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Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*

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Abstract Food web studies based on stable C and N isotope ratios usually assume isotopic equilibrium between a consumer and its diet. In the Arctic, strong seasonality in food availability often leads to diet switching, resulting in a consumer's isotopic composition to be in flux between different food sources. Experimental work investigating the time course and dynamics of isotopic change in Arctic fauna has been lacking, although these data are crucial for accurate interpretation of food web relationships. We investigated seasonal (ice-covered spring vs. ice-free summer) and temperature (1 vs. 4°C) effects on growth and stable C and N isotopic change in the common nearshore Arctic amphipod *Onisimus litoralis* following a diet switch and while fasting in the laboratory. In spring we found no significant temperature effect on N turnover [half-life (HL) estimates: HL-N = 20.4 at 4°C, 22.4 days at 1°C] and a nonsignificant trend for faster growth and C turnover at the higher temperature (HL-C = 13.9 at 4°C, 18.7 days at 1°C). A strong seasonal effect was found, with significantly slower growth and C and N turnover in the ice-free summer period (HL-N = 115.5 days, HL-C = 77.0 days). Contrary to previous studies, metabolic processes rather than growth accounted for most of the change in C and N isotopic composition (84–89 and 67–77%, respectively). This study provides the first isotopic change and metabolic turnover rates for an Arctic marine invertebrate and demonstrates the risk of generalizing turnover rates based on taxon, physiology, and environment. Our results highlight the importance of experimental work to determine turnover rates for species of interest.

Keywords Food web · Sea ice · Diet switching · Temperature · Metabolic turnover

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Introduction

Brine channels and pockets in sea ice create a unique habitat for a specialized community of organisms, including bacteria, protozoans and metazoans, and ice algae (Horner et al. 1992; Gradinger 2002). During early spring, when light penetration into the water column is low and phytoplankton production is limited, ice algal abundance and biomass can be orders of magnitude higher than phytoplankton abundance, providing an important early food source (Horner 1985; Sakshaug 2004). Sympagic (ice-associated) fauna, specifically amphipods, utilize this rich food source near the ice-water interface (Werner 2000; Gradinger and Bluhm 2004), thereby channeling ice-derived organic C to pelagic and benthic food webs, including fish, birds, and mammals (Bradstreet and Cross 1982; Bluhm and Gradinger 2008).

Stable isotopes have been used to investigate these and other trophic interactions in the ice-covered waters of the Arctic (Hobson and Welch 1992; Iken et al. 2005; Lovvorn et al. 2005; Tamelander et al. 2006) and Antarctic (Frazer 1996; Schmidt et al. 2003) for nearly two decades. Analysis of naturally occurring stable isotope ratios of C and N has become a standard method in food web studies, as the

isotopic composition of a food source is reflected in the isotopic composition of the consumer in a fairly predictable manner (Hobson and Clark 1992). The stable C isotope composition ($\delta^{13}C$) of a consumer is similar to that of its diet generally enriched by 0–1‰, while a consumer's stable N isotope composition ($\delta^{15}N$) reflects a stepwise increase from diet to consumer of 2–4‰ (Peterson and Fry 1987). Sea ice algae differ in both C and N isotope signatures from pelagic phytoplankton (Gradinger and Bluhm 2005; McMahon et al. 2006; Tamelander et al. 2006; Gradinger 2008), making isotope analysis a potential tool to resolve the seasonal importance of ice algae to coastal Arctic food webs.

One common assumption made in interpreting stable isotope data in a food web context is that the consumers measured are in isotopic equilibrium with their diet. However, in seasonally ice-covered regions temporal changes in the ice algal isotopic baseline can confound interpretation if recent changes in the isotopic baseline are not yet fully expressed in the tissues of consumers. Moreover, diet switching occurs in the Arctic, where strong seasonal pulses of production lead to seasonally available food sources that are exploited by consumers during the short productive season (Dower et al. 1996; Sakshaug 2004). The time course over which consumer tissues come into isotopic equilibrium with a new diet (isotope turnover) can vary widely among tissues and species. Despite wide use of stable isotope techniques to investigate Arctic marine food webs (Iken et al. 2005; McMahon et al. 2006; Tamelander et al. 2006), no study has investigated isotope turnover in organisms that might be exposed to such a diet shift.

We chose the common Arctic gammarid amphipod species *Onisimus litoralis* as a target species as it migrates between the ice and benthos and seasonally switches its diet (Carey 1992). In laboratory experiments, we studied the rate at which isotopic changes occur following a diet switch as well as under fasting conditions. These data provide the foundation for using stable isotope ratios to examine the temporal dynamics of stable isotopic composition in ice-associated fauna in the field that exhibit habitat or dietary changes as a response to seasonally available sea ice algal production in coastal Arctic waters.

Materials and methods

Collection of animals

Specimens of *O. litoralis* were collected in baited minnow traps under shore-fast sea ice in the Chukchi Sea near Barrow, Alaska (71°19.911′N, −156°40.470′W), in March 2004. During open water conditions, *O. litoralis* were collected in Elson Lagoon (71°20.502′N, −156°33.504′W) in September 2004. Bait was wrapped in filter paper and screen material to prevent ingestion. Animals were subsequently transported to the University of Alaska, Fairbanks (UAF) laboratory and placed in incubation chambers in the dark at 1°C to acclimate for 1 week.

Turnover experiments

Two long-term feeding experiments [63 and 72 days for experiments 1 (Exp. 1) and 2 (Exp. 2), respectively] were performed to estimate C and N turnover rates in amphipods collected during the ice-covered and the ice-free periods. Exp. 1 assessed the turnover of C and N at two different temperatures and for two different diets, while Exp. 2 was conducted to compare the turnover in amphipods collected during an ice-free period to those collected during an ice-covered period.

Prior to the start of each feeding experiment, amphipods were blotted dry, weighed to the nearest 0.1 mg, and transferred to 500-ml plastic cups filled with artificial seawater (Instant Ocean, practical salinity 30) at 1 or 4°C in the dark. Each cup contained two animals, one serving as a backup in case the primary specimen died prior to sampling, separated by a screen to prevent cannibalism.

Experimental diets

We created isotopically distinct experimental feeds (Table 1) using different combinations of commercial algal-based aquaria fish food (Wardley Premium Algae Discs) and ice algae collected from the study site in June 2003. Ice algal cells were cultured in artificial seawater at 4°C/24 h light and constant aeration. Fresh artificial seawater and Guillard's f/2 (Sigma G9903) nutrient solution were added to the culture weekly. Ice algae were isotopically enriched through incorporation of heavy isotopes during algal incubations with ^{15}N and ^{13}C labeled compounds ($Na^{15}NO_3$ and $NaH^{13}CO_3$, respectively). For this purpose, each week 2 l of the culture was transferred to a separate container and 0.8 ml labeled $Na^{15}NO_3$ solution (0.086 g/l) and 4 ml labeled $NaH^{13}CO_3$ solution (4.3 g/l) were added. Algal cells in the 2 l culture were incubated under the same environmental conditions as the main culture for 24 h. After 24 h, the enriched culture was centrifuged, water was decanted, and algal cells were frozen.

All isotopically enriched algal samples were pooled, dried for 3 days at 60°C, and homogenized (final pooled values: $\delta^{13}C = 605.8‰$, $\delta^{15}N = 44.0‰$). Enriched experimental diets (Table 1) were formulated by mixing different ratios of the isotopically enriched algae with the commercial food [$\delta^{13}C = -22.8$ (SD ± 0.4)‰, $\delta^{15}N = 2.0$ (SD ± 0.2)‰, $n = 5$]. Ratios of ice algae to

commercial food were 0.25:1 for diet 1 and 0.004:1 for diet 2. Non-enriched ice algae were added to the commercial food in the ratio of 0.004:1 to create the control diet. An insufficient amount of diet 1 was available for the second experiment so the highly enriched diet was reformulated (diet 1a) using a ratio of 0.6:1 of enriched ice algae and the commercial food. Deionized water was added to make a paste, and pellets of 2 mm diameter were portioned onto aluminum foil using a syringe. The pellets were dried at 60°C for 48 h and stored at −18°C. Pellets were subsequently soaked in artificial seawater to determine the stability of the isotopic values under experimental conditions. After soaking for 72 h (the average time a food pellet would sit in an experimental cup before being replaced with a fresh pellet), pellets were re-dried and δ^{13}C and δ^{15}N values of the soaked pellets were measured. Soaking reduced the enrichment level of the enriched diets by approximately 10‰ for δ^{13}C and 3‰ for δ^{15}N. Diet values reported (Table 1) are for soaked pellets. Soaking had no effect on the isotopic signature of the non-enriched diet. For both experiments a non-enriched diet served as a control.

Experimental setup

Exp. 1 took place from 2 April to 3 June 2004, using amphipods collected in March 2004. Amphipods were randomly assigned to one of five treatments as outlined in Table 1 (four experimental treatments and one control treatment). Each treatment consisted of five replicate animals and their backups for each of the ten sampling periods. Two experimental treatments received the highly enriched diet (diet 1), one maintained at 1°C and the other at 4°C. All other treatments were maintained at 1°C. The third experimental treatment received the moderately enriched diet (diet 2) with a δ^{13}C value similar to values found in Barrow fast ice communities in late spring under bloom conditions (Gradinger et al., in review). The fourth treatment received no food but otherwise experienced the same conditions as the treatments above. The control group received the non-enriched diet (diet 3). Due to a feeding error, data for this group are only available for weeks 1–3. Amphipods were kept in the dark and fed pellets of an average of 13.5 ± 1.9 mg dry weight. Fresh feed pellets were added every 3 days, at which time uneaten food (considered a sign of feeding ad libidum) and fecal pellets were suctioned off the bottom of the cups, and molts were collected. Incubation temperature was surveyed daily and dead animals were removed.

Initial amphipod δ^{13}C and δ^{15}N ratios were determined at the start of each experiment. Thereafter, five replicate amphipods (and their backups) were sampled weekly from each treatment and were allowed to clear their guts for 24 h. They were then blotted dry, weighed to the nearest 0.1 mg wet weight, and frozen at −18°C until processed for stable isotopic analysis.

Exp. 2 took place from 1 October to 25 December 2004, and had two treatments: one receiving a highly enriched diet (diet 1a) and the other receiving the non-enriched diet as control. The enriched diet in Exp. 2 was more than twice as enriched for C and 5 times more enriched for N than in Exp. 1 (Table 1). Both control and experimental groups were maintained in the dark at 1°C. During Exp. 1 much of the isotopic turnover occurred in the first 3 weeks; therefore, amphipods in Exp. 2 were sampled every 4 days in the first 2 weeks. Sampling was extended to every 7 days at week 3 and every 10 days from week 6 to the end of the experiment. Upon sampling, amphipods were processed as described for Exp. 1.

Stable isotope and particulate organic C and particulate organic N analysis

Amphipods and experimental diet samples were oven dried for 24 h at 60°C, fumed with concentrated HCl to remove carbonates, and re-dried for 48 h at 60°C. Feed samples

Table 1 *Onisimus litoralis* initial and final wet weights, growth rates, and dietary stable C isotope composition (δ^{13}C) and stable N isotope composition (δ^{15}N) for experiments 1 (*Exp.* 1; run from April to June 2004) and 2 (Exp. 2; run from October to December 2004). Wet weight (*WW*) growth rates, dietary δ^{13}C and δ^{15}N values reported as mean ± SD. *T* Temperature

Exp.	Treatment	*T* (°C)	Diet	Dietary δ^{13}C ($n = 5$)	Dietary δ^{15}N ($n = 5$)	Initial WW (mg) ($n = 50$ per treatment)	% Amphipods that molted	Final WW (mg) ($n = 45$)	Mean growth rate (mg/day)
1	High δ^{13}C	1	1	20.6 ± 1.0	3.7 ± 0.6	51.9 ± 13.6	72	64.5 ± 19.3	0.4 ± 0.5
1	High δ^{13}C	4	1	20.6 ± 1.0	3.7 ± 0.6	54.6 ± 12.0	82	68.8 ± 14.8	0.6 ± 0.6
1	Moderate δ^{13}C	1	2	−15.4 ± 0.6	2.5 ± 0.6	54.4 ± 10.4	78	66.5 ± 15.9	0.4 ± 0.5
1	Control	1	3	−22.8 ± 0.2	2.0 ± 0.2	56.3 ± 12.7	22[a]	68.8 ± 13.8	0.4 ± 0.8
1	Fasting	1	–	–	–	55.0 ± 11.1	36	60.8 ± 16.6	0.2 ± 0.9
2	High δ^{13}C	1	1a	49.3 ± 0.81	22.8 ± 1.0	54.9 ± 28.1	31	57.0 ± 26.9	0.0 ± 0.1
2	Control	1	3	−22.8 ± 0.2	2.0 ± 0.2	55.6 ± 21.8	20	57.5 ± 21.7	0.0 ± 0.1

[a] Control molting rate reported for weeks 1–3 only

and whole amphipods were homogenized prior to analysis. Lipids were not extracted from the samples prior to analysis. Lipids are depleted in $\delta^{13}C$ relative to protein or muscle. However, *O. litoralis* have relatively low lipid stores (Percy and Fife 1981; Sainte-Marie 1986; Graeve et al. 1997), and any lipid effect on the data was expected to be minimal. $\delta^{13}C$ and $\delta^{15}N$ were measured by continuous flow isotope ratio mass spectrometry using a Costech elemental analyzer interfaced with a Thermo Finnigan Delta Plus isotope ratio mass spectrometer at the UAF Alaska Stable Isotope Facility. Isotope ratios were reported in per mil (‰) using standard delta notation:

$$\delta X = \{(R_{\text{sample}} - R_{\text{std}})/R_{\text{std}}\} \times 1000(‰) \quad (1)$$

where $X = {}^{13}C$ or ${}^{15}N$, $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, and std (standard) = Vienna-Pee Dee Belemnite or air N_2, respectively. Analytical precision was 0.1‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{15}N$ and was established by analyzing eight peptone standards throughout each run of 50 samples.

Turnover rate modeling

Turnover rates were calculated as a function of days since the diet switch using the following exponential turnover equation (Tieszen et al. 1983):

$$\delta_{(t)} = \delta_f + (\delta_0 - \delta_f)e^{-ct} \quad (2)$$

where $\delta_{(t)} = \delta^{13}C$ or $\delta^{15}N$ (‰) at time t, $\delta_f =$ the value (‰) being approached asymptotically, $\delta_0 =$ the amphipod $\delta^{13}C$ or $\delta^{15}N$ at the onset of the experiment (‰), $c =$ the fractional turnover rate constant (day^{-1}), and $t =$ time (days) since diet switch. $\delta_{(t)}$, δ_0, and t were known. By fitting the model to the data, we estimated the parameters c and δ_f for each treatment group.

Half-life (HL) was calculated as HL = ln(0.5)/c and refers to the amount of time required for the stable isotope signature of the consumer's tissues to reach a midpoint value between the equilibrium value of the consumer before the diet switch and the expected equilibrium value of the consumer on the new diet (Bosley et al. 2002).

In addition, to understand the processes governing isotopic turnover in *O. litoralis*, we used a model that partitions the fractional turnover rate, c, into two components: growth and metabolic turnover according to Hesslein et al. (1993):

$$\delta_{(t)} = \delta_f + (\delta_0 - \delta_f)e^{-(g+m)t} \quad (3)$$

where $g =$ the growth rate in day^{-1} and $m =$ the metabolic turnover rate in day^{-1}.

The growth rate was calculated as $g = \ln(W_f/W_0)/t$, where W_f is the amphipod wet weight at time of sampling, and W_0 is the initial amphipod weight at the start of the experiment. The sum of (g + m) corresponds to the constant, c, and describes total isotopic change resulting from both growth (g) and metabolic turnover (m). Final equilibrium values (δ_f) estimated using Eq. 1 were used in Eq. 2.

Statistical analysis

Most statistical analyses were performed in SYSTAT version 6.0 (SPSS, Evenston, Ill.). The estimates of c and m were obtained using nonlinear, iterative least squares minimization techniques. Differences in isotopic turnover between temperature treatments were tested using a likelihood ratio test (Haddon 2001). We performed a power analysis to identify the sample size needed for significant differences in the mean final $\delta^{13}C$ ratio for the medium and highly enriched feeds based on our results. A t-test comparison between initial (first two sampling events) and final $\delta^{13}C$ (last two sampling events) for Exp. 1 (highly enriched and fasting) and Exp. 2 (highly enriched) was done with the statistics tool package of Microsoft Excel.

Results

Growth and mortality

Growth rates of fed *O. litoralis* in Exp. 1 ranged from 0.4 to 0.6 mg/day and were similar among the fed treatments (Table 1), with no significant difference between the fed treatments at 1 and 4°C (t-test, P 0.310). Unfed amphipods grew significantly slower than amphipods in the fed treatments (t-test, $P \leq 0.0001$). Amphipods in Exp. 2 experienced little growth, with mean growth rates significantly lower than those for Exp. 1 (t-test, $P < 0.001$). Mortality during both experiments was between 2 and 4% in all treatments with at least one animal in each tank surviving until sampling, so no replicates were lost.

C and N turnover

In Exp. 1, initial amphipod $\delta^{13}C$ and $\delta^{15}N$ values averaged for all treatments were −21.6 (±1.2) and 13.2 (±0.8)‰, respectively, reflecting their natural diet in the field (Table 2).

The $\delta^{13}C$ and $\delta^{15}N$ values of the amphipods in all fed treatments of Exp. 1 approached those of their experimental diets asymptotically toward the end of the 9-week experiment (Fig. 1). For C, these asymptotic values were, on average, approximately 10‰ below the $\delta^{13}C$ values of the enriched diets. For N, these asymptotic values ranged from 9.7‰ (moderate diet) to 10.6‰ (high and control diets), suggesting a large trophic enrichment of 6–8‰. In

Table 2 Initial and final amphipod $\delta^{13}C$ and $\delta^{15}N$ values for Exp. 1 and 2. t_0 Initial isotope value, t_f final isotope value ($n = 5$ for all samples)

Exp.	Treatment	T (°C)	$\delta^{13}C$ Amphipod (t_0) Mean ± SD	$\delta^{13}C$ Amphipod (t_f) Mean ± SD (‰)	$\delta^{15}N$ Amphipod (t_0) Mean ± SD (‰)	$\delta^{15}N$ Amphipod (t_f) Mean ± SD (‰)
1	High $\delta^{13}C$	1	−22.0 ± 1.0	8.0 ± 4.8	13.2 ± 0.8	10.6 ± 0.4
1	High $\delta^{13}C$	4	−20.7 ± 1.6	10.3 ± 4.7	13.1 ± 0.8	9.7 ± 0.2
1	Moderate $\delta^{13}C$	1	−21.8 ± 1.2	−18.0 ± 0.7	14.1 ± 0.5	10.6 ± 0.4
1	Control	1	−22.0 ± 0.9	−22.9 ± 0.6	12.5 ± 0.0	11.4 ± 0.6
1	Fasting	1	−21.7 ± 1.5	−21.4 ± 1.1	13.2 ± 0.4	14.1 ± 0.7
2	High $\delta^{13}C$	1	−19.6 ± 0.6	7.9 ± 14.4	15.9 ± 0.6	19.9 ± 0.6
2	Control	1	−20.1 ± 1.2	−20.8 ± 0.7	15.4 ± 0.5	12.3 ± 0.4

Exp. 2, amphipods did not reach asymptotic values by the end of the 10 weeks (Fig. 2). C turnover in the two "high" $\delta^{13}C$ treatments of Exp. 1 was faster at 4°C (HL = 13.9 days) than at 1°C (HL = 18.7 days; Table 3); however, the difference was not significant (likelihood ratio, $\chi^2 = 4.778$, $P = 0.114$). N turnover was similar among the fed treatments in Exp. 1, with HL ranging from 20.4 to 22.4 days. No temperature effect was observed for N. C turnover could not be estimated for the treatment receiving the moderately enriched diet (diet 2) because the difference between the $\delta^{13}C$ diet and the initial amphipod $\delta^{13}C$ (approximately 5‰) could not resolve the isotopic dynamics from the background variability (Fig. 1e). The rate of $\delta^{15}N$ turnover was similar to that found for the highly enriched treatments. Fasting amphipods exhibited no change in $\delta^{13}C$ over the course of the experiment (Fig. 1g), while $\delta^{15}N$ showed a 3.3‰ enrichment from week 1 [12.6 (±1.1)‰] to week 5 [15.9 (±3.2)‰; Fig. 1h]. A linear regression of the $\delta^{15}N$ change over time showed a significant increase ($r^2 = 0.34$, $P < 0.0001$) from weeks 1 to 5, but no change was detected in $\delta^{15}N$ from week 6 through the end of the experiment ($r^2 = 0.09$, $P = 0.07$). The control group showed no change in $\delta^{13}C$. The C/N ratio of the fed animals in Exp. 1 did not change significantly (t-test) between the initial mean (5.9 ± 3.4) and the final mean (6.0 ± 0.1). However, in the fasting treatment, C/N ratios significantly (t-test, $P < 0.001$) decreased from 7.0 ± 1.1 initially to 5.2 ± 0.7.

In Exp. 2, amphipods did not equilibrate with diets 1 and 3 during the 10-week experiment (Fig. 2a, b, d). Isotopic variability between individuals was greater in Exp. 2 than in Exp. 1, and the exponential models fit the data poorly, causing lower confidence in the estimated rate constants for Exp. 2. However, they are reported here for comparison to Exp. 1 and to illustrate the magnitude of difference in fractional turnover rates between the two experiments. The estimated C turnover rate for the highly enriched treatment [$c = 0.009$ (±0.002) day^{-1}, HL = 77.0 days] was 75% slower than C turnover in Exp. 1 at the same temperature. Amphipods receiving the highly enriched diet did not approach an asymptotic $\delta^{15}N$ value; therefore a N turnover rate could only be calculated for the control group [$c = 0.006$ (±0.001) day^{-1}, HL = 115.5 days]. Amphipods receiving the non-enriched diet as a control maintained constant $\delta^{13}C$ values, with less than 0.8‰ difference between the initial [−20.1 (±0.9)‰] and the final [−20.8 (±0.7)‰] mean $\delta^{13}C$ (Fig. 2c). The C/N ratios in the animals fed with highly enriched feed was significantly lower (t-test, $P = 0.05$) at the end of the experiment (5.6 ± 0.3) when compared to the start (6.3 ± 0.6).

Metabolic turnover vs. growth

Relative to total isotopic change ($g + m$), metabolic turnover (Table 3) was responsible for 84–89% of the observed change in C and 74–77% of the observed isotopic change in N in Exp. 1 (Fig. 3a–d). In Exp. 2 metabolic turnover was slower. However, as total observed isotopic change was also slower, the relative contribution of metabolic turnover was similar to Exp. 1, accounting for 89% of C and 67% of N turnover in Exp. 2 (Fig. 4).

Discussion

Turnover in *O. litoralis* was relatively rapid despite slow growth (Table 4). Our data indicate that metabolic turnover (Hobson and Clark 1992), not growth (Fry and Arnold 1982), was the dominant process causing isotopic change. This is in contrast to observations in rapidly growing ectotherms where isotopic change is usually dominated by growth (Herzka and Holt 2000; Bosley et al. 2002; Jardine et al. 2004) and in agreement with data from non- or slow-growing endotherms (Hobson and Clark 1992; MacAvoy et al. 2005). We found that metabolic turnover accounted for the majority (75–90%) of isotopic change in *O. litoralis* at low temperatures similar to field conditions. These rates are high compared to those of other ectothermic taxa, particularly in light of the low ambient temperatures

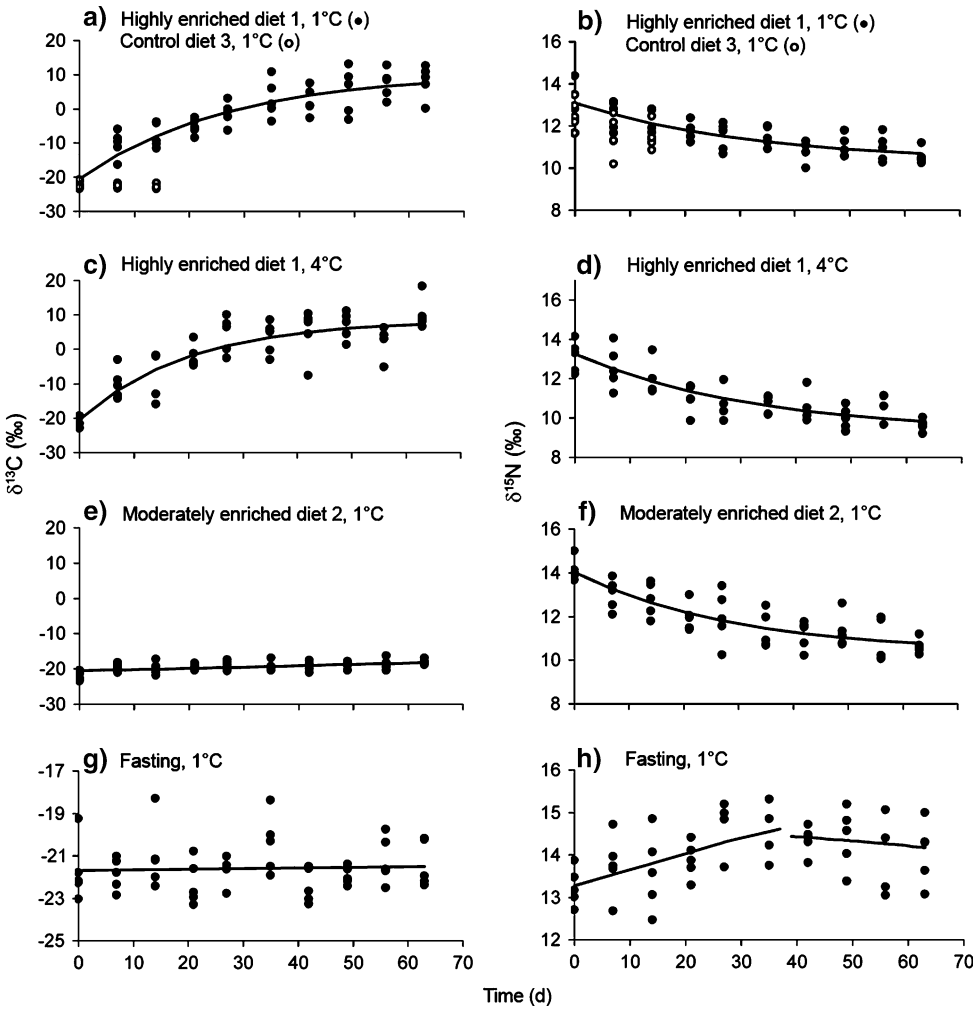

Fig. 1a–h Changes in δ^{13}C and δ^{15}N in *Onisimus litoralis* amphipods on highly enriched, moderately enriched or control diets, and while fasting as a function of time since the diet shift (experiment 1). **a–f** *Lines* represent best fit nonlinear regression. For fasting plots *lines* represent least squares regression with separate regression lines in δ^{15}N plot for weeks 1–7 and 7–9. **g**, **h** Note the expanded *y*-axis scale. *d* Days

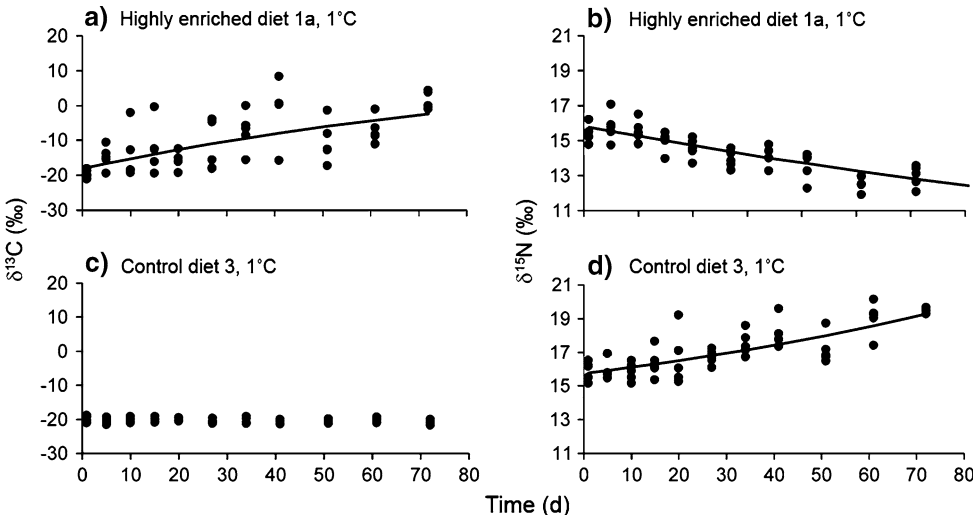

Fig. 2 Changes in δ^{13}C and δ^{15}N in *O. litoralis* amphipods on **a**, **b** highly enriched or **c**, **d** control diets at 1°C as a function of time since the diet shift (experiment 2). *Lines* represent best fit nonlinear regression. The model was unable to resolve a solution for the change in δ^{15}N in amphipods receiving diet 1a, therefore no turnover rate was calculated for **b**

(Hesslein et al. 1993; Frazer et al. 1997; Herzka and Holt 2000), and are among the fastest rates reported for an ectotherm (Jardine et al. 2004). This dominance of metabolic turnover in *O. litoralis* isotopic change might be typical of polar ectotherms that tend to grow slowly (Peck 2002).

Determination of turnover rates largely depends on sufficient difference between the initial isotopic value of the

Table 3 Isotopic change constants (c) and corresponding half-lives (HL) calculated according to Tieszen et al. (1983)

Exp.	Treatment	T (°C)	Element	c (day^{-1}) ± SE	HL (day)	m^a (day^{-1}) ± SE	Hesslein's g^a (mg day^{-1}) ± SE
1	High δ^{13}C	1	^{13}C	0.037 ± 0.009	18.7	0.033 ± 0.003	0.007 ± 0.001
1	High δ^{13}C	4	^{13}C	0.050 ± 0.012	13.9	0.042 ± 0.005	0.009 ± 0.001
1	High δ^{13}C	1	^{15}N	0.031 ± 0.013	22.4	0.024 ± 0.003	0.007 ± 0.001
1	High δ^{13}C	4	^{15}N	0.031 ± 0.013	22.4	0.023 ± 0.003	0.009 ± 0.001
1	Moderate δ^{13}C	1	^{15}N	0.034 ± 0.013	20.4	0.026 ± 0.003	0.008 ± 0.001
2	High δ^{13}C	1	^{13}C	0.009 ± 0.002	77.0	0.008 ± 0.001	0.002 ± 0.000
2	Control	1	^{15}N	0.006 ± 0.001	115.5	0.004 ± 0.000	0.002 ± 0.001

[a] Metabolic turnover rate (m) and growth rate (g) constants calculated using the model from Hesslein et al. (1993) for relative contribution of metabolic turnover to total observed isotopic change in *O. litoralis*

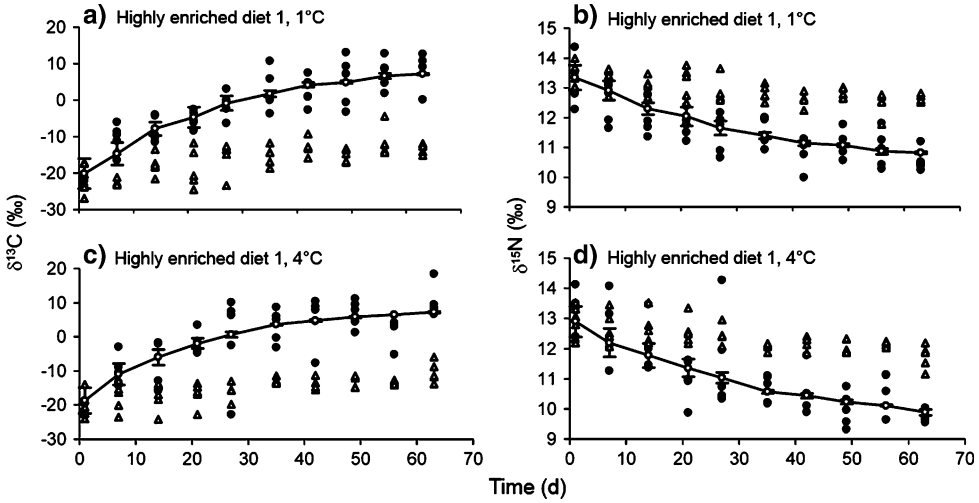

Fig. 3 Relative contribution of metabolic turnover to isotopic change in *O. litoralis* amphipods on highly enriched diets at 1°C (**a**, **b**) and 4°C (**c**, **d**) (experiment 1). Experimental observations (*filled circle*) are plotted with predicted data points based on growth alone (no metabolic turnover, *open triangle*). *Lines* represent theoretical curves describing fractional turnover (growth + metabolic turnover). *Lines* are means ± SD of five theoretical data points calculated using the model from Hesslein et al. (1993)

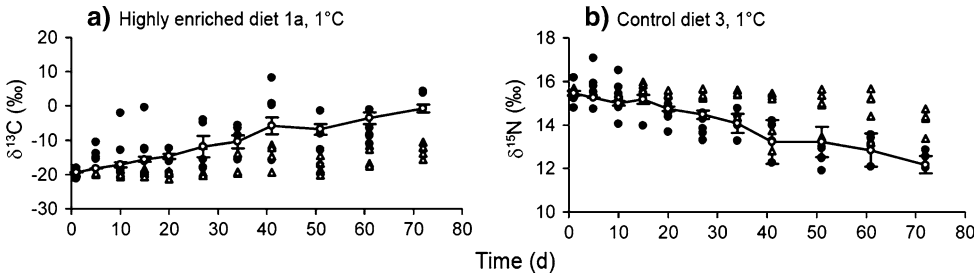

Fig. 4 Relative contribution of metabolic turnover to isotopic change in *O. litoralis* amphipods on **a** highly enriched and **b** control diets (experiment 2). Experimental observations (*filled circle*) are plotted with predicted data points based on growth alone (no metabolic turnover, *open triangle*). *Lines* represent theoretical curves describing fractional turnover (growth + metabolic turnover). *Lines* are means ± SD of five theoretical data points calculated using the model from Hesslein et al. (1993)

species of interest and the isotopic value of the experimental feed. Natural isotopic variability and analytical error associated with isotope measurements can limit the ability to estimate metabolic turnover (Fry and Arnold 1982). In our experiments, the moderately enriched diet 2 in Exp. 1 was approximately 5‰ δ^{13}C more enriched than initial amphipod values, but this difference was overwhelmed by the natural and experimental variability of amphipod δ^{13}C values. A power analysis (based on power of 0.9 and $P = 0.05$) based on the final δ^{13}C of our experiments

Table 4 Published isotopic change and metabolic turnover rates for comparison. *BW* Body weight; for other abbreviations, see Table 3

Organism	*T* (°C)	Growth (day^{-1})	*c* (day^{-1})		HL (days)		Study
			C	N	C	N	
Crustacean (Krill; *Euphausia superba*)	−1.5	140	–	–	–	–	Frazer et al. (1997)
Crustacean (Krill; *Euphausia superba*)	1.5	70	–	–	30.4	25	Frazer et al. (1997)
Crustacean (*Onisimus litoralis*; spring)	1	180	0.037	0.013	18.7	22.4	This study
Crustacean (*Onisimus litoralis*; spring)	4	130	0.05	0.013	13.9	22.4	This study
Crustacean (*Onisimus litoralis*; autumn)	1	>300	0.009	0.006	77	115.5	This study
Mollusc (snail; *Tarebia granifera*)	20–27	–	–	0.034	–	20.2	McIntyre and Flecker (2006)
Mollusc (snail; *Lavigeria grandis*)	25–27	–	–	0.014	–	49.5	McIntyre and Flecker (2006)
Amphibian (tadpole; *Rana palmipes*)	20–27	–	–	0.005	–	138.6	McIntyre and Flecker (2006)
Fish (*Ancistrus triradiatus*)	20–27	–	–	0.038	–	18.2	McIntyre and Flecker (2006)
Fish (*Paralichthys olivaceus*; mean BW 0.26 g)	14.8–18.9	3–7	0.04–0.05	–	14–17	–	Tominaga et al. (2003)
Fish (*Paralichthys olivaceus*; mean BW 1.06 g)	14.8–18.9	<6	0.14	–	5	–	Tominaga et al. (2003)
Fish (*Lateolabrax japonicus*)	23	35[b]	0.033	0.036	21	19.3	Suzuki et al. (2005)
Fish (*Oncorhynchus nerka*; BW 9 to 15 g)	10–13	26.7[b]	–	0.048	–	14.4	Sakano et al. (2005)
Fish (*Oncorhynchus nerka*; BW 71 to 170 g)	10–14	86.6[b]	–	0.04	–	17.3	Sakano et al. (2005)
Fish (*Oncorhynchus nerka*; BW 169 to 308 g)	10–15	231.0[b]	–	0.017	–	40.8	Sakano et al. (2005)
Fish (*Salmo salar*)	–	69.3[b]	–	–	71.9	–	Jardine et al. (2004)
Fish (*Salmo salar*)	–	86.6[b]	–	–	21.9	–	Jardine et al. (2004)
Fish (*Salmo salar*)	–	173.3[b]	–	–	19.2	–	Jardine et al. (2004)
Fish (*Rhinogobius* sp.)	–	>30[c]	–	–		33–99	Maruyama et al. (2001)
Fish (*Sciaenops ocellatus*)	24	1–2[c]	–	–	<2	<2	Herzka and Holt (2000)
Fish (*Sciaenops ocellatus*)	28	1–2[c]	–	–	<2	<2	Herzka and Holt (2000)
Fish (*Pseudopleuronectes americanus*)	13	<8[c]	0.17	0.18	4.1	3.9	Bosley et al. (2002)
Fish (*Pseudopleuronectes americanus*)	18	<8[c]	0.32	0.22	2.2	3.1	Bosley et al. (2002)
Fish (*Paralichthys dentatus*; larvae)	13	<2	0.08	0.09	9.2	7.5	Witting et al. (2004)
Fish (*Paralichthys dentatus*; larvae)	22	<3	0.24	0.22	2.9	3.2	Witting et al. (2004)
Fish (*Paralichthys dentatus*; young juvenile)	13	<4	0.06	0.05	11.6	13.6	Witting et al. (2004)
Fish (*Paralichthys dentatus*; young juvenile)	22	<2	0.14	0.11	5	6.1	Witting et al. (2004)
Fish (*Paralichthys dentatus*; older juvenile)	13	<9	0.04	0.01	16.9	70[a]	Witting et al. (2004)
Fish (*Paralichthys dentatus*; older juvenile)	22	<8	0.12	0.01	6	70[a]	Witting et al. (2004)
Fish (*Ictalurus furcatus*)	11–19	77–187.5[b]	<0.004	<0.004	>173	>173	MacAvoy et al. (2001)

[a] Values calculated using the HL equation; HL = ln(0.5)/*c*, where *c* is the isotopic change constant including change attributed to both growth and metabolic turnover

[b] Value calculated using published growth rate constants (*k*) and applying the equation; growth rate (doubling time) = ln 2/*k*

[c] Values estimated from published plots in original literature references

revealed that 46 replicates would have been needed at each sampling event with the moderately enriched feed to detect significant differences between initial and final values. This is higher than our number of ten replicates (five control, five experimental feed) and explains why C turnover rate could not be calculated for this treatment. This is in striking contrast to the comparison of the initial and final values for the highly enriched feed, where a smaller number of replicates (only three replicates per group: control/enriched feed) would have been sufficient to detect significant differences (power of 1, $P = 0.05$).

The final $\delta^{13}C$ values reached by the experimental amphipods receiving the highly enriched diets were approximately 10‰ lower than the diet. We consider two possibilities that could account for this discrepancy. First, we reject the possibility that C fractionation could have been higher than the commonly found 0–1‰ (Peterson and Fry 1987), as *O. litoralis* fed the same commercial feed used in the current experiments (without enriched ice algae) showed a fractionation of 0–1‰. Alternatively, the multi-component nature of the experimental diets used in this study (enriched ice algae and a commercial algal-based

fish food) may have caused this finding. The loss of enrichment could be explained by leaching of inorganic ^{13}C from the pellets or by differential assimilation rates among the feed components via selective feeding or assimilation processes. This possibility highlights the advantage of using a single-component experimental diet, as recently suggested by Yokoyama et al. (2005).

In diet-switch experiments, final equilibrium values are typically determined by adding a fractionation factor to the value of the diet (Frazer et al. 1997; Jardine et al. 2004). In this study, final equilibrium $\delta^{13}C$ and $\delta^{15}N$ values were obtained by fitting the Tieszen et al. (1983) model to the data and estimating the asymptotic values being approached by the amphipods (δ_f). We recommend our approach because of the following advantage. Though there are generally accepted ranges, C and N fractionation rates vary between individual consumers and can be unpredictable because they are affected by factors such as food type and physiological state (McCutchan et al. 2003; Yokoyama et al. 2005). Using experimentally determined end equilibrium values avoids the necessity of assigning arbitrary fractionation factors.

The fasting animals in our experiments did not change their $\delta^{13}C$ over the 9-week period, which is consistent with previous studies on fish (*Salmo salar*, Jardine et al. 2004), mysids (*Mysis mixta* and *Neomysis integer*, Gorokhova and Hansson 1999), and Antarctic krill (Frazer et al. 1997). However, other studies showed that starving animals can show a progressive enrichment in ^{13}C or ^{15}N as the lighter isotopes are preferentially excreted in the catabolism of body tissues (Hobson et al. 1993; Gannes et al. 1997). Unlike $\delta^{13}C$ *O. litoralis* exhibited starvation related changes in $\delta^{15}N$, which became enriched over the first 5 weeks of the experiment, after which the curve flattened. We propose that this change after 5 weeks was related to a delayed conservation of somatic N after a prolonged period without food, similar to the energy conservation strategy of the pelagic Arctic amphipod *Themisto libellula* (Percy 1993). The significant decrease in the C/N ratios in the starving animals supports the idea that C and N metabolism, and therefore turnover rates in those two elements, differed during the periods of starvation, with higher somatic N than C retention.

The rate of isotopic change was nearly an order of magnitude slower in Exp. 2 versus Exp. 1. This difference requires that both growth and metabolic turnover be dramatically suppressed in late-summer animals relative to animals collected in the spring. Indeed, growth rates were an order of magnitude slower in Exp. 2 than Exp. 1, and we infer that metabolic turnover was similarly reduced. The fastest growth rates for *O. litoralis* in the southwestern Beaufort Sea occur in late May at the peak of ice algal production (Boudrias and Carey 1988), the main food at this time (Carey and Boudrias 1987). Our data on turnover and growth both suggest a slower metabolism in summer, but previous studies have not found evidence for this strategy in other *Onisimus* species (Collie 1985; Werner and Auel 2005; Arndt and Beuchel 2006). Both a change from summer to winter conditions and the lack of appropriate food affect metabolism and growth rates in polar crustaceans (Chapelle and Peck 1995; Attkinson et al. 2002). We propose that the contrast between Arctic nearshore summer field conditions (24 h daylight and up to 9°C seawater temperatures) and laboratory conditions (24 h darkness and 1°C seawater) in Exp. 2 essentially amounted to an artificially introduced summer/winter transition. Antarctic krill reduce their metabolism in the austral winter as an energy saving strategy (Attkinson et al. 2002), and the Antarctic under-ice amphipod *Paramoera walkeri* had a reduced growth rate during winter that was attributed to low food availability during the winter period (Rakusa-Suszczewski 1972). Our results suggest a similar metabolic suppression in *O. litoralis*, although we consider the meal sizes provided appropriate. Meal sizes in *O. litoralis* from Frobisher Bay, maintained at 2°C, ranged from 0.6–1.6 mg dry weight after starvation for 2–15 days (Sainte-Marie et al. 1989). Therefore, the amount provided every 3 days in our experiments would supply at least eight meals with starvation times of 9 h or less (assuming feeding was similar between the studies).

While *O. litoralis* has a primarily algal diet in the spring, its summer diet consists of a mixture of plant material and carrion (Carey and Boudrias 1987; Sainte-Marie 1989). It is possible that the experimental diet offered to the amphipods supported growth sufficiently in the first experiment but was lacking in important components for amphipods collected during open water conditions. While we were trying to keep variables constant between the two experiments, a parallel experiment under conditions more consistent with in situ open water field conditions would have been desirable for determining rates of growth, metabolism, and isotopic change at that time. Based on Boudrias and Carey's (1988) finding that *O. litoralis* growth is fastest in late May, the small temperature effect found in this study (but larger effects found in other studies), and the mean temperature in the nearshore Beaufort Sea ranging around 4°C (Weingartner et al. 2005) (not 9°C as in the point sampling in our study), we would expect that turnover in such an open water experiment would be somewhat similar to and not much faster than our first experiment.

The effect of temperature on growth and isotopic turnover on *O. litoralis* in Exp. 1 was minor compared to other marine invertebrates in general (Hochachka and Somero 2002) and more specifically to Antarctic krill (Frazer et al. 1997), which had significantly slower C turnover at –1.5°C

compared to 1.5°C. The different responses between the Arctic and Antarctic species is likely related to differences in the temperature regime with stable temperatures (−1.96° to 1.64°C; Robertson et al. 2001) and narrow physiological temperature tolerance in offshore Antarctica (McWhinnie 1964). In contrast, *O. litoralis* experiences a wider range of seasonal temperatures in shallow coastal Arctic waters. Slower growth and slower C turnover in amphipods at 1°C compared to 4°C, although not statistically significant, suggests that both processes are temperature sensitive in this species but beyond the detection limit with our approach. Using a Q_{10} approach (Schmidt-Nielsen 1997) to estimate the in situ under-ice turnover rate (with a Q_{10} of 2.69 calculated for C turnover between the experimental temperatures 1 and 4°C), a C HL of 24.6 days is expected at −1.8°C, approximately 6 days slower than at 1°C.

Our present study shows that in the spring, a diet switch (e.g., from isotopically heavy ice algae to lighter phytoplankton) can be reflected in the tissues of *O. litoralis* within 4 weeks, given sufficient difference in isotope composition between the diets and a sufficient number of replicates (see power analysis above). The slower isotopic turnover rates observed in *O. litoralis* collected in September suggest that *O. litoralis* will integrate their diet composition over a period of months and reduce the temporal resolution under conditions applied in Exp. 2 (see discussion about artificial winter conditions above). However, experimental conditions of Exp. 2 probably underestimated actual growth and metabolic turnover in *O. litoralis* in the field at that time given that similar Arctic amphipods, including two sympagic *Onisimus* species (*Onisimus nanseni* and *Onisimus glacialis*), continue to grow and mature at this time (Collie 1985; Arndt and Beuchel 2006).

Based on previous work and assumptions about low physiological rates in polar species, metabolic turnover rates found here are higher than what would have been predicted for a polar ectotherm (Chapelle and Peck 1995; Peck 2002). These results highlight the risk of generalizing isotopic turnover in organisms based on physiology, taxon, and environmental temperatures and stress the need for experimental investigations of stable isotope dynamics in species of interest to accurately interpret isotopic data from the field. Additionally, the wide range of HL found for *O. litoralis* in the two experiments suggests that C and N turnover rates may be seasonally variable.

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