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Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*

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Abstract

The ability of the cold-water coral *Lophelia pertusa* to exploit different food sources was investigated under standardized conditions in a flume. All tested food sources, dissolved organic matter (DOM, added as dissolved free amino acids), bacteria, algae, and zooplankton (*Artemia*) were deliberately enriched in ^{13}C and ^{15}N. The incorporation of ^{13}C and ^{15}N was traced into bulk tissue, fatty acids, hydrolysable amino acids, and the skeleton (^{13}C only) of *L. pertusa*. Incorporation rates of carbon (ranging from 0.8–2.4 $\mu g\,C\,g^{-1}\,DW\,d^{-1}$) and nitrogen (0.2–0.8 $\mu g\,N\,g^{-1}\,DW\,d^{-1}$) into coral tissue did not differ significantly among food sources indicating an opportunistic feeding strategy. Although total food assimilation was comparable among sources, subsequent food processing was dependent on the type of food source ingested and recovery of assimilated C in tissue compounds ranged from 17 % (algae) to 35 % (*Artemia*). De novo synthesis of individual fatty acids by *L. pertusa* occurred in all treatments as indicated by the ^{13}C enrichment of individual phospholipid-derived fatty acids (PLFAs) in the coral that were absent in the added food sources. This indicates that the coral might be less dependent on its diet as a source of specific fatty acids than expected, with direct consequences for the interpretation of in situ observations on coral nutrition based on lipid profiles.

1 Introduction

Cold-water corals (CWC) form reef structures in the cold and deep oceanic waters around the world (Davies and Guinotte, 2011; Roberts et al., 2009b). These reefs form hotspots of biodiversity (Roberts et al., 2006) and are important in carbon cycling along continental margins (van Oevelen et al., 2009). The high metabolic demand of CWC communities implies high food processing rates and indeed a close relationship between food availability and the occurrence of CWC reefs has been reported in many studies (Roberts et al., 2006; Thiem et al., 2006).

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In the North Atlantic Ocean, CWC reef communities are primarily formed by the scleractinian coral *Lophelia pertusa* (Roberts et al., 2006). Recent in situ investigations using stable isotope and fatty acid analyses point to a close coupling of *L. pertusa* with pelagic resources such as zooplankton and phytodetritus (Duineveld et al., 2004; Kiriakoulakis et al., 2005; Spiro et al., 2000). While tidal pumping (Davies et al., 2009) and internal waves (Duineveld et al., 2004; Frederiksen et al., 1992) deliver a diverse range of particles to the coral, ranging from fresh to resuspended material, the vertical migration (daily or seasonal) of zooplankton can also contribute to the linkage between surface-water production and CWC nutrition (Dodds et al., 2009; Hind et al., 2000; Valle-Levinson et al., 2004).

Although organic food sources of various size, type and quality reach the cold-water coral reefs, very little is currently known about their importance to the metabolism of CWCs or the biogeochemical processing that occurs following nutritional uptake. Analysis of natural stable isotope signatures in tissues allow insight into the coral nutrition as described above (Dodds et al., 2009; Duineveld et al., 2004; Kiriakoulakis et al., 2005; Roberts et al., 2009a; van Oevelen et al., 2009), but to enhance the resolution of bulk tissue isotope data, fatty acids are often used as biomarkers in these studies (Dodds et al., 2009; Duineveld et al., 2012; Kiriakoulakis et al., 2005). However, the processing and production of fatty acids by CWCs has not yet been studied. This limits their interpretation since the use of fatty acids as biomarker for a specific food source critically depends on the assumption that these markers cannot be synthesized by the consumer itself (Kelly and Scheibling, 2012).

Feeding studies of *L. pertusa* so far have focused on uptake rates of *Artemia salina* (Purser et al., 2010; Tsounis et al., 2010) in the laboratory, but other food sources and particle sizes below 100 µm have not been considered yet. The nutritional importance of a food source does not only depend on its availability, but also on uptake and physiological processing by *L. pertusa*. In addition to particulates, dissolved resources may also contribute to coral dietary requirements. For tropical corals, it is known that dissolved organic matter (DOM) can be an important food source even under low ambi-

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ent DOM concentrations (Grover et al., 2006, 2008; Hoegh-Guldberg and Williamson, 1999). Recently, Naumann et al. (2011) reported DOM uptake by the CWC *Desmophyllum dianthus*, thus DOM may also form an additional resource for *L. pertusa* that has not been accounted for so far.

In addition to a demand of organic resources for energy and tissue growth, *L. pertusa* also needs an inorganic carbon source to sustain calcification. Two carbon sources are possibly involved in the calcification process in corals: dissolved inorganic carbon (DIC) from the surrounding seawater or metabolically generated CO_2. While calcification in tropical zooxanthellae scleractinian corals is mainly (70–75 %) based on metabolic CO_2 (Furla et al., 2000), the opposite seems to be true for the azooxanthellaete octocoral *Leptogorgia virgulata* (Lucas and Knapp, 1997). Based on stable isotope data ($\delta^{18}O$, $\delta^{13}C$), Adkins et al. (2003) suggested that C for calcification in azooxanthellae scleractinian CWCs is primarily derived externally rather than metabolically. Direct measurements distinguishing between the different calcification pathways in CWCs are however not available.

In this study we used standardized food quantities in a laboratory setting to trace the incorporation of stable isotope labelled food sources (^{13}C and ^{15}N) to measure food uptake rates and potential preferences by the CWC *L. pertusa*. Different food sources were selected to cover different particle sizes and nutritional values (C : N ratio), comprising dissolved organic matter, bacteria, algae and zooplankton (*Artemia*). Following food uptake we traced ^{13}C and ^{15}N into two of the most important biochemical components, hydrolysable amino acids (HAAs) and lipids represented by the sum of total fatty acids (TFAs) to follow metabolic processing. Within the lipid pool we especially followed food-derived C further into phospholipid-derived fatty acids (PLFAs) to have a more detailed look into the synthesis of structural and therefore functional fatty acids. Additionally, we traced food-derived C into the coral skeleton to investigate the metabolic contribution to coral calcification.

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2 Methods

2.1 Sampling location and maintenance

All corals used in the experiment were harvested at the Tisler Reef, one of the largest and shallowest inshore reefs known so far. It is located at a depth of 70 to 155 m in the Skagerrak, on a sill forming the submarine border between Norway and Sweden. The current velocity over the reef varies from 0 to 50 cm s^{-1} throughout the year while the flow direction fluctuates irregularly between NW and SE (Lavaleye et al., 2009; Wagner et al., 2011). The amount and quality of particulate organic carbon (POC) entering the reef depend on the location within the reef, and concentrations vary between 43 to 106 µg POC L^{-1} (Wagner et al., 2011). Temperature at the reef site typically fluctuates between 6 and 9 °C throughout the year (Lavaleye et al., 2009; Wagner et al., 2011).

Corals were collected from a depth of 117 m (58°59 800′ N 10°58 045′ E) using an ROV (Remotely Operated Vehicle, Sperre Subfighter 7500 DC). Within a few hours after sampling, corals were transported in cooling boxes filled with cold seawater (7–8 °C, salinity 31) to the laboratory at the Sven Lovén Centre for Marine Sciences, Tjärnö, Sweden. Until the start of the experiment (3 months), corals were kept in a dark thermostated room at 7 °C with a flow through of sand-filtered bottom water from 45 m depth in the adjacent Koster-fjord (7–8 °C, salinity 31). During this time the corals were fed with larvae (nauplii) of the Brine Shrimp *Artemia spp.* every 3 to 4 days. The Sven Lovén Centre has kept *L. pertusa* alive and growing under these conditions for a number of years.

Coral samples used in this experiment were clipped to approximately the same size with 4.5 ± 1.9 g dry weight (DW) and 8 ± 4 polyps per fragment (average ± SD) about a week before the experiments started.

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2.2 Preparation of particulate labelled substrates

CWCs are thought to thrive mainly on particulate organic matter (Duineveld et al., 2012). To test for assimilation of different food particle sizes, we chose bacteria to represent picoplankton and microalgae to represent nanoplankton. *Artemia nauplii* were chosen to represent mesozooplankton because they can be cultured in high densities, are the essential food source for successfully keeping *L. pertusa* in the laboratory and have been used in earlier cold-water coral feeding studies (Naumann et al., 2011; Purser et al., 2010; Tsounis et al., 2010). While DOM was added in the form of a commercially available algal-derived mixture of dissolved free amino acids (Cambridge Isotopes, U ^{13}C 97–99 %, U ^{15}N 97–99 %, CNLM-452-0.5), the labelled POM food sources were prepared by culturing the respective organisms in the presence of ^{13}C and ^{15}N labelled substrates. A natural community of bacteria was derived from a few ml of natural seawater, obtained from the Oosterschelde estuary (salinity 30) in the SW of the Netherlands. The water sample was added to 1 L culture medium (M63) containing 0.02 mol L^{-1} glucose (10 atom % ^{13}C, Cambridge Isotopes) and 0.01 mol L^{-1} ammonium chloride (10 atom % ^{15}N, Cambridge Isotopes). After 3 days of culturing in the dark, bacteria were concentrated by centrifugation (14 500 g) and rinsed with 0.2 µm filtered seawater to remove residual labelled substrates. Bacteria in the concentrate were kept frozen until use in the experiment.

The diatom *Skeletonema costatum* was cultured axenically in 4 L F/2 culture medium containing 0.8 mmol L^{-1} $NaNO_3$ (10 atom % ^{15}N, Cambridge Isotopes) and 2 mmol L^{-1} $NaHCO_3$ (20 atom % ^{13}C, Cambridge Isotopes, 99 % ^{13}C). After 3 weeks of culturing in 12 h light 12 h dark cycles (at a cell density of around 3–4 $\times 10^6$ cells mL^{-1}), algae were concentrated by centrifugation at 450 g, rinsed three times with 0.2 µm filtered seawater to remove residual labelled substrates and kept frozen until use in the experiment.

For culturing ^{13}C and ^{15}N enriched *Artemia nauplii*, 6 × 0.1 g *Artemia* cysts (Sera) were incubated in 5 L incubation chambers filled with 0.2 µm filtered seawater under

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natural light conditions and light aeration. After the larvae had developed to the state that they take up particulate food (1 to 2 days after eclosion of larvae), they were fed every second day with around 7 to 10 mg C derived from ^{13}C and ^{15}N enriched pre-cultured algae (cultured as described above, 4 atom % ^{13}C, 10 atom % ^{15}N). The uptake of algae by *Artemia* was visually confirmed under the microscope. After seven days of feeding, the larvae were concentrated by filtration, rinsed with filtered seawater, counted under the binocular and stored frozen. Within the filtrate, different early larvae stages could be identified.

To standardize the amount of carbon added to the incubations, all substrates were measured for carbon and nitrogen content. ^{13}C and ^{15}N enrichment and the fatty acid composition (PLFAs) of organic food sources were also measured to trace and calculate coral food uptake (see below for methodological description).

2.3 Experimental set up and procedure

During the incubations, corals were placed in recirculation flumes (60 L) in a thermostated room at 7 °C (Fig. 1). Water circulation was maintained by a motor-driven propeller situated in the returning pipe (for more details see Purser et al., 2010). Prior to the experiment, the flume was filled with 0.2 µm filtered seawater from 45 m depth out of the Koster-fjord (salinity 33, 7 °C, pH 7.9 on NBS) and the motor was set to ensure a flow speed of 7 cm s^{-1}, which is within the natural range found at the Tisler Reef (Lavaleye et al., 2009; Wagner et al., 2011).

Three coral fragments were randomly selected and placed in the test section of each flume (Fig. 1). The three pieces were gently inserted into a 1 cm elastic silicone tube on an acrylic plate that could be attached to the flume base (Purser et al., 2010). Corals were left in the flume for 12 h to acclimatize to the conditions. After acclimation, 10 mg C of the respective food source per treatment was gently pipetted into the water column of each flume (final concentration 170 µg C L^{-1}). Visual observations confirmed that the circulating water kept the particulate food in suspension. Each flume contained three coral pieces and each food source was replicated twice. As a control treatment, corals

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were incubated for the same time without any food addition. After an incubation time of 4 days in darkness, coral samples were frozen at −20 °C, freeze-dried and stored frozen for further analysis.

2.4 Sample treatment and analyses

After freeze-drying, coral samples were weighed and homogenized by grinding with a ball mill for 20 s (MM 2000, Retsch, Haan, Germany). A subsample of around 30 mg of ground material (organic and inorganic fraction) was transferred to pre-combusted silver boats and analyzed for isotopic ratio and C / N content using a thermo Electron Flash EA 1112 analyzer (EA) coupled to a Delta V isotope ratio mass spectrometer (IRMS). Another subsample was transferred to a silver boat, acidified stepwise with drops of increasing concentrated HCl until the inorganic C fraction was removed (no bubbling after acid addition). The remaining material was analyzed on the EA-IRMS for isotopic ratio and organic C content. Incorporation of C in the inorganic skeleton was determined by subtraction of the organic carbon fraction (tissue + organic matrix) from the total carbon pool.

Total fatty acids (TFAs) were extracted with an adjusted Blight Dyer method. A part of the total fatty acid extract was further eluted over a silica column (Merck Kieselgel 60) to isolate the phospholipid derived fatty acids (PLFAs) (Boschker et al., 1999). The TFA and PLFA extracts were then further derivatized by mild alkaline transmethylation to obtain fatty acid methyl esters (FAME). Preparation of methyl esters was carried out following the method of Boschker et al. (1999). For extraction, 0.7 g DW of coral samples, ∼ 100 µL of DOM and smaller particulate food sources, and 100 *Artemia* (equivalent to 500 µg C and 50 µg C respectively) were used. Concentration and carbon isotopic composition of individual TFAs and PLFAs were measured on a gas-chromatograph combustion-interface isotope-ratio mass spectrometer (GC-c-IRMS) according to Boschker et al. (1999).

Hydrolysable amino acids (HAAs) were extracted and analyzed following Veuger et al. (2005). Ground coral samples were first treated with 12 mol L^{-1} HCl to dissolve the

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skeleton by repeated addition of HCl drops to avoid loss of sample through bubbling. The remaining material was then hydrolyzed in 6 mol L^{-1} HCl at 110 °C for 20 h and purified by cation-exchange chromatography (Dowex 50WX8 resin). The hydrolysable amino acids were derivatized with isopropanol and pentafluoropropionic anhydride and analyzed by GC-c-IRMS for concentrations and ^{13}C and ^{15}N content.

Stable isotope data are expressed in delta notation as: δX (‰) = ($R_{sample}/R_{ref} - 1$) × 1000, in which X represents C or N, R_{sample} is the heavy/light isotope ratio in the sample (e.g. $^{13}C/^{12}C$) and R_{ref} is the heavy/light isotope ratio of the reference material (R_{ref} = 0.01118 for C and R_{ref} = 0.00368 for N). The atomic % of the heavy isotope in a sample (e.g. $^{13}C/[^{13}C + ^{12}C]$) was calculated as $F = R_{sample}/(R_{sample}+1)$. The excess (above background) atom % is the difference between the F in an experimental sample and the atom % in a background (untreated) coral sample: $E = F_{sample} - F_{background}$, so that zero values of E imply no uptake of the isotopically labelled food source and positive values indicates food uptake. To correct for differences in isotope enrichment among the food sources, the excess incorporation was divided by the atom % of each specific food source, e.g. 0.09 for bacteria C and 0.1 for bacteria N respectively. To arrive at total elemental uptake, E was multiplied with C or N content of 1 g DW sample (µg C g^{-1} DW sample, µg N g^{-1} DW sample). All results are reported as average ± SD derived from all coral pieces per treatment (n = 6).

2.5 Statistical analyses

To be able to perform statistical analyses of the obtained data we treated pseudo-replicates as true replicates if no significant different between flumes were found by using Kruskal–Wallis–Test ($p \geq 0.05$). However, all statistical values still need to be considered with care. The potential influence of food sources on C and N uptake in bulk tissue and specific components was investigated using Kruskal–Wallis–Test since a normal distribution for some data could not be achieved by data transformation. However, in cases where all requirements for an ANOVA were met, the results did not

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differ from the ones obtained by Kruskal–Wallis–Tests. Therefore we decided to use Kurskal–Wallis–Tests for all factors. Differences among treatments were then further investigated using Wilcoxon rank-sum test for pair wise comparison with an adjustment of p values by the method of Bonferroni.

3 Results

3.1 Biogeochemical characteristics of particulate food sources

All food sources were significantly isotopically enriched above background and differed considerably in food quality represented by C / N ratio and PLFAs contents as well as compositions in case of particulate organic food sources (Table 1, Fig. 2a). Accordingly, the bacteria derived PLFA pool was dominated by C 16 : 1ω7 c/t, C 16 : 0 and C 18 : 1ω7 c and the algae-derived PLFA pool by C 16 : 0, C 16 : 1ω7 c, followed by C 16 : 3ω4, C 20 : 5ω3 and C 22 : 6ω3 (Fig. 2a). *Artemia* derived-PLFAs mainly comprised C 18 : 3ω6, followed by C 16 : 0, C 18 : 1ω7 c, C 18 : 1ω9 t/c and C 18 : 2ω6 t/c (Fig. 2a).

3.2 Biogeochemical characteristics of *L. pertusa*

Corals used in this experiment had a total C content of 128 ± 5 mg C g^{-1} DW coral. This total C was partitioned into an organic tissue fraction of 13 % and inorganic skeleton fraction of 87 %. The organic C in the tissue fraction could be further partitioned into 24 % of THAAs, 7 % TFAs and 0.04 % PLFAs (Table 2). Dominant PLFAs in the coral tissue were C 16 : 0, C 18 : 0, C 20 : 4ω3, C 20 : 4ω6, C 20 : 5ω3, C 22 : 4ω6 and C 22 : 5ω3 (all > 5 %), followed by C 20 : 1ω9 c and C 22 : 1ω9 c (~ 5 %, Fig. 2b). No significant difference in coral C content in tissue, TFA or PLFA was detected between the coral pieces in the different food treatments (Kruskal–Wallis $p > 0.05$ for all comparisons). Organic N content of corals used in this experiment was 3 ± 1 mg N g^{-1} DW coral, with 12 % of the N present in the THAA fraction (Table 2). No significant difference in

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coral N content in tissue and THAA was detected between the coral pieces in the different food treatments (Kruskal–Wallis $p > 0.05$).

3.3 Total C and N assimilation

The assimilation of C from the food sources into coral tissue was not significantly different among treatments (Wilcoxon $p > 0.05$ for all comparisons, Fig. 3a). *Artemia*-derived C was assimilated at a rate of $1884 \pm 1067\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$, algal-derived C with $1520 \pm 498\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$, bacterial-derived C with $750 \pm 458\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$ and DOM with $2393 \pm 1221\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$. Also N was assimilated comparably among different food sources by *L. pertusa* (Wilcoxon $p > 0.05$ for all comparisons) with *Artemia*-derived N assimilated with $797 \pm 399\,\mathrm{ng\,N\,g^{-1}\,DW\,coral\,d^{-1}}$, algal-derived N with $247 \pm 174\,\mathrm{ng\,N\,g^{-1}\,DW\,coral\,day^{-1}\,d^{-1}}$), bacterial-derived N with $399 \pm 200\,\mathrm{ng\,N\,g^{-1}\,DW\,d^{-1}}$ and DOM with $797 \pm 258\,\mathrm{ng\,N\,g^{-1}\,DW\,coral\,d^{-1}}$ (Fig. 3a).

With the exception of corals fed with DOM (Kruskal–Wallis $p = 0.006$, Fig. 3a), C assimilation did not differ significantly from N assimilation among corals fed with particulate sources (Kruskal–Wallis $p > 0.05$), regardless of different N additions per treatment due to fixed C additions and variable C / N ratios of food sources. This points to a higher retention of nitrogen during assimilation and metabolic processing (Fig. 3e).

3.4 Food processing: tracer incorporation in amino acids

Between 14 to 32 % of the total assimilated carbon was incorporated into the total hydrolysable amino acid pool (THAA) of *L. pertusa*. DOM-derived C was assimilated into THAAs at a significantly higher rate ($746 \pm 244\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$) than bacteria and *Artemia*-derived C ($178 \pm 69\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$ and $272 \pm 88\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$ respectively, Wilcoxon $p_{\mathrm{DOM\text{-}BAC/ART}} = 0.03$). The incorporation algal-derived C ($484 \pm 311\,\mathrm{ng\,C\,g^{-1}\,DW\,coral\,d^{-1}}$) did not differ significantly from that of the other food sources (Wilcoxon $p > 0.05$ for all comparisons).

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The incorporation of N into THAAs represented up to 30 % of the total N assimilated by the coral and did not differ significantly between food treatments (Kruskal–Wallis $p = 0.2$) with 152 ± 67 ng N g^{-1} DW coral d^{-1} for DOM, 137 ± 87 ng N g^{-1} DW coral d^{-1} for *Artemia*, 73 ± 43 ng N g^{-1} DW coral d^{-1} for algae and 72 ± 27 ng N g^{-1} DW coral d^{-1} for bacteria (Fig. 3b).

3.5 C incorporation into fatty acids

Of the total C assimilated up to 4 % was traced in the total fatty acids pool (TFA) of *L. pertusa*. The ingested food source hereby significantly influenced the amount of C incorporated into TFAs. (Kruskal–Wallis $p = 0.0003$, Fig. 3c). DOM-derived C incorporation was significantly lower than that of the particulate sources (0.3 ± 0.2 ng C g^{-1} DW coral d^{-1}, Wilcoxon $p_{\text{DOM-ART/ALG/BAC}} = 0.03$). *Artemia*- and algal-derived C (Wilcoxon $p > 0.05$) were incorporated in TFA at comparable rates, 49 ± 23 and 59 ± 40 ng C g^{-1} DW coral d^{-1}, respectively, but bacteria-derived C was incorporated at a significantly lower rate of 15 ± 5 ng C g^{-1} DW coral d^{-1} (Wilcoxon $p_{\text{BAC-ART}} = 0.03$, Wilcoxon $p_{\text{BAC-ALG}} = 0.05$, Fig. 3c).

The incorporation into the phospholipid-derived fatty acid (PLFA) C-pool accounted for 0.6 % of total assimilated C. Like for TFAs, also C incorporated into PLFAs was significantly different between different food sources (Kruskal–Wallis $p = 0.002$). Again, DOM-derived C was incorporated at a significant lower rate (1 ± 1 ng C g^{-1} DW coral d^{-1}) than any of the particulate sources (Wilcoxon $p_{\text{DOM-ART/ALG}} = 0.03$, Wilcoxon $p_{\text{DOM-BAC}} = 0.05$, Fig. 3d). The particulate sources however did not differ significantly in their incorporation (Wilcoxon $p > 0.05$ for all comparisons). On average *Artemia*-derived C was incorporated with 10 ± 6 ng C g^{-1} DW d^{-1}, algae-derived C with 8 ± 7 ng C g^{-1} DW coral d^{-1} and bacteria-derived C with 5 ± 4 ng C g^{-1} DW coral d^{-1}.

The incorporation of C into PLFAs in corals fed with DOM was solely caused by de novo synthesis, since the DOM source did not contain any PLFAs. The PLFAs C 16 : 0, C 16 : 1ω7 and C 18 : 1ω 7c showed highest C incorporation but also long chain PLFAs like C 22 : 2ω 6 and C 22 : 4ω 6 incorporated tracer C in DOM fed corals (Fig. 2d). For

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particulate sources over 40–60 % of the assimilated PLFA-C by the corals was incorporated in PLFAs characterizing the respective food source (Fig. 4). PLFAs not present in the diet but with substantial tracer incorporation (> 4 % contribution to tracer uptake) were C 18 : 0, C 18 : 1ω9c and C 20 : 4ω6 in *Artemia* fed corals, C 18 : 1ω7c and C 22 : 4ω6 in algae fed corals and C 22 : 2ω6 and C 22 : 1ω9c in bacteria fed corals (Fig. 2c).

3.6 Carbon incorporation into coral skeleton

Incorporation of metabolic C derived from the processing of organic food sources into the inorganic carbonate skeleton was highly variable among coral samples (Fig. 3f), partly because only 1–2 coral pieces out of 6 showed measurable incorporation. Incorporation into the coral skeleton was highest in the algal treatment ($1.6 \pm 1.0\,\mu g\,C\,g^{-1}\,DW\,coral\,d^{-1}$), followed by the *Artemia* ($0.2 \pm 0.5\,\mu g\,C\,g^{-1}\,DW\,coral\,d^{-1}$) and DOM ($0.08 \pm 0.15\,\mu g\,C\,g^{-1}\,DW\,coral\,d^{-1}$) treatment. Coral pieces fed with bacteria did not incorporate tracer C in their skeleton.

4 Discussion

4.1 Biochemical characteristics of *L. pertusa*

The overall contribution of amino acids and fatty acids to C tissue is in agreement with observations on other organisms, including tropical corals, in which proteins form the largest fraction before sugars and lipids (Achituv et al., 1994; Szmant-Froelich and Pilson, 1980).

The concentration of total fatty acids ($20\,mg\,g^{-1}$ DW tissue with tissue DW contributing 5 % to total DW, as observed in this study) however was below the range of 55–$124\,mg\,g^{-1}$ DW tissue reported by Dodds et al. (2009) for *L. pertusa* from Rockall Bank, Mingulay Reef and New England Seamounts. Local differences can be responsible for this discrepancy as Larsson et al. (2013a) reported storage fatty acids concentrations

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of 15 to 19 mg g^{-1} DW tissue from *L. pertusa* harvested at the Tisler Reef but also the maintenance in aquaria (3 month in this study) might have altered the lipid content (Larsson et al., 2013b).

4.2 Food assimilation and source preferences

In line with aquaria studies and in situ observations (Buhl-Mortensen, 2001; Freiwald et al., 2002; Tsounis et al., 2010) our study confirms that *L. pertusa* can utilize various particulate resources from a broad range of sizes including bacteria, algae and zooplankton. The assimilation of DOM by *L. pertusa* is in accordance with the observation that *Desmophyllum dianthus* took up DOM (~ 6 µg C g^{-1} DW d^{-1}) during core incubations at a 10–100 × lower DOC concentration (Naumann et al., 2011). The comparable assimilation rates among resources hereby suggest that *L. pertusa* feeds rather unselectively at equivalent concentrations. This, together with the indication that coral food uptake is primarily driven by external factors such as food availability and current velocity (Purser et al., 2010), suggests that *L. pertusa* is an opportunistic feeder that utilizes resources depending on availability.

Rates of C assimilation into the tissue/biomass of *L. pertusa* in this study (~ 2 µg POC g^{-1} DW coral d^{-1}) are lower than the *Artemia* capture rates measured by Purser et al. (2010) under comparable flow and food conditions (324 µg POC g^{-1} DW coral d^{-1}). These measurements however are difficult to compare, because capture rates may overestimate actual ingestion if not every prey item is successfully transferred to the gut (Purser et al., 2010) and tissue assimilation only represents a fraction of the total uptake as respiration and mucus excretion are ignored. Especially latter can be a significant component of the energy budget of *L. pertusa* (Maier et al., 2011; Wild et al., 2008).

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4.3 Food composition governs transfer into amino acids and lipids

Although the food sources were unselectively assimilated, there were clear differences in the metabolic processing. The most pronounced difference was observed between DOM and POM derived C incorporation. While POM derived C was incorporated at a higher rate than DOM derived C in fatty acids, DOM derived C was incorporated at higher rates in amino acids than POM derived C, excluding algae derived C. This difference was most likely caused by the differences in composition between the sources. The DOM consisted solely of dissolved free amino acids, which can be directly incorporated into coral tissue amino acids whereas fatty acids had to be produced de novo using amino acids as C-substrate. The POM sources contained among others amino acids and fatty acids. The comparatively high POM incorporation into coral fatty acids most likely results from their availability in the source and their (direct) assimilation by the coral as illustrated by the effective incorporation of dietary PLFAs into coral PLFAs (Fig. 4).

Our results further indicate that not only the quantity (concentration) of amino acids/fatty acids, present in a food sources, but also their quality (composition) might affect food source processing. This is especially illustrated by the assimilation of algae in comparison to other POM sources. Algal-derived C was incorporated into coral PLFAs at a comparable rate to other POM sources, despite containing 10 times less PLFA-derived C (Table 1). Additionally, algal-derived N incorporation into coral tissue and amino acids did not significantly differ from the incorporation of other POM sources despite a higher C / N ratio, i.e. a lower N concentration in the algal source. This suggests that while total assimilation can be comparable among sources, their nutritional importance in sustaining tissue components can still differ.

4.4 Assimilation and synthesis of PLFAs

Fatty acids are often used as biomarkers to infer the diet of animals (Braeckman et al., 2012; Kelly and Scheibling, 2012). This approach relies on the assumption that the

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relative composition of the PLFA pool in the animal reflects that of its food source(s) and hence that there is no alteration/modification or production of PLFAs occurring during the transfer from food source to animal. However this approach is only valid if the respective animal cannot synthesize the biomarker.

On the first look the labeled PLFA profiles (Fig. 2c, d) indeed reflect more the dietary PLFA profiles (Fig. 2a) than the one of the coral itself (Fig. 2a) with highest tracer recovery in PLFAs < C 20 : 0 chain length. However looking more detailed it becomes apparent, that in case of POM a direct assimilation of dietary PLFAs can only explain 40 to 60 % of the total C incorporation into PLFAs while in the case of DOM dietary transfer of PLFAs was not an option since this source did not contain any PLFAs. This indicates that not only direct transfer of PLFAs occurs but also alteration/modification and even de novo production as especially illustrated in the case of DOM fed corals. This implies that the assumption "you are what you eat" is not completely true for *L. pertusa*.

Additionally, the de novo synthesis of FAs by *L. pertusa* includes also FAs which have previously been used as biomarkers. For example, C 20 : 5ω3 and C 22 : 6ω3 (biomarkers for diatoms and dinoflagellates, respectively, Harwood and Russell, 1984) synthesized by *L. pertusa* from *Artemia*. Furthermore C 22 : 1ω9c, a zooplankton biomarker (Sargent and Falkpetersen, 1988), was synthesized by *L. pertusa* when fed bacteria (detected in one of three samples). Although the variation in de novo synthesis is high, it may complicate the interpretation of fatty acid profiles from field collected specimens, because presumed "unique" fatty acids may have been (partly) synthesized by *L. pertusa*. Our study thus adds to the growing evidence that care should be taken using fatty acids as dietary tracers in benthic food webs (Kelly and Scheibling, 2012; McLeod et al., 2013).

4.5 Metabolic versus external C incorporation into coral skeleton

Inorganic carbon to sustain calcification can either originate from an external (dissolved inorganic C) or from an internal pool (metabolic-derived C). In this study we directly

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measured the transfer of metabolic-derived C transfer into the coral skeleton, which ranged from 0.1–1.6 µg C g^{-1} DW d^{-1} coral depending on the food source. This rate is considerably lower than separate, but comparable, incubations with ^{13}C-bicarbonate that showed a direct external inorganic C uptake of 46 ± 25 µg C g^{-1} DW coral d^{-1} (C. E. Mueller et al. unpubl. data). Maier et al. (2009) measured a total calcification rate, i.e. sum of internal and external usage, of 23–78 µg C g^{-1} DW d^{-1} coral with ^{45}Ca on freshly collected corals. These results indicate that metabolic derived C only plays a minor role as C source for calcification, which confirms the suggestion by Adkins et al. (2003) based on isotopic data analysis in the coral skeleton (δ^{18}O, δ^{13}C), that calcification of *L. pertusa* mainly relies on an external DIC source which decreases the effect of isotopic fractionation during the calcification process. Together with the lack of autotrophic symbionts in the coral this makes *L. pertusa* skeletons an excellent study object for climatic reconstructions (Adkins et al., 2003).

5 Conclusions and implications

In this study we investigate the capability of *L. pertusa* to take up different food sources ranging from dissolved organic matter, bacteria and algae to zooplankton. We also explored for the first time the processing of theses food sources by the coral. The comparable assimilation rates of the different food sources hereby indicate that *L. pertusa* is an opportunistic feeder, able to exploit a wide variety of food sources. The ability to utilize DOM further underlines the nutritional flexibility of *L. pertusa* and might be especially important in reef locations like Rockall bank, where POM concentrations can be very low during a period of several months (Duineveld et al., 2007). The assimilation of external DOM and the re-assimilation of DOM from coral mucus release, responsible for high DOM concentrations above CWC reef (van Duyl et al., 2008; Wild et al., 2009), might help the coral to withstand several months without POM supply.

The observed differences in food processing suggest that the nutritional value of a food source is determined by its composition (quantity and quality of fatty acids and

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amino acids). Our findings further indicate that phytoplankton is a valuable resource for *L. pertusa* due to the efficient transformation into coral fatty acids. This might be especially relevant in locations where downwelling events (Tisler Reef, Mingulay Reef) supply the reefs with a high availability of phytoplankton (Davies et al., 2009; Duineveld et al., 2004; Wagner et al., 2011). Furthermore, the high flow velocities characterizing many CWC reef locations (Messing, 1990; Thiem et al., 2006; White et al., 2007) might also favour the uptake of smaller particles such as algae, since particle retention is negatively affected by particle size especially at higher flow velocities (Shimeta and Koehl, 1997).

Additionally we found de novo synthesis within the fatty acid metabolism, indicating that corals do not only rely on dietary fatty acids to obtain certain fatty acids. This especially concerns bacteria, since they are often considered as low quality food based on their lack of long-chain fatty acids (Leroy et al., 2012; Phillips, 1984). However, given the ability of the coral to synthesized long chain fatty acids such as C 22 : 2ω6 and C 22 : 1ω 9c from bacteria, our results suggest that bacteria can be a valuable addition to coral nutrition. This might be especially relevant since bacteria occur in high abundance around cold-water coral reefs and food uptake in *L. pertusa* is positively correlated with prey abundance (Purser et al., 2010). Additionally, bacteria are constantly available to the coral since they are fertilized by the coral itself via mucus production (Maier et al., 2011; Wild et al., 2009), while POM availability can vary spatially and temporally (Duineveld et al., 2007).

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Table 1. Characteristics of food sources used during the experiment.

Food source	^{13}C (at%)	^{15}N (at%)	Molar C / N ratio	PLFA content (% C)
Amino acids (DOM)	99	99	5.0	0.00
Bacteria (BAC)	9	10	3.6	0.31
Algae (ALG)	3	10	9.8	0.03
Zooplankton (ART)	3	2	4.2	0.32

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Table 2. Total carbon (Total C), organic carbon (org C), total nitrogen (total N), total hydrolysable amino acids (THAAs), total fatty acids (TFAs) and PLFAs composition of *L. pertusa*. Values are presented in [mg C g^{-1} DW coral ± SD] and [mg N g^{-1} DW coral ± SD] respectively.

Total C	Org C	Total N	THAAs	TFAs	PLFAs
128.05 ± 4.95	1.60 ± 4.81	2.79 ± 0.95 (N)	3.61 ± 0.55 (C) 0.34 ± 0.05 (N)	1.02 ± 0.03	0.06 ± 0.02

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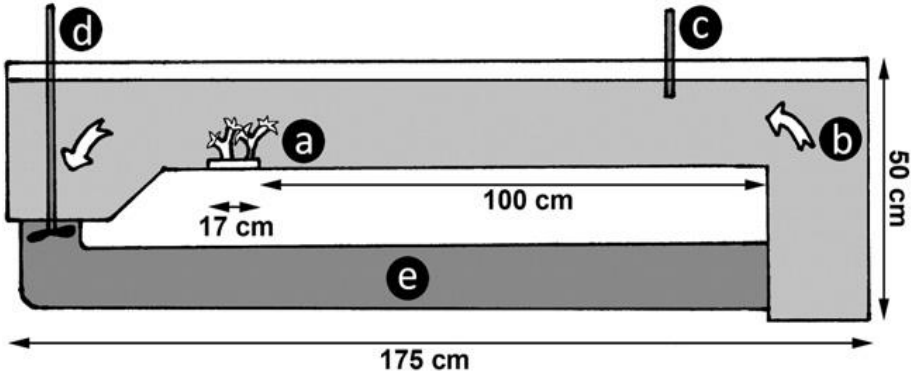

Fig. 1. Scale diagram of recirculation Plexiglas flume setup adopted from Purser et al. (2010). **(a)** Test section with coral branches in plastic mount (depth 8 cm). **(b)** Direction of circulation, **(c)** food delivery point, **(d)** motor, **(e)** opaque plastic return pipe.

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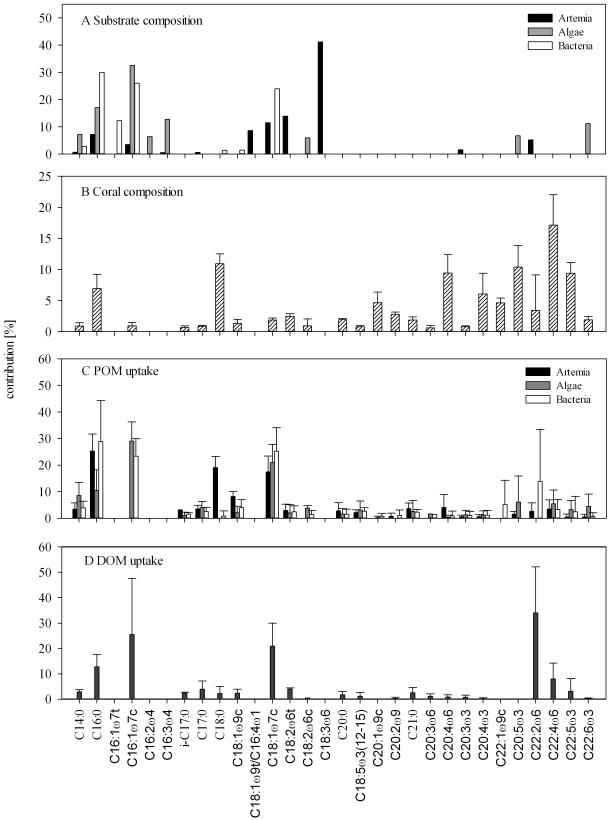

Fig. 2. PLFA profiles of **(A)** the particulate organic food sources *Artemia*, algae and bacteria (% contribution to total concentration), **(B)** *L. pertusa*, **(C)** POM-derived C incorporation into coral PLFAs by *L. pertusa* and **(D)** DOM transformation into coral PLFAs by *L. pertusa* (% contribution to total uptake). The bars in each figure represent average ± SD.

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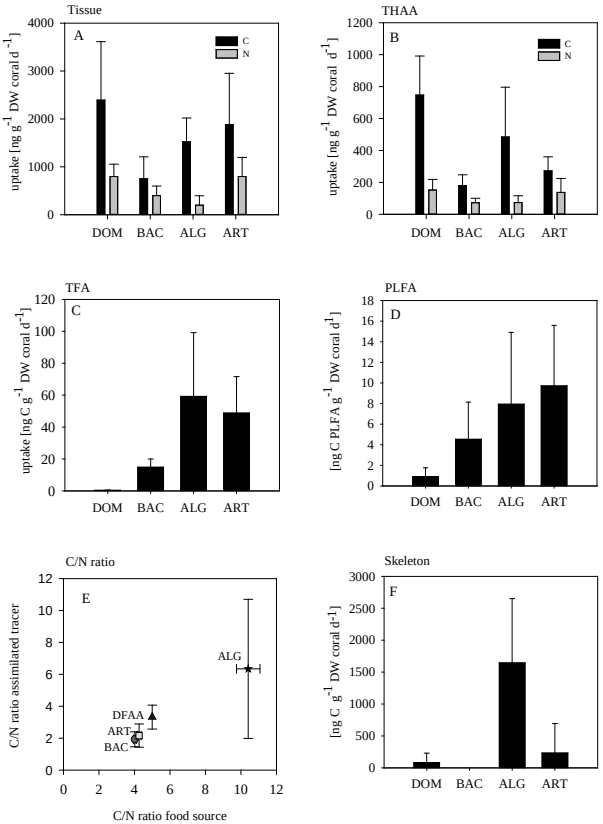

Fig. 3. (A) C and N uptake in coral tissue (note: different C / N ratios of sources), **(B)**, C and N uptake in THAAs of coral samples (note: different C / N ratios of sources), **(C)** C uptake in TFA of coral samples, **(D)** C uptake in PLFA of coral samples, **(E)** C / N ratio of food provided and of assimilation, **(F)** C uptake in coral skeleton. The bars in each figure represent average ± SD.

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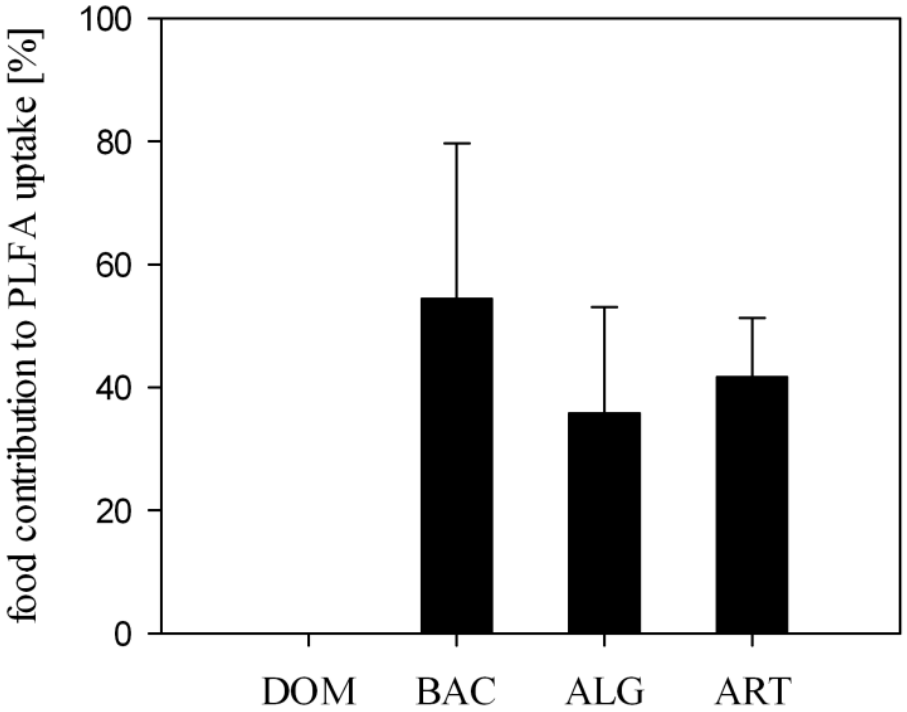

Fig. 4. Contribution of food-derived PLFAs to total PLFA synthesis in corals during the experiment. Based on the assumption that food-derived PLFA are directly incorporated into animal PLFAs, the food contribution was calculated by summing the uptake in food characteristic PLFAs by *L. pertusa* and dividing it by its the total PLFA uptake. The bars in the figure represent average ± SD.

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