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Dual-fuels: intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish

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Running headline: Seasonal resource use of subarctic whitefish

Summary

1. Ecological systems are often characterised as stable entities. However, basal productivity in most ecosystems varies between seasons, particularly in subarctic and polar areas, but how this variability affects higher trophic levels or entire food webs remains largely unknown, especially in high latitude regions.

2. We undertook a year-long study of benthic (macroinvertebrate) and pelagic (zooplankton) resource availability, along with short- (day/days: stomach content), medium- (month: liver $\delta^{13}C$ and $\delta^{15}N$ isotopes) and long-term (season: muscle $\delta^{13}C$ and $\delta^{15}N$ isotopes) assessments of resource use by a generalist fish, the European whitefish. in a deep, oligotrophic, subarctic lake in northern Europe. Due to the long ice-covered winter period, we expected to find general benthic reliance throughout the year, but also a seasonal importance of zooplankton to the diet, somatic growth and gonadal development of whitefish.

3. Benthic and pelagic resource availability varied between seasons: peak littoral benthic macroinvertebrate density occurred in mid-winter, whereas maximum zooplankton density was observed in summer. Whitefish stomach content revealed a reliance on benthic prey items during winter and pelagic prey in summer. A seasonal shift from benthic to pelagic prey was evident in liver isotope ratios, but muscle isotope ratios indicated a year-round reliance on benthic macroinvertebrates. Whitefish activity levels as well as somatic and gonadal growth all peaked during the summer, coinciding with the zooplankton peak and the warmest water temperature.

4. Stable isotopes of muscle consistently depicted the most important resource, benthic macroinvertebrates, whereas short-term indicators, i.e. diet and stable isotopes of liver, revealed the seasonal significance of pelagic zooplankton for somatic growth and gonad development. Seasonal variability in resource availability strongly influences consumer growth and reproduction and may also be important in other ecosystems facing pronounced annual weather fluctuations.

Keywords benthic macroinvertebrates; C:N ratio; *Coregonus lavaretus*; $\delta^{13}C$; $\delta^{15}N$; diet; multiple tissues; subarctic; trophic subsidies; zooplankton

Introduction

Seasonal variation in the abundance of basal resources has a profound effect on ecosystems and ecosystem function. In arid regions, seasonal variation in precipitation regulates whole terrestrial ecosystems (Reynolds *et al.* 2004). In freshwater habitats, seasonal variation in precipitation, temperature and light drives production pathways which, in temperate regions, typically peak during summer. Such temporal fluctuations in prey availability determines the diet and trophic activity of consumers encompassing a full range of diversity from sharks (Matich & Heithaus 2014) to terrestrial mammals (Ben-David, Flynn & Schell 1997). Consequently, when assessing the ecology of an organism or the trophic interactions within an ecosystem it is important to consider the effects of seasonal variation in resources. However, the majority of studies addressing ecological questions do so under comparatively controlled conditions, either by regulating the environment in an experiment or conducting field studies of a limited duration (Carmel *et al.* 2013). Such approaches fail to address the underlying variability inherent in almost all ecosystems. Here, we outline how seasonal variability in environmental conditions, principally light and temperature, alter the relative abundance of pelagic and benthic dwelling invertebrate species within a subarctic lake, ultimately effecting the trophic ecology and development of the principal generalist consumer.

Lake ecosystems are predominantly fuelled by either pelagic (e.g. phytoplankton) or benthic (e.g. periphytic algae) basal productivity. The relative level of pelagic and benthic production is typically associated with limnological factors such as nutrient load, water colour and pelagic volume (Vadeboncoeur *et al.* 2008). Mobile consumers feeding at the next trophic level, such as fish, can act as specialists feeding exclusively on either pathway or as generalists, integrating both (Vander Zanden & Vadeboncoeur 2002). As such, factors which govern the basal productivity levels in lakes are likely to have an effect on higher trophic levels. In subarctic regions, the majority of lakes are oligotrophic and ice covered for 6 - 8 months per year, limiting peak phytoplankton productivity to a brief summer period (de Senerpont Domis *et al.* 2013), hence benthic productivity is often dominant (Vadeboncoeur *et al.* 2003). However, zooplankton communities, predominantly consumers of pelagic phytoplankton, in these regions typically display a population boom during the late summer (de Senerpont Domis *et al.* 2013), providing an additional resource for generalist fishes.

An additional level of complexity is added by the contribution of dead phytoplankton and other pelagic detritus in the diet of benthic invertebrates (Jónasson 2004). This is particularly true in the profundal zone of deep lakes where light levels are too low to stimulate benthic algal production. As such, profundal invertebrate communities are largely powered by pelagic derived energy, but consumed by benthic feeding fish. In the current study, we are primarily concerned with the feeding activities of fish. As such we divide their potential prey items into three categories (pelagic, littoral and profundal) based on their location within the lake rather than the primary resources from which they are derived.

Research detailing seasonal variation in fish diet is predominantly limited to temperate lakes, and thus may not be representative of subarctic regions (but see Amundsen & Knudsen 2009; Eloranta *et al.* 2013). Traditional netting approaches are impossible when lakes are ice covered and, as such, seasonal sampling requires specific under-ice techniques (see Materials and Methods). As the majority of studies in subarctic lakes have been conducted during the ice-free summer season and do not include any assessment of putative prey resources, they may not adequately reflect the relative importance of pelagic and benthic resources to fishes through the year. The European whitefish *Coregonus lavaretus* L. (hereafter whitefish) is the most abundant fish species in European subarctic lakes. Previous studies of whitefish, conducted during ice-free summer periods have revealed a generalist foraging strategy, including both benthic macroinvertebrates and zooplankton (Hayden *et al.* 2013). Year-round studies of whitefish in subarctic lakes, are based solely on stomach content data, and as such provide a snapshot of an individual fish's diet rather than a conclusive time-integrated analysis (Tolonen 1998; Hayden, Harrod & Kahilainen 2013).

Stable isotope ratios provide an opportunity to develop such a time-integrated assessment of diet as isotope values of a particular tissue reflect that of the fish's diet while that tissue was being metabolised (West *et al.* 2006). Body tissues vary in terms of their metabolic activity, their turnover and their isotopic half-life (Tieszen *et al.* 1983), therefore isotope values from different tissues can be used to characterise diet over different time scales (Boecklen *et al.* 2011). It is difficult to precisely estimate the isotopic turn-over time of a specific tissue in any population, however, in studies which standardise for species and life stage, the turn over time of liver is typically faster than muscle (Logan *et al.* 2006). In rainbow trout *Oncorhynchus mykiss* Walbaum liver tissue represents the organism's diet over the preceding 3-4 weeks (Heady & Moore 2013). In broad whitefish *Coregonus nasus* Pallas muscle tissue reflects seasonal diet, i.e. 3-6 months (Hesslein, Hallard & Ramlal 1993), it should be noted that in this study no variation was observed in the turn-over rate of liver and muscle, most likely due to very slow somatic growth obscuring any difference between tissues.

To determine the relative contribution of pelagic and benthic derived energy to the annual diet and assimilation of tissues of whitefish, we studied seasonal variation in benthic and pelagic resource availability, along with short- (stomach content), medium- (liver δ^{13}C and δ^{15}N isotope values) and long-term (muscle δ^{13}C and δ^{15}N isotope values) indicators of whitefish diet in a large, deep and oligotrophic lake in Finnish Lapland. We investigated three principal hypotheses: 1.) In light of previous studies of invertebrate populations in the region (Rautio, Sorvari & Korhola 2000), we suggested that zooplankton density would peak in late summer while benthic macroinvertebrate (BMI) density would remain comparatively stable throughout the year. 2.) Based on a previous seasonal study of Arctic charr *Salvelinus alpinus* L. we expected that an indicator of long term whitefish resource use (stable isotopes of muscle) would indicate an overall annual reliance on benthic prey (Eloranta, Kahilainen & Jones 2010). We predicted that the generalist diet of whitefish, reflects the opportunistic utilisation of pelagic prey during summer, and thus is most evident in short (stomach content) and medium (stable isotopes of liver) term measures of resource use. 3.) Finally, that despite its limited temporal duration, the peak summer abundance of zooplankton plays a fundamental role supporting growth and reproduction in whitefish, as it coincides with the maximum increase in feeding activity, condition, gonad and somatic mass.

Materials and methods

FIELD STUDY

Sampling was conducted Lake Kilpisjärvi (N 69° 03', E 20° 49'; hereafter L. Kilpis) on six occasions between December 2011 and September 2012 (Table 1). L. Kilpis is a large (37 km^2), deep (max. depth 57, mean depth 19.4 m), clear water (colour 8 Pt L^{-1}, TOC 2.8 mg L^{-1}, turbidity <0.01 NTU), oligotrophic lake situated 473 meters above sea level. The lake is located below the treeline and its catchment area consists of birch forest and tundra. The fish fauna is dominated by whitefish (Table 1) but also includes Arctic charr, brown trout *Salmo trutta* L., grayling *Thymallus thymallus* L., pike *Esox lucius* L., burbot *Lota lota* L., alpine bullhead *Cottus poecilopus* Heckel and minnow *Phoxinus phoxinus* L. (Kahilainen *et al.* 2007). On each sampling occasion, light attenuation levels were measured using a LI-COR LI-250A Light Meter (LI-COR Biosciences, Nebraska, USA) at 1 m intervals from the surface to a max depth of 20 m. During the ice covered period, the light meter was lowered though a drilled hole which was subsequently filled with crushed ice and light measurements were recorded below solid ice using an iron frame. Water temperature and dissolved oxygen levels (%) were measured along the same gradient using a YSI Professional Plus meter (YSI Inc., Ohio, USA). On each occasion, three replicate samples of zooplankton were collected using a zooplankton net (50 µm mesh size, 25 cm diameter) hauled vertically through the water column from a depth of 20 m. Samples were stored in a 5 % formalin solution. Additional composite zooplankton samples, three replicates where possible, were collected on each occasion for stable isotope analysis (SIA). Littoral (1 m) and profundal (20 m) BMI communities were sampled using an Ekman grab (sampling area 272 cm^2). On each occasion, three replicate samples were taken at each depth. Fish were sampled using benthic gill net series, set at depths between 2 and 16 m. Each gill net series consisted of seven, 1.8 × 30 m panels (knot-to-knot mesh sizes: 12, 15, 20, 25, 30, 35 and 45 mm) and a 1.5 × 30 m Nordic multi-mesh net (12 equidistant 2.5 m panels with knot-to-knot mesh sizes ranging between 5 and 55 mm). Nets were collected after approximately 10-12 hours during the open water period (June – September) and 24-48 hours during the ice covered (December – May) period. Total length (± mm) and blotted wet mass (± 0.1 g) of all fish was recorded and individually coded whitefish were frozen (-20 °C) for later stomach content and stable isotope analysis. The number of fish caught $hour^{-1}$ net $series^{-1}$ (catch per unit effort, CPUE) was calculated for each sampling event and interpreted as a crude proxy for fish activity.

LABORATORY ANALYSIS

Zooplankton and BMIs were identified to family level. The density of each zooplankton (n l^{-1}) and BMI (n m^{-2}) family was estimated from the number of individuals recorded in each vertical tow and Ekman grab sample respectively. The composite zooplankton sample and a subsample of profundal and littoral BMI families (n = 3 – 10) were frozen for stable isotope analysis.

Both sagittal otoliths were collected from whitefish for age determination. Gonads were dissected and weighed (± 0.001 g). Whitefish stomachs were dissected and individual stomach fullness was measured on a scale of 0 – 10, where 0 reflects an empty stomach and 10 represents a fully extended stomach. Stomach contents were identified to family level and the relative volumetric proportion of each family to stomach fullness was visually estimated using the points method (Swynnerton & Worthington 1940). The proportion of benthic (BMI) and pelagic (zooplankton, chironomid pupae and terrestrial adult insects) prey consumed was estimated for each fish. In addition, *Diphyllobothrium* spp. tapeworm cysts in stomach wall were counted using a binocular microscope, in order to estimate the long-term consumption of pelagic prey (Kahilainen *et al.* 2011). As the density of parasites accumulates over time, we only present the data for the most abundant year class (2003). Muscle and liver tissue were dissected from a representative subset (n = 40 when possible) of each whitefish sample and freeze dried (48 hours at -75°C). Fish and invertebrate tissue samples were then ground to a fine powder and a subsample (0.5 ± 0. 1 mg) was encapsulated in aluminium foil cups for analysis. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope values were determined using a FlashEA 1112 elemental analyser attached to a Thermo Finnigan Delta^{PLUS} Advantage mass spectrometer, located at the University of Jyväskylä. Isotope values are presented relative to international standards PeeDee Belemite (for carbon) and atmosphereic nitrogen (for nitrogen). Analytical error (SD) for δ^{13}C and δ^{15}N was estimated at 0.1 ‰ from the repeated analysis of internal standards.

DATA ANALYSIS

Temporal variation in whitefish activity level (mean CPUE), and the density of zooplankton and BMIs between consecutive samples was assessed using Welch's t-test. PERMANOVA, a non-parametric, probability based analogue of analysis of variance (McArdle & Anderson 2001), was employed to test for seasonal variation in zooplankton and BMI community structure. A Bray-Curtis similarity index was created from untransformed abundance values of both datasets. A single factor PERMANOVA (sample month; 6 levels; fixed) was performed on the zooplankton matrix. A second factor (Habitat; profundal/littoral; fixed) was added when analysing the BMI dataset.

Four independent metrics were used to assess temporal variation in growth and condition of whitefish; mass at age of the dominant year class, whitefish age was determined from burnt and cracked otoliths and mass-at-age was calculated for each fish (Bagenal & Tesch 1978). Fulton's condition factor (*k*), derived as:

$$k = \left(\frac{M}{TL^3}\right) \times 100$$

where *M* is blotted wet mass (g) and *TL* is total fish length (cm), was calculated for each sample of whitefish (Froese 2006). The gonadosmatic index (GSI) of each mature whitefish was calculated as:

$$GSI = \left(\frac{GM}{SM}\right) \times 100$$

where *GM* is gonad mass (g) and *SM* is somatic mass (g) i.e. total mass excluding gonad mass. (Bagenal & Tesch 1978). Finally, the ratio of elemental carbon and nitrogen (C:N ratio) from whitefish liver and muscle tissue, a useful proxy for lipid content (DeNiro & Epstein 1977), was determined. Lipid is rich in carbon but contains no nitrogen; pure protein has a C:N ratio approximately equal to 3, therefore C:N values above 3 indicate lipid reserves within the sampled tissue. Temporal variation in each of these indices was assessed using a Welch t-test to compare mean values between consecutive samples. Due to limited sample sizes, mass-at-age values were restricted to the dominant 2003 year class, while analysis of condition, GSI and C:N ratios were limited to mature specimens (>25 cm).

The relationship between whitefish diet and resource availability was assessed using short (stomach content), medium (liver isotope values) and long-term (muscle isotope values) characterisations of resource use. A Bray-Curtis similarity index was created from untransformed stomach content data. A single factor PERMANOVA (Month; 6 levels; fixed) was performed on the data to test for temporal variation in whitefish diet. Dietary niche width was determined using the Levins index (Levins 1968). Variation in niche width between seasons was tested by a multiple comparison Welch t-test.

Due to the accumulation of ^{13}C in lipids, $\delta^{13}C$ values of fish tissue were arithmetically corrected prior to analysis using the arithmetic correction model of Kiljunen *et al.* (2006), which is partly based on subarctic whitefish samples. In the absence of a pre-existing model for whitefish liver tissue, these were corrected using the specific fish liver tissue model of Logan *et al.* (2008). Single factor PERMANOVA (Month; 6 levels; fixed) was performed on a Euclidean distance matrix of untransformed whitefish $\delta^{13}C$ and $\delta^{15}N$ values to test for seasonal variation in both isotope ratios. Separate analyses were performed for isotope values of liver and muscle tissues. The stable isotope analysis in R (SIAR) Bayesian mixing model was used to determine medium and long term resource use of whitefish (Parnell *et al.* 2010). A likelihood test, implemented in SIAR, was used to test for a significant shift in pelagic resource use between samples. The annual mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of littoral and profundal BMIs and zooplankton were used to define the littoral, profundal and pelagic isotopic baselines respectively (Post 2002). Mean ± SD trophic fractionation values $\Delta^{13}C = 1.3 \pm 0.3$ for and $\Delta^{15}N = 2.9 \pm 0.3$ for, derived from McCutchon *et al.* (2003) were used in the mixing model. When insect pupae were observed in fish stomachs, they were considered as evidence for foraging on pelagic prey. Pupae were not obtained in sufficient numbers during our sampling of putative prey to be included in the isotope analysis. Temporal variation in the isotopic niche width of whitefish across medium (liver) and long-term (muscle) periods was derived from small sample size corrected standard ellipses (SEA_c) of the $\delta^{13}C$ and $\delta^{15}N$ values of each sample (Jackson *et al.* 2011). PERMANOVAs were performed using PAST ver. 2.17c (Hammer, Harper & Ryan 2001). SIAR and SIBER analyses and Welch t-tests were performed in R (R Development Core Team 2012).

Results

PHYSICAL ENVIRONMENT

During the study period, L. Kilpis was ice covered between early December 2011 and mid June 2012 (Table 1). During the polar night (late November – mid January), the light compensation depth was zero. The compensation depth increased to 2 m in February, despite the presence of snow on the ice. In May, after snow melt but before ice break-up, compensation depth increased to 9 m. During the ice-free summer months, compensation depth reached a maximum of 14 m during the midnight sun period. Surface water temperature ranged from < 1°C in winter to a maximum of 10°C in July and water column was well-oxygenated across the year (Table 1).

INVERTEBRATE COMMUNITY

Littoral BMI density was highest in December (mean ± SD: 6341 ind m^{-2} ± 1143), during the polar night, and steadily decreased until June (2919 ind m^{-2} ± 297; Fig 1a). There was a smaller summer peak in July (4452 ind m^{-2} ± 1440), followed by the minimum recorded density in September (527 ind m^{-2} ± 85). In contrast, densities of profundal BMIs peaked in July (1129 ind m^{-2} ± 617) whereas the lowest density was recorded in February (699 ind m^{-2} ± 127; Table S1; Fig 1a). In general, profundal BMI densities were 3-6 times lower than littoral BMIs, except at the minimum littoral density in September. BMI community structure (as proportion of total density) varied seasonally, in both habitats (littoral: $Pseudo\ F_{(6,17)} = 23.37$, $P < 0.01$; profundal: $Pseudo\ F_{(6,17)} = 11.25$, $P < 0.01$). BMI communities in both habitats were dominated by chironomid larvae and oligochaeta throughout the year, while an increased density of *Eurycercus* sp. and *Megacyclops* sp. was observed in July and September (Table S1). The pelagic zooplankton community was dominated by copepods throughout the year, with a single peak of both cladocerans and copepods observed in July (Fig. 1b).

Zooplankton δ^{13}C values (-31.8 ‰ ± 1.2) were ^{13}C depleted by approximately 10 ‰ relative to littoral BMIs (-17.5 ‰ ± 2.5; Fig 2). Profundal BMI δ^{13}C values (-27.6 ‰ ± 2.1) were intermediate between both groups. Zooplankton displayed intra-annual variability, a circa 2 ‰ difference was evident between annual maximum (May: -30.1 ‰ ± 0.3) and minimum (July: -33.3 ‰ ± 0.2) values. Littoral BMI values in June (-20.8 ‰ ± 3.4) were depleted in δ^{13}C relative to the annual mean, δ^{13}C values of profundal BMIs were stable through the year (Fig. 2, Table S2).

Profundal BMIs (7.1 ‰ ± 0.8) were ^{15}N enriched relative to littoral (3.3 ‰ ± 1.4) populations. The δ^{15}N values of both communities were relatively stable through the year (Fig. 2). Zooplankton δ^{15}N values (4.5 ‰ ± 1.4) were intermediate between both BMI groups and displayed high levels of intra-annual variability (Fig. 2, Table S2). High fluctuations were observed between relatively ^{15}N enriched values in December just after the lake surface froze (6.3 ‰) and June (6.4 ‰ ± 0.1) just after ice melt and depleted values in May (2.9 ± 0.2).

WHITEFISH GROWTH AND ACTIVITY

Whitefish (*n* = 617) was the most frequently caught fish species, contributing between 78 and 97% of each survey catch (Table 1). Mean (± SD) whitefish CPUE was the highest in September (6.27 ± 0.07) and consistently low during the polar night (December: 0.59 ± 0.07) and winter (February: 0.54 ±0.15) period (Fig. 1c). The lowest CPUE was recorded during the mid-night sun in May-June (0.2 ± 0.13; Table 1; Fig 1c). Fulton's condition factor (*k*) of both male and female whitefish increased significantly from June to September (Table S3;

Fig 3a). At the time of sampling, the L. Kilpis whitefish population was dominated (58 %; *n* = 358) by a single year class (2003). Consequently, the comparison of incremental increase in fish mass between seasons was restricted to this year class. The mean mass of these fish increased during the summer; both male and female whitefish displayed maximum growth between May and July (Fig 3b). In females, the most significant increase of gonad weight (GSI) occurred between September and December, whereas males had reached their pre-spawning GSI in September (Table S3; Fig. 3c). Female GSI was the highest in December 2011, just prior to spawning, and dropped significantly thereafter (Table S3). Liver C:N ratios, a proxy for lipid content, decreased through the year in both sexes, although the trend was particularly evident in male whitefish (Fig. 3d). No seasonal variation was evident in the C:N ratios of whitefish muscle tissue (3.21 ± 0.05 SD; Table S3).

SHORT TERM DIET – STOMACH CONTENT

Whitefish stomach content varied considerably through the year (Table 2; Fig. 4). Levins' index values observed at each sampling occasion were low (< 0.25), suggesting that at any particular period whitefish were predominantly consuming one prey type (Table 2; Fig 4), e.g. chironomid larvae in December (mean ± SD: 59 % ± 41) and February (70 % ± 39), and chironomid pupae in June (67 % ± 44). Whitefish displayed a wider trophic niche in May (0.24) and July (0.18), feeding on both zooplankton and benthic invertebrates (Table S4; Fig. 4). In September, whitefish predominantly fed on small benthic crustaceans (63 % ± 37), most notably *Eurycercus* spp (Fig. 4). The feeding activity of whitefish, characterised by a high level stomach fullness values (> 4.5 / 10) and the lowest amount of empty stomachs (0 – 1 %; Table S4), was highest during late summer (July-September), when pelagic zooplankton and small benthic crustaceans were prevalent in the diet. The shift towards a pelagic diet in spring and early summer was also evident in the amount of copepod transmitted *Diphyllobothrium* spp. tapeworm cysts in the stomach wall of whitefish: the maximum mean infection intensity of cysts (cysts host^{-1} ± SD) was recorded in May (112.9 ± 69.5) and June (128.1 ± 72.4; Table S4; values relate solely to the 2003 year class). Infection intensity fell later in the summer (July: 58.3 ± 30.5; September: 96.2 ± 56.4), potentially reflecting a successful immune defence.

MEDIUM TERM DIET – LIVER SIA

The δ^{13}C and δ^{15}N isotopic values of whitefish liver were stable between December and June, but pairwise PERMANOVA analysis indicated that isotopic shifts took place July and September (Fig. 2, Table 2, isotope biplots are presented in Fig. S1). In July, this related primarily to variation in δ^{13}C, which was ^{13}C depleted (-25 ‰ ± 1.9) relative to June (-22.7 ‰ ± 1.7) indicating a greater reliance on pelagic prey. In September, the variation was principally due to δ^{15}N, which was ^{15}N depleted (7.5 ± 0.5) relative to the annual mean (8.2 ± 0.6), indicative of foraging at a lower trophic level.

The SIAR mixing model reflected this annual variation (Fig 5b, Table S5). Between December and June, mixing model results based on whitefish liver δ^{13}C and δ^{15}N isotope values indicated a predominance of benthic foraging. Modal pelagic resource utilisation estimates ranged between 11 % (June) and 18 % (December), which combined with the limited 95% credibility limits for pelagic resource use during this period (9 – 26 %) indicated an overall reliance on benthic prey items. Increased assimilation of pelagic derived prey was evident in both July (mode: 33; 95% credibility limits: 26 – 40), a significant increase from

June (likelihood 99%), and September (mode: 32%; 95% C.L. 26 – 40). Isotopic niche width (SEA_c) was also significantly reduced (likelihood 99%) in July (2.51) and September (2.49) relative to the preceding months (4.78 – 3.69; Table S5, Fig 5b)

LONG TERM DIET – MUSCLE SIA

Pairwise PERMANOVA analyses of whitefish muscle $\delta^{13}C$ (annual mean: -24.8 ‰ ± 1.6 SD) and $\delta^{15}N$ (annual mean: 8.6 ‰ ± 0.3 SD) isotope ratios indicated no significant intra-annual variation (Table 2, Fig 2). The SIAR mixing model (Fig. 5c) indicated a reliance on benthic resources for all samples (modal estimate for pelagic resource use: 17 – 24 %; 95% credibility limits: 6 – 30 %). Pelagic resource use in May (mode: 19 %; 95% C.L. 14 – 24) was lower than in February (mode: 24 %; 95% C.L. 19 – 30) at a close to significant level (likelihood 93 %), however benthic resources were dominant in both cases (Fig. 5c). SEA_c based on muscle tissue also varied minimally between samples (Fig. 5c). Muscle SEA_c values (1.09 – 1.99) were smaller than the SEA_c values based on liver tissue (2.49 – 4.78).

Discussion

We found clear annual differences in whitefish trophic ecology and activity reflecting seasonal changes in both the physical environment and prey resources. Whitefish predominantly foraged in the benthic zone throughout the year, but displayed a significant seasonal shift to pelagic feeding during the period of peak zooplankton abundance. This seasonal shift coincided with the highest feeding activity, growth, condition and investment in gonad tissue of whitefish. The data supported the utilization of muscle tissue to track the most important annual resource, in this case BMIs, for fish in cold water systems, but also revealed that finer scale analyses such as diet and liver isotope ratios are needed to reveal the seasonal importance of pelagic resources during the summer.

Changes in prey availability are well established for many terrestrial systems in Arctic, where the vole and lemming population cycles strongly contribute to predator diet selection and reproductive output (Killengreen *et al.* 2011; Giroux *et al.* 2012), our data reveal similar trends in subarctic lakes. There was a clear indication of different dynamics between littoral and profundal BMI's, with the latter showing the highest densities during the period of peak water temperatures in July and the lowest densities in December. In contract, the maximum density of littoral BMIs was observed at the lowest water temperatures in December and densities steadily decreased until June. The profundal BMI community is characterised by low diversity and dominated by chironomids and oligochaetes, whereas the littoral community is more diverse and includes insect larvae, molluscs and benthic cladocerans. The littoral samples contained a large proportion of insect larvae and as such were likely influenced by patterns of emergence through the summer months (Pinder 1986). In L. Kilpis, the initial intensive hatching period of insects occurs in concert with increasing water temperature and light in June. This corresponds with the observed decrease in abundance between ice-covered May and open water June. The increase of BMI abundance between the first hatching period in early June and late July may be related to recruitment of insect larvae and molluscs, as previously observed within the region (Kahilainen, Lehtonen & Könönen 2003). Subsequent hatching or alternatively, increased predation by whitefish, during the summer and autumn may have reduced the density of littoral BMIs in September. Alternatively, the sampling effort, three replicates at a single location, may have been insufficient to adequately account for patchily distributed littoral BMI community. Additional statistical power, derived from a greater number of sample sites and the division of the heterogeneous littoral habitat into distinct sub-habitats, in addition to a thorough assessment of BMI biomass, would be required to fully examine this trend in the data.

Zooplankton provided an alternative source of energy and nutrients for whitefish during the summer. Although copepods were available year-round, both they and cladocerans displayed a seasonal peak at the end of July, coinciding with the highest water temperatures. The lowest densities were observed in May just before the loss of surface ice. This single summer peak in July-August is typical of zooplankton communities in this region (Kahilainen, Alajärvi & Lehtonen 2005). Despite the brief abundance of pelagic, and most likely also benthic zooplankton (especially *Eurycercus* spp.), they represented the main prey of whitefish in July and September, a period associated with increased movement (assessed by CPUE), condition and the formation of new somatic and gonadal tissues by the fish. It is also noteworthy, that whitefish apparently selected zooplankton prey in July, even though, BMIs were relatively abundant in both littoral and profundal habitats.

The highest increments of condition and mass of whitefish coincided with the highest water temperature, zooplankton abundance and the end of mid-night sun period in July. Both sexes exploited the temporary abundance of pelagic prey during the summer, as indicated by the similar increases in condition factor and mean mass. Variation in GSI and liver C:N ratios succinctly displays the variation in development between sexes. In males, GSI was already at spawning level in September and C:N ratios indicated significant lipid stores during winter. In females, maximum gonad development occurred after September and it is likely that pelagic derived energy was directed towards gonad development, as winter lipid stores were lower than in males. This apparent routing of resources from recently consumed prey into a particular tissue is supported by the high concentration of zooplankton-derived essential fatty acids in whitefish eggs (Brett & Müller-Navarra 1997). Tyler and Sumpter (1996) detail that increased female mass immediately prior to spawning is related primarily to the uptake of water into eggs. While the water content of eggs was not measured during this study, water uptake may account for the large increase in GSI prior to spawning in December.

Our time integrated characterisation of whitefish diet highlights the interaction between variation in resource availability and the increased growth and condition of whitefish. Whitefish stomach content, indicative of short term resource use, revealed a high degree of seasonal variation, as fish used the most abundant prey. During the winter months, chironomid larvae and molluscs dominated whitefish diet, but in early spring as insect larvae began to pupate, prior to emerging at ice-break, whitefish fed increasingly on these pupae. During summer, whitefish shifted to a zooplankton dominated diet, coinciding with peak zooplankton density. While in September, whitefish diet was dominated by *Eurycercus* spp. and *Megacyclops* spp. which were also abundant in the BMI samples during that period. These findings mirror results seen in other subarctic lakes, revealing the seasonal importance of pelagic and benthic zooplankton (i.e. *Eurycercus* spp.) to whitefish across northern Fennoscandia (Kahilainen, Lehtonen & Könönen 2003; Harrod, Mallela & Kahilainen 2010; Hayden, Harrod & Kahilainen 2013). The consumption of zooplankton coincided with the fewest empty stomachs, the highest average stomach fullness and notable increase in both whitefish condition and gonad development, highlighting the importance of a temporally-limited pelagic resource to the annual somatic and gonad growth of whitefish.

Whitefish liver stable isotope values, indicative of medium term resources use, reflected this temporal variation in diet. The results of the SIAR mixing model indicate that this variation is directly related to a greater reliance on pelagic resources during summer. Such temporal variation was not detected in the muscle isotope values of whitefish which indicated a reliance on prey obtained from the benthic zone throughout the year. As muscle tissue turns over at a slower rate than liver, it is likely that the brief temporal shift towards a pelagic diet is too short to be revealed in the muscle isotope ratios. This variation between tissues has a broad ecological relevance as stable isotopes are used to track the diet and migration of a wide variety of animals (Rubenstein & Hobson 2004). The slow somatic growth, and by default tissue turnover, of organisms in cold environments may obscure short term variation in a consumers diet, causing a variety researchers using only stable isotopes of muscle to overlook seasonally important prey types (Dalerum & Angerbjorn 2005). Our findings reinforce the ‘best practise’ protocol of integrating stable isotopes with an additional measure of diet, such as rumen or scat analysis.

The stability of muscle isotope values and the importance of benthic resources in oligotrophic L. Kilpis is in sharp contrast to almost complete pelagic reliance of whitefish in larger, deeper and more productive alpine Lake Geneva (Perga & Gerdeaux 2005). In this meso-eutrophic lake, seasonal variation in whitefish muscle and liver isotope values reflected the changes of isotopic values of their main prey, pelagic zooplankton. The faster muscle turn-over rates in warm water and higher degree of baseline variability likely explain the difference between these two whitefish populations. It is interesting to note that the same species, whitefish, is predominantly associated with pelagic resources in southern lakes and benthic resources in northern lakes, attesting to variation in the relative productivity of both basal resources across a latitudinal gradient (Vadeboncoeur *et al.* 2003). Such variation in the resource use of generalist consumers has also been recorded in birds and mammals overcoming spatial variation in prey resources (Terraube & Arroyo 2011).

The relative annual importance of benthic and pelagic prey to whitefish documented here provides a possible means of evaluating functional changes in subarctic lake ecosystems subjected to climate change. Long term air temperature and ice data from the Kilpisjärvi region indicates a general warming over the last 30 years and an increased duration of the open water period (Lei *et al.* 2012). In a closed system, an increased summer period would likely be a benefit to whitefish. It may be surmised that a moderate increase in temperature would extend the zooplankton succession (de Senerpont Domis *et al.* 2013) and thus, availability to whitefish, potentially increased somatic growth and gonadal development allowed by warmer water temperatures and an extended growing season. In general, the relative proportion of pelagic habitat is likely to increase due to higher carbon run-off from the catchment area, decreasing the area for benthic primary production through light limitation (Hansson *et al.* 2013). However, subarctic lakes are typically a part of large interconnected waterways and cannot be considered as closed systems. Cool-water adapted competitors and predators of cold water adapted whitefish are becoming established at previously thermally inaccessible latitudes and as a consequence additional resources are shared in more complex food webs (Byström *et al.* 2007; Hayden *et al.* 2013; Hayden, Harrod & Kahilainen 2014). The outlook for whitefish populations under these conditions is less clear and provides an interesting topic for future investigations. Climate envelope models of predicted future distributions of terrestrial mammals in subarctic regions suggest that the influx rate of new species will exceed the limited local extinctions of cold adapted residents, resulting in increased mammalian biodiversity in the region (Hof, Jansson & Nilsson 2012). Our data tentatively supports the extension of this hypothesis to whitefish, and potentially other cold-adapted species, which may benefit from increased productivity and prey availability resulting from modest climate warming, but maybe adversely affected by an invasion of warmer water adapted species.

The data presented here display how consumers may respond to temporal variation in prey abundance, a trend which is also relevant to terrestrial and marine ecosystems. In the introduction, we highlighted examples of the response of consumers to seasonal variation in prey abundance. While numerous authors have observed this trend, few have linked such variation in diet with the annual growth and reproductive development of an organism, particularly in the context of temporarily scarce prey. In addition, most studies in Arctic and subarctic regions are based on a coarse temporal resolution i.e. comparing resources and consumer diet with snap-shot sampling once per year (e.g. Killengreen *et al.* 2011; Terraube *et al.* 2011), while far less is known of how seasonally fluctuating prey resources influence to growth and reproduction (but see Giroux *et al.* 2012). In light of this, we suggest that investigating annually migrating species or stationary consumers using annually migrating prey may be a fruitful area for future research.

To conclude, we confirmed that, on an annual basis, in low productivity subarctic regions, benthic invertebrates are the most important prey for this dual-fuelled generalist fish. However, pelagic production, facilitating by a switch to zooplankton foraging during the summer, plays a key role in the development of somatic and gonadal tissues. Our results suggest that muscle isotopic values provide robust evidence of the most important annual resource, whereas additional analyses of recent diet through stomach content analysis and liver stable isotopes provide the means to resolve finer scale seasonal shifts of slow growing fish in subarctic lakes.

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Figure Legends

Fig. 1. Seasonal variation in mean density of (a) littoral and profundal benthic macroinvertebrates, (b) pelagic zooplankton and (c) the relative density of whitefish in L. Kilpis. Error bars indicate 95% confidence intervals in all cases. Whitefish density values are presented as catch per unit effort (CPUE). Broken line indicates the spring ice-break.

Fig. 2. Seasonal variation in (a) δ^{13}C and (b) δ^{15}N of invertebrates (left panels) and whitefish tissues (right panels). Error bars indicate 95% confidence limits in all cases.

Fig. 3. Seasonal variation in (a) Fulton's condition factor, (b) mean somatic mass of the dominant 2003 year class, (c) gonadosomatic index and (d) the liver C:N ratio of mature male and female whitefish. Mean somatic mass values for June were omitted from figure 2b due to small sample size ($n = 3$). Error bars indicate 95 % confidence limits in all cases.

Fig. 4. Seasonal variation in the stomach content of whitefish. Mean proportion of chironomid larvae (Chiro), insect pupae (Insect P: Chironomid & Trichoptera pupae), Zooplankton (ZPL: *Bosmina* sp, Calanoida and Cyclopoida), small benthic crustaceans (SBC: *Eurycercus* sp & *Megacyclops* sp.) and other prey items (Other: *Pisidium* sp., *Lymnaea* sp. and *Valvata* sp., Trichoptera & Plecoptera larvae). Broken line indicates the spring ice-break.

Fig. 5. Seasonal variation in proportion of pelagic resources in (a) stomach content, (b) liver and (c) muscle stable isotope ratios of whitefish. Left panel denotes resource use, right panel denotes niche width. Stomach content is displayed as a box plot (median, 1st and 2nd quartiles are displayed, outliers are shown as circles). Gradations in (b) and (c) indicate 50%, 75% and 95% credibility intervals. Black circles indicate mean SEA values.

Table 1. Seasonal environmental characteristics and fish density values recorded in L. Kilpis.

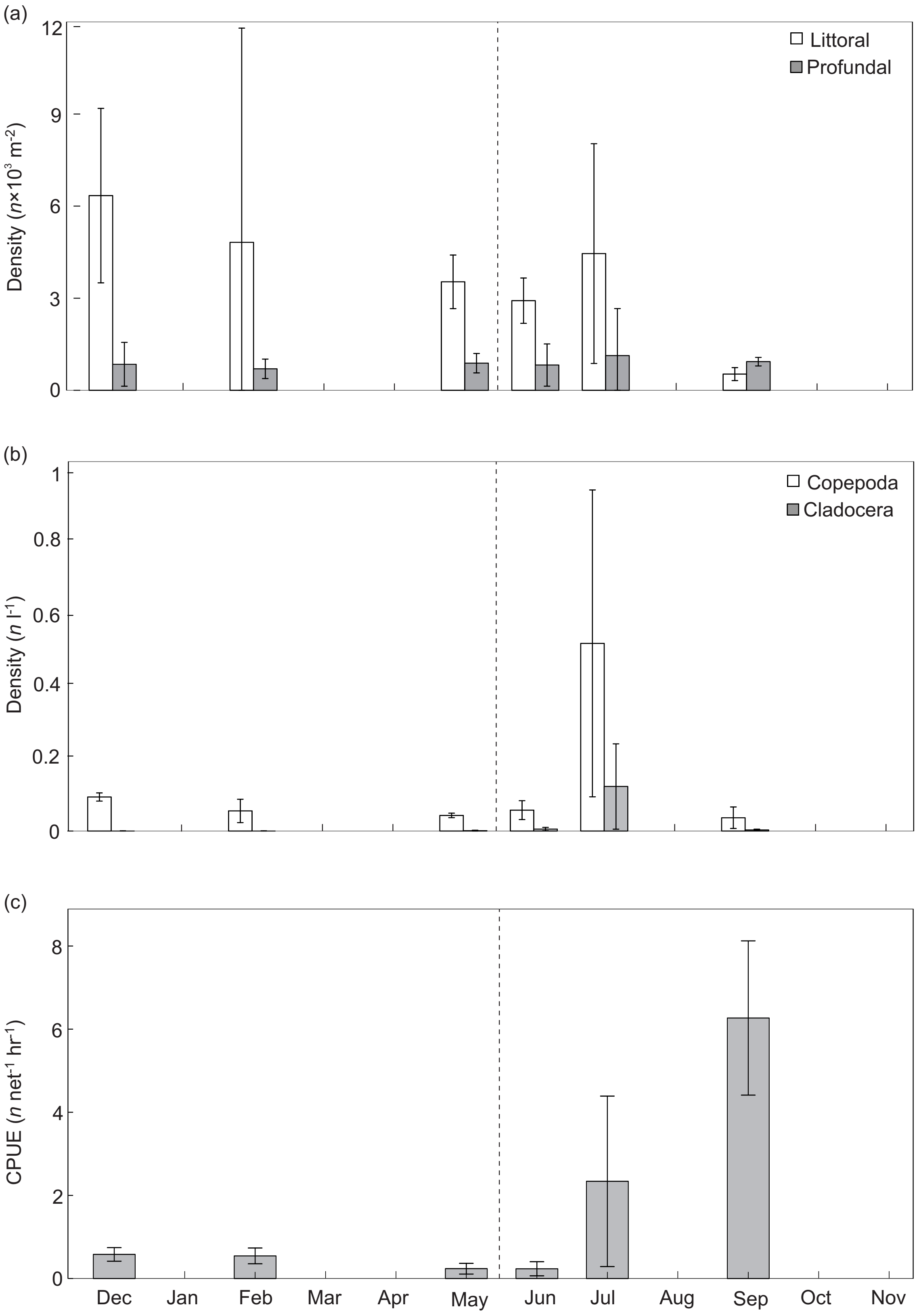
Parameter	December	February	May	June	July	September
Snow depth (cm)	0 - 10	15 - 25	0 - 5			
Ice depth (cm)	12.3 (2.1)	85 (4.4)	76.3 (1.2)			
Mean water temperature (°C)	0.4*	0.65	1.27	3.02	9.33	8.63
Compensation depth (m)	0	2	9	13	14	13
Water chemistry						
Oxygen (mg l^{-1})		14.5		12.1	11.3	10.8
Oxygen saturation (%)		100		91	97	88
pH		7.08		7.28	7.16	7.08
Total nitrogen (µg l^{-1})		140		110	120	110
Total phosphorus (µg l^{-1})		4		4	3	3
Chlorophyll-a (µg l^{-1})				1.5	1	1.1
CPUE (*n* net series^{-1} hour^{-1})						
Whitefish	0.59 (0.07)	0.54 (0.15)	0.2 (0.11)	0.2 (0.13)	4.68 (3.74)	6.27 (0.21)
Combined other species	0.07 (0.06)	0.07 (0.06)	0.04 (0.02)	0.07 (0.03)	0.13 (0.06)	0.25 (0.14)

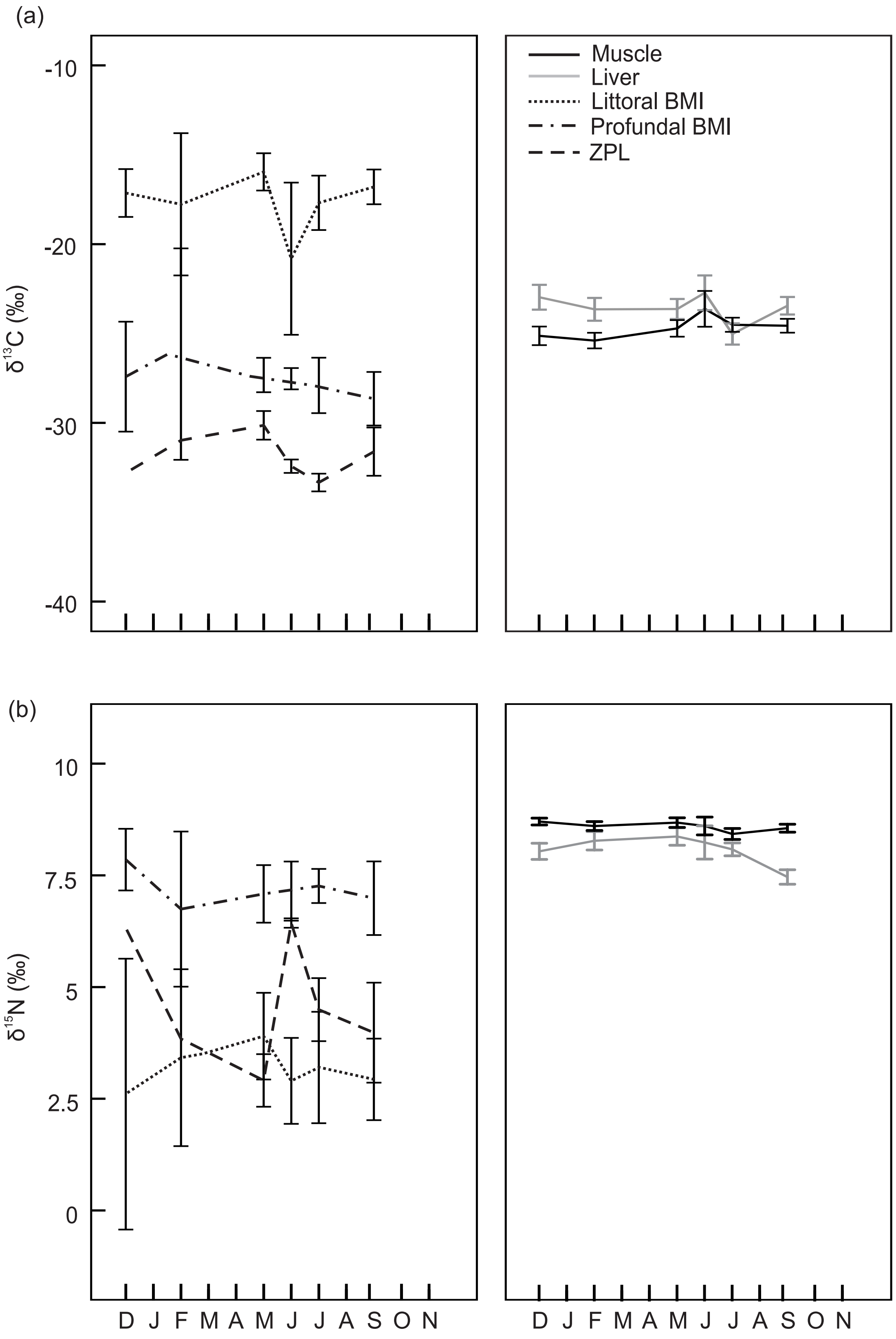
The December sample was obtained in 2011, all other sampling occurred in 2012. *December water temperature values refer to surface water temperature only. Water chemistry data is provided courtesy of Lapland Centre for Economic Development, Transport and the Environment. Combined other species includes Arctic charr, burbot, alpine bullhead, brown trout and grayling. Standard deviations are provided in parentheses.

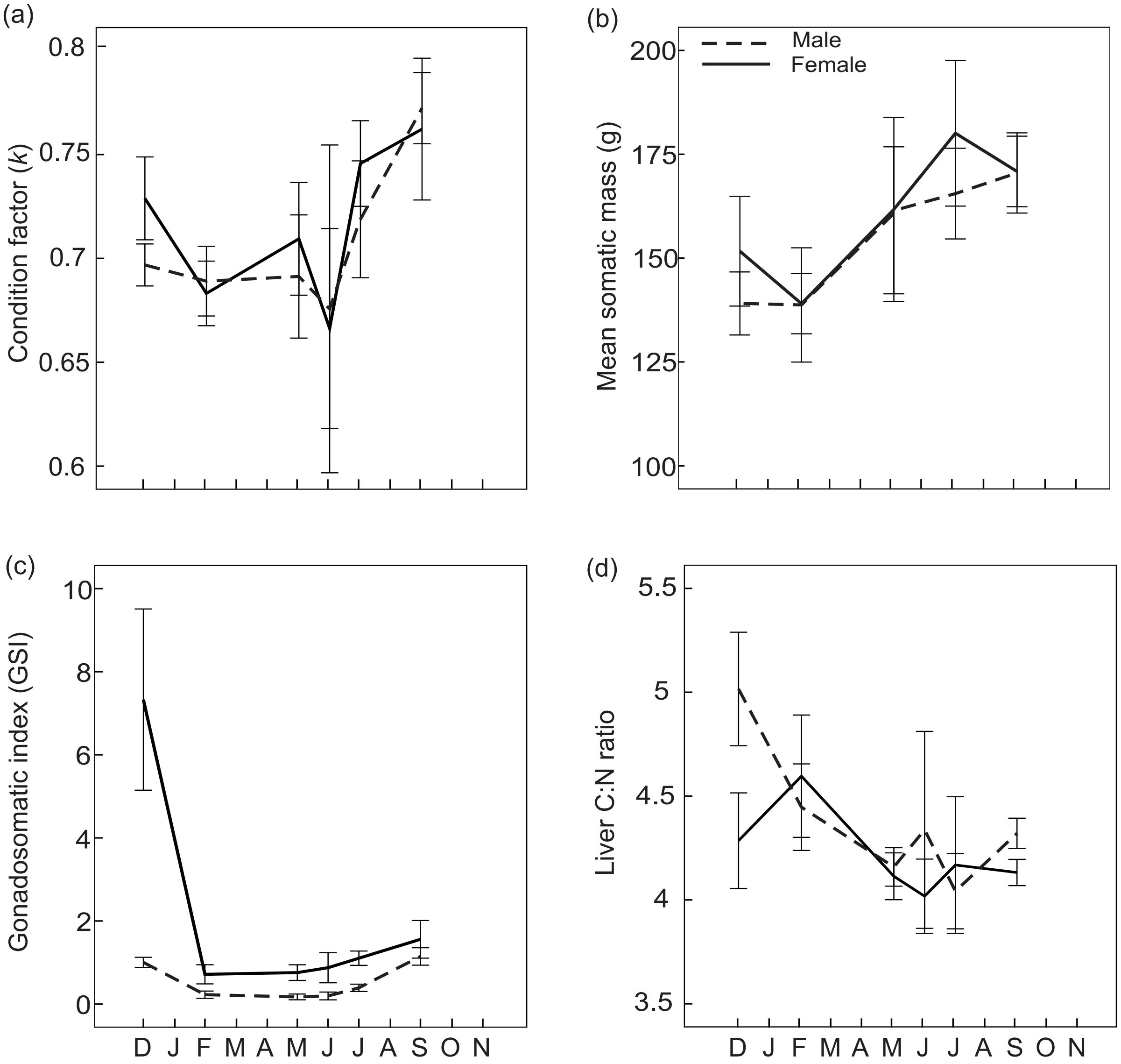
Table 2. Pairwise PERMANOVAs of stomach content, liver and muscle $\delta^{13}C$ and $\delta^{15}N$ values (SIA) of whitefish from December 2011 to September 2012. Each row represents variation with preceding sample.

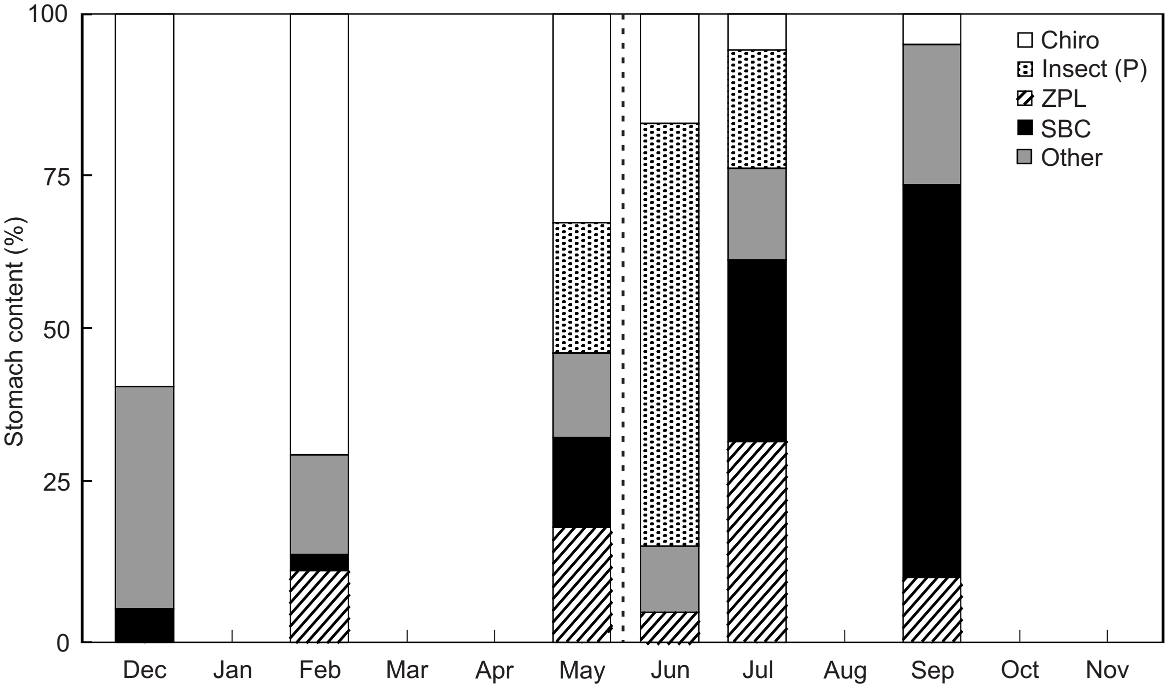
	Stomach content			Liver SIA			Muscle SIA		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
December*	176	49.9	**< 0.001**	89	2.6	0.1	89	2.9	1
February	123	2.7	0.65	89	2.1	0.15	89	0.7	1
May	146	13.8	**< 0.001**	88	0.1	0.93	88	4.3	0.57
June	72	6.5	**< 0.001**	61	2.3	0.13	61	4.7	0.48
July	128	12.8	**< 0.001**	52	15.7	**<0.01**	52	4.2	0.59
September	255	42.6	**< 0.001**	79	18.6	**<0.01**	79	0.24	1

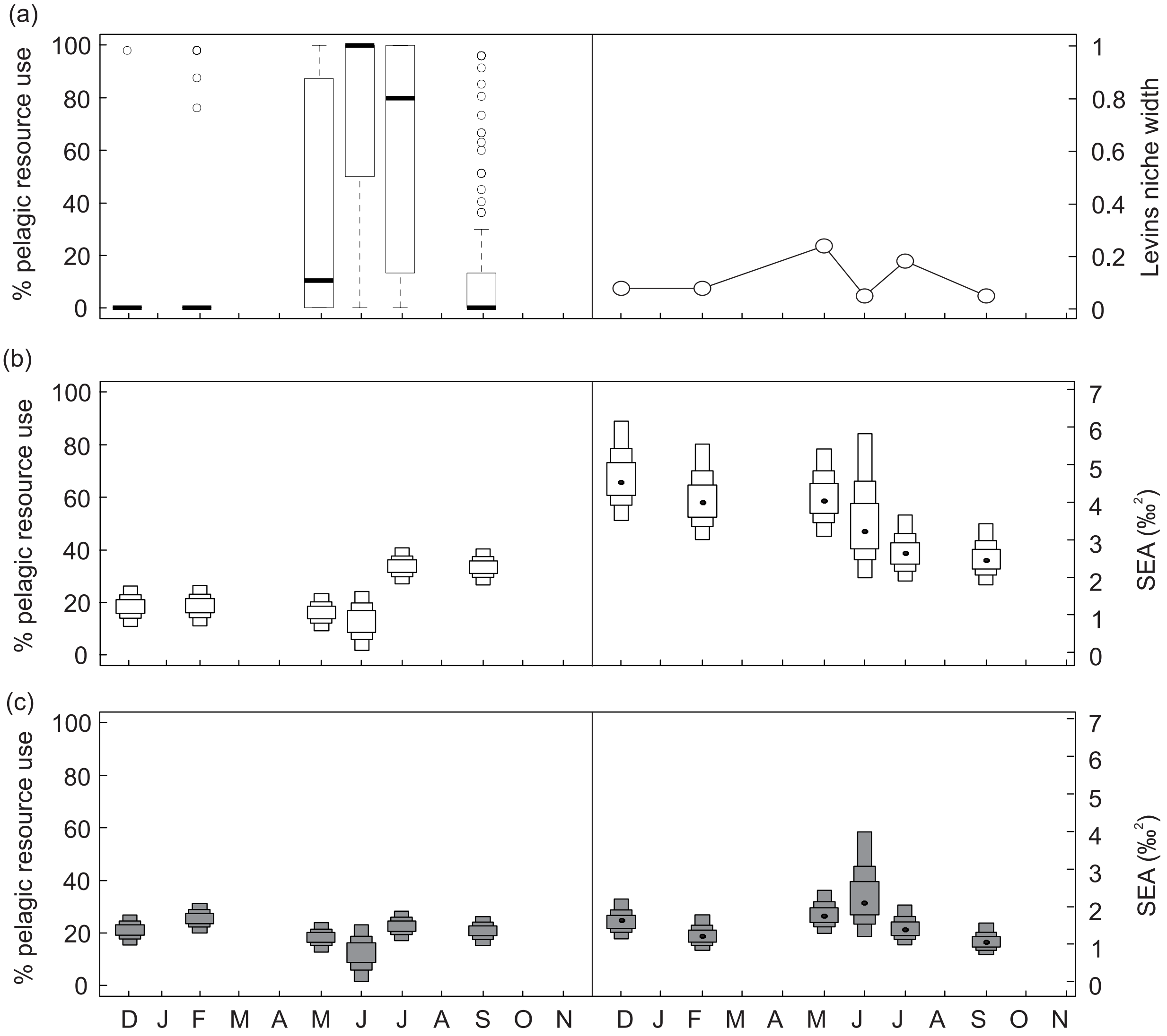
*December 2011 values are compared with September 2012


(a)
12
9
6
3
0
Density (n×10^3 m^{-2})
☐ Littoral
▨ Profundal
(b)
1
0.8
0.6
0.4
0.2
0
Density (n l^{-1})
☐ Copepoda
▨ Cladocera
(c)
8
6
4
2
0
CPUE (n net^{-1} hr^{-1})
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov


(a)
-10
-20
-30
-40
δ13C (‰)
Muscle
Liver
Littoral BMI
Profundal BMI
ZPL
(b)
10
7.5
5
2.5
0
δ15N (‰)
D J F M A M J J A S O N
D J F M A M J J A S O N


(a)
Condition factor (k)
0.8
0.75
0.7
0.65
0.6
(b)
Male
Female
Mean somatic mass (g)
200
175
150
125
100
(c)
Gonadosomatic index (GSI)
10
8
6
4
2
0
D J F M A M J J A S O N
(d)
Liver C:N ratio
5.5
5
4.5
4
3.5
D J F M A M J J A S O N


100
75
50
25
0
Stomach content (%)
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Chiro
Insect (P)
ZPL
SBC
Other


(a)
% pelagic resource use
Levins niche width
(b)
% pelagic resource use
SEA (‰^{2})
(c)
% pelagic resource use
SEA (‰^{2})
0
20
40
60
80
100
0
0.2
0.4
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1
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