Dear Dr. Woulds,

We thank you for your earlier suggestions to clarify our manuscript and the reviewers for their suggestions and favourable evaluation of our manuscript "Food selectivity and processing by the cold-water coral *Lophelia pertusa*". Below, we describe how we will address these issues in the revised version of our manuscript.

To address your initial concern regarding the experimental design, we have added Fig. 1B to clarify the issue. Note that we have also updated Fig. 4 (Fig. 5 in the revision) as a few data points were incorrect in the original figure.

On behalf the authors,
Dick van Oevelen

Reviewer William Hunter

Review of van Oevelen et al. Food Selectivity and processing by the cold-water coral Lophelia pertusa.

General Comments

The manuscript by van Oevelen et al. presents a very elegant experiment that tests the food selection and processing by the cold-water coral *Lophelia pertusa*. The experiments conducted provide a novel insight into the whether this coral is capable of feeding selectively and the potential mechanisms that underlie this. The authors' experimental design was excellent, particularly the neat use of 13C and 15N tracers to independently trace the uptake of algal and bacterial derived C and N into the corals. One broad concern I have with the paper is the low level of replication within the paper, it would have been nicer to see a greater number of experimental replicates to improve statistical power. I recognise that there are both logistical and ethical considerations to take into account when sampling cold-water corals, but I think the authors need to justify the limited replication within the study. On a further note, I believe the manuscript could be further developed to address how consumer and resource stoichiometry may help to explain the observed differences in food assimilation. It may be useful to look at the relative carbon and nitrogen content of each food source (%C, %N and C:N ratios) and the C:N ratios of the corals, and investigate the changes in food selectivity as responses to these parameters. Overall, I believe this paper is worthy of publication once the authors have addresses the
specific comments outlined below.

We thank the reviewer for his compliments on our experimental work and design. Our experimental design was aimed at a replication at n=3, which we achieved in most cases although we agree that a higher number of replicates would be better. The field station where the experiments were conducted (Tjaerno Marine Laboratory in Sweden) collects corals from the nearby Tisler reef, which is in Norwegian waters. Hence, approval needs to be granted by the Norwegian authorities for the collection of corals. Permission has been given but with restrictions on the amount of corals to collect, so we were unfortunately restricted in the number of replicates we could conduct. We acknowledge this now in the manuscript in the "Materials and methods - Experimental design" by stating "Replication in this study was limited due to collection restrictions for *Lophelia pertusa* from the Tisler reef." *The stoichiometry remark will be discussed under point 4 below.*

Specific Comments
1. This is an experimental study, as such I believe that the authors need to state a working hypothesis or at the minimum a clearly articulated set of aims. At present the introduction provides a nice review of the current knowledge around Lophelia pertusa feeding, but this is not just a descriptive study.
We partially agree on this point with the reviewer. It is true that it is not a purely descriptive study, but we do consider this an explorative study to identify feeding preferences and better quantify the energy budget of Lophelia. The reviewer also states, see point 2 below, that we should refrain from statistical testing. Hence, we decided to not end the introduction with a specific hypothesis (that typically requires statistical testing), but better articulated the aims of this study.

2. I do not believe that the authors' use of analysis of variance is appropriate. I would recommend that the authors remove the statistical tests and seek to describe and interpret the

results graphically. Analysis of variance relies upon the assumption that a mean and variance can be estimated from the data. Given that the lowest food concentrations (8.3 µmol C l-1) treatment had only two replicates, this means that estimating a reliable sample mean for this treatment is not possible. Furthermore, given that the bacterial / algal proportions are not repeated over all 3 food concentration treatments, I cannot see how a two-way interaction can be tested within this study. The experimental design is confounded by the fact that the algal:bacterial biomass was 1:1 in two of the treatments but 3:1 in the third. I would ask the authors to acknowledge the limitation this places on the study and interpret their results accordingly.

Thanks for pointing this out. We have removed the statistical tests and now take the different food ratios into account when discussing the results in section 4.2, as in section 4.1 we discuss the response to total (i.e. algal + bacterial) food availability.

3. I believe that more could be learned about the feeding responses of L. pertusa by investigating the relative quality of each food source, in terms of average particle size and the %C and %N content. Given that the algal cells where 5 times larger than the bacteria, what can be said about the relative nutritional content of each?

Unfortunately, our method of algal and bacteria collection leaves a variable proportion of salt in the residue. Hence, the %C and %N content measurements are unreliable and we therefore decided not to discuss this any further. We however do discuss the effect of cell size on food selectivity in section 4.2. Despite the difference in cell size, mechanical selection cannot explain the observed selectivity.

4. Furthermore, some exploration of consumer and resource stoichiometry may help to elucidate selective uptake and incorporation. I would ask the authors to do some data exploration of the C:N ratios and if it is possible to derive a 13C:15N ratio for the food sources and corals. This would potentially allow a greater insight into resource portioning by the corals.

This is a good point and we looked further into this. As a result, we found a surprising uncoupling of C and N uptake in one treatment (see the new figure 4). We explicitly state that the stoichiometric effects are clearly visible, but it does not modifiy the observed food selectivity at higher food concentrations.

Minor Comments & Technical Corrections
Page 1 Line 10: Comma missing – "In this study, we investigated…" *OK*

Page 2 Line 14: "it is presently unclear whether cold-water corals exhibit selective resource utilisation or feed proportionally to resource availability" Do you have a reference which would support this supposition. *No, we were referring to the fact that there have not been studies that have assessed this. We have modified the sentence accordingly.*

Page 2 Line 20-21: "However, to advance our understanding of cold-water coral physiology…" This sentence is rather poorly structured. Consider revising to "In order to advance our knowledge of cold-water coral physiology, we must understand how dietary carbon partitioning affects the organismal energy budget." or similar. *OK*

Page 2 Line 26-31: Please state the hypothesis for this study. *See our response above.*

Page 4 Line 10-13: What were the %C, and %N values of the algal and bacterial food sources? *See our response above.*

Page 4 Line 14: Poor grammar, please revise to "Prior to the start of the experiment, incubation chambers (10 L) were placed in a temperature-controlled room at 7oC and…" *OK*

Page 6 Line 2-5: Please can you clarify the terms in the equation. Looking at the I cannot tell if the uptake of resource is per unit time or total? Also is the availability of the resource a ratio or does it have units? *We have better explained the terms in this equation.*

Figure 2: Given that there were only two replicates of the lowest food concentrations (8.3 µmol C l-1) I would suggest that the authors plot the raw data. Sample mean and variance cannot be reliably estimated with less that 3 replicates. This would also apply for figure 4. *We tried this, but the figure becomes quite messy and unclear. To address this comment we have therefore noted in the legend explicitly that the mean ± 'sd' is mean ± range for the low food treatment. In addition, we have added Fig.1B to clarify the design.*

Reviewer Evina Gontikaki

General comments

This is well-written, well-designed concise paper on food selectivity of the CWC *Lophelia pertusa*. The experimental design, experimental procedure and sample and data analysis are sound and reflect the extensive experience of the team of authors on the study of CWC reefs and isotope tracers experiments in general. I highly recommend publication of the present manuscript with only minor modifications.

We thank the reviewer for these compliments on our experimental work and design.

Specific comments

It is mentioned that the selectivity index normalises the food uptake for the differences in the availability of food sources. Does that mean that the different bacterial: algal C ratio in the high load treatment compared to the other two does not affect the result?
Correct

Technical comments

All the subheadings in section 2 should be corrected (e.g. 2.1 experimental design instead of 1.1).
This has now been corrected.

Page 2, line 24: consider changing the word "feasible" to "effective".
Changed accordingly.

Page 5, line 5: After "incorporation", add "of isotopic tracers".
Changed accordingly.

Page 7, lines 2-4: these lines would fit better into section "2.5 Data Analysis"
Changed accordingly.

Figure 2: For the "sum" (open circles), there are error bars only for the calcium incorporation. Keep it consistent, either present only the mean or add error bars to all graphs. Also, I would remove the lines connecting the "sum" between the treatments, as these are appropriate to use in time series rather than independent concentration treatments.
The figures are consistent, i.e. also in the calcium carbonate figure there are only error bars (though large) in the C-algae and C-bacteria data.
We disagree that it would be inappropriate to draw lines between the concentration treatments. There is a large body of scientific work on functional responses (e.g. Holling type functional responses or Michaelis-Menten kinetics) that is focussed on relating uptake to concentration.

Food selectivity and processing by the cold-water coral *Lophelia pertusa*

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Abstract. Cold-water corals form prominent reef ecosystems along ocean margins that depend on suspended resources produced in surface waters. In this study, we investigated food processing of ^{13}C and ^{15}N labelled bacteria and algae by the cold-water coral *Lophelia pertusa*. Coral respiration, tissue incorporation of C and N and metabolic-derived C incorporation into the skeleton were traced following the additions of different food concentrations (100, 300, 1300 µg C l^{-1}) and two ratios of suspended bacterial and algal biomass (1:1, 3:1). Respiration and tissue incorporation by *L. pertusa* increased markedly following exposure to higher food concentrations. The net growth efficiency of *L. pertusa* was low (0.08±0.03), which is consistent with their slow growth rates. The contribution of algae and bacteria to total coral assimilation was proportional to the food mixture in the two lowest food concentrations, but algae were preferred over bacteria as food source at the highest food concentration. Similarly, the stoichiometric uptake of C and N was coupled in the low food treatment, but was uncoupled in the high food treatment and indicated a comparatively higher uptake or retention of bacterial carbon as compared to algal nitrogen. We argue that behavioural responses for these small-sized food particles, such as tentacle behaviour, mucus trapping and physiological processing, are more likely to explain the observed food selectivity as compared to physical-mechanical considerations. A comparison of the experimental food conditions to natural organic carbon concentrations above CWC reefs suggests that *L. pertusa* is well adapted to exploit temporal pulses of high organic matter concentrations in the bottom water caused by internal waves and downwelling events.

1 Introduction

Cold-water corals have a global distribution in the deep sea and are typically found at locations with high bottom-water velocities such as continental margins, seamounts and mid-ocean ridges (Roberts et al., 2009; Davies and Guinotte, 2011; Yesson et al., 2012). Some cold-water corals are scleractinians and produce a three-dimensional carbonate structure, which provides settlement, refuge and feeding ground for many associated organisms (Henry and Roberts, 2007; Kutti et al., 2015).

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As a result, these reef communities are diverse, have high biomass and consume up to 20 times more organic carbon per square meter as compared to surrounding soft-sediment communities (Van Oevelen et al., 2009; White et al., 2012; Cathalot et al., 2015; Rovelli et al., 2015).

The main reef-building coral species in the North Atlantic Ocean is the branching coral *Lophelia pertusa*, which is a passive suspension feeder that uses tentacles to 'catch' particles from the water column. Field observations on stable isotopes and fatty acids suggest that *L. pertusa* feeds on a broad range of food sources including particulate suspended matter, bacteria, phytoplankton and zooplankton (Kiriakoulakis et al., 2005; Duineveld et al., 2007; Sherwood et al., 2008; Dodds et al., 2009). Laboratory studies have confirmed the uptake of suspended particles, bacteria, phytoplankton and zooplankton by cold-water corals (Purser et al., 2010; Mueller et al., 2014; Orejas et al., 2016). Recently, *L. pertusa* was also shown to take up dissolved organic matter in the form of free amino acids (Gori et al., 2014; Mueller et al., 2014) and to fix inorganic carbon into its biomass, supposedly through chemo-autotrophic activity of associated microbes (Middelburg et al., 2015). This flexibility in resource utilization clearly indicates an opportunistic feeding strategy (Mueller et al., 2014; Orejas et al., 2016).

In natural reefs the diversity of organic matter sources is high (Jensen et al., 2012) and it is presently unclear whether cold-water corals exhibit selective resource utilization or feed proportionally to resource availability. Moreover, organic matter supply to cold-water reefs is temporally variable due to seasonality in organic matter production in the surface ocean and the dynamic physical environment in which cold-water reefs occur (Duineveld et al., 2007; Davies et al., 2009; Findlay et al., 2013; Hebbeln et al., 2014; Mohn et al., 2014). Freshly hatched *Artemia salina* nauplii, which are often used as food in aquarium studies of scleractinians, were increasingly taken up by the cold-water coral *L. pertusa* with increasing concentration in the incubation vessel (Purser et al., 2010), indicating that *L. pertusa* responds to changes in food supply. In order to advance our understanding of cold-water coral physiology, we must better understand resource partitioning within the energy budget of the organism. For the cold-water coral *Desmophyllum dianthus* it was shown that zooplankton contributed to various components of the energy budget, including calcification, respiration and mucus release, following food withdrawal for 1 week (Naumann et al., 2011). The slow (i.e. months) response time of *L. pertusa* to changing food conditions renders this approach less effective to directly link food uptake to physiological processing (Larsson et al., 2013).

The aims of this study are twofold. Firstly, we wanted to assess whether the cold-water coral *Lophelia pertusa* exhibits selective uptake when exposed to a mixed diet. Secondly, we aimed to quantitatively elucidate the energy budget of *L. pertusa* following feeding on different food quantities. To this end, we investigated food uptake, food selectivity and subsequent processing with a novel dual isotope labelling technique using mixed diets of ^{13}C-labeled algae/ ^{15}N-labeled bacteria and ^{15}N-labeled algae/^{13}C-labeled bacteria. This approach provided the high sensitivity needed to eliminate long-term incubations and allowed us to trace not only uptake but also subsequent processing of algal and bacterial carbon and

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nitrogen. This experimental mixed diet study better represents the diversity of food available under natural coral reef conditions than traditional single food source studies and enables the quantitative tracing of individual food sources.

2 Materials and methods

2.1 Experimental design

Our dual isotope tracer design involved exposing separate coral fragments either to a food mixture of ^{13}C-labelled algae (^{13}C-Algae) + ^{15}N-labelled bacteria (^{15}N-Bacteria) or to a mixture of ^{15}N-labelled algae (^{15}N-Algae) + ^{13}C-labelled bacteria (^{13}C-Bacteria) (Fig. 1). Uptake, respiration and calcification rates are subsequently summed to obtain total C or N uptake/processing (i.e. by dividing rates with the fractional ^{13}C or ^{15}N enrichment of each food source, see below). Three food concentrations were tested in this study: 8.3 (n=2 per food mixture), 25 (n=3 per food mixture) and 108 (n=3 per food mixture) µmol C l^{-1}. Replication in this study was limited due to collection restrictions for *Lophelia pertusa* from the Tisler reef. The bacterial-C to algal-C ratio was 1:1 in the 8.3 and 25 µmol C l^{-1} treatment, but, due to technical issues, appeared to be 3:1 in the 108 µmol C l^{-1} exposure.

2.2 Sampling location and maintenance

Corals were collected at the Tisler Reef, located 70 to 155 m deep in the Skagerrak, at the Norwegian-Swedish border. The Tisler reef is located at a sill, which connects the Kosterfjord deep trough with the open Skagerrak. The current velocity at the reef varies from 0 to 50 cm s^{-1}, with peaks in excess of 70 cm s^{-1}, and the bottom-water temperature varies normally between 6 to 9 ºC throughout the year (Lavaleye et al., 2009; Wagner et al., 2011) though peaks in excess of 12°C have been observed in recent years (Guihen et al., 2012). The particulate organic carbon (POC) concentration at the reef varies between 3.6 and 8.9 µmol C l^{-1} and the depositional POC fluxes averages at 38 µmol C m^{-2} d^{-1} (Wagner et al., 2011).

Fragments of the cold-water coral *Lophelia pertusa* were collected from a depth of around 110 m using the remotely operated vehicle Sperre Subfighter 7500 DC. Fragments were placed in cooling boxes filled beforehand with cold seawater (7 - 8 ºC) and transported within a few hours to the laboratory at the Sven Lovén Centre in Tjärnö (Sweden). After arrival, the coral fragments were clipped to approximately the same size (7.90±2.12 g dry weight (DW) fragment^{-1}; 14.1±2.4 polyps fragment^{-1} as mean ± standard deviation) and were subsequently acclimated for 6 weeks in aquaria (~20 L) placed in a dark thermo-constant room (7 ºC). Sand-filtered (1-2 mm particle size) bottom water from 45 m depth out of the adjacent Koster fjord (salinity 31) was continuously flushed through the aquaria (~1 L min^{-1}). Experience at the station and our earlier experiments showed that the sand-filtered water still contains sufficient organic particles, so that no extra food was provided during the acclimation period (Mueller et al., 2014).

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2.2 Preparation of isotopically labelled algae and bacteria

[15]N-labeled algae were cultured axenically in F/2 culture medium adjusted after Guillard (Guillard, 1975). The culture medium was prepared by replacing 80% of the $NaHCO_3$ (^{13}C-Algae) or 70% of the $NaNO_3$ with its heavy isotope equivalent (Cambridge Isotopes, 99% [13]C-$NaHCO_3$, 99% [15]N-$NaNO_3$). Subsequently, a sterile inoculum of the diatom *Thalassiosira*

5   *pseudonana* (~5 μm) was added. After a 3-week culture period with a 12-hour light-dark cycle, the culture had reached a cell density of $3 - 4 \cdot 10^6$ cells ml^{-1}. The diatoms were concentrated by centrifugation at 450 g and the concentrate was rinsed three times with 0.2 μm filtered seawater to remove residual label and the algal suspension was kept frozen until further use.

Bacteria (±1 μm diameter) were cultured by adding a few ml of natural seawater from the Oosterschelde estuary (Netherlands) to M63 culture medium adjusted after Miller (1972). In the culture medium, 50% of glucose (3 g l^{-1}) or 50% of

10 NH_4Cl (1.125 g l^{-1}) was replaced by its heavy isotope equivalent (Cambridge Isotopes, 99% ^{13}C-glucose, 99% ^{15}N-NH_4Cl) to obtain ^{13}C or ^{15}N isotopically labeled bacteria. After 3 days of culturing in the dark, bacteria were concentrated by centrifugation (14,500 g), rinsed 3 times with 0.2 μm filtered seawater to remove residual label and the bacterial suspension was stored frozen until the start of the experiment.

Subsamples of the algae (n = 3) and bacteria (n = 3) were measured for ^{13}C, ^{15}N, C and N (see below). The algae used in

15 the experiment had a molar C:N ratio of 7.8±0.5, 44 at% [13]C and 65 at% [15]N, while bacteria had a C:N ratio of 4.8±0.2, 58 at% [13]C and 47 at% of [15]N.

2.3 Experimental procedure

Prior to the start of the experiment, 10-L incubation chambers were filled with 5-μm filtered bottom water from the nearby Koster fjord and placed in a temperature-controlled room that was maintained at 7 ºC. Each coral fragment was

20 inserted into an elastic silicone tube, which was mounted on an acrylic plate to allow easy fixing onto the chamber base and to ensure that the fragments retained an upright position. A continuous level of turbulence and water circulation was maintained during the experiment by a motor-driven paddlewheel in the upper part of the incubation chamber (speed: 2 rpm).

The corals were exposed to the isotopically labelled food for 12 h per day during 10 consecutive days (i.e. the 'feeding

25 period'). A food suspension dosage of a few millilitres was given at the beginning of each day during the feeding period with the respective concentration and ratio of ^{13}C bacteria/^{15}N algae and ^{13}C algae/^{15}N bacteria (see above and Fig. 1). After a 12-hour exposure to the food dosage, the chambers were flushed with 5-μm filtered Koster fjord (140 ml min^{-1}) for 12 h to remove food particles, avoid accumulation of waste products and renew the O_2 supply. Corals for background isotope measurements (controls) were incubated in parallel under 'acclimatization' conditions: i.e. only exposed to sand-filtered

30 seawater.

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After the last flushing period on day 10, the incubation chambers were closed for 48 hours to measure the production of ^{13}C dissolved inorganic carbon (^{13}C-DIC) as a proxy for respiration (Moodley et al., 2000). Filtered (GF/F) water samples were taken for DIC analysis before (control) and after the incubation period and stored in a 10 ml headspace vial. Biological activity was stopped by adding 10 µl $HgCl_2$ to the vials. The vials were closed with an aluminium cap fitted with a rubber septum and stored upside down for further analysis. Calculations based on literature respiration rates (Dodds et al., 2007) and pilot experiments indicated that the expected changes in pH, and oxygen and ammonium concentration during the incubations are limited, so that no negative affect on coral or sponge physiology was expected. Coral fragments were stored frozen (-20°C) at the end of the incubation for further analysis.

2.4 Sample analysis

Coral fragments were freeze-dried, weighed and subsequent grinded with a ball Mill for 20 seconds (MM 2000, Retsch, Haan, Germany). This ground coral material, comprised of skeleton and organic tissue, was measured for the incorporation of isotopic tracers in the skeleton and tissue (following Tanaka et al., 2007 and Mueller et al. 2013). Around 30 mg of a coral sample was transferred to silver measuring boats and measured for C content and ^{13}C at% using a thermo Electron Flash EA 1112 analyzer (EA) coupled to a Delta V isotope ratio mass spectrometer (IRMS). Another 30 mg of ground coral was transferred to pre-combusted silver boats and gently decalcified by acidification by placing them in an acidic fume for 3 to 4 days to remove most of the inorganic C and then further acidified by stepwise addition of HCl with increasing concentration (maximum concentration 12 mol L^{-1}) until the inorganic skeleton was removed (as evidenced by the absence of bubbling after further acid addition) (Mueller et al. 2013). After acidification, the samples were analyzed on the EA-IRMS for C and N content and ^{13}C and ^{15}N at% in the organic fraction. Incorporation of ^{13}C into the inorganic skeleton, as proxy for calcification (sensu Tanaka et al., 2007), was obtained by subtracting the ^{13}C in the organic fraction from the total ^{13}C in the ground coral material. Note that this calcification proxy only tracks the incorporation of 'metabolically-derived' carbon, as the ^{13}C needs to be liberated by metabolism from the organic resource (algae or bacteria) before it can be incorporated. Calcification based on metabolically-derived C may only be a small fraction of total calcification, but it can still be used as a tracer to detect changes in calcification (Mueller et al., 2013).

In the headspace vials taken for DIC analysis, a headspace of ~3 ml was created by injecting N_2 gas through the vial septum (Mueller et al., 2013). Samples were acidified with 20 µl of concentrated H_3PO_4 to transform DIC into gaseous CO_2. A 10-µl sample of the headspace was injected into (EA-IRMS) for analysis of CO_2 concentration and at% ^{13}C-CO_2.

The incorporation of ^{13}C and ^{15}N in coral tissue and ^{13}C in $CaCO_3$ is the excess (E) ^{13}C or ^{15}N in a sample and is calculated as $E = F_{experiment} - F_{background,}$ in which F represents the at% of ^{13}C or ^{15}N (i.e. $^{13}C/[^{12}C+^{13}C]$ and $^{15}N/[^{14}N+^{15}N]$, respectively) in an experimental or background sample. Hence, E is the above-background at% of ^{13}C or ^{15}N and positive values indicate transfer of isotope from the original algal or bacterial source to the coral. The excess values are multiplied

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with the C or N content in the ground coral material (i.e. μmol C g^{-1} DW and μmol N g^{-1} DW, respectively) and divided with the at% enrichment of the specific food source to obtain total incorporation rate during a 'feeding period' in μmol C g^{-1} DW and μmol N g^{-1} DW. Incorporation rates throughout the paper are expressed as the daily rates by dividing total incorporation with the length of the feeding period (i.e. 10 days). Total respiration is calculated similarly, in which excess values of DIC

5   are multiplied with the DIC concentration (μmol C L^{-1}) and chamber volume (10 L). Moreover, daily respiration rates are calculated over the length of the incubation period (2 days) and normalized to the coral (g DW) in an incubation chamber.

2.5 Data analysis

Selective uptake of algae or bacteria was assessed with the Chesson index (Chesson, 1983)

$$\alpha_i = \frac{r_i/n_i}{\sum_j r_j/n_j} \quad\quad\quad\quad\quad (1)$$

10 in which α_i is the selectivity index for resource i, r_i is the uptake of resource i expressed as C or N uptake g^{-1} DW d^{-1}, n_i is the initial concentration of resource i in the incubation chamber and j is the total number of resources (i.e. $j = 2$ here). The Chesson index was calculated per food concentration tested and indicates selective uptake as the uptake is normalized to the respective food concentration, i.e. the algae versus bacterial uptake is normalized for the differences in their availability. The selectivity indices sum to 1 and in the present experiment a selectivity index of 0.5 implies no selectivity, >0.5 indicates

15 'positive' selectivity (i.e. higher uptake than proportional availability) and <0.5 indicates 'negative' selectivity. This selectivity index normalizes the food uptake against food availability of the different food mixtures for each food concentration tested.

A net growth efficiency (NGE) was calculated from the C incorporation rate into tissue and respiration rates as: NGE = Tissue incorporation / (Tissue incorporation + Respiration).

20 We explored resource stoichiometry in this experiment by comparing the C:N ratio of the food uptake from the algal and bacterial resources with the C:N ratio of the food in the incubation chamber (algal-bacterial mixture has a C:N of 5.9 in the low and medium food treatment and 5.3 in the high food treatment).

Data presented are mean ± standard deviation, except were stated otherwise, and figures were made in R (R Development Core Team, 2015). The bacteria:algae ratio was not constant over the food concentrations tested (see 'Experimental design'

25 above) and therefore we refrained from statistical comparisons and instead discuss the trends in the data.

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3 Results

3.1 Tissue incorporation and processing of food sources

Both bacterial and algal C and N were incorporated into the coral tissue and their incorporation rates increased with increasing food concentrations (Fig. 2A, B). Incorporation of algal C increased from 0.013 to 0.09 µg C g^{-1} DW day^{-1} and bacterial C from 0.017 to 0.14 µg C g^{-1} DW day^{-1} over the food concentration range (Fig. 2A). The incorporation rate into the carbonate skeleton tended to increase with food concentrations, but the estimated rates were associated with a high variability (Fig. 2C). Respiration of algal C increased substantially from 0.11 to 0.98 µg C g^{-1} DW day^{-1} and bacterial C from 0.10 to 2.6 µg C g^{-1} DW day^{-1} with increasing food concentration (Fig. 2D). The higher bacterial uptake and processing in the highest food treatment can be the result of the (unplanned) deviating bacteria:algae ratio in this treatment as compared to the other two treatments (3:1 vs. 1:1, respectively). A total of 2.6±0.6%, 4.8±0.8% and 3.6±1.4% of the total added organic carbon was recovered in the investigated pools with increasing food concentrations, respectively.

The incorporation rates into tissue were low compared to respiration losses (Fig. 3) resulting in comparatively low net growth efficiencies (NGEs, see Methods for calculation) of 0.08±0.03, independently of food concentration or type (Fig. 3).

The comparison of resource stoichiometry show that a low food concentrations, the C:N incorporation into the coral tissue was equal to or lower than the bulk tissue C:N ratio of the coral (6.3±1.5, mean ± standard deviation) and the offered suspended food (i.e. ^{13}C-algae + ^{15}N-bacteria and ^{15}N-algae + ^{13}C-bacteria, Fig. 4). In the high food concentration treatment however, the C:N incorporation into the coral tissue was evidently different between the two treatments (Fig. 4), with values ranging from 4.9 to 6.8 in the ^{13}C-algae + ^{15}N-bacteria treatment and 9.6 to 14.2 in the ^{15}N-algae + ^{13}C-bacteria. The high C:N values of the coral tissue indicate a comparatively higher uptake or retention of bacterial carbon as compared to algal nitrogen in the ^{15}N-algae + ^{13}C-bacteria treatment.

3.2 Food selectivity

We found the mean C-based Chesson index for bacteria ranging from 0.56 to 0.35 over the food treatments and for algae ranging from 0.44 to 0.65 (Fig. 5A). When food concentration and food uptake are expressed in N-equivalents, the mean Chesson index ranged from 0.30 to 0.61 for bacteria and from 0.39 to 0.70 for algae (Fig. 5B). There was a clear tendency for selective uptake of algae at the higher food concentration treatment.

4 Discussion

4.1 Concentration-dependent food uptake and processing by *Lophelia pertusa*

Higher suspended food concentrations resulted in increased assimilation and respiration rates by *L. pertusa*, indicating that food uptake and metabolism is tightly coupled to food availability. This is consistent with observations by Purser et al.

5   (2010) and Larsson et al. (2013) showing higher respiration and removal rates of zooplankton with increased particle concentration. Interestingly, food capture rates in Purser et al. (2010) and metabolic activity in this study start to saturate at food concentrations of more than hundred μmol C l^{-1}. POC concentrations above CWC reefs vary between 1 to 11 μg C l^{-1} (Kiriakoulakis et al., 2007; Wagner et al., 2011), which implies that *L. pertusa* is well adapted to exploit temporal pulses of high organic matter concentrations in the bottom water caused by internal waves and downwelling event such as observed on

10 Mingulay reef (Davies et al., 2009), Tisler reef (Wagner et al., 2011) and the Logachev Mounds at Rockall Bank (Duineveld et al., 2007; Soetaert et al., In press).

In contrast to assimilation and respiration rates, calcification rates increased less pronounced with increasing food concentration and were associated with a high variability. Hennige et al. (2014) found a short-term response in respiration rates by *L. pertusa* to higher pCO$_2$ conditions, but calcification rates were not significantly affected. Similarly, Larsson et al.

15 (2013) did not find a response of skeletal growth of *L. pertusa* after long-term exposure (months) to different food concentrations. Hence, it seems that the response time of calcification acts on a longer time scale than does food availability. Also for tropical coral it is known that calcification processes can be less responsive to environmental conditions than tissue growth (Anthony and Fabricius, 2000; Tanaka et al., 2007; Tolosa et al., 2011). One explanation why a longer time period is needed before a response in calcification to altered food conditions can be measured may be the relatively low metabolic

20 costs related to calcification in *L. pertusa* (McCulloch et al., 2012; Larsson et al., 2013). Naumann et al. (2011) however did measure significantly higher calcification in fed compared to unfed specimens of the CWC *Desmophyllum dianthus*, but *D. dianthus* is a faster growing species and may therefore respond more rapidly to food availability.

The net growth efficiency (NGE) is the percentage of assimilated organic carbon that is transferred into biomass. Hence, a high NGE means that a food source is efficiently shunted into biomass. We are not aware of NGE estimates for cold-water

25 corals in the existing literature. The NGEs of *L. pertusa* in our study ranged from 4% to 17% and these values are low compared to values of >50% for zooplankton (Anderson et al., 2005), a taxonomic group for which NGE is well studied. The shallow-water anemone *Anthopleura elegantissima*, taxonomically closely related to corals, also has substantially higher NGEs ranging from 30% to 60% (Zamer, 1986). The NGE is positively correlated with growth rate for the sponge *Halichondria panicea* (Thomassen and Riisgard, 1995) and the bivalve *Mytilus edulis* (Kiørboe et al., 1981) and we

30 therefore speculate that the low NGE of the cold-water coral *L. pertusa* is related to their slow growth rates (Roberts et al., 2009). The NGE tended to be higher when *L. pertusa* was feeding on algae compared to bacteria (Fig. 3), but were

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associated with a high variability. Hence, although it is known that the NGE can depend on food quality and quantity (Anderson et al., 2005), additional research is necessary to determine that relation for cold-water corals.

4.2 Food-composition dependent uptake by *L. pertusa*

Food assimilation at the lower two food concentrations responded proportionally to resource stoichiometry (Fig. 4) and
5 food composition (Fig. 5), which indicates that *L. pertusa* is an opportunistic and seemingly unselective feeder. This opportunistic feeding strategy is consistent with uptake of various organic resources in aquarium experiments (Gori et al., 2014; Mueller et al., 2014; Orejas et al., 2016) and inferences from natural abundance stable isotope and fatty acid compositions from field-collected CWC (Duineveld et al., 2007; Dodds et al., 2009). Interestingly however, at higher food concentrations it appears that *L. pertusa* feeds selectively on algae (Fig. 5) and the C:N uptake or retention becomes
10 unbalanced. This conclusion is tentative, because the high food concentration treatment contained proportionally more bacteria than algae (see *Methods – Experimental design*), but these results do suggest that that *L. pertusa* assimilates food in proportion to availability at comparatively lower food concentrations, but when food is in ample supply, *L. pertusa* starts to feed preferentially on algal organic matter and differentially process the carbon and nitrogen derived from the resources.

Our data do not allow us to identify which mechanisms drive the observed food selectivity. The algal cells (5 μm) are a
15 factor 5 larger in diameter than bacteria, so food size may be a trigger that induces selective behaviour. Consistently, Tsounis et al. (2010) found that several CWCs, amongst other *L. pertusa*, fed at higher rates on adult *Artemia salina* compared to the smaller-sized *A. salina* nauplii. Shimeta and Koehl (1997) conducted a theoretical analysis of selective feeding by passive suspension feeders and found particle selection to be a function of encounter, retention and handling. For the particles considered in this study, i.e. bacteria and algae that are substantially smaller than the feeding tentacles, Shimeta and Koehl
20 predict that encounter rates increase with particle size, while particle retention is likely to be independent of particle size. Sole mechanical predictions for the food handling stage provide only part of the story, because behavioural choices may play an important role as well (Shimeta and Koehl, 1997). In this study, a role for behavioural is further suggested by the uncoupling of C and N processing at higher food concentrations. Additional behavioural triggers that may increase encounter and retention include enhanced polyp extension in the presence of the preferred food source or environmental conditions
25 (Orejas et al., 2016) and trapping of food particles with the aid of mucus secretion (Mortensen, 2001). Zetsche et al. (2016) recently showed that mucus by *L. pertusa* is produced in small amounts and very localized in response to different stimuli. When exposed to *A. salina* nauplii, mucus strings and so-called 'string balls' were seen to enhance food trapping. Given the comparatively small particle size used in this study and the uncoupling of C and N processing at higher food concentrations, we suggest that behavioural responses and subsequent physiological processing are more likely to explain the observed food
30 selectivity as compared to the physical-mechanical considerations.

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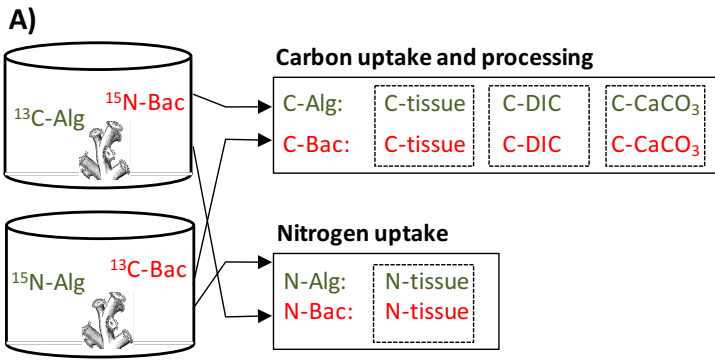
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A)

Carbon uptake and processing

| C-Alg: | C-tissue | C-DIC | C-CaCO$_3$ |
| C-Bac: | C-tissue | C-DIC | C-CaCO$_3$ |

Nitrogen uptake

| N-Alg: | N-tissue |
| N-Bac: | N-tissue |

(^{13}C-Alg, ^{15}N-Bac)
(^{15}N-Alg, ^{13}C-Bac)

B)

Food	^{13}C-Alg + ^{15}N-Bac	^{15}N-Alg + ^{13}C-Bac
Low		
Medium		
High		
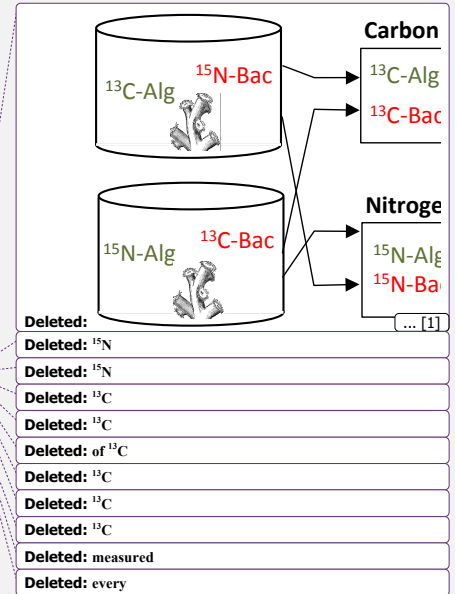
Figure 1: Experimental design of the dual-isotope labelling study. A) Different coral fragments were exposed to a food mixture of ^{13}C-labelled algae (^{13}C-Alg) + ^{15}N-labelled bacteria (^{15}N-Bac) or to a mixture of ^{15}N-labelled algae (^{15}N-Alg) + ^{13}C-labelled bacteria (^{13}C-Bac). The N uptake in tissue (N-tissue), C uptake in tissue (C-tissue), respiration to dissolved inorganic carbon (C-DIC) and C incorporation into the skeleton (C-CaCO$_3$) was calculated for each incubation from the ^{13}C and ^{15}N transfer (see Methods). B) Full experimental design with 8 incubations for the ^{13}C-Alg + ^{15}N-Bac treatment and 8 incubations for the ^{15}N-Alg + ^{13}C-Bac treatment, partitioned over a low, medium and high food concentration treatment.

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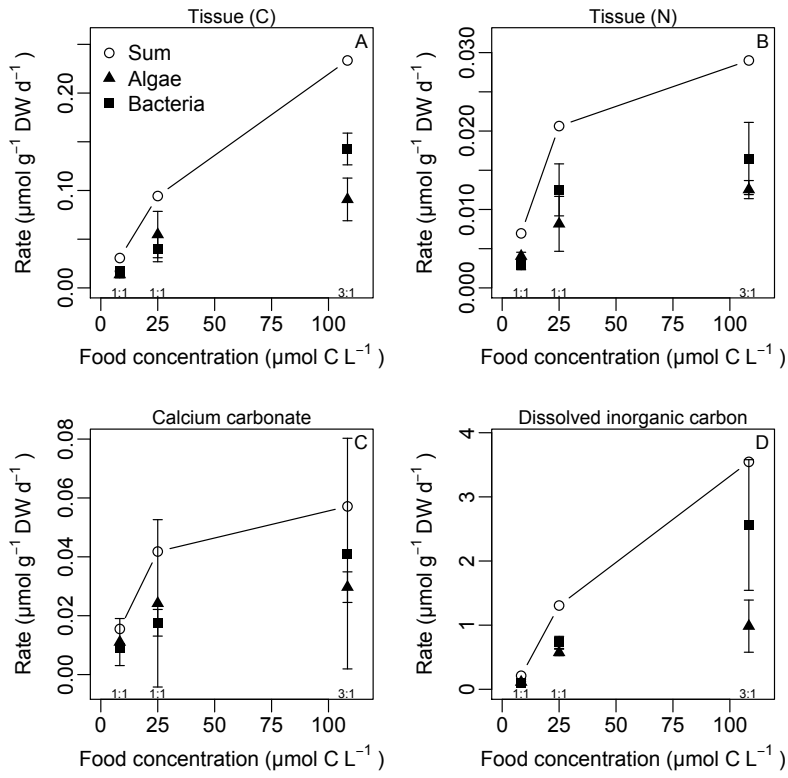
Figure 2: Food processing by the cold-water coral *L. pertusa* at different food concentrations and compositions. A) Carbon assimilation in tissue, B) nitrogen assimilation in tissue, C) carbon incorporation into coral skeleton, D) carbon respiration. The mean ± range is shown for the low food concentration treatment (n = 2). The ratios 1:1 and 3:1 in the subpanels indicate the ratio of bacteria : algae in the respective food concentration treatment.
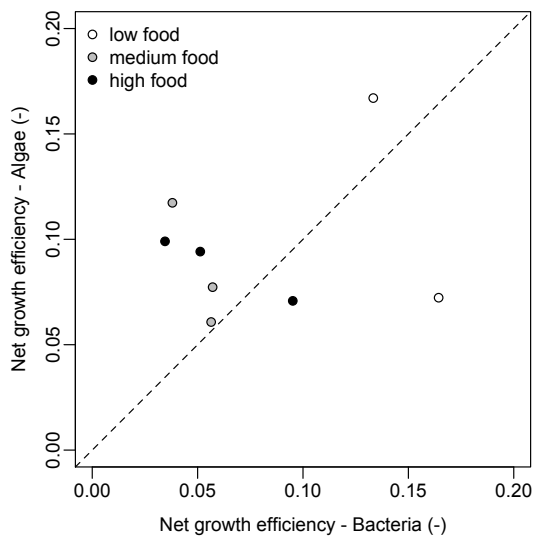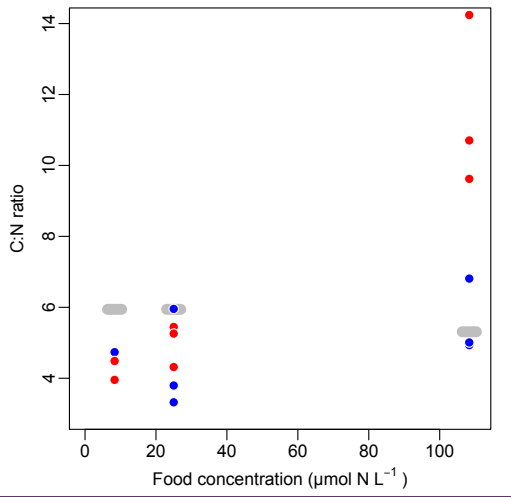
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Figure 3: The net growth efficiency of *L. pertusa* when feeding on algae versus bacteria. The colors represent the low, medium and high food concentration as in Fig. 2.

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Figure 4: Resource stoichiometry in the experiment, presented as the C:N ratio of the resource versus the C:N ratio in the coral tissue after the incubation. The grey bar is the C:N ratio of the suspended food (i.e. algae + bacteria), the blue dots are the C:N ratios of the coral tissue in the treatment ^{13}C-algae + ^{15}N-bacteria and the red dots are the C:N ratios of the coral tissue in the treatment ^{15}N-algae + ^{13}C-bacteria.
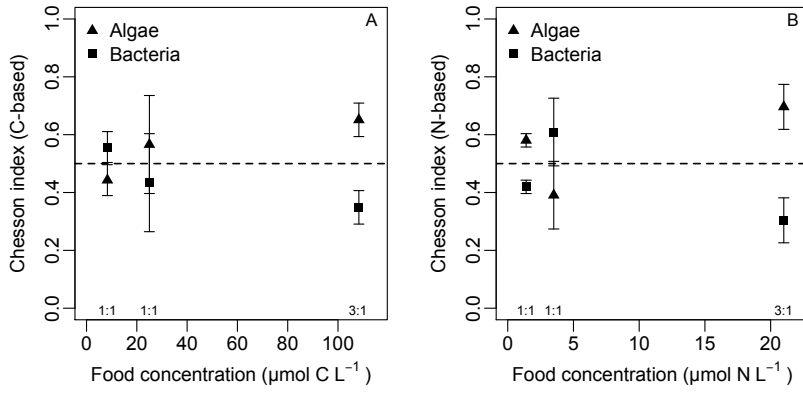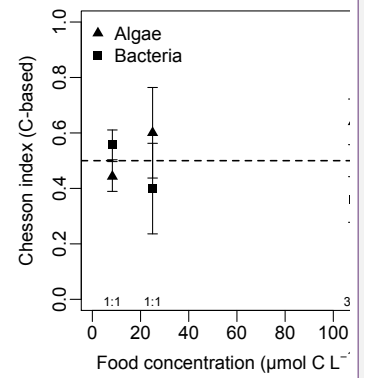
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Figure 5: The Chesson index of *L. pertusa* for feeding on bacteria and algae expressed in A) carbon and B) nitrogen. The mean ± range is shown for the low food concentration treatment (n = 2). The ratios 1:1 and 3:1 in both subpanel indicate the ratio of bacteria : algae in the respective food concentration treatment.

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Carbon uptake and processing

| ^{13}C-Alg: | ^{13}C-tissue | ^{13}C-DIC | ^{13}C-CaCO$_3$ |
| ^{13}C-Bac: | ^{13}C-tissue | ^{13}C-DIC | ^{13}C-CaCO$_3$ |

^{15}N-Bac
^{13}C-Alg

Nitrogen uptake

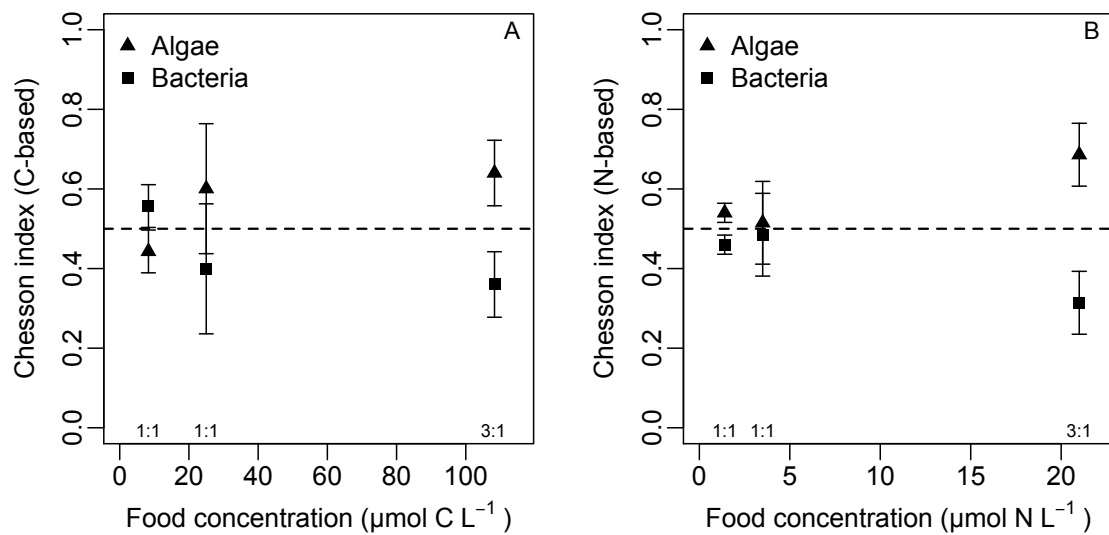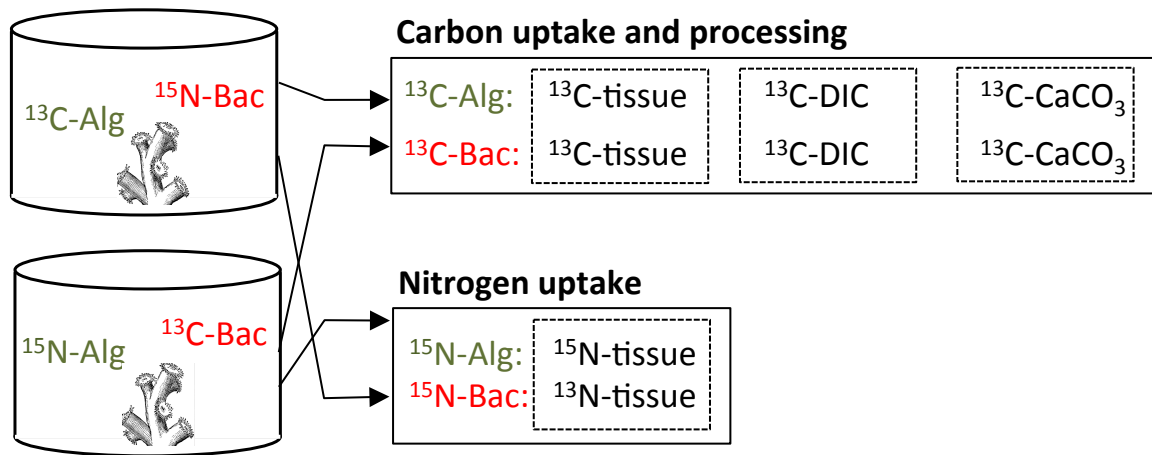| ^{15}N-Alg: | ^{15}N-tissue |
| ^{15}N-Bac: | ^{13}N-tissue |

^{13}C-Bac
^{15}N-Alg

Figure 4: The Chesson index of *L*.