also been suggested as corresponding declines in acidity can increase DOC solubility (Evans *et al.,* 2006)

Whilst climate and anthropogenic changes may be leading to greater exports of allochthonous organic carbon from terrestrial ecosystems, lakes already contribute to significant mineralisation of terrestrial organic carbon. Quantifying global carbon emissions and uptake for components of the biosphere (Table 2) identifies lakes as significant contributors and demonstrates that they should be included in global carbon budgets. The last IPCC report (2001) did not account for the transformation of carbon within aquatic systems although it did acknowledge the role of rivers in transporting carbon to the sea.

Table 2. Global carbon dioxide emissions (+) & uptake (-) for components of the biosphere

Component	Flux (Gt C yr^{-1})	Reference
Oceans	-2.2	Takahashi *et al.,* (2002)
Rivers	0.3	Cole & Caraco (2001)
Lakes	0.14	Cole *et al.* (1994)
Amazon	0.5	Richey *et al.* (2002)
Net terrestrial sink	-0.4	IPCC (2001)

Influence of allochthonous organic carbon on lake ecosystems

Allochthonous organic carbon exerts its greatest effects upon lake trophic dynamics in two principal ways:

1. By altering the light climate. Allochthonous DOC affects the attenuation of photosynthetically active radiation (PAR) and the spectral quality of light and thus influences photosynthetic production (Jones, 1992; Jewson & Taylor, 1978; Jackson & Hecky, 1980), phytoplankton community composition (Wall & Briand, 1979) and the mixing depth in small lakes (Fee *et al.*, 1996). Allochthonous organic carbon can therefore have a significant bearing upon autochthonous energy mobilisation.

2. By serving as a substrate for primary consumers. DOC can be metabolised by heterotrophic bacteria (Tranvik, 1988,1992; Moran & Hodson, 1990) and its consumption is one the largest fluxes of carbon in most aquatic ecosystems (Cole *et al.*, 1999). Although considered recalcitrant to microbial attack with less than 10% typically available for bacterial metabolism, the large relative pool size of allochthonous DOC in many lakes allows a small utilisable fraction to contribute significantly to energy mobilisation (Hessen *et al.*, 1990). DOC can thus enter pelagic food webs via zooplankton grazing of bacteria. Furthermore evidence is emerging that zooplankton may also directly ingest and assimilate POC (Cole *et al.,* 2006).

Many species of benthic macro-invertebrate, particularly those inhabiting unproductive habitats display morphological and behavioural adaptations that enable them to exploit both autochthonous and allochthonous organic carbon (Iversen, 1974; Moore, 1975; Frieberg & Jacobson, 1994; Murphy & Giller, 2000). Allochthonous carbon can therefore directly support a considerable proportion of secondary production in lakes.

Aquatic ecosystem metabolism, in terms of gross primary production (GPP) and respiration (R) is a powerful descriptor of overall ecosystem functioning as it incorporates metabolism of allochthonous organic carbon (e.g. Vannote *et al.,* 1980). Aquatic ecosystems are characterised as net autotrophic when GPP exceeds or equals R and net heterotrophic when R exceeds GPP (Odum, 1956). Net heterotrophic lakes will therefore be sources of carbon dioxide to the atmosphere. Studies examining carbon dioxide concentrations in the surface waters of a wide range of lakes have found that most are supersaturated with regard to carbon dioxide and are thus heterotrophic (Kling *et al.*, 1992; Cole *et al.*, 1994). It is generally accepted that bacterial respiration of allochthonous DOC is largely responsible for estimates of R exceeding GPP.

Across a wide range of allochthonous organic carbon loading and nutrient availability, lakes tend to function as net heterotrophic systems due to respiration of terrestrial carbon subsidies. The base for production by primary and higher consumers can therefore be both autochthonous and allochthonous. Which carbon source is utilised more by consumers depends upon a variety of factors. The lower nutritional value of allochthonous organic carbon means it is unable to support the same magnitude of production as autochthonous organic carbon. Optimal feeding strategies and the feeding adaptations of consumers therefore show a tendency to rely upon autochthonous organic carbon and only switch to significantly utilising allochthonous carbon where primary production is low or depressed. Numerous studies have shown strong zooplankton reliance upon

allochthonous organic carbon in oligotrophic lakes with estimates ranging from 20-82 % reliance (Jones *et al.*, 1998; Hessen *et al.*, 1990; Pace *et al.*, 2004; Meili *et al.*, 1996, Carpenter *et al.*, 2005; Karlsson *et al.*, 2003; Pulido-Villena *et al.*, 2005). Carpenter *et al.* (2005) found that the degree of allochthony (reliance on allochthonous carbon) was highest for a humic lake and lowest in a lake that was experimentally fertilised.

Determining food web reliance on allochthonous organic carbon

Trophic structure and feeding relationships within ecosystems are commonly conceptualised as food chains and food webs. In food chain studies species are assigned to one of several discrete trophic levels. This classification can only provide a simplified view of energy flow and trophic interactions and inadequately represent the complexity of ecosystems. Given sufficient taxonomic resolution of dietary preferences by consumers food webs can describe the complexity of natural systems, however many feeding interactions cannot be observed and feeding links are not weighted according to their energetic importance. Gut content analyses have been used to assign organisms a measure of trophic position but often quantitative dietary data is unattainable or biased and may not reflect actual matter assimilated by a consumer.

Natural abundance carbon and nitrogen stable isotope ratios can provide time-integrated information about feeding relationships and energy flow in food webs. They are powerful tools for assessing food web relationships and have been extensively used across a range of freshwater systems in the last 25 years (Salonen & Hammar, 1986; Hessen *et al.*, 1990; France, 1995; Meili *et al.,* 1993, 1996; Jones *et al.*, 1998; Vander Zanden & Rasmussen, 2001; Grey *et al.,* 2001, Pace *et al.*, 2004; Carpenter *et al.*, 2005; Karlsson *et al.*, 2003; Pulido-Villena *et al.*, 2005).

Consumer carbon stable isotope signatures ($\delta^{13}C$) are similar to that of their food, whereas the typical carbon sources for production in aquatic systems: phytoplankton, benthic algae and terrestrial primary production generally exhibit distinct $\delta^{13}C$ signatures. Given that $\delta^{13}C$ signatures are conserved up food chains and that the potential bases for production exhibit distinct $\delta^{13}C$ signatures, the carbon source to a consumer can be inferred from its $\delta^{13}C$ signature.

In contrast consumers become substantially but consistently enriched in the heavier nitrogen stable isotope (^{15}N) relative to their food. This results in a stepwise trophic level enrichment that can be used as an indicator of a time integrated trophic position based on pathways of energy flow. Low order consumers in natural systems tend towards omnivory and allochthonous and autochthonous carbon sources may both be consumed. Given sufficient distinction between the isotopic signatures (carbon or nitrogen) of each potential source the proportions assimilated by a consumer can be calculated using a mass balance equation. Carbon stable isotopes are more commonly employed for this purpose as the analytical precision obtained is better.

Summary

Due to extensive areas of peatland in Ireland a great number of lakes are humic stained with terrestrially derived organic matter dominating the organic carbon pool. Although several studies

have shown that allochthonous organic carbon can significantly fuel food webs in humic lakes, the degree to which this occurs in Irish lakes has yet to be investigated.

Despite a considerable pool of terrestrial organic carbon in the form of peatlands no high-resolution temporal data on drainage water DOC has been recorded in Ireland. Increasing DOC exports from the landscape to watercourses from a variety of different geographical regions have been reported, but with no consensus as to the influencing factors there is a need to expand upon existing datasets.

Increasing terrestrial organic matter loading to lakes has the potential to significantly alter ecosystem structure and function and more research is required to better understand the impacts of what may be an inevitable process of terrestrial organic matter enrichment.

Lough Melvin is unique amongst Irish lakes due to its salmonid fish community, high quality flora, nutrient status and geographical position. Determining the energetic importance of allochthonous organic carbon as well as quantifying the inputs, sources and factors influencing the supply will provide information to help safeguard the future an immensely valuable resource.

Purpose of study

■ To determine the relative importance of allochthonous and autochthonous organic carbon to Lough Melvin's food webs: a stable isotope approach.

■ To quantify the inputs and determine the sources of allochthonous organic carbon to Lough Melvin and their subsequent influence on productivity.

Methods: Carbon Budget

Lake Sampling

Lough Melvin was sampled monthly from March to August 2006 and fortnightly from September 2006 to September 2007. A mooring buoy was deployed over the deepest point to maintain a constant position between sampling visits and during sampling. Discrete water samples were taken from the surface, 20, 30 and 40 metres depth using a Kemmerer water sampler (Wildco, USA). A composite sample to 10m was taken using an epilimnetic tube sampler (Lund & Talling, 1957).

River Sampling

Seven inflowing rivers that account for ~80% of the catchment plus the outflow (River Drowse) were sampled on the same days that lake sampling took place (Table 3). Six headwater tributaries were also sampled in the two largest Roogagh and County Rivers.

Table 3. Grid references for river sampling points and year(s) in which they were sampled.

River	Irish Grid reference	Catchment area (km^2)
Muckenagh	G 918 543	10.4
Roogagh	G 939 520	59.2
County	G 937 507	56.1
Ballagh	G 925 495	14.1
Glenaniff	G 921 497	27.4
Kinlough	G 815 558	3.4
Clancys	G 860 543	7.5
Drowse	G 832 567	240.2*
Drumgormly[a]	H 020 485	7.37
Glen East[a]	G 994 517	10.60
Glen Bridge[a]	G 993 521	5.66
Lattone[b]	G 947 469	9.25
Deans[b]	G 978 454	2.17
Sraduffy[b]	G 973 453	10.99

[a] denote tributaries of the Roogagh river, [b] denote tributaries of the County river. * includes lake area of 22.7 km^2

Laboratory Analyses

Samples were stored in the dark and filtered through 0.45 µm Durapore (polyvinylidene fluoride) filters within 5 hours of collection, and analysed within 24 hours in most cases. When it was not possible to analyse samples within 24 hours filtered samples were stored frozen. River and lake water samples were analysed as follows.

Dissolved Organic Carbon (DOC) was analysed using a Teledyne Techmar Apollo 9000 TOC analyser (Pt-catalysed high temperature combustion method) following automated removal of the inorganic fraction by acidification and sparging with zero-grade air.

Light attenuation of samples was measured on filtered samples using a Unicam UV1 spectrophotometer between 250 nm and 710 nm (2 nm bandwidth) in a 1cm quartz cuvette. Readings were taken against a blank of ultra-pure Milli-Q water.

The absorption coefficients (m^{-1}) were obtained by,

$$a_\lambda = 2.303 \, . \, A_\lambda / L$$

where a_λ = absorption coefficient at wavelength λ (m^{-1})
A_λ = absorption at wavelength λ
L = path length / cuvette size (m)

The absorption value per mass unit of particles, the specific absorption coefficient, a^*_λ ($m^{2} \cdot mg^{-1}$), was determined as:

$$a^*_\lambda \ / \ DOC \ (mg \ L^{-1})$$

Decreasing light absorption with increasing wavelength follows an exponential decline and can be modelled as,

$$a_\lambda = a_{\lambda o} \, e^{S(\lambda o - \lambda)}$$

where a_λ = absorption coefficient at wavelength λ (m^{-1})
$a_{\lambda o}$ = absorption coefficient at reference wavelength λo (m^{-1})
S = exponential slope coefficient.

DOC Loading and Export Estimation

Flow data was available at 15 minute intervals for the Roogagh and the County rivers that lie within Northern Ireland. For the Drowse, Glenaniff, Ballagh and Clancy's rivers that lie within the Republic of Ireland mean daily flows were available.

A number of algorithms are commonly used for estimating river loads. Here we employ mean daily flows for each river with 'Method 5' (eq. 1) according to Walling & Webb (1985). For comparison, loads for the Roogagh and County rivers were estimated using both instantaneous flow data and mean daily flows. Loadings from monitored streams without flow gauges were estimated using flows in adjacent gauged sub-catchments scaled by sub-catchment area.

$$\mathbf{L^{SC} = Q_r \, . \, K \, . \, [\sum (C_i \, Q_i) \, / \sum Q_i \,] \, / \, 10^6} \qquad \mathbf{(1)}$$

where $\mathbf{C_i}$ = concentration on day of sampling (g m^{-3})
$\mathbf{Q_i}$ = mean flow on day of sampling, (m^3 sec^{-1}, mean daily flow)
$\mathbf{L^{SC}}$ = annual sub-catchment DOC load (tonnes)
$\mathbf{Q_r}$ = Mean discharge for the period of record (m^{-3} sec-1, n= 365)
$\mathbf{K}$ = Conversion factor (for the period of record, 24.60.60.365)

Sub-catchment export rates are then the annual sub-catchment load divided by the sub-catchment area:

$$\mathbf{M^{SC}_{EXPORT} = L^{SC} \, / \, A^{SC} \, * 10^3} \qquad \mathbf{(2)}$$

where $\mathbf{A^{SC}}$ = sub-catchment area (ha)
$\mathbf{M^{SC}_{EXPORT}}$ = sub-catchment export rate (kg ha^{-1} yr^{-1})

Loadings from un-monitored areas of the catchment were estimated using DOC export rates from specific sub-catchments considered to be most representative in terms of land use (CORINE, 2000). On this basis the un-monitored areas of the catchment were divided into 7 areas with export rates from gauged sub-catchments assigned as follows:

North-west	Muckenagh sub-catchment export rate
North-east	Roogagh sub-catchment export rate
South-east	County sub-catchment export rate
South-west	Clancy's sub-catchment export rate
Islands	Clancy's sub-catchment export rate
Breffni sub-catchment	Clancy's sub-catchment export rate
Derrynaseer sub-catchment	Muckenagh sub-catchment export rate

Loading and export within the Roogagh and County sub-catchments

The sampling of an additional three tributaries within each of the Roogagh and County catchments effectively divided these sub-catchments into four discrete areas. Flow data for these rivers was recorded at the inflow to Lough Melvin at 15 minute intervals allowing instantaneous flow data (to the nearest 15 minutes) to be used with equation 1. Flows within each tributary catchment were estimated as the proportion, by area, of the total flow assuming uniform precipitation over the sub-catchment.

To calculate loads and exports for the downstream area of the catchment between the inflow and the tributary sampling points, loads for the tributary sub-catchments are summed and subtracted from the load estimated for the entire river sub-catchment (at inflow point).

Balance of organic carbon within the lake

Annual retention of carbon in the lake was calculated as the difference between annual riverine inflow and outflow.

Methods: Carbon and nitrogen stable isotope analysis of food webs: determining the importance of terrestrial organic matter

Stable isotope analysis of food webs requires that the different basal resources (energy sources) available to consumers exhibit distinct isotopic signatures. These signatures can then be traced through the food web because the isotopic signatures of consumers reflect those of their diet in a dependable manner. While the carbon isotopic signature of a consumer ($\delta^{13}C$) closely reflects that of its diet with only minor enrichment (<1 ‰), consumer nitrogen isotopic signatures ($\delta^{15}N$) show considerable enrichment of ~3‰ relative to their diet. The combination of carbon and nitrogen isotope analysis therefore yields information on an animal's food sources and trophic position.

Carbon and Nitrogen stable isotope analysis was carried out at the Stable Isotopes in Nature Laboratory, Canadian Rivers Institute at the University of New Brunswick, Canada, with a Finnigan

Delta Plus IRMS coupled to a NC2500 Elemental Analyser. Analytical precision was typically +/- 0.15‰ for carbon and +/- 0.2‰ for nitrogen.

Dissolved organic and inorganic carbon were analysed for their stable isotopic signature at the GG Hatch laboratory, University of Ottawa, Canada using an OI Analytical "TIC-TOC" Analyser Model 1010 interfaced to a Finnigan Mat Delta Plus IRMS. Analytical precision was +/- 0.2‰.

Results are given using the δ notation in per thousand units (‰)

where $\delta\ (‰) = [\ (\ R_{sample} / R_{reference}\ )\ -1\ ] \times 1000$

and $R = {}^{13}C / {}^{12}C$ or ${}^{15}N / {}^{14}N$

The reference standards were secondary standards of known relation to the international standards of Pee Dee Belemnite for carbon and N_2 air for nitrogen.

Lakes consist of three principal habitats: the pelagic, littoral and profundal zones. These differ considerably in their physical characteristics and the nature and supply of energy in the form of organic matter. Accordingly consumers show adaptations peculiar to each habitat thus dividing the lake into three distinct food webs. Inputs of energy to lake food webs from primary producers within the lake and from catchment exports are seasonally variable and consumers may switch from one source to another as the relative proportions change during the seasonal cycle. Assessing the annual importance of terrestrial organic matter to lake production therefore requires a temporal examination of each food web.

Methods: Pelagic food web

Lake sampling

Consumers Zooplankton were sampled by vertical hauls of the water column using a 180µm plankton net. On some occasions the net was towed in the surface waters to obtain sufficient material for analysis. On shore larger zooplankton were coarsely separated by filtration through 1000µm & 350µm meshes and stored separately in surface lake water until return to the lab.

Potential energy sources Phytoplankton were sampled using a 53µm plankton net that was towed to achieve sufficient material for isotopic analysis. The contents of the tows were stored in 2L sample jars until return to the laboratory. An epilimnetic composite sample to 10m depth was taken for analysis of bulk particulate organic matter. Epilimnetic lake water (10m composite) was used for the determination of the isotopic signatures of lake dissolved organic and inorganic carbon. We used the isotopic signatures of inflow particulate and dissolved organic matter from the Roogagh and County rivers (>50% Catchment) to estimate the isotopic signal of terrestrially derived organic matter and catchment inorganic carbon.

Spatial variation in the isotopic signatures of zooplankton was investigated by sampling nine widely separated sites on one occasion during August 2006. The sites ranged from sheltered macrophyte dominated littoral areas to exposed rocky littoral areas and true pelagic sites. Zooplankton were sampled from littoral areas using over-night light traps (chemi-luminescent light sticks) set 1.5 m from the bottom in 2 m of water at each site. Vertical net tows were used to sample pelagic habitats

following recovery of the light traps. There was no significant difference for either stable isotope for any species between sites justifying a sampling programme at one pelagic site.

Temporal variation Plankton communities can change rapidly in response to changing environmental conditions and significant differences can be observed within days. Components of the pelagic food web were sampled fortnightly between September 2006 and September 2007 over the deepest point on the lake in conjunction with the water quality monitoring programme providing a background of environmental data.

Laboratory methods

Samples were returned to the lab within 4 hours of collection and stored refrigerated until processing.

Zooplankton With the exception of *Chaoborus sp.,* which were manually removed unharmed using fine forceps, *Daphnia hyalina* var. *galeata* were sufficiently large compared to other species to permit separation by filtration through a 1000 µm mesh. *Arctodiaptomus laticeps, Eudiaptomus gracilis and Cyclops abyssorum* were filtered onto gauzes of 250-800 µm and re-suspended in filtered lake water in a large petri dish. At intervals copepods were narcotized using carbonated water and sorted to species using a fine pipette and binocular dissecting microscope. Separated individuals of each species were placed in filtered lake water overnight to allow gut clearance. The following day samples of each species were re-filtered, washed with ultra-pure milli-Q water and collected on pre-combusted glass fibre filters (24hrs, 500°C) and oven dried at 60 °C for 48 hours. For analysis zooplankton samples were divided into 3 parts, each consisting of at least 20 individuals to give 3 composite replicates. The numbers of individuals used per replicate was as high as logistically possible and was typically > 50.

Phytoplankton samples were transferred to 1L glass beakers and allowed to stand. Buoyant blue-green algae that accumulated at the surface were removed and re-suspended in filtered lake water and the process repeated until zooplankton were no longer visible in the sample. Blue green algae were then removed from the surface using a pipette, re-suspended in ultra-pure milli-Q water and filtered onto pre-combusted (24hrs, 500°C) glass fibre filters ((Whatman GF/C). Filters were screened for purity under a dissecting microscope and a subsample removed for species identification. With one exception, a sample taken during a bloom of *Microcystis aeruginosa,* samples consisted of >95% *Woronichinia naegliana*. Samples were oven dried at 60°C for 48 hours. In most cases sufficient material collected to allow removal of the algal sample from the filter, which were placed in acid washed (15% HCl) glass vials and stored in a dessicator prior to dispatch for stable isotopic analysis.

Following removal of the surface accumulated blue-green algae, the 'middle' part of the phytoplankton sample that contained mostly zooplankton (particularly small *Cyclops* and copepod *nauplii*) was discarded leaving sedimented diatoms and detritus. These were resuspended in filtered lake water and transferred to several 200ml measuring cylinders. The process was repeated until all zooplankton were removed. A subsample of the sediment was removed to examine species composition and purity. The sediment was then resuspended in ultra-pure milli-Q water and filtered onto pre-combusted (24hrs, 500°C) Whatman glass fibre filters (GF/C). Samples contained >85%

diatoms in every case. On some occasions during the summer during repeated sedimentation we was found that *Aulacoseira italica* sank at far slower rates than other material present (they dominated the diatom biovolume at such times). This species was decanted and onto filtered onto pre-combusted (24hrs, 500°C) Whatman glass fibre filters (GF/C) and rinsed with ultra-pure milli-Q water.

For isotopic analysis three composite replicates of each sample were used.

Lake and inflow particulate organic matter Composite lake samples and river water samples from the county and Roogagh rivers were filtered onto pre-combusted (24 hrs, 500°C) glass fibre filters (Whatman GF/C) and rinsed with ultra-pure milli-Q water. Each filter was examined under a binocular microscope and all visible invertebrates were removed with fine forceps. Filters were dried at 60°C for 48 hours and placed in sealed, sterile petri dishes and stored in a dessicator prior to dispatch.

Three individual filters of each sample were collected and one subsample of each was analysed providing three replicates.

Dissolved organic and inorganic carbon Samples were filtered (0.45µm) into amber borosilicate glass vials with silicon-teflon septa containing mercury chloride (final conc. 0.2 mg l^{-1}) and filled without headspace. These were stored refrigerated in the dark until dispatch.

Methods: Littoral food web

The carbon and nitrogen stable isotopic signatures of basal resources and consumers are known to vary spatially and temporally between and within systems (Cabana & Rasmussen, 1996; Syväranta *et al.,* 2006). Spatial variation is generally considered to increase with ecosystem size in response to increasing habitat heterogeneity, and temporal variation is principally affected by seasonal constraints upon the supply of nutrients, light and temperature. We investigated temporal variation of resource utilisation at six spatially distinct sites on Lough Melvin (Table 4 and Figure 3).

Field Sampling

Invertebrates were collected in the field by kick sampling and hand searches. The sampling depth was standardised between sites to approximately 70 cm. Taxa were sorted on the shore and stored separately alive in lake water for return to the laboratory. As far as was possible individuals of the same instar / size were sampled between sites throughout the year. Three fist sized rocks were randomly collected and stored as for invertebrates for subsequent preparation of epilithon samples. Where macrophytes were present three samples were taken from three different plants and stored as for invertebrate samples.

Table 4. Location, timing and description of sites for littoral invertebrate sampling.

Site	Irish grid reference	Description	Months sampled
1	G880 532	Exposed rocky littoral subject to moderate wave action with shoreline patches of *Littorella uniflora.* No overhanging riparian vegetation.	Aug '06 Nov '06 Jul '07 Oct '07
2	G904 520	Exposed rocky littoral adjacent to 45m basin, subject to strong / moderate wave action. Overhanging broadleaved riparian vegetation. Stands of *Littorella uniflora* and *Potamogeton spp.*	Nov '06 Feb '07 Jun '07 Oct '07
3	G939 520	Exposed rocky littoral <50m from the Roogagh river inflow. Subject to strong onshore wave action. Few patches of *Littorella uniflora* and most rocks with some growth of *Cladophora glomerata*	Feb '07 Jul '07 Oct '07
4	G931 531	Moderately sheltered rocky littoral with broadleaved riparian vegetation. Extensive areas of *Littorella uniflora* and numerous stands of *Potamogeton spp.* Some rocks with conservative growths of epilithic blue-green algae	Aug '06 Feb '07 Jun '07 Oct '07
5	G877 556	Moderately exposed rocky littoral with riparian vegetation consisting of scrub (gorse, hawthorn, birch)	Mar '07 June '07 Oct '07
6	G824 555	Sheltered with riparian vegetation consisting mostly of rough pasture. Loose stand of emergent *Phragmites australis* interspersed with *Potamogeton spp..* Benthos with rocky areas but generally of fine sediment.	Sep '06 Feb '07 Jul '07 Oct '07

Figure 3. Map showing the locations of littoral invertebrates sampling sites. Number codes refer to those in Table 4.

Laboratory methods

Invertebrate and macrophyte / algal samples were returned to the laboratory within 5 hours of collection and identified to species in the majority of cases. Once sorted, a number of individuals of each invertebrate species were left overnight in filtered lake water (0.45µm) to allow gut evacuation. Samples were rinsed with ultra pure Milli-Q water, dried at 60°C for 48 hrs, placed in sealed acid washed glass vials (15% HCl) and stored in a dessicator prior to dispatch. 3 individuals of each species were analysed separately providing 3 replicates.

Macrophytes were shaken in ultra pure Milli-Q water and their surfaces wiped down to remove epiphytic algae and biofilm. In cases where macrophytes were abundant the residual shaken water was filtered onto pre-combusted glass fibre filters (Whatman GF/C, 24hrs 500°C) and dried at 60°C for 48 hrs for subsequent isotopic analysis. Epilithon was individually removed from each rock using a toothbrush and rinsing with ultra pure Milli-Q water. Three replicate epilithon solutions were then treated as for epiphytic samples. The following keys were used for identification of biota:

Wallace *et al.* (2003), Friday (1988), Edington & Hildrew (1995), Wilson & Ruse (2005), Haslam *et al.* (1975), Macan (1960), Hynes (1977), Hynes *et al.* (1960), Whitton & Brook (2003), Scourfield & Harding (1966), Harding & Smith (1974), Pontin (1978) Huber-Pestalozzi (1975), Savage (1989), Macan (1979), Brinkhurst (1982) and Weiderholm (1983).

Methods: Profundal food web

We examined the spatial and temporal variation of carbon and nitrogen isotopic signatures for profundal invertebrates (Table 5, Figure 4.). Logistic and budget constraints prohibited an examination of effect of depth and all samples were taken from 10m depth, close to the mean depth of the lake (~10.9m).

Table 5. Location and dates of sampling for profundal invertebrates

Site	Irish grid reference	months sampled
1	G884 534	Nov ’06, Apr ’07, Jul ’07, Oct ‘07
2	G903 522	Nov ’06, Apr ’07, Jul ’07, Oct ‘07
3	G935 523	Nov ’06, Apr ’07, Jul ’07, Oct ‘07
4	G877 553	Apr ’07, Jul ’07, Oct ‘07

Field Sampling

Samples were taken using an Eckman Grab. The entire contents of at least 3 grabs (sediment plus inverts) were stored together in plastic buckets for return to the laboratory.

Figure 4. Map showing locations of sites for profundal invertebrate sampling.

Laboratory methods

Samples were successively sieved through 10 mm, 3 mm and 0.5 mm wire meshes to remove larger coarse particulate matter and silt/mud. The contents of the 0.5 mm sieve were washed under cold tap water to remove remaining silt and then rinsed into a white bottomed tray. All visible invertebrates were manually sorted using fine forceps or a fine pipette. Indiviudally sorted taxa were then transferred to filtered lake water (0.45 µm) overnight to allow gut evacuation. The following day samples were filtered, washed with ultra-pure milli-Q water, dried at 60°C (48hrs) and stored in acid washed glass vials in a dessicator prior to dispatch. In most cases three specimens were analysed separately providing three replicates per species.

Methods: Isotopic sampling of Lough Melvin Fishes

Sampling for fishes initially took place in February 2007 with overnight gill netting. It was our intention to repeat the process in the summer in order to pick up seasonal variation. However netting was biased towards the more abundant fishes in the lake and certain species such as *Gillaroo* were notably absent. Attempts were made to obtain samples of Arctic Charr by netting in deep water and the use of specific angling techniques but these were unsuccessful.

Additional samples were taken at the weigh-in of the Melvin Open Fly fishing competition in August 2007 where a good number of samples from *Gillaroo* were achieved. Dorsal muscle tissue was analysed for samples obtained in February 2007 and fin clips taken from the adipose were analysed for samples obtained during the fishing competition.

Results: Carbon budget

For the Roogagh and County Rivers, flow data were available at 15 minute resolution but this greater temporal resolution did not result in markedly different estimates of dissolved organic carbon (DOC) load compared to estimates based on mean daily flows (Table 6). For the purpose of comparison the loads analysed are those based on mean daily flows.

Table 6. Annual loads, export rates and balance of dissolved organic carbon for the period October 2006 – September 2007 calculated according to equation 1 with mean daily flows and instantaneous flows.

	Mean daily flows		Instantaneous flows	
Catchment	**Load (tonnes)**	**Export rate (kg ha^{-1} yr^{-1})**	**Load (tonnes)**	**Export rate (kg ha^{-1} yr^{-1})**
Roogagh	1342	224	1353	225
County	954	172	976	176
Ballagh	140	101		
Glenaniff	153	56		
Kinlough	88	221		
Clancys	68	89		
Muckenagh	227	250		
Small streams	741			
Drowse*	2967			
Drumgormly[a]	177	240.67	172	225
Glen East[a]	240	226.30	240	225.96
Glen Bridge[a]	100	176.25	109	192
Roogagh downstream[a]	825	226.78	833	229
Lattone[b]	200	181.50	200	182
Deans[b]	420	184.67	419	184
Sraduffy[b]	172	156.55	172	156
County downstream[b]	163	131.59	186	150
Total in	3714			
Total out	2967			
Retention	747			

* denotes the outflow, [a] denotes tributaries of the Roogagh River and [b] tributaries of the County River

Dissolved organic carbon export

Export rates within the catchment ranged between 56.3 to 240.7 kg ha^{-1} yr^{-1} (Table 6). These rates are markedly higher than the values presented for a variety of vegetation types in Table 1. For

comparison a range of twelve sites in Nova Scotia exhibited DOC export rates: 30 – 123 kg ha^{-1} yr^{-1}, 21 catchments in central and northern Sweden: 23 – 102 kg ha^{-1} yr^{-1}, 23 sites in North-Eastern Scotland: 20 – 115 kg ha^{-1} yr^{-1} and peat dominated upland catchments in North East Scotland and Mid Wales: 191 and 121 kg ha^{-1} yr^{-1} respectively (Aitkenhead-Peterson *et al*., 2004; Algesten *et al*., 2003; Hope et *al*., 1997; Dawson et *al*., 1997).

Export rates for the Lough Melvin catchment may be markedly higher than those observed in other regions for a number of reasons. Positive relationships have been observed between DOC export and wetland area in a number of studies (Curtis, 1998; Xenopoulos *et al*., 2003) and since soils in Ireland retain high levels of moisture with many areas are frequently waterlogged this could be a partial explanation for above average DOC exports. Additionally much of the geology of the Lough Melvin catchment consists of carbonate limestone resulting in well buffered, high pH drainage water despite large tracts of peatland. Some studies have suggested that DOC release is positively related to pH (Kennedy *et al.*, 1996) so other sites in peatland catchments may release relatively less DOC by nature of the more typical lower pH.

Export rates were positively related to the proportion of coniferous forestry and negatively related to the proportion of peat bogs (Fig. 5).

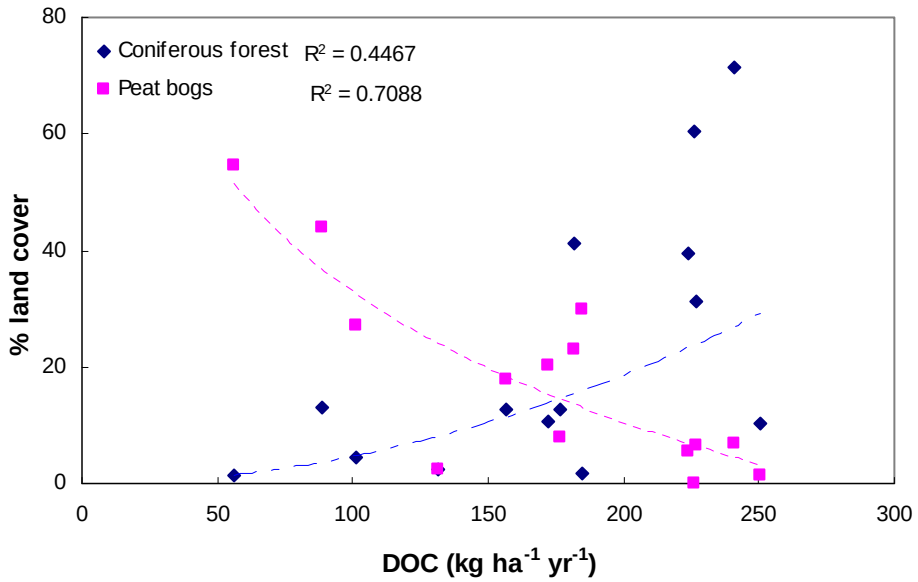

Figure 5. Sub-catchment export rates against % land cover occupied by peat bogs and coniferous forestry.

Results: Carbon and nitrogen stable isotope analysis of food webs

The $\delta^{13}C$ and $\delta^{15}N$ of consumers from littoral, pelagic and profundal habits overlapped to varying degrees (Figures 6 & &). Littoral consumers generally exhibited signatures distinct from those of pelagial and profundal consumers, consistent with a diet based upon biofilms, attached algae, macrophytes and terrestrial organic matter. The $\delta^{13}C$ of pelagic and profundal invertebrates indicated similar degrees of reliance upon phytoplankton and terrestrial organic matter. Zooplankton exhibited significantly more enriched $\delta^{15}N$ values consistent with intermediate trophic links.

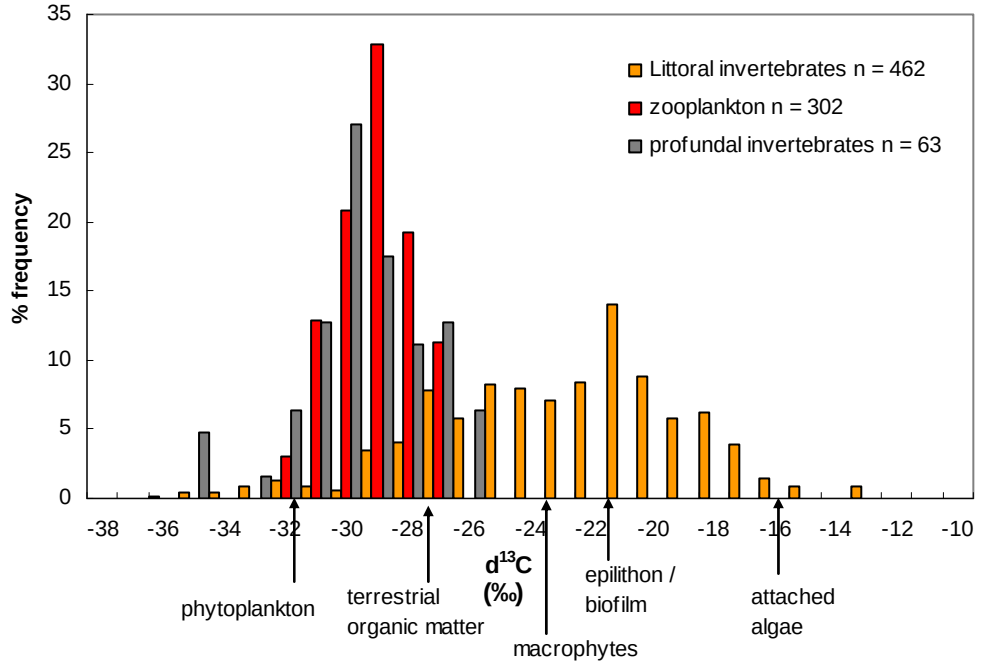

Figure 6. Frequency distribution of δ13C signatures for littoral, pelagic and profundal consumers. Arrows indicate the mean signatures of potential energy sources.

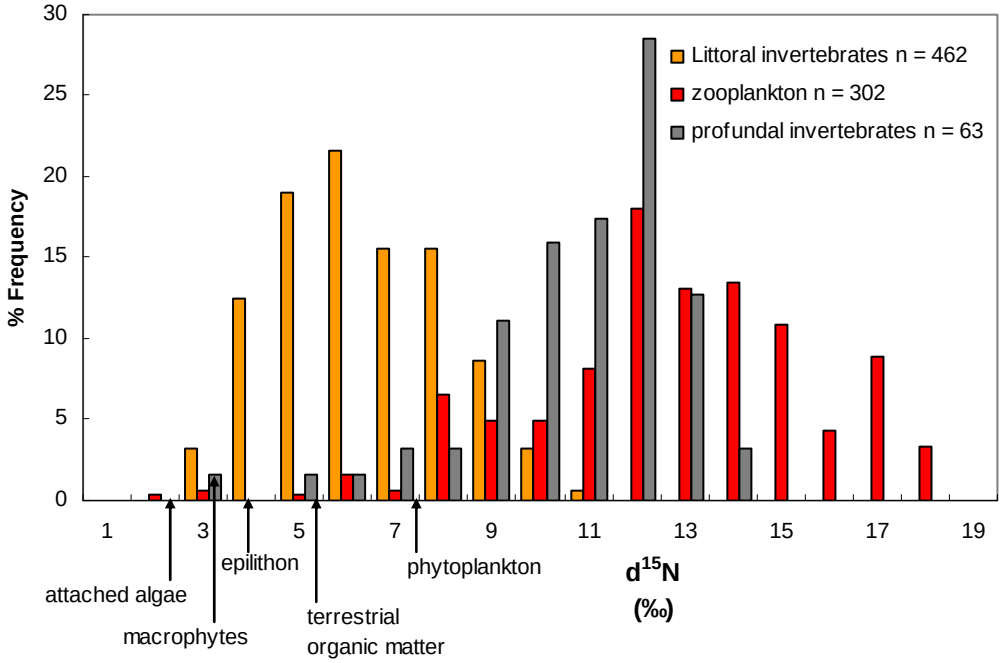

Figure 7. Frequency distribution of d15N signatures for littoral, pelagic and profundal consumers. Arrows indicate the mean signatures of potential energy sources.

Pelagic food web

Inflow and lake dissolved organic matter (DOM) $\delta^{13}C$ were indistinguishable throughout the study period demonstrating that any algal derived DOM present in lake water was completely masked by the high proportion of allochthonous DOM.

The $\delta^{13}C$ of DOM (mean -28.8‰) was consistently depleted relative to allochthonous POM (mean 27.8‰), which exhibited values close to the average for terrestrial C3 plants (~-27‰). Grey *et al.* (2001) also observed DOM in Loch Ness with a lighter $\delta^{13}C$ than POM with annual mean values of -27.6 and -25.5‰ respectively. Microbial processing of POM into DOM leachates would be expected to result in isotopic enrichment making degradation an unlikely causative factor. Alternatively depletion of atmospheric $\delta^{13}CO_2$ by recent fossil fuel use (~1.5‰) suggests that lighter DOM could be of more recent origin than POM. Billet *et al.* (2007) and Guo & Macdonald (2006) also observed riverine DOM of recent origin on the basis of ^{14}C dating, and in the latter study POM was also enriched in ^{13}C relative to DOM. These observations are consistent with DOM entering water courses from more recent upper soil horizons and POM from deeper, older soils.

This difference between the $\delta^{13}C$ of allochthonous sources (DOM & POM), although relatively slight (~1‰) presents a difficulty as to which to employ for the purposes of assessing their contribution to consumer production. Utilisation of allochthonous DOM by zooplankton consumers requires at least one intermediate trophic step in the form of bacterial utilisation, incurring an additional level of carbon and nitrogen stable isotopic fractionation, whereas utilisation of POM will occur by direct ingestion. Although we do not have $\delta^{15}N$ data for DOM, values have previously shown it to be relatively similar, if not depleted compared to POM (Guo & Macdonald, 2006). During the winter of 2007 zooplankton exhibited $\delta^{13}C$ values consistent with a diet of a mixture of allochthonous DOM, POM and phytoplankton. But in terms of $\delta^{15}N$, zooplankton were enriched by at least 6‰ compared with allochthonous POM, far exceeding the typical enrichment for animal consumers of ~3.4‰ (DeNiro & Epstein, 1981) and thus eliminating POM as a dietary component. Nevertheless both $\delta^{15}N$ and $\delta^{13}C$ values of zooplankton could not be explained simply on the basis of a diet consisting of phytoplankton alone. These observations suggest zooplankton fed upon bacterial and subsequent consumer production (eg. bacterivorous ciliates) based upon allochthonous DOM evidenced by $\delta^{13}C$ and $\delta^{15}N$ values equivalent to 2-3 trophic levels, with the assumption that the $\delta^{15}N$ of DOM was comparable to that of POM.

Over the study period the carbon isotopic signatures ($\delta^{13}C$) of phytoplankton were distinct from those of allochthonous organic matter (mean difference 5.3‰, SD 0.88‰) allowing assessment of the relative contributions to consumers (Fig. 8). Although different phytoplankton species can exhibit markedly different carbon and nitrogen isotopic signatures within lakes (Vuorio *et al.* 2006) the close isotopic similarity of *Aulacoseira italica* and *Woronichinia naegliana,* members of different algal phyla, suggest that their values are representative of the algal community as a whole (Fig. 8).

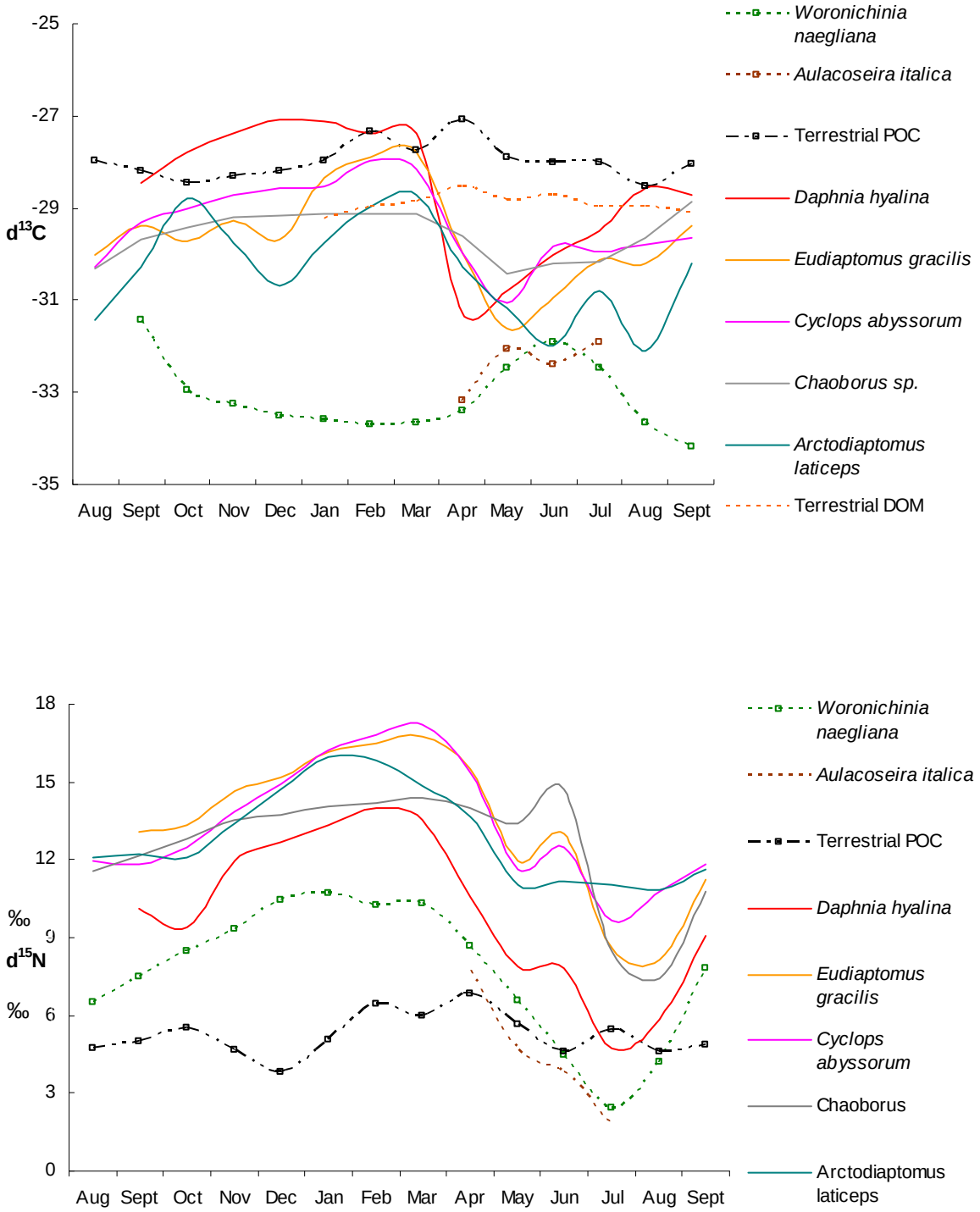

Figure 8. Seasonal variation of carbon and nitrogen stable isotopic signatures for components of the pelagic food web, based on monthly mean values. POM- particulate organic matter. DOM- dissolved organic matter. Putative autochthonous sources are represented by the blue-green alga *Woronichinia naegliana* and the diatom *Aulacoseira italica* and allochthonous sources by terrestrial POM and DOM.

Results: Pelagic food web

Carbon of allochthonous origin in zooplankton

In freshwater zooplankton and planktivorous fish lipids are present as fatty acids in the form of phospholipids and triglycerides (Olsen, 1999), which can be depleted by up to 9‰ relative to the tissues (DeNiro & Epstein, 1977). Samples with high lipid content can therefore hinder accurate interpretation of carbon stable isotope data. Here we use the mass balance correction model of Fry *et al.* (2003) to correct for the lipid content:

$$\delta^{13}C_{ex} = \delta^{13}C_{bulk} + D\,(\,C{:}N_{bulk} - C{:}N_{ex} / C{:}N_{bulk}\,)$$

where

$\delta^{13}C_{ex}$ = lipid extracted carbon isotopic signature

$\delta^{13}C_{bulk}$ = non lipid extracted carbon isotopic signature

D = mean difference between $\delta^{13}C$ of lipids and protein

$C{:}N_{bulk}$ = atomic carbon to nitrogen ratio of non extracted sample

$C{:}N_{ex}$ = atomic carbon to nitrogen ratio of extracted lipid

Since we did not determine $\delta^{13}C$ or C:N of lipid extracted material, mean values from the literature are used. Smyntek *et al.* (2007), in a study encompassing 10 zooplankton species from nine lakes, determined a mean value for $C{:}N_{ex}$ of 4.2. The low coefficient of variation of 9.1% suggests that this value is widely applicable to other lake systems. Apart from *Arctodiaptomus laticeps* all species exhibited C:N ratios very close to the mean value determined for $C{:}N_{ex}$ suggesting that lipids exerted a minor effect on their $\delta^{13}C$ (Fig. 9). Correction for lipids was not carried out for *Daphnia* and *Cyclops* or *Eudiaptomus* on the basis that values determined for D were found to vary significantly between lakes (Smyntek *et al.,* 2007) and the low $C{:}N_{bulk}$ values resulted in changes between $\delta^{13}C_{bulk}$ and $\delta^{13}C_{ex}$ within the limits of analytical precision (~0.2‰) for a range of values of D. For *Arctodiaptomus laticeps* we set D at 6.3 on the basis that Smyntek *et al.* (2007) determined this figure for *Eudiaptomus gracilis* and *Arctodiaptomus laticeps* from the Lake District.

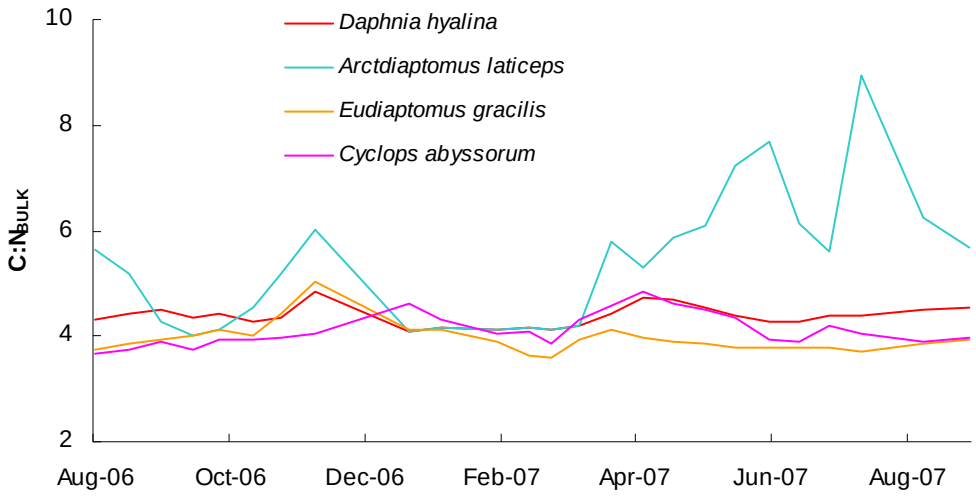

Figure 9. Seasonal variation of atomic C : N ratios for Lough Melvin Zooplankton.

Carbon of allochthonous origin in zooplankton

A mass balance equation was use to determine the % allochthonous carbon present in zooplankton, for which the $\delta^{13}C$ of the cyanobacterium, *Woranichinia naegliana* and riverine DOM were employed as autochthonous and allochthonous end members respectively. Since we do not have isotopic data for heterotrophic intermediaries, the $\delta^{13}C$ of riverine DOM are been adjusted to reflect enrichment equivalent to one trophic level. ^{13}C fractionation between consumer tissues and their diet result in enrichment of ~1‰ (Michener and Schell, 1994). However Grey *et al.*, 2001 determined a value of 0.43 ‰ for Loch Ness zooplankton based on laboratory studies. To give a measure of the sensitivity of this method to estimates of F, % allochthony was calculated by employing fractionation factors of 0.43‰ and 1‰.

$$\text{\% allochthonous carbon} = \frac{(\delta^{13}C_{zoopl} - F - \delta^{13}C_{phyto}) \times 100}{(\delta^{13}C_{RDOM} - \delta^{13}C_{phyto})}$$

Where $\delta^{13}C_{zoop}$ = carbon isotopic signature of zooplankton species

$\delta^{13}C_{phyto}$ = carbon isotopic signature of phytoplankton species

$\delta^{13}C_{RDOM}$ = carbon isotopic signature of riverine DOM (allochthonous)

F = fractionation factor

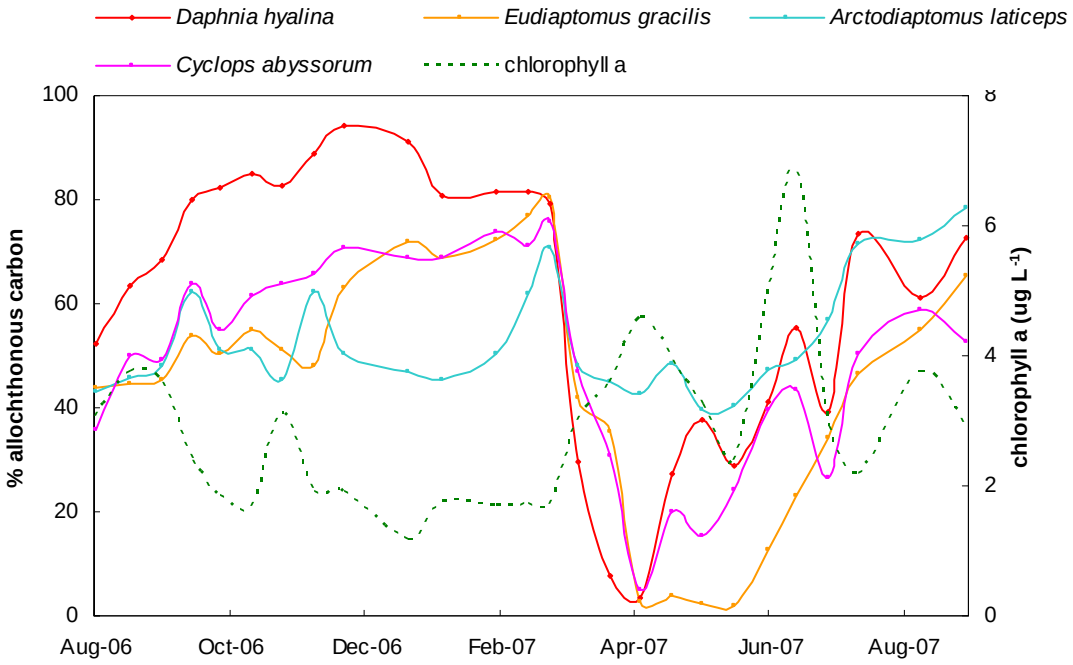

Figure 10. Seasonal variation of % contribution of allochthonous carbon to zooplankton consumers and annual cycle of chlorophyll a. Mean values are presented based upon upper and lower limits calculated according to fractionation factors of 0.43 and 1‰.

Carbon of allochthonous origin in zooplankton

The percentage reliance of zooplankton upon allochthonous carbon at any point in time, whilst providing specific dietary information, must be combined with measures of abundance to determine the extent to which allochthonous carbon contributes to production. Quantitative zooplankton

samples taken on the same day as sampling for stable isotopes provided such measures. Table . shows the mean annual % allochthony and the annual mean abundance/biomass-weighted reliance upon allochthonous carbon for each zooplankton species. This is calculated as the percentage of annual production based on allochthonous organic matter divided by the total annual production:

Abundance / Biomass weighted allochthonous reliance (%)

$$= \sum(\text{\% allochthony} \times \text{Zoopl}_{AB}) / \sum \text{Zoopl}_{AB} \cdot 100$$

where Zoopl_{AB} = abundance / biomass for individual zooplankton species

% allochthony = proportion of body carbon derived from allochthonous matter

Table 7. Annual abundance-weighted allochthonous reliance for principal components of the Lough Melvin pelagic food web. Note range of allochthony is determined by variations of the value of F used for the mass balance calculation; here 0.43 & 1.0‰.

Zooplankton species	Mean annual allochthony (%)	Annual abundance-weighted allochthonous reliance (%)
Daphnia hyalina var. *galeata*	54 - 67	49 - 61
Eudiaptomus gracilis	36 - 50	37 - 50
Arctodiaptomus laticeps	44 - 58	42 - 57
Cyclops strenuus abyssorum	42 - 56	34 - 48

Seasonal variation of zooplankton diets

Each zooplankton species displayed a pronounced dietary switch from a high degree of reliance upon allochthonous carbon during the winter to autochthonous carbon during the productive summer months (Fig. 10). Within the community a marked difference was apparent between the $\delta^{13}C$ and $\delta^{15}N$ of *Daphnia* and the copepod species. *Daphnia* exhibited the lowest $\delta^{15}N$ during the winter months, that was on average 6.9‰ enriched relative to allochthonous POM (here a proxy for the $\delta^{15}N$ of DOM) and was enriched by 1.7‰ relative to the $\delta^{13}C$ of DOM. These levels of ^{15}N and ^{13}C enrichment both approximately equate to two trophic levels and are consistent with a diet of bacterial production based on allochthonous DOM. In contrast copepods displayed $\delta^{15}N$ & $\delta^{13}C$ values consistent with a diet consisting principally of matter derived from allochthonous DOM but with an additional bacterivorous trophic component consisting of protozoa and rotifers.

Between late March and early April zooplankton $\delta^{13}C$ displayed a sudden shift to a diet derived almost exclusively from phytoplankton production. On the basis of the ^{15}N enrichment *Daphnia* directly consumed phytoplankton whereas copepod $\delta^{15}N$ values suggested an additional trophic link was present transferring autochthonous production to them.

These observations are consistent with suggestions (Kankaala, 1988) and reports of similar pathways of resource utilisation where bacteria provide the link between allochthonous DOM and microplankton (Karlsson *et al.*, 2003; Work *et al.*, 2003). More specifically the likely importance of additional bacterivorous heterotrophs, such as protozoa, to the diets of copepods but not filter feeding cladocerans has also been reported (Grey *et al.* 2001; Karlsson *et al.* 2007).

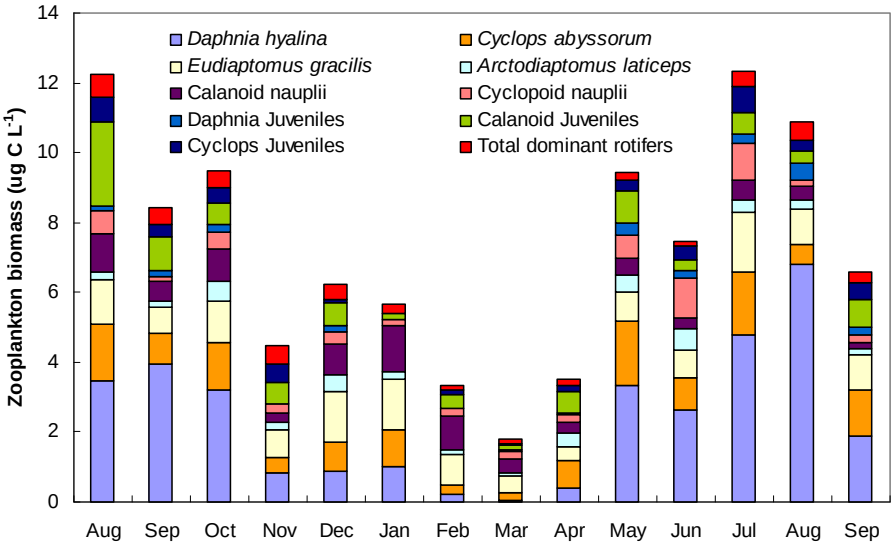

Figure 10. Seasonal variation of the biomass (as carbon) for components of the zooplankton community.

Seasonal variation of zooplankton diets

The different pathways of resource utilisation between copepods and filter feeding cladocera stem from their different feeding mechanisms, which can also affect their relative ability to gain nutrition during the seasonal cycle. Calanoid copepods, like *Daphnia*, are filter feeders but are known to be highly selective and are able to asses the nutritional quality of prey items on a unit by unit basis. In contrast *Daphnia* is more passive and although it can modify its feeding apparatus to filter within a small range of different prey sizes, collected material is largely dependent on the ambient concentrations of items of a particular size. *Daphnia* can also select what to ingest however this is only possible once a ball or *bolus* of prey items has been collected; a process that is energetically expensive in poor prey quality environments.

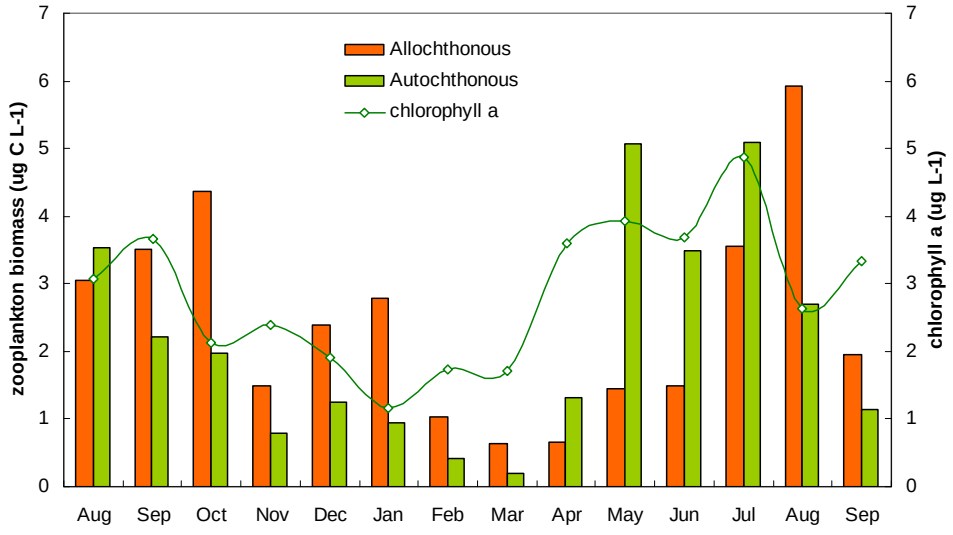

Figure 11. Monthly biomass of *Daphnia hyalina, Eudiaptomus gracilis, Arctodiaptomus laticeps* and *Cyclops abyssorum* apportioned into allochthonous and autochthonous derived carbon.

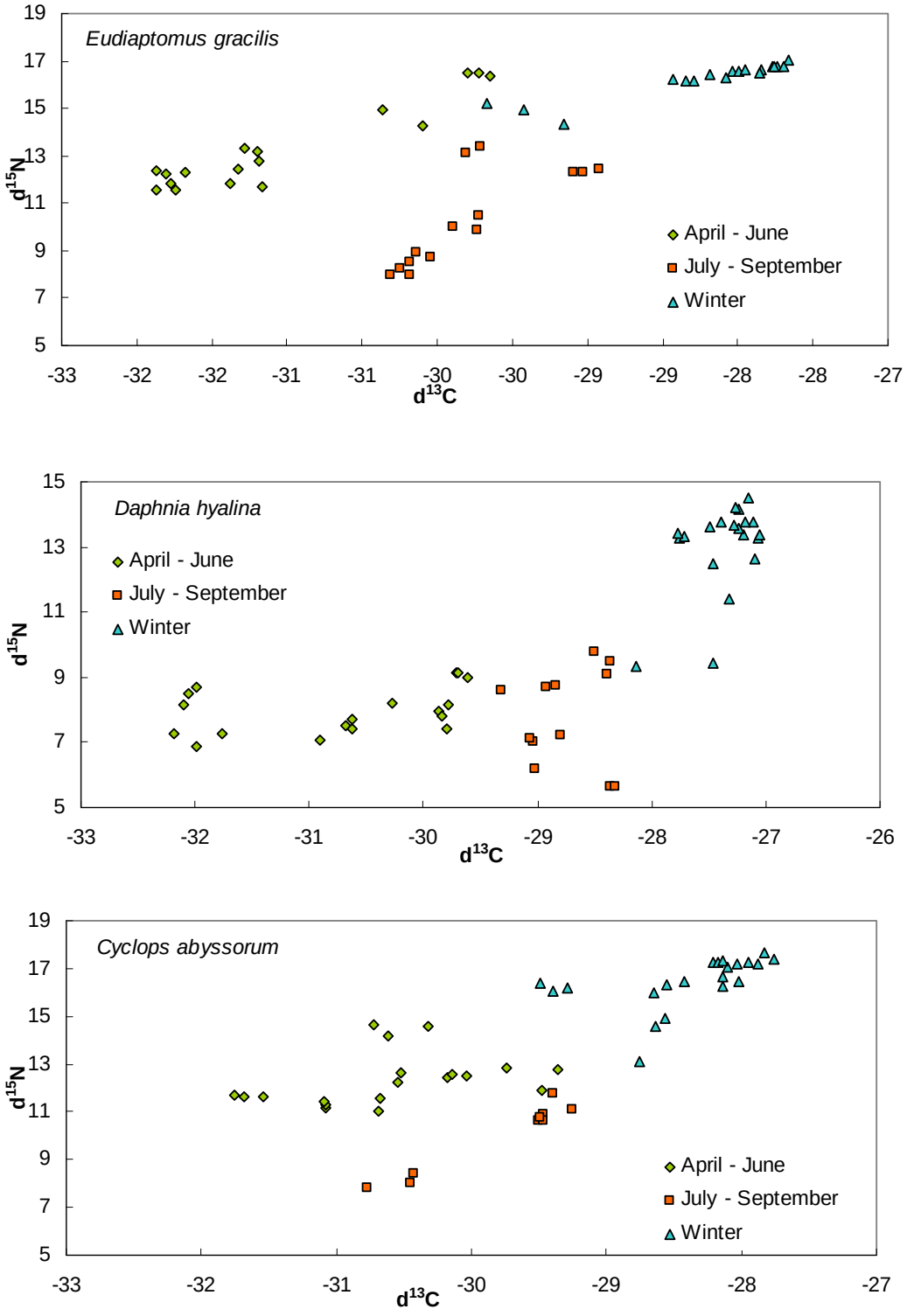

Figure 12. Carbon and nitrogen stable isotopic signatures for *Cyclops abyssorum, Daphnia hyalina* and *Eudiaptomus gracilis* divided into Winter (October – March) and 1st and 2nd halves of the growing season.

The principal zooplankton species rely upon allochthonous organic matter for between 34-61% of their body carbon annually. The co-existence of these species throughout the year with an absence of any pronounced seasonal succession relies upon their differing feeding habits and abilities to

utilise phytoplankton and allochthonous energy sources. Bacterial production is more dependent upon temperature and likely lags phytoplankton production during the seasonal cycle. Furthermore lake temperatures remain warm into mid-October after phytoplankton production has declined and coincide with increasing inputs of allochthonous organic matter. For these reasons most production occurs between April and October with a transition between predominant reliance upon autochthonous production between April and June to reliance upon allochthonous production between July and March (Fig. 11).

There is a clear distinction in resource utilisation between the two periods that results in separate carbon and nitrogen isotopic groupings (Fig. 12) with a cyclic seasonal pattern in response to changing food availability and decline and increase of the phytoplankton $\delta^{15}N$ in mid to late summer.

Determining the trophic pathways between allochthonous organic matter and higher trophic levels is frequently confounded by the inability to sample and separate sufficient mass of primary and secondary consumer species or taxonomic groups. Microzooplankton (35-180µm) are generally too small to be employed in stable isotope analysis despite the fact that they have been shown to account for approximately 70 and 83% of zooplankton grazing upon phytoplankton and bacteria respectively (Kim *et al.*, 2000). In 2006 the colonial rotifer *Conochilus unicornis* which was first recorded in 2001/02 became abundant in the plankton between October and November (Figure 13) and it was possible to manually separate and concentrate sufficient colonies for stable isotopic analysis on three consecutive fortnightly occasions.

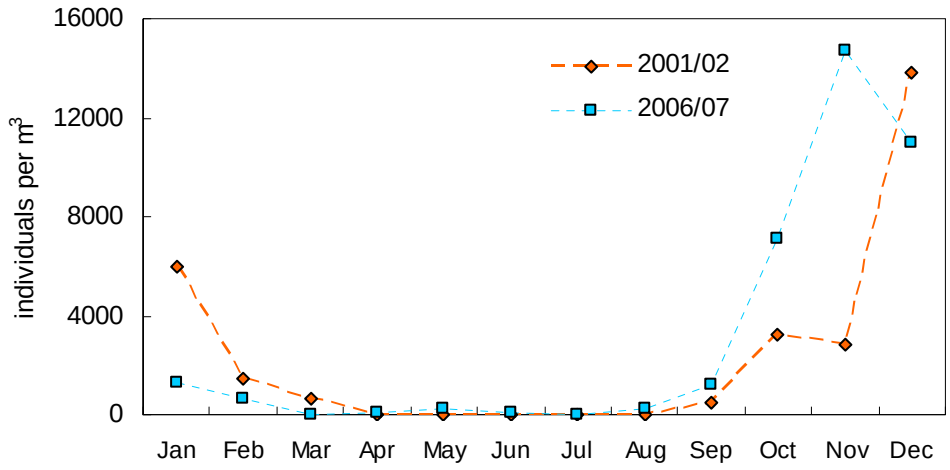

Figure 13. Seasonal cycles of abundance for *Conochilus unicornis* in 2001/02 and 2006/07.

Conochilus exhibited $\delta^{13}C$ signatures indicating 83% reliance upon allochthonous carbon at the end of September and 100% reliance at the beginning and end of October. The $\delta^{15}N$ signatures were also consistent with an increasing reliance upon allochthonous carbon, equivalent to approximately 2 trophic levels when the $\delta^{13}C$ signatures indicated 100% allochthonous reliance. This suggest that *Conochilus* preyed upon bacterial production based upon allochthonous organic matter.

Results: Littoral food web

The $\delta^{15}N$ and $\delta^{13}C$ of invertebrates, biofilms and macrophytes showed a considerable overlap (Fig. 14) both across and within individual sites. Attached algae (colonial and filamentous species) displayed the most distinctive $\delta^{13}C$ but had $\delta^{15}N$ values similar to approximately 50% of biofilm samples and 55% of macrophyte samples.

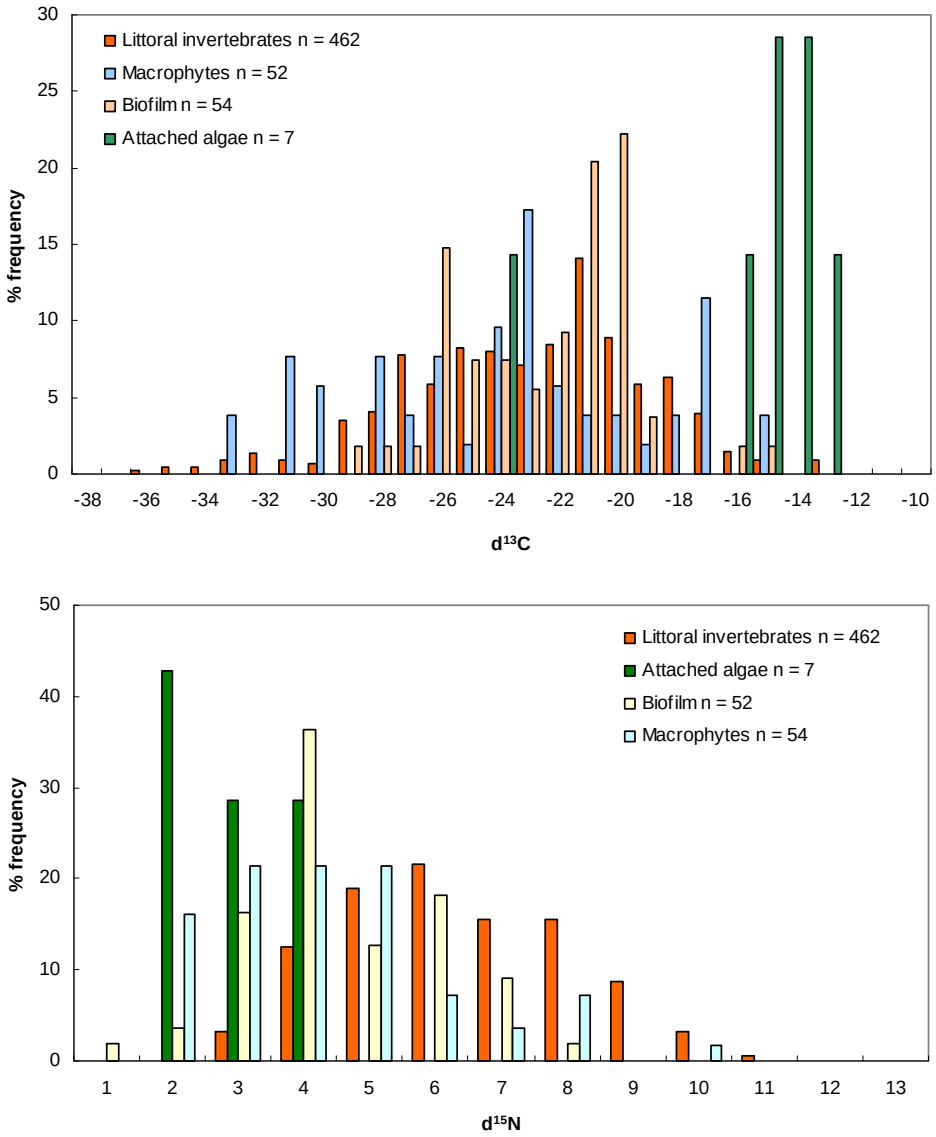

Figure 14. Frequency distributions of δ13C (top) and δ15N (bottom) signatures for components of the littoral food web

Assessing littoral consumer reliance upon autochthonous and allochthonous matter

Biofilms are a food resource for many littoral invertebrates and consist of a polysaccharide matrix derived from the attached algae and heterotrophic bacteria present. They can thus be a mixture of autochthonous and allochthonous matter via assimilation of DOM by bacteria. Attached colonial and filamentous algae and specific invertebrate grazers were considerably enriched in ^{13}C and

depleted in ^{15}N relative to biofilms at all but one site[2], suggesting that the algal component of the biofilms was isotopically heavier in carbon and lighter in nitrogen. A prerequisite for determining the contributions of different dietary resources to consumers is that they display distinct isotopic signatures. The biofilm isotopic signatures are therefore deemed unsuitable as end members in mass balance calculations here.

An alternative method is to estimate the basal autochthonous isotopic signature from those of primary consumers (Post, 2002). This approach was used to estimate the $\delta^{13}C$ of algae in biofilms in conjunction with the mean $\delta^{13}C$ of inflow DOM and POM in a mass balance to determine consumer reliance upon each source for Summer and Winter values (Fig. 15). The larvae of *Metalype fragilis,* a grazing / scraping species of trichoptera (Edington & Hildrew, 1995), was found at 4 sites and exhibited the most enriched and relatively consistent $\delta^{13}C$ signatures between sites during the summer (-15.51, -16.44, -17.21, -18.39 ‰), consistent with a diet composed of attached algae. Although the $\delta^{13}C$ for this species varied seasonally the algal signature was assumed to be constant throughout the year. At one site where this species was not present the $\delta^{13}C$ of the grazing freshwater limpet, *Ancylus fluviatilis* was used (winter value: -13.73 ‰).

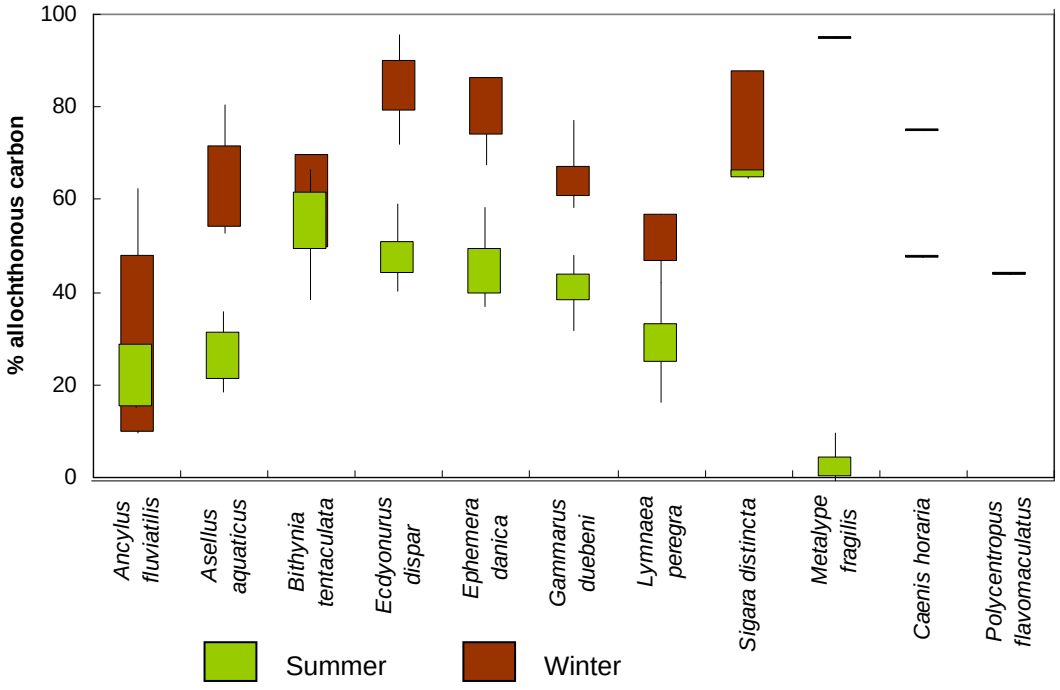

Figure 15. Summer and winter reliance upon allochthonous organic matter (%) for littoral consumers calculated on a site specific basis. Vertical bars show the range and vertical box plots are the standard error (+/-) the mean across sites.

Although there are potentially large errors associated with this methodology the substantial depletion of consumer $\delta^{13}C$ towards that of the allochthonous signature during the winter demonstrates a clear seasonal switch in the importance of each source. Additionally the switch was least marked for grazer species, particularly the gastropod molluscs *Lymnaea peregra* and *Ancylus*

[2] Site 6 is considered an outlier and is examined separately; see page 35

fluviatilis supporting the assumption that the algal signature is relatively consistent throughout the year. A summer-winter switch was not evident for the gastropod *Bithynia tentaculata*, however this species has the capacity to filter feed and may have utilised ^{13}C depleted phytoplankton (Fink & Von Elert, 2006; Brendelburger & Jürgens, 1993). This may also explain the high calculated % allochthony observed during the summer for this species.

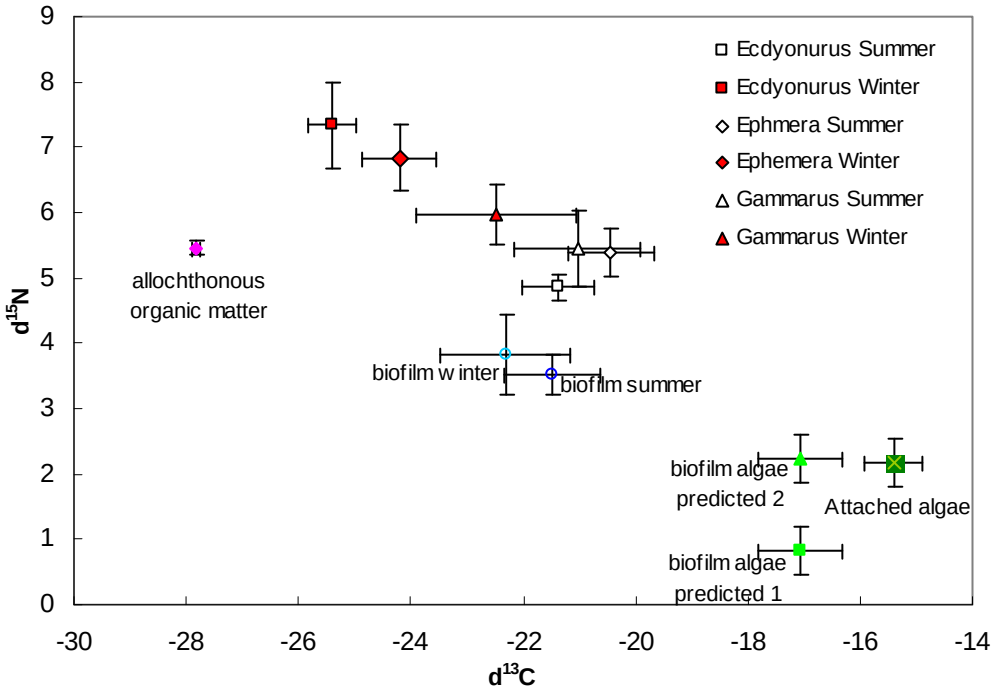

Figure 16. Plot of summer and winter $\delta^{13}C$ & $\delta^{15}N$ values for *Ecdyonurus dispar, Ephemera danica, Gammarus duebeni,* attached algae and biofilms. Data presented are means of values from all sites. Errors bars denote standard error. Predicted algal biofilm components are those estimated from the isotopic signatures of *Metalype fragilis* and *Ancylus fluviatilis*; calculated assuming ^{15}N fractionation factors of 3.4‰ and 2.0‰ per trophic level for nos. 1 & 2 respectively.

The mayfly nymphs, *Ecdyonurus dispar, Ephemera danica* and *Caenis horaria* and the isopod, *Asellus aquaticus* exhibited wide shifts in their $\delta^{15}N$ and $\delta^{13}C$ signatures at all sites, consistent with a switch from a diet of biofilm in the summer to a greater proportion allochthonous matter in Winter (figure x). Each of the mayfly species and *Asellus* are described as collector-gatherers and *Ecdyonurus* can also feed as a scraper (Moore, 1975; Elliot *et al.,* 1988), these species are therefore capable of exploiting allochthonous resources. The amphipod *Gammarus duebeni,* also exhibited a seasonal switch but not of the same magnitude as other species (Fig. 16). This species feeds as a collecting omnivore and can be predaceous (Dick *et al.,* 2002) and therefore has the capacity to utilise allochthonous matter.

Figure 16 shows that the $\delta^{15}N$ and $\delta^{13}C$ values of biofilm fell approximately midway between those of attached algae and allochthonous POM. This suggests that each source may contribute equally to biofilm matter as a whole. The values predicted for the algal component of the biofilm based on the signatures of grazing consumers agreed relatively well with those obtained for pure samples of

attached algae, however in terms of $\delta^{15}N$ a fractionation factor of 2‰ provided a closer match. Furthermore the summer $\delta^{13}C$ of the mayfly nymphs and *Gammarus* are consistent with a diet based upon biofilms (Fig. 16), however in terms of $\delta^{15}N$ a fractionation factor of 2‰ again appears more accurate.

The summer and winter $\delta^{13}C$ and $\delta^{15}N$ of biofilm samples were similar suggesting that the relative proportions of allochthonous and autochthonous matter present do not vary seasonally. However the transition to a diet based more upon allochthonous POM during the winter by several species suggests that the overall biomass of biofilms may be reduced beyond a point where it is no longer energetically viable for consumers to feed upon it.

Trophic position

The vast majority of consumers examined can be classed as primary consumers on the basis of their stable isotopic composition in agreement with functional feeding group designations. The general increase in $\delta^{15}N$ during the transition from summer to winter observed for several species was not indicative of more predaceous winter feeding habits but rather a switch in dietary reliance to allochthonous matter with a higher $\delta^{15}N$. However this interpretation is dependent upon the ^{15}N trophic level fractionation employed, which can be both species and site specific. The mean value of 3.4‰ (Post, 2002) appears to be high on the basis of the observed enrichment of consumers relative to biofilms and grazers to attached algae of about 2‰ found here. With this fractionation factor the $\delta^{15}N$ of *Ecdyonurus* and *Ephemera* observed at some sites during the winter could only be explained by partial dietary reliance upon primary consumers. The only distinctive secondary consumer signatures were those of the damselfly nymph, *Coenagrion pulchellum* and the dytiscid beetle *Stictotarsus duodecimpustulatus* that were only found in areas rich in detritus or vegetation.

Macrophytes

Macrophytes at many sites exhibited isotopic signatures that were indicative of potential food resources for invertebrates. However species such as *Isoetes lacustris* and *Littorella uniflora* are not effectively grazed by herbivores and probably do not enter the food web until they become detritus. Alternatively some species are known to feed upon *Potamogeton spp.* but these are somewhat patchy distributed in Lough Melvin and were sparse at the sites examined. In terms of the general habitat type of the lake these species unlikely to be of significant energetic importance.

Site 6.

As noted above the isotopic signature of biofilms differed at site 6 from other sites in the Lough. This site is in sheltered location close to the most westerly point of the lake near Kinlough (Fig. 3). At site 6 consumers and biofilms were markedly depleted in ^{13}C and enriched in ^{15}N relative to those at the other sites examined and approached values more typical of the pelagic system (Fig. 17). The physical characteristics of site 6 were distinct by nature of its sheltered location, fine silt / mud substratum and extensive stands of emergent *Phragmites australis*. In general a more sheltered location would be expected to result in ^{13}C enrichment of primary producers due to greater restrictions upon inorganic carbon diffusion by larger boundary layers but this was not the case here. The general consensus is that phytoplankton tend to be depleted in ^{13}C relative to terrestrial producers due to the fixation of inorganic carbon derived from the mineralisation of

terrestrial production (~-28‰) in addition to that derived from the atmosphere or carbonate rock weathering (~ -8 - -5‰). The nature of the substratum at this site, its sheltered location and position at the eastern end of the lake beyond a large expanse of water < 5m depth suggests that it is a depositional area and likely experiences higher sedimentation rates than the other sites. Greater deposition of both allochthonous and autochthonous organic material would lead to greater heterotrophic activity and a consequent rise in CO_2 and ^{13}C depletion of the inorganic carbon pool. Subsequent uptake of this depleted carbon would then be reflected in the $\delta^{13}C$ of primary producers such as those in biofilms.

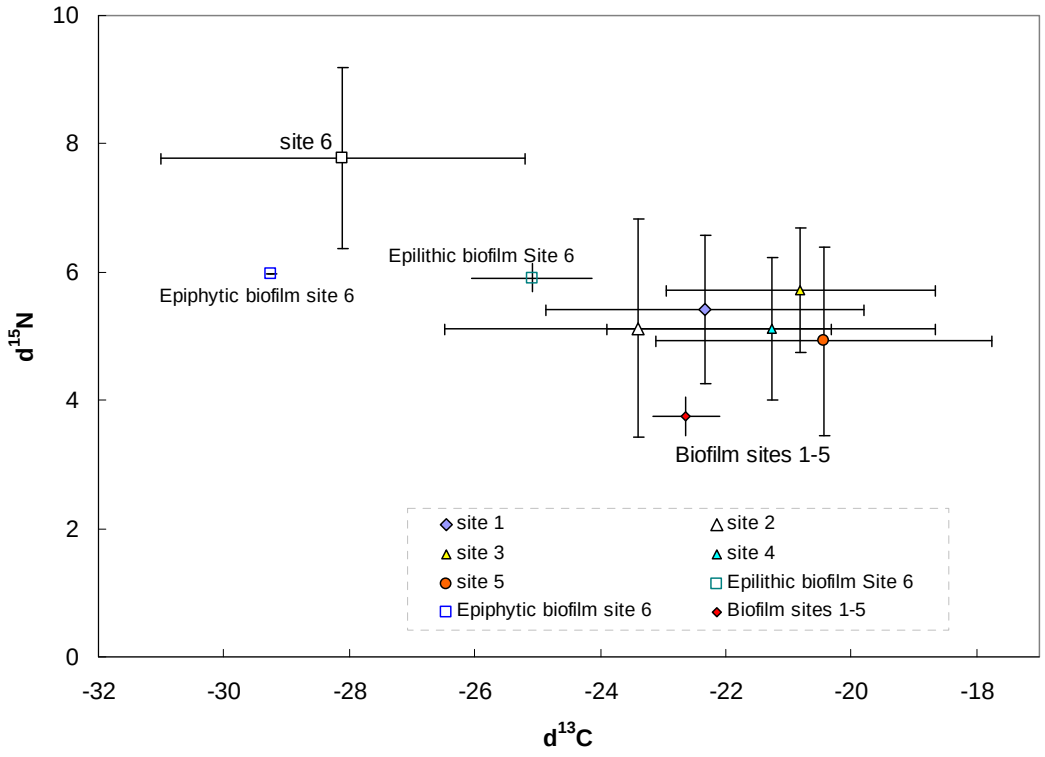

Figure 17. Plot of consumer carbon and nitrogen stable isotopic signatures for consumers by site (Error bars represent 1 standard deviation (+/-) the mean) and mean values for biofilm for sites 1-5 and site 6 (Error bars denote the standard error).

The most depleted $\delta^{13}C$ of -34.7 was exhibited by the trichopteran schredder, *Anabolia nervosa*. The closest possible dietary component analysed from this site was the macrophyte *Potamogeton lucens* which had a $\delta^{13}C$ of -33.6‰ and a $\delta^{15}N$ 2‰ lighter. *Anabolia* is known to feed upon *Potamogeton sp.* in addition to terrestrial leaf detritus (Jacobson & Friberg, 2006). Nevertheless a number of different species including a grazers exhibited $\delta^{13}C$ < -30‰. There was no discernable seasonal pattern in the isotopic signatures of any consumer which tended to be highly variable both within and between dates. This suggests that the resources utilised by consumers could be spatially or isotopically patchy. Assessing the contributions of allochthonous and autochthonous matter to consumers at this site was not possible to due the very similar $\delta^{13}C$ and $\delta^{15}N$ signatures exhibited by biofilms and allochthonous POM. Another interesting feature of this site was that the $\delta^{15}N$ signatures were markedly higher for consumers and primary producers.

Summary

It was beyond the logistical scope of the work to carry out a quantitative analysis of invertebrates in order to apportion allochthonous and autochthonously derived biomass. However this work has demonstrated that consumers rely upon allochthonous carbon for a significant proportion of their body carbon during the winter months. Although the analysis is based upon the assumption that biofilms are a mixture of autochthonous and allochthonous matter, if we were to set the isotopic signatures of biofilms as the autochthonous baseline, a lower but significant contribution of allochthonous matter to consumers would still be evident.

Results: Profundal food web

Sediment samples taken with an Eckman grab and filtered through a 500µm mesh revealed a relatively low abundance of invertebrates. This is consistent with a low supply of organic matter evidenced by the relatively low mean sedimentation rate of 0.032g cm^{-1} yr^{-1} (Anderson *et al.*, 1996). Biomass at each site was dominated by the larvae of the phantom midge, *Chaoborus sp.* which had an abundance of approximately 20-125 individuals m^{-2}. This species is planktivorous and is known to hide in the surficial sediments during the day and migrate into the water column at night. It is also a component of the diet of *Sonaghen* trout making up approximately 14% of the food volume (Ferguson, 1985). *Holotanypus sp.* (Tanypodinae, Chironomidae) was the next most abundant invertebrate at relatively low abundances of approximately 1-50 individuals m^{-2}. Chironomid pupae constitute approximately 20% by volume of the diet of *Sonaghen*. Oligochaetes, particularly *Stylodrilus heringianus* and *Aulodrilus pleuriseta*, were present at most sites but due to their small diameter, some may have been lost during the sieving process and an assessment of their abundance is not attempted.

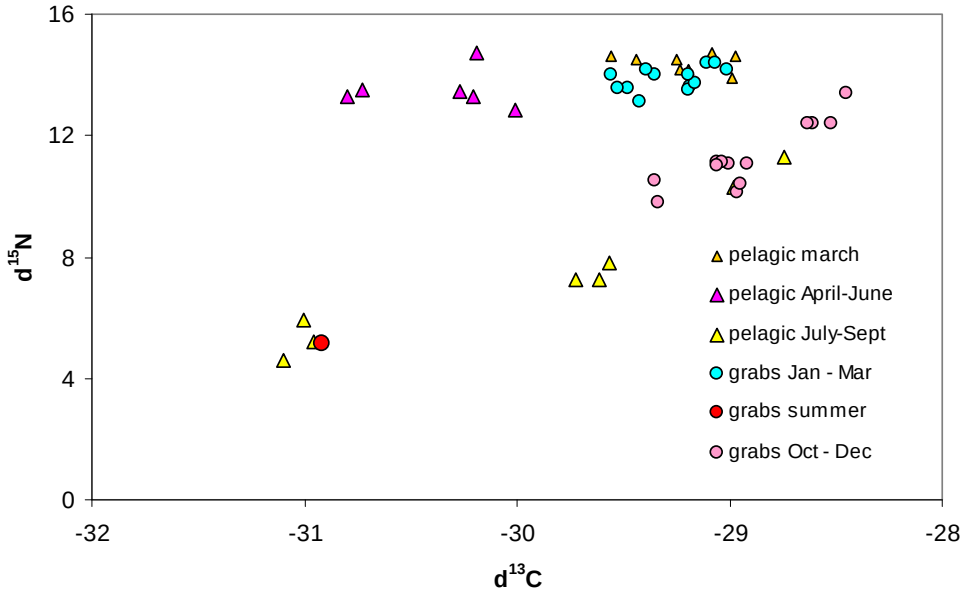

Figure 18. Comparison of seasonal changes in the carbon and nitrogen isotopic signatures of *Chaoborus sp.* sampled by Eckman grabs at spatially distinct sites and from pelagic net tows over the 45m basin**.**

Spatial variation of the $\delta^{13}C$ and $\delta^{15}N$ of *Chaoborus* was small on each sampling occasion during the year (<1‰ and < 1.4‰ respectively) and signatures very similar to those for individuals sampled over the deep water basin in association with the zooplankton hauls. The seasonal cyclic pattern displayed by *Daphnia* and copepods was also observed for *Chaoborus*. *Chaoborus* displayed an enriched $\delta^{15}N$ relative to *Daphnia* during the summer which it therefore relied upon for nutrition. However during the winter months *Chaoborus* exhibited $\delta^{13}C$ and $\delta^{15}N$ values similar to the copepods consistent with selective feeding upon bacterivorous heterotrophic intermediaries.

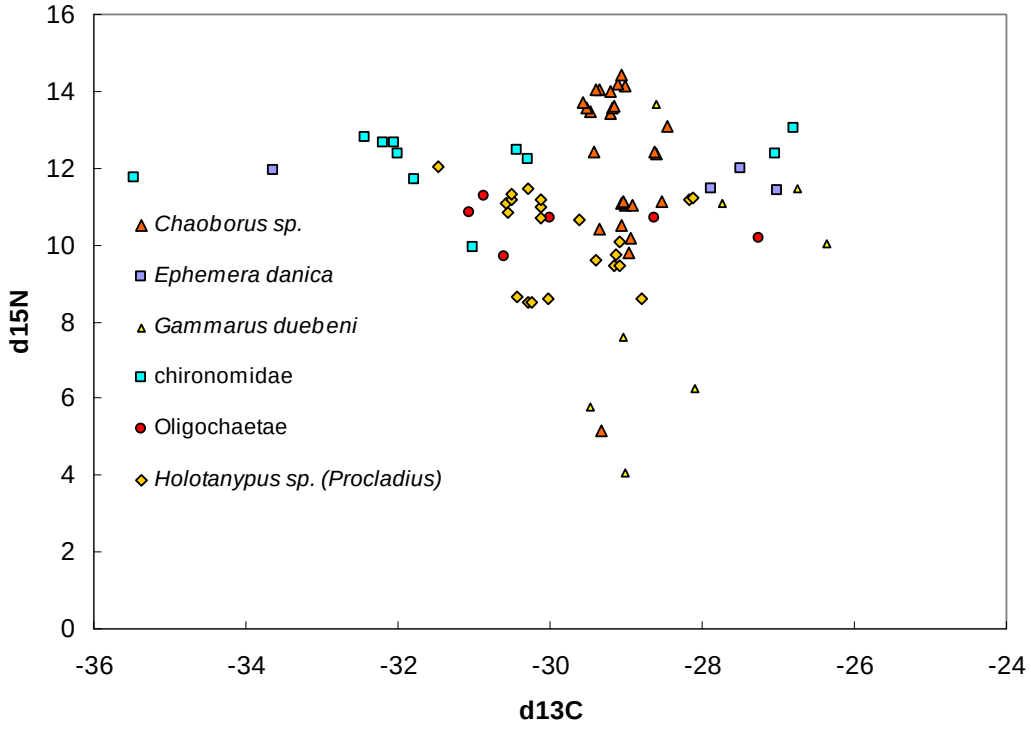

Figure 19. $\delta^{13}C$ and $\delta^{15}N$ signatures for profundal consumers at all sites.

Gammarus duebeni and *Ephemera danica,* species more typical of littoral habitats, were also sampled at 10m depth. The $\delta^{13}C$ and $\delta^{15}N$ of these species fell in a similar range to those of the more typical profundal invertebrates suggesting similar resource utilisation. The individuals of *Gammarus duebeni* sampled were significantly smaller than those found in littoral habitats suggesting that the profundal benthos may be a nursery area for this species.

At site 3 the benthos had a much greater abundance of coarse particulate organic matter (CPOM) such as sticks and leaves, probably resulting from the close proximity of the Roogagh river inflow. Chironomid larvae of the sub-family chironominae were sampled on one occasion at this site (July '07) where they exhibited among the most depleted $\delta^{13}C$ observed in the study (-35.3 - -35.9‰) and highly variable $\delta^{15}N$ (2.2 – 11.8‰). The lowest algal signature observed in this study was for the diatom *Aulacoseira italica* var. *subarctica* at -34.8‰, other this one sample phytoplankton $\delta^{13}C$ remained above -34‰. A number of studies have reported chironomid larvae with $\delta^{13}C$ signatures lower than those of potential food resources and consumption of depleted methotrophic bacteria is suggested as a possible explanation. Although most reports of far ^{13}C depleted chironomid larvae are from seasonally stratified lakes where periods of hypolimnetic anoxia occur, the existence of methanotrophic bacteria is possible though only likely to occur at specific atypical sites. Site 3 may

have been conducive due to the high amounts of CPOM that could restrict mixing and promote localised deoxygenation.

Assessing profundal consumer reliance upon autochthonous and allochthonous matter

Profundal consumers exhibited $\delta^{13}C$ and $\delta^{15}N$ signatures indicative of a diet consisting of a mixture of autochthonous phytoplankton carbon and allochthonous organic matter (Fig 20). The plot for nitrogen suggests a greater dependency on phytoplankton, however phytoplankton $\delta^{15}N$ became depleted during the growth season with a mean of 6.2‰. This suggests that the bulk of the pelagic production exhibits a similar $\delta^{15}N$ and profundal consumer $\delta^{15}N$ of 12-15‰ are therefore a result of additional trophic levels rather than phytoplankton utilisation.

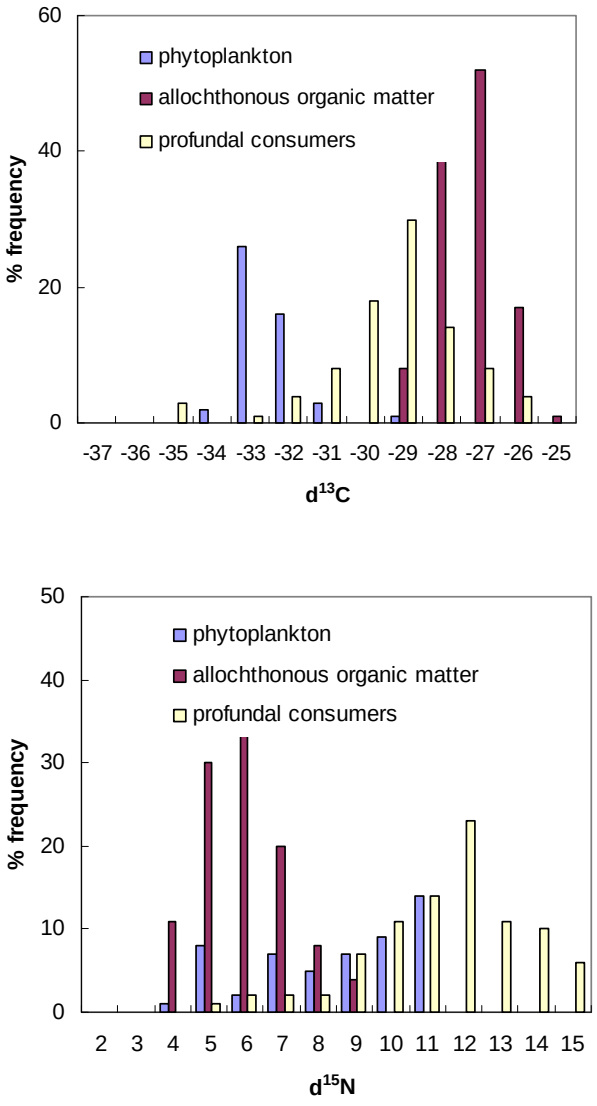

Figure 20. Frequency distribution of profundal consumers, allochthonous organic matter, and phytoplankton carbon and nitrogen isotopic signatures.

No consistent temporal pattern could be observed for any consumer species with either stable isotope within or between sites. Again this may be facet of a low sedimentation rate, where a pulse of allochthonous or autochthonous matter is not delivered to the profundal benthos during any part

of the seasonal cycle. For this reason consumers likely have access to similar proportions of allochthonous and autochthonous matter throughout the year and therefore consistently utilise the same proportions year round. On this basis the mean $\delta^{13}C$ signatures +/- 1 SD for each consumer species across sites was employed with the mean $\delta^{13}C$ signatures for phytoplankton and allochthonous POM in a mass balance calculation to asses the relative contributions of each source (Table 8.)

Table 8. Mean and mean +/- 1SD for $\delta^{13}C$ and % allochthonous carbon calculated according to mean values for allochthonous POM and phytoplankton.

	$\delta^{13}C$		
	Mean	**+1SD**	**-1SD**
Chironomidae	-30.6	-28.5	-32.7
Holotanypus sp.	-29.8	-29.0	-30.7
Oligochaetae	-30.0	-28.5	-31.5
	% Allochthonous Carbon		
	Mean	**+1SD**	**-1SD**
Chironomidae	39	78	0
Holotanypus sp.	54	70	38
Oligochaetae	51	80	21

Importance of allochthonous organic matter to higher consumers: Fishes

The C:N ratio of fishes analysed from Lough Melvin exhibited a mean of 3.25 and standard deviation of 0.2 (Fig. 21). As C:N ratios below 3.4 have been generally found to result in minimal changes to $\delta^{13}C$ signatures (Logan *et al.,* 2008) lipid correction models were not applied to the data.

Sonaghen exhibited $\delta^{13}C$ and $\delta^{15}N$ signatures consistent with a diet based upon a mixture of *Daphnia*, *Chaoborus* and emerging profundal inverts and consequently derive a large proportion of their carbon from allochthonous sources. Gillaroo exhibited $\delta^{13}C$ signatures consistent with a diet of littoral invertebrates however their $\delta^{15}N$ signatures were somewhat more enriched than expected. Gillaroo were sampled in August and exhibited signatures more consistent with a diet based upon winter invertebrates in line with the data assuming an average tissue turnover time of 5-6 months. Coarse fish exhibited signatures consistent with a diet similar to that of Gillaroo with an almost identical range of $\delta^{15}N$ values. In contrast the $\delta^{13}C$ of the coarse fishes was depleted relative to that of Gillaroo suggesting that they may have fed in deeper waters upon invertebrates that would have a lower $\delta^{13}C$ signature more towards that of the pelagic food web. This would be consistent with feeding behaviours more suited to a muddy substrate compared to the shallower, more boulder like areas inhabited by Gillaroo.

In agreement with the findings of Ferguson (1985), who carried out gut contents analysis for the Melvin trout, Sonaghen and Gillaroo appear completely segregated in regard to their diet. Interestingly juvenile trout (~15cm length) sampled in February (these could not be assigned to

species based on their morphology) exhibited a range of carbon and nitrogen signatures, two of which were typical of adult Sonaghen at the time and two consistent with a more varied diet. Trout of this size would be relatively new to the lake having entered from the inflowing/outflow rivers and their isotopic signatures may therefore reflect that of their riverine diet. Alternatively it is possible that different species of juvenile trout rapidly assume the feeding behaviours characteristic of each species almost immediately upon entering the lake.

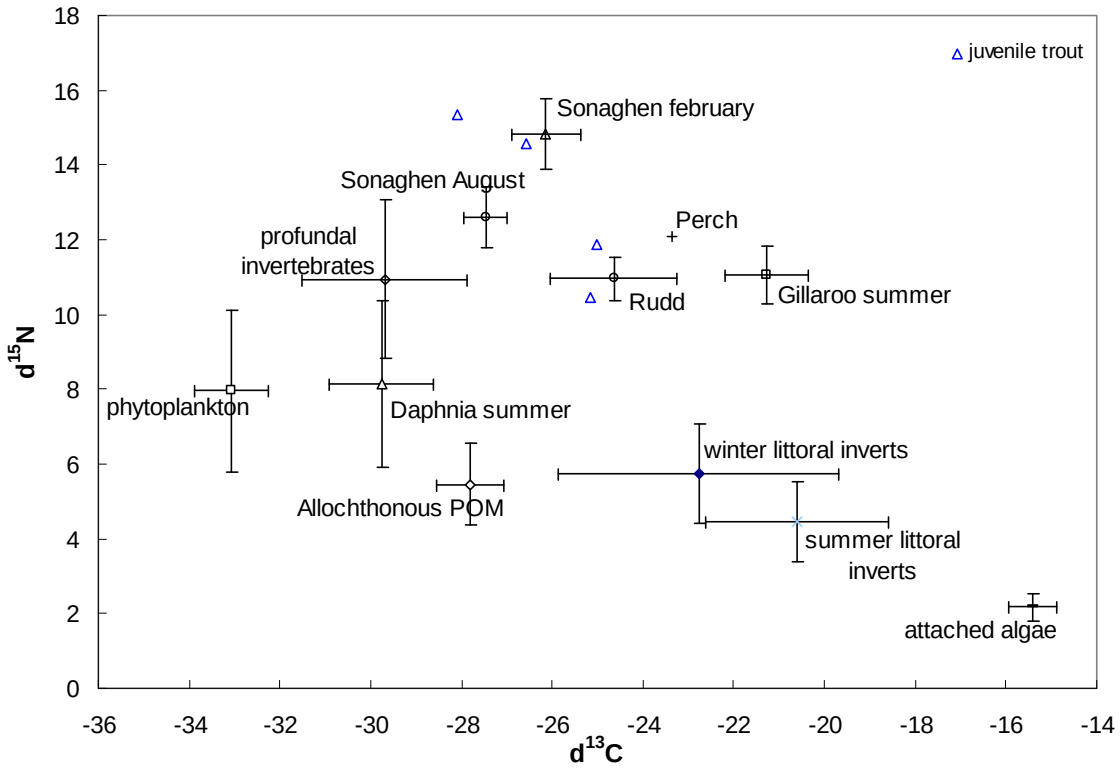

Figure 21. $\delta^{13}C$ and $\delta^{15}N$ plot of components of the Lough Melvin food web. Error bars denote 1 standard deviation.

The pronounced difference in the carbon and nitrogen isotopic signatures of Gillaroo and Sonaghen could have applications for fisheries management. The accuracy of stock assessments relies in part upon correct identifications of each species, however netting surveys frequently disfigure fishes making correct identifications difficult and even certain unaffected individual fish can be naturally hard to distinguish. Stable isotope analysis could therefore provide a relatively simple and cost effective means of correctly assigning unknown fish to species. This would be particularly useful if juvenile trout could be shown to exhibit the distinctive signatures of adult Gillaroo and Sonaghen.

No samples of Arctic char or Ferox were achieved during the study despite considerable efforts.

Discussion

The importance of allochthonous organic carbon to Lough Melvin

Ireland has several relatively deep, polymictic, humic lakes including Lough Melvin. In these lakes the optical depth is a particularly strong determinant of primary production as circulating algal cells spend the majority of time in darkness. In Lough Erne for example, where total phosphorus concentrations are indicative of eutrophic conditions, light reduction by humic compounds limit the algal response to levels that merit mesotrophic classification (Foy *et al.,* 1993). Such humic mediated 'trophic stability' (Girvan & Foy, 2006) has been observed in Lough Melvin where annual mean chlorophyll a concentrations have remained < 5µg L^{-1} despite a 35% increase in total phosphorus over 18 years. Without significant changes to pattern of mixing and the mixing depth in Lough Melvin it is reasonable to expect that increases in allochthonous organic carbon loading will result in a concomitant increase in light attenuation, a decrease to the photic depth and a reduction in algal production. In fact there are several lines of circumstantial evidence to suggest that allochthonous loadings may have increased over the last 15 years:

i. The abundance of mixotrophic phytoplankton species that have the capacity to utilise allochthonous matter has increased since 1990.

ii. A number of new mixotrophic phytoplankton species have been recorded

iii. The abundance of certain rotifer species has increased suggesting they may be benefiting from greater prey abundances in the form of bacterial production based upon allochthonous DOC

iv. The rotifer *Conochilus unicornis* was recorded for the first time in 2001/02 and again at similar abundances in 2006/07. Abundance peaks for this species in around mid-November at a time when algal volumes are low suggesting that it utilises different dietary sources. Stable isotope analysis of this species revealed that it was almost entirely reliant upon allochthonous organic matter.

v. The abundance of the copepod *Cyclops abyssorum* that can feed raptorially upon prey such as rotifers has increased suggesting that stimulation of microbial components of the food web by allochthonous matter is being passed up the pelagic food web. This is supported by the high dietary reliance upon allochthonous organic matter determined for this species (34-48% annually).

vi. Chlorophyll a concentrations have failed to reach mean annual or annual maxima of the same magnitude as recorded in 1990. In view of increasing nutrient availability over the same period it is possible that light limitation caused by greater allochthonous loading has reduced the photic depth sufficiently to affect primary production. Alternatively stimulation of the zooplankton community by allochthonous carbon may in turn have increased the grazing pressure upon phytoplankton.

Whilst the high degree of organic matter loading to Lough Melvin may be beneficial in regard to trophic status, reductions to *in situ* photosynthetic production caused by greater loads could have

undesirable consequences. The lower nutritional quality of allochthonous organic matter relative to autochthonous organic matter means that it can support lower production per unit mass. Energy mobilisation for lake consumers will therefore decrease and the effects would be passed up food chains, potentially affecting species such as salmonids that have a high conservation importance.

The pelagic food web

Significant contributions of allochthonous organic carbon to lake food webs are most commonly reported from oligotrophic, humic lakes; lakes of higher trophic status typically rely more upon autochthonous production. However, polymictic, humic mesotrophic lakes that are also alkaline, such as Lough Melvin, can be considered as distinct lake types. The phytoplankton communities of these lakes are somewhat specialised and tend to be dominated by relatively large colonial and filamentous cyanobacteria and diatoms. Cyanobacteria, although more typical of eutrophic conditions, have a competitive advantage in such lakes for several reasons:

i. Many posses active transport mechanisms for bicarbonate (Badger *et al.,* 2002) and there is evidence that such mechanisms are more efficient in cyanobacteria compared with other algae (Raven, 1995)

ii. Many posses gas vacuoles conveying positive buoyancy allowing them to float into the illuminated surface waters and increase their light dose during periods of water column stability (Walsby *et al.,* 1997)

iii. The dominant colonial cyanobacteria in Lough Melvin are >50µm in diameter exceeding the effective grazing size of many herbivorous zooplankton (Burns, 1968).

iv. Some species, such as members of the genus *Planktothrix* (*Oscillatoria*) have very low light requirements enabling them to compete with diatoms and green algae in light limited conditions.

v. Many species produce toxins that have been shown to have adverse affects on the growth, reproduction, survival and filtration of zooplankton grazers (Rohrlack *et al.*, 1999a; Rohrlack *et al.,* 1999b). The toxin microcystin produced by species of *Microcystis* has been found to be poisonous to *Daphnia galeata* (Rohrlack *et al.,* 1999c).

Cyanobacteria, particularly *Woronichinia naegliana,* dominate the phytoplankton community of Lough Melvin for the vast majority of the year. In view of the large colonial size of this species, that potentially makes them inedible to zooplankton, the net phytoplankton biomass available for grazing may be more representative of oligotrophic situations thus increasing the relative importance of allochthonous sources of organic matter to the food web. Furthermore, a significant proportion of the phytoplankton biomass of these lakes consists of diatoms of the genus *Aulacoseira*, which are reported to be inedible to small zooplankton due to their long filamentous structure (Thompson *et al.,* 1982). Phytoplankton grazing resistance may therefore explain the high degree of reliance upon allochthonous carbon sources in Lough Melvin that is similar to that reported for other humic-stained oligotrophic lakes (Dysotrophic, Rodhe, 1969).

References

Aerts, R., Wallen, B. & Malmer, N. Growth limiting nutrients in Sphagnum-dominated bogs subject to low and high atmospheric nitrogen supply. J. Ecol 80: 131-140

Aiken, G.R., McKnight, D.M., Wershaw, R.L. & MacCarthy, P., 1985. Humic substances in soil, sediment and water- Geochemistry, Isolation and Characterisation. John Wiley & Sons, New York p.692

Aitkenhead-Peterson, J.A., Alexander, J.E. & Clair, T.A. 2004. Dissolved organic carbon and dissolved organic nitrogen export from forested watersheds in Nova Scotia: Identifying controlling factors. *Global Biogeochemical cycles.* 19: GB4016

Algesten, G., Sobek, S., Bergstrom, A., Agren, A., Tranvik, L.J. & Jansson, M. 2003. Role of lakes for organic carbon cycling in the boreal zone. *Global change Biology.* 10:141-147

Anderson, N.J., Patrick, S.T. & Appleby, P.G. 1996. Palaeolimnological surveys of Lough Erne and Lough Melvin (NI). Final report to the Department of the Environment (NI) Inter-reg programme. Environmental Change Research Centre. UCL.

Anderson, N.J. & Stedmon, C.A. 2007. The effect of evapoconcentration on dissolved organic carbon concentration and quality in lakes of SW Greenland. Freshwater Biology 52: 280-289

Azam, F., Fenchel, T., Field, J.G., Gray J.S., Meyer-Reil. L.A., Thingstad, F. 1983. The ecological role of water-column microbes in the sea. Marine Ecology-Progress Series 10: 257-263.

Badger, M.R., Hanson, D. & Price, G.D. 2002. Evolution and diversity of CO_2 concentrating mechanisms in cyanobacteria. Functional plant biology. 29(3) 161 – 173.

Bertilsson, S, & Tranvik, L.J., 1998. Photochemically produced carboxylic acids as substrates for freshwater bacterioplankton. Limnol. Oceanogr. 43(5): 885-895.

Billet, M.F., Garnett, M.H. & Harvey, F. 2007. UK peatland streams release old carbon dioxide to the atmosphere and young dissolved organic carbon to rivers. Geophysical research letters 34: L23401.

Birge, E.A. & C. Juday. 1927. The organic content of the water of small lakes. Proc. Amer. Phil. Soc. 666:357-372.

Bogdan, K.G. & Gilbert, J.J. 1982. Seasonal patterns of feeding by natural populations of Keratella, Polyartha and Bosmina, clearance rates, selectivites and contributions to community grazing. Limnol.Oceanogr., 27: 918-934.

Bouvy, M., Arfi, R., Guiral, D., Pagano, M. & Saint-Jean, L. 1994. Role of bacteria as food for zooplankton in a eutrophic tropical pond (Ivory Coast). Neth. J. Aquat. Ecol. 28: 167-174.

Brendelburger, H. & Jürgens, S. 1993, Suspension feeding in Bithynia tentaculata (Prosobranchia, Bithyniidae), as affected by body size, food and temperature Oecologia 94(1): 36-42.

Burns, C.W. 1968. Maximum particle size ingested by cladocera. Limnol Oceanogr, 13: 675-678.

Cabana, G. & Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Science U.S.A. 93: 10844-10847.

Carpenter, S.R., Cole, J.J., Pace, M.L., Van De Bogert, M., Bade, D., Bastiviken, D., Gille, C.M., Hodgson, J.R., Kitchell, J.F. & Kritzberg, E.S., 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from 13C addition to contrasting lakes. Ecology 86: 2737-2750.

Cole, J.J., Carpenter, S.R., Pace, M.L., Van de Bogert, M.C., Kitchell, J.L. & Hodgson, J.R. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecology Letters 9:558-568.

Cole, J.J., Carpenter, S.R., Kitchell, J.F. & Pace, M.L., 2002. Pathways of organic carbon utilisation in small lakes: results from a whole-lake 13C addition and a coupled model. Limnol. Oceanogr. 47: 1664-1675..

Cole, J.J. 1999. Aquatic microbiology for ecosystem scientists: new and recycled paradigms in ecological microbiology. Ecosystems 2: 215-225..

Dawson, J.J.C., Billett, M.F., Neal, C. & Hill, S. 2002. A comparison of particulate, dissolved and gaseous carbon in two contrasting upland streams in the UK. *Journal of Hydrology* 257: 226-246.

Del Giorgio, P.A., Cole, J.J. & Cimberlis, A. 1999. Respiration rates in bacteria exceed phytoplankton production in unproductive systems. Nature: 385: 148-151.

Demott, W.R. 1999. Foraging strategies and growth inhibition in 5 daphnids feeding on mixtures of a toxic cyanobacterium and a green alga. Freshwater biology 42 (2): 263-274.

DeNiro, M. J. & Epstein, S. 1977. Mechanism of carbon isotopic fractionation associated with lipid synthesis. Science 197: 261-263.

DeNiro, M. J. & Epstein, S. 1981. Influenece of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta. 45: 341-351.

Dick, T.A., Platvoet, D. & Kelly D.W. 2002. Predatory impact of the freshwater invader Dikerogammarus villosus (Crustacea: Amphipoda) Can.J. of Fish. and Aquat. Sci. 59: 1078-1084.

Driscoll, C. T., Baker, J.P., Bidogni, J.J. & C. L. Schofield. 1980. Effects of aluminum speciation on fish in dilute acidified waters. Nature 284: 161–164.

Edington, J.M. & Hildrew, A.G. 1995. A revised key to the caseless caddis larvae of the British Isles with notes on their ecology. Freshwater Biological Association. Scientific publication No. 53.

Edmonson, W. T. 1991. The uses of ecology: Lake Washington and beyond. Univ. Washington.

Edzwald, J. K., Becker, W.C. & Wattier, D.L. 1985. Surrogate parameters for monitoring organic matter and THM precursors. J. Am. Waterworks Assoc. 77: 122–132.

Engstrom, D.R., 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Can J. Fish. Aquat. Sci. 44: 1306-1314.

Epp, G.T. 1996. Grazing on Filamentous Cyanobacteria by Daphnia pulicaria. Limnol. Oceanogr, 41(3): 560-567.

Evans, C.D., Chapman, P.J., Clark, J.M., Montieth, D.T. and Cressers, M.S. 2006. Alternative explanations for rising dissolved organic carbon export from organic soils. Global Change Bioloogy 12: 2044-2053.

Fee, E.J., Hecky, R.E., Kasian, S.E.M.& Cruickshank, D.R., 1996. Effects of lake size, water clarity and climatic variability on mixing depths in Canadian shield lakes. Limnol. Oceanogr. 41: 912-920.

Ferguson, A. 1985. Lough Melvin- A unique fish community. Went Memorial Lecture.

Fink, P. & von Elert, E. 2006. Food quality of algae and cyanobacteria for the freshwater gastropod Bithynia tentaculata: the role of polyunsaturated fatty acids. Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie 29 (3): 1235-1240.

France, R. L. 1995a. Carbon-13 enrichment in benthic compared to planktonic algae: Food web implications. Mar. Ecol. Prog. Ser. 124: 307–312.

Freeman, C., Fenner, N., Ostle, N.J., Kang, H., Dowrick, D.J., Reynolds, B., Lock, M.A., Sleep, D., Hughes, S. & Hudson, J., 2004. Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. Nature 430: 195-198.

Frieberg, N. & Jacobson, D. 1994. Feeding plasticity of two detritivore-shredders. Freshwater Biology 32: 133.

Friday, L.E. 1988. A key to the adults of British Water Beetles. Field Studies Council. Field studies 7: 1-151.

Fry, B., Baltz, D.M., Benfield, C., Fleefer, J.W., Gace, A., Haas, H.L. & Quinones-Riviera, Z.J. 2003. Stable isotope indicators of movement and residency for brown shrimp (Farfantepenaes aztecus) in coastal Louisiana marshscapes. Estuaries 26: 82-97.

Gorham, E., 1991. Northern peatlands; role in the carbon cycle and probable responses to climatic warming. Ecol. App. 1: 182-195.

Graneli, W., Lindell, M.J., Tranvik, L.J., 1996. Photo-oxidative production of dissolved inorganic carbon in lakes of different humic content. Limnol. Oceanogr. 41(4): 698-706.

Grey, J., Jones, R.I. & Sleep, D. 2000. Stable isotope analysis of the origins of zooplankton carbon in lakes of differing trophic state. Oecologia 123: 232-240.

Grey, J., Jones, R.I. & Sleep, D. 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. Limnol. Oceanogr. 46: 505-513.

Gulati, R.D., Bronkhorst, M. & Van Donk, E. 2001. Feeding in Daphnia galeata on Oscillatoria limnetica and on Detritus Derived from It. Journal of Plankton Research 23 (7): 705-718.

Guo, L. & Macdonald, R.W. 2006. Source and transport of terriginous organic matter in the upper Yukon River: Evidence from isotope ($\delta^{13}C$, $\Delta^{14}C$ and $\delta^{15}N$) composition of dissolved, colloidal and particulate phases. Global Biogeochemical Cycles 20: GB2011.

Hansen, B., Bjornsen, P.K. & Hansen, P.J. 1994. The size ratio between planktonic predators and their prey. Limnol. Oceanogr. 39(2): 395-403.

Harding, J.P. & Smith, W.A. 1974. A key to the British Freshwater Cyclopoid and Calanoid Copepods. Freshwater Biological Association. Scientific Publication No. 18.

Haslam, S., Sinker, C. & Wolesley, P. 1975. British Plants. Field Studies Council. Field Studies 4 243-351.

Hecky, R.E. & Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. J. N. Am. Benthol. Soc. 14: 631-653.

Hessen, D.O., Andersen, T. & Lyche, A. 1990. Carbon metabolism in a humic lake: pool sizes and cycling through zooplankton. *Limnol. Oceanogr.* 35: 84-99.

Hope, D., Billett, M.F. & Cresser, M.S. 1997. Exports of organic carbon in two river systems in NE Scotland. *Journal of Hydrology* 193: 61-82.

Huber-Pestalozzi, G. (1975). Das Phytoplankton des Süsswassers. 2. Teil, 2. Hälfte, Diatomeen. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart 1942.

Hynes, H.B.N., Macan, T.T., Williams, D.M. 1960. A key to the British species of Crustacea: Malacostraca occurring in fresh water with notes on their ecology and distribution. Freshwater Biological Association. Scientific Publication No. 19.

Hynes, H.B.N. 1977. Adults and Nymphs of British Stoneflies (Plecoptera). Freshwater Biological Association. Scientific publication No. 17.

IPCC 2001. The third assessment report of the intergovernmental panel on climate change (IPCC): Climate change 2001. Cambridge University Press.

Iversen T.M. (1974) Ingestion and growth in Sericostoma personatum (Trichoptera) in relation to nitrogen content of ingested leaves. Oikos 25: 278-282.

Jackson, T.A. & Hecky, R.E., 1980. Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone. Can. J. Fish. Aquat. Sci. 37: 2300-2317.

Jansson, M., Bergstrom, A.-K., Blomqvist, P. & Drakare, S. 2000. Allochthonous organic carbon and phytoplankton/bacterioplankton relationships production relationships in lakes. Ecology 81: 3250-3255.

Jansson, M,. Karlsson, J. & Blomqvist, P. 2003. Allochthonous organic carbon decreases pelagic energy mobilisation in lakes. Limnol. Oceanogr. 48(4): 1711-1716.

Jenkinson, D.S., Adams, D.E. 7 Wild, A., 1991. Model estimates of CO_2 emissions from soil in response to global warming. Nature 351: 304-306.

Jewson, D.H. & Taylor, J.A. 1978. The influence of turbidity on net phytoplankton photosynthesis in some Irish lakes. Freshwater Biology 8: 573-584.

John, D.M., Whitton, B., Brook, A.J. (eds). 2002. The freshwater algal flora of the British Isles. Cambridge University Press.

Jones, R. I., 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229:73-91.

Kankaala, P. 1988. The relative importance of algae and bacteria as food for Daphnia longispina (Cladocera) in a polyhumic lake. Freshwater Biology. 19: 285-296.

Karlsson, J. Jonsson, A. Meili, M. Jansson, M. 2003. Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. Limnol. Oceanogr. 48(1): 269-276.

Karlsson, J. Lymer, D. Vrede, K. Jansson, M. 2007. Differences in efficiency of carbon transfer from dissolved organic carbon to two zooplankton groups: an enclosure experiment in an oligotrophic lake. Aquat. Sci. 69: 108-114.

Kennedy, J., Billet, M.F., Duthie, D. Fraser, A.R., Harrison, A.F. 1996. Organic matter retentionin an upland humic podzol; the effects of pH and solute type. European Journal of Soil Science 47: 615-625.

Kerner, M. 2003. Self organisation of dissolved organic matter to micelle-like microparticles in river water. Nature 422: 150-154.

Kling, G.W., Kipphut, G.W. & Miller, M.M. 1992. The flux of CO_2 and CH_4 from lakes and rivers in arctic Alaska. Hydrobiologia, 240: 23-36.

Knulst, J. C. C. 1992. Effects of pH and humus on the availability of 2,29,4,495,59 hexachlorobiphenyl-^{14}C in lake water. Environ. Toxicol. Chem. 11: 1209–1216.

Kritzberg, E. S., Cole, J.J., Pace, M.L., Graneli, W. & Bade, D. 2004. Autochthonous versus allochthonous carbon sources for bacteria: Results from whole-lake 13C addition experiments. Limnol. Oceanogr. 49 (2): 588-596.

Kritzberg, E.S., Cole, J.J., Pace, M.L. Graneli, W., 2005. Does autochthonous primary production drive variability in bacterial metabolism and growth efficiency in lakes dominated by terrestrial C inputs? Aquatic Microbial Ecology, 38: 103-111.

Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A. & Lutcavage, M.E. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of lipd extraction and modelling methods. J. Animal Ecol. 10.1111/j.1365-2665.2008.01394x.

Macan, T.T. 1960. A key to the British fresh and brackish water Gastropods. Freshwater Biological Association. Scientific publication No. 13.

Macan, T.T., 1979. A key to the nymphs of the British Species of Ephemeroptera with notes on their ecology. Freshwater Biological Association. Scientific publication No. 50.

Maguire, C.M. & Grey, J. 2006. Determination of zooplankton dietary shift following a zebra mussel invasion as indicated by stable isotope anlaysis. Freshwater biology. 51 (7), 1310–1319.

McCauley, E., Downing, J.A. & Watson, S. 1989. Sigmoid relationships between nutrients and chlorophyll among lakes. Can. J. Fish. Aquat. Sci. 46: 1171–1175.

Meili, M. 1992. Sources, concentrations and characteristics of organic matter in softwater lakes and streams of the Swedish forest region. Hydrobiologia 229: 23-41.

Meili, M., Fry, B. & Kling, G.W. 1993. Fractionation of stable isotopes (^{13}C, ^{15}N) in the food web of a humic lake. Verh. Int. Ver. Limnol. 25: 501–505.

Meili, M., Fry, B. & Kling, G.W., Bell, R.T. & Ahlgren, I. 1996. Sources and partitioning of organic matter in a pelagic microbial food web inferred from the isotopic composition (d13C and 15N) of zooplankton species. Arch. Hydrobiol. Spec. Issues Adv. Limnol. 48: 53–61.

Mitchener, R.H. & Schell, D.M. 1994. Stable isotope ratios as tracers in marine aquatic food webs pp. 138-157. In Lajtha, K & Michener, R.H. (eds) Stable isotopes in ecology and environmental science. Blackwell.

Moore, J.W. 1975. The Role of algae in the diet of Asellus aquaticus L. and Gammarus pulex L.. Journal of Animal Ecology 44 (3): 719-730.

Moran, M.A. & Hodson, R.E.1990. Bacterial production on humic and non humic components of dissolved organic carbon. Limnol Oceanogr. 35:1744-1756

Murphy, J.S. & Giller, P.S., 2000. Seasonal dynamics of macro-invertebrate assemblages in the benthos and associated with detritus packs in two low order streams with different riparian vegetation. Freshwater biology 43: 617-631.

Nauman, E. 1919. Nagra synpunkter angaende limnoplanktons okologi med sarskild hansyn till fytoplankton. Svensk Bot. Tidskr. 13:129-163. (English translat. By the Freshwater Biological Association, no. 49).

Odum, H. T. 1956. Primary production in flowing waters. Limnol Oceanogr 1:112-117.

Olsen, Y. 1999. Lipids and essential fatty acids in aquatic food webs: What can freshwater ecologists learn from mariculture? P. 161-2-2. In Arts, M.T. & Wainman, B.C. (Eds.), Lipids in Freshwater Ecosystems. Springer-Verlag.

Ooms-Wilhms, A.L., Postema, G. & Gulati, R.D. 1993. Clearance rates of bacteria by the rotifer Filinia longiseta (Ehrb.) measured using three tracers. Hydrobiologia,255: 255-260.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitc2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427: 240-243.

Pace, M.L., Carpenter, S.R., Cole, J.J., Coloso, J.J., Kitchell, J.F., Middelburg, J.J., Preston, N.D., Solomon, C.T. & Weidel, B.C. 2007. Does terrestrial organic carbon subsidise the planktonic food web in a clear-water lake. Limnol. Oceanogr. 52(5): 2177-2189.

Pomeroy, L.R. 1974. The oceans food web, a changing paradigm. Bioscience 499-504.

Pontin, R. M. 1978. A key to the British Freshwater Planktonic Rotifera. Freshwater biological Association. Scientific Publication No. 38.

Porter, K.G. 1984. Natural bacteria as food resources for zooplankton. In Klug, M.J. & Reddy, C.A. (Eds.), Current Perspectives in Microbial Ecology. Washington, pp. 340-345.

Prakash, A., Rashid, M.A., Jensen, A. Subba Rao, D.V., 1973. Influence of humic substances on the growth of marine phytoplankton: diatoms. Limnol. Oceanogr. 18: 516-524.

Pulido-Villena, E., Reche, I. & Morales-Baquero, R. 2005. Food web reliance on allochthonous carbon in two high mountain lakes with contrasting catchments: a stable isotope approach. Can J. Aquat. Sci., 62: 2640-2648.

Raven J. A. 1995. Photosynthetic and non-photosynthetic roles of carbonic anhydrase in algae and cyanobacteria. Phycologia. 34: 93–101.

Reckhow, D. A. & Singer, P.C. 1990. Chlorination by-products in drinking waters: From formation potentials to finished water concentrations. J. Am. Waterworks Assoc. 82: 173-180.

Reckhow, D. A. & Malcolm, R.A. 1990. Chlorination of humic materials: By-product formation and chemical interpretations. Environ. Sci. Technol. 24: 1655-1664.

Roditi, H.A., Fisher, N.S. & Sanudo-Wilhelmy, S.A. 2000. Uptake of dissolved organic carbon and trace elements by zebra mussel. Nature 407: 78-80.

Rohrlack, T., Dittmann, E., Henning, M.,Börner, T. & Kohl J. 1999a. Role of Microcystins in Poisoning and Food Ingestion Inhibition of Daphnia galeata Caused by the Cyanobacterium Microcystis aeruginosa. Applied and Environmental Microbiology, 65(2): 737-739.

Rohrlack, T., Henning, M. & Kohl, J. 1999b. Mechanisms of the inhibitory effect of the cyanobacterium Microcystis aeruginosa on Daphnia galeata's ingestion rate. J. Plank. Res, 21: 1489-1500

Rohrlack, T., Henning, M. & Kohl, J. 1999c. Does the toxic effect of Microcystis aeruginosa on Daphnia galeata depend on microcystin ingestion rate? Arch. Hydrobiol,146,(4): 385-395.

Salonen, K. & Hammer, T. 1986. On the importance of dissolved organic matter in the nutrition of zooplankton in somelake waters. Oecologia 68: 246–253.

Savage, A.A. 1989. Adults of the British aquatic Hemiptera Heteroptera: a key with ecological notes. Freshwater Biological Association. Scientific Publication No. 50.

Scavia, D. and Laird, G.A. 1987. Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. Limnol. Oceanogr.32, 1017–1033.

Sherr, E. & Sherr, B. 1988. Role of Microbes in Pelagic Food Webs: A Revised Concept Limnol. Oceanogr.33 (5): 1225–1227.

Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes: Implications for lake management. Science 184: 897–899.

Schram, M.D. & Schmitz, E.H. 1983. Correlation of total organic carbon and dry weight data as indices of freshwater zooplankton biomass. Hydrobiologia 106(3): 283-284.

SNV, 1986. Monitor 1986 (ed. C. Bernes): Sura och forstsurade vatten (Acidic and acidified waters in Sweden). Swedish National Environmental Protection Board, Solna. Pp. 180.

Scourfield, D.J. & Harding, J.P. 1966. A key to the British Freshwater Cladocera. Freshwater Biological Association. Scientific publication No. 5.

Starkweather, P.L. 1980. Aspects of feeding behaviour and trophic ecology of suspension feeding. Hydrobiologia, 73: 63-72.

Steinberg, C.E.W, Kamara, S., Prokhotskaya, V.Y., ‡Manusadzˇ Ianas, L., Karasyova, T.A., Timofeyev, M.A., Jie, Z., Paul, A., Meinelt, T., Farjalla, V.F., Matsuo, A.Y.O., Burnison, B.K.O & Menzel, R.A. 2006. Dissolved humic substances – ecological driving forces from the individual to the ecosystem level. Freshwater Biology, 51: 1189-1210.

Stevens, R.J. & Stewart, B.M., 1982. Concentration, fractionation and characterisation of soluble organic phosphorus in river water entering Lough Neagh. Wat. Res. 16: 1507-1519

Stedmon, C. A., & Markager, S., 2001. The optics of chromophoric dissolved organic matter (CDOM) in the Greenland sea: an algorithim for differentiation between marine and terrestrially derived organic matter. Limnol. & Oceanogr. 46: 2087-2093.

Stewart, A.J. & Wetzel, R.G., 1982. Influence of dissolved humic materials on carbon assimilation and alkaline phosphatase activity in natural algal-bacterial assemblages. Freshwater Biol. 12: 369-380.

Strayer, D. & Likens, G.E. 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology 67(2): 303-312.

Syväranta, J. Hämäläinen, H. & Jones, R.I. 2006. Within-lake variability in carbon and nitrogen stable isotope signatures. Freshwater Biology 51: 1090-1102.

Tranvik, L. 1992. Allochthonous dissolved organic matter as an energy source for pelagic bacteria and the concept of the microbial loop. Hydrobiologia 229: 107-114.

Tranvik, L., 1988. Availability of dissolved organic carbon for planktonic bacteria in oligotrophic lakes of differing humic content. Microb Ecol 16:311-322.

Vander Zanden, M. J. & Rasmussen, J. 2001. Variation in d15N and d13C trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. 46: 2061–2066.

Vander Zanden, M. J. & Vadeboncoeur, Y. 2002. Fish as integrators of benthic and pelagic food webs in lakes. Ecology 83(8): 2152-2161.

Vannote, R.L., Minshall, G. W., Cummins, K. W. Sedell, J.R. & Cushing, E.G. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

Vollenweider, R. A. 1968. Water management research. OECD. Paris. DAS/CSI/68.27. National Academy of Sciences. 1969. Eutrophication: Causes, consequences, correctives. Natl. Acad. Sci.

Vuorio, K., Meili, M. & Sarvala, J. 2006. Taxon-specific variation in the stable isotopic signatures of lake phytoplankton. Freshwater Biology. 51: 807-822.

Wall, D. & Briand, F., 1979. Response of lake phytoplankton communities to in situ manipulations of light intensity and colour. J. Plankton Res.1: 103-112.

Wallace, I.D., Wallace, B. & Philipson, G.N. 203. Keys to the case bearing caddis larvae of Britain and Ireland. Freshwater Biological Association. Scientific publication No. 61.

Walling, D.E. & Webb, B.W., 1985. Estimating the discharge of contaminants to coastal waters by rivers: some cautionary comments. Mar. Pollut. Bull., 16:488-492.

Walsby, A.E., Hayes, P.K., Boje, R. &. Stal, L. J. 1997. The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. New Phytologist 136 (3): 407–417.

Welch, I.M., Barrett, P.R.F., Gibson, M.T. & Ridge, I. 1990. Barley straw as an inhibitor of algal growth: studies in the Chesterfield canal. Journal of Applied Phycology, 2: 231-239.

Welsh, P. G., 1993. Effect of pH and dissolved organic carbon on the toxicity of copper to larval fathead minnow (Pimephales promelas) in natural lake waters of low alkalinity. Can. J. Fish. Aquat. Sci. 50: 1356–1362.

Wetzel, R.G., 2001. Limnology. Lake and river ecosystems. 3rd Edition. Academic press. P. 734.

Williamson, C.E., Morris, D.P, Pace, M.L. & Olson, O.G., 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. Limnol. Oceanogr. 44: 795-803.

Wilson, R.S. & Ruse, L.P. 2005. A guyide to the identification of genera of chironomidae pupal exuviae in Britain and Ireland. Freshwater Biological Association. Special publication NO. 13.

Work, K., Havens, K., Sharfstein, B. & East, T. 2005. How important is bacterial carbon to planktonic grazers in a turbid, subtropical lake? J. Plank. Res. 27(4): 357-372.

Worrall, F., Burt, T. & Shedden, L., 2003 Long term records of riverine dissolved organic matter. Biogeochemistry 64: 165-178.

Worrall, F., Harriman, R., Evans, C.D., Watts, C., Adamson, J., Neal, C., Tipping, E., Burt, T., Grieve, I., Monteith, D., Naden, P., Nisbet, T., Reynolds, B. & Stevens, P. 2004. Trends in dissolved organic carbon in UK rivers and lakes. Biogeochemistry 70, 369-402.

Wiederholm, T. 1983. Chironomidae of the Holarctic region : keys and diagnoses. Pt.1. Entomologica scandinavica. no.19 Motala : Borgströms Tryckeri.