The carbon and nitrogen budget of *Desmophyllum* dianthus - a voracious cold-water coral thriving in an acidified Patagonian fjord (#63798)

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The carbon and nitrogen budget of *Desmophyllum dianthus* - a voracious cold-water coral thriving in an acidified Patagonian fjord

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In the North Patagonian fjord region, the cold-water coral (CWC) Desmophyllum dianthus occurs in high densities, in spite of low pH and aragonite saturation. These conditions may enhance the energy demand of the corals, which is so far unknown. In a laboratory experiment, we investigated the carbon and nitrogen (C, N) budget of D. dianthus from Comau Fjord under three feeding treatments: (1) live fjord zooplankton (>100 µm), (2) live fjord zooplankton plus krill, and (3) four-day food deprivation. In closed incubations, C and N budgets were derived from the difference between C and N uptake during feeding and subsequent C and N loss through respiration, ammonium excretion, release of particulate organic carbon and nitrogen (POC, PON). Feeding on zooplankton plus krill significantly increased coral respiration (35 %), excretion (131 %), and POC release (67 %) compared to feeding on zooplankton only. Nevertheless, the higher C and N losses were overcompensated by the threefold higher C and N uptake from krill (plus zooplankton), indicating a high assimilation and growth efficiency for the krill diet. In contrast, short food deprivation caused a substantial reduction in respiration (59 %), excretion (54 %), release of POC (73 %) and PON (87 %) compared to feeding on zooplankton, suggesting a high potential to acclimatize to food scarcity (e.g. in winter). To balance their relatively high C and N losses, the corals have to consume 4 % of their tissue-C and -N every day, equivalent to almost 800 zooplankton individuals. The capture of a single krill, however, provides enough C and N to compensate daily C and N losses and grow tissue reserves,

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suggesting that krill plays an important nutritional role for the fjord corals. Efficient krill and zooplankton capture, as well as dietary and metabolic flexibility, may enable *D. dianthus* to thrive under adverse environmental conditions in its fjord habitat; however, it is not known how combined anthropogenic warming, acidification and eutrophication jeopardize the energy balance of this important habitat-building species.



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Abstract

- 29 In the North Patagonian fjord region, the cold-water coral (CWC) Desmophyllum dianthus
- 30 occurs in high densities, in spite of low pH and aragonite saturation. These conditions may
- 31 enhance the energy demand of the corals, which is so far unknown. In a laboratory experiment,
- 32 we investigated the carbon and nitrogen (C, N) budget of D. dianthus from Comau Fjord under
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- 34 krill, and (3) four-day food deprivation. In closed incubations, C and N budgets were derived
- 35 from the difference between C and N uptake during feeding and subsequent C and N loss
- 36 through respiration, ammonium excretion, release of particulate organic carbon and nitrogen
- 37 (POC, PON). Feeding on zooplankton plus krill significantly increased coral respiration (35 %),
- as excretion (131 %), and POC release (67 %) compared to feeding on zooplankton only.
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Introduction

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54 Cold-water coral (CWC) reefs and assemblages range amongst the most diverse and productive deep-sea ecosystems, but may be found in shallower waters in temperate fiords (Freiwald et al., 55 2004). On the steep, partly overhanging walls of the North Patagonian Comau Fjord (Los Lagos 56 57 Region, Chile; Fig. 1), the cosmopolitan, solitary CWC Desmophyllum dianthus (Scleractinia) 58 forms vast banks between 20 and 280 m depth (Försterra & Häussermann, 2003; Fillinger & Richter, 2013; Försterra et al., 2016), in spite of low pH and aragonite undersaturation (Fillinger 59 & Richter, 2013; Jantzen et al., 2013a). The low pH in the North Patagonian fjord region may 60 relate to the high organic matter concentration from high productivity (Montero et al., 2011) and 61 terrestrial run-off (Försterra & Häussermann 2003, Jantzen et al. 2013a). To maintain 62 63 calcification under these conditions, the corals may up-regulate their internal pH (Trotter et al., 64 2011; Anagnostou et al., 2012; McCulloch et al., 2012). This is an energy-costly process requiring a corresponding energy supply (Gattuso, Allemand & Frankignoulle, 1999; Cohen & 65 66 Holcomb, 2009). Also, terrestrial run-off (Försterra & Häussermann 2003, Jantzen et al. 2013a) 67 may increase the concentration of suspended particles, creating energetic costs of cleaning and mucus production to protect the sensitive coral tissue from smothering (Larsson & Purser, 2011; 68 Larsson et al., 2013; Zetsche et al., 2016). The sheltered occurrence of D. dianthus in Comau 69 Fjord, in an upside-down position under overhangs, has been interpreted as avoidance to 70 sedimentation (Försterra & Häussermann, 2003). 71

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The natural conditions of low pH and relatively high turbidity in the fjord region are exacerbated by climate change and intense salmon aquaculture (Buschmann et al., 2009; Mayr et al., 2014; Iriarte, 2018). It is therefore important to (1) know the energetic costs involved in coping with present and future fjord environments and (2) estimate the resilience to disturbance affecting the energy budget, growth and reproduction of these ecosystem engineers (Melzner et al., 2009; Findlay et al., 2011; Vidal-Dupiol et al., 2013).

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The energy budget of the fiord corals, i.e. their food supply against energetic costs, is presently 80 unknown. The carbon and nitrogen isotopic composition of D. dianthus from Comau Fjord 81 indicates consumption of zooplankton (Mayr et al., 2011). With its large polyps (up to 6 cm in 82 diameter, Försterra & Häussermann 2003), D. dianthus is able to capture large zooplankton such 83 84 as copepods and euphausiids (krill) (Sokol, 2012; Höfer et al., 2018). To fuel its respiratory carbon demand, D. dianthus from the Mediterranean deep sea requires the equivalent of three 85 adult brine shrimps (Artemia salina) per day (Naumann et al., 2011). However, A. salina does 86 not occur in the coral habitat and feeding on natural prey may entail a different carbon budget 87 (Møller & Riisgård, 2007). In the North Patagonian fjord region, the zooplankton abundance 88 89 shows a pronounced seasonality, with a maximum following the spring phytoplankton bloom and a minimum in Austral winter (Iriarte et al., 2007; González et al., 2010). In experiments, 90 increased availability of zooplankton food enhanced the skeletal growth of the fiord corals 91 92 (Martinez-Dios et al., 2020), but it is unknown whether food is currently limiting coral growth in 93 the fjord region.

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Here, we investigate the carbon and nitrogen (C and N) budget and natural zooplankton demand of *D. dianthus* from Comau Fjord, Chile. The C and N budget of a consumer is the difference between C and N uptake and C and N loss (Fig. 2). CWCs release the indigestible parts of their food and coral mucus (Wild et al., 2008) as particulate and dissolved organic matter (POM, DOM), measurable as particulate and dissolved organic carbon and nitrogen (POC, PON; DOC, DON). CWC metabolism involves oxygen consumption and carbon dioxide production through respiration, as well as ammonium production via excretion (Khripounoff et al., 2014; Maier et al., 2019). The remaining, non-released C and N is available for growth of somatic and reproductive tissue and therefore termed 'scope for growth' (Warren & Davis 1967). We determined the C and N budget (uptake versus loss) of the fjord corals under three different feeding treatments, simulating the varying zooplankton availability in the fjord region (Iriarte et al., 2007; González et al., 2010): (1) live fjord zooplankton, (2) live fjord zooplankton plus krill, and (3) short-term food deprivation. From these budgets, we estimated the minimum C, N and zooplankton demand of *D. dianthus* in the North Patagonian fjord region and evaluated the scope for growth of this important foundation species.

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Materials & Methods

Coral sampling and maintenance

- Thirteen similar-sized D. dianthus specimens (calyx height: 3.4 ± 0.4 cm, calyx length:
- 114 1.4 ± 0.2 cm, calyx width: 2 ± 0.4 cm, Fig. 3a) were collected live from 20 m water depth in
- 115 Comau Fjord (Cross Huinay, Liliguapi, Fig. 1) in January 2012. The collection of *D. dianthus* for
- scientific purposes was approved by the Chilean Ministry of Economy, Development & Tourism,
- sub-secretariat of fisheries and farming (ref. 1742). The corals were chiseled off the substrate by
- 118 SCUBA divers and immediately placed into water-tight, sealed plastic containers, ensuring no
- 119 contact with either the brackish surface water layer or air during transport to the laboratory.



Desmophyllum dianthus from the shallow parts of Comau Fjord typically has live tissue only on 120 the apical end of the corallum (skeleton), while the basal end is bare and inhabited by diverse 121 organisms (Försterra & Häussermann, 2003). To remove those organisms, the bare corallum was 122 carefully cut off with a submerged diamond blade (3.2 mm thick), connected to an electric 123 124 grinder (Jantzen et al. 2013b). The fracture zone was sealed with cyano-acrylate gel (super flex glue gel) and glued to a polyethylene screw (Jantzen et al., 2013b). For maintenance before and 125 during the experiment, the corals were fixed in their natural 'upside-down' growth position in 28 126 L-maintenance tanks (Fig. 3a, maximum seven corals per tank) with a flow-through of 10 min-127 filtered fiord water, continuously pumped from 25 m depth off Huinay (flow: 0.07 L min⁻¹): 128 temperature: 11.9 °C; salinity: 31.6; particulate organic matter concentration: 12.8 ± 4.2 umol 129 POC L⁻¹; 1.4 ± 1.2 µmol PON L⁻¹). Corals were fed for two hours per day with live, freshly-130 collected fjord zooplankton (for collection, see next section) at a concentration of 571 ± 203 131 zooplankton individuals L⁻¹, equivalent to $85 \pm 30 \mu mol C L^{-1}$ and $16 \pm 6 \mu mol N L^{-1}$. During 132 133 feeding, water exchange was interrupted. Before the start of the feeding treatments, all corals were weighed in seawater of ambient temperature and salinity (density 1.026 g cm⁻³) with an 134 analytical balance equipped with an underfloor weighing basket (Sartorius CPA225DOCE). 135 Polyp dry mass was derived from buoyant weight according to Davies (1989), using a species-136 specific aragonite density of 2.835 g cm⁻³ (Naumann et al., 2011). Corals were given a recovery 137 and acclimatization time of one week from collection to the start of the experiment. 138

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Zooplankton and krill sampling

For the feeding treatments, live fjord zooplankton was collected ca. 1 km off Huinay Scientific Field Station (Fig. 1) in the afternoon, by a single vertical haul from 20 m water depth with a 100 µm-Nansen net (diameter 0.7 m). The zooplankton sample was split with a Motodo plankton sample splitter into equal 1/8 portions, which were split again with measurement cylinders into ten equal portions (1/80 of the original sample). Live zooplankton was used in the experiment (see next section).

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Krill (*Euphausia vallentini*, adult and pre-adult stages) was collected at night in Comau Fjord between 20 and 80 m water depth, in a 45-min horizontal trawl at 2 knots with a ring trawl net (0.5 m diameter, 500 μ m mesh size). Krill was drained on paper tissue, individuals were measured (cephalo-thoracic length, ca. 7 cm), weighed (wet mass) and stored frozen (-13°C) until the experiment. Six individuals were dried (40 °C, three days) and weighed again (dry mass, 3.3 ± 1.5 mg).

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Experimental design and set-up

Corals were split into two batches of six and seven corals, respectively. All corals (n=13) were initially fed with zooplankton (treatment 'zooplankton'). Subsequently, coral batch I was fed with zooplankton plus one krill individual and on the next day remained unfed (treatment 'zooplankton+krill'). Coral batch II was food-deprived for four days (treatment 'unfed'). The C



- and N uptake of the corals was determined during feeding (as described in Section 'Feeding').
- After each feeding treatment, the C and N losses of the corals were measured in 9-11 h
- incubations (see Section 'Incubations'). In the treatments 'zooplankton' and 'zooplankton+krill',
- incubations were started 1-3 h after feeding (incubations called 'zoopl', 'krill.d1'); in the
- 'zooplankton+krill' treatment, corals were incubated a second time 24 h after feeding ('krill.d2').
- 165 In the 'unfed' treatment, corals were incubated after four days of food deprivation.

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- Feeding and incubations were carried out at 11°C (representing in situ temperature) in 0.5 L-
- 168 SCHOTT-DURAN® bottles (total volume: 0.8 L; in the following referred to as 'SCHOTT
- bottles'), filled with 10 µm-filtered fjord water from 25 m depth off Huinay (Fig. 3b, c). One
- 170 coral per bottle was fixed in its natural 'upside-down' position in the custom-built bottle lid
- 171 (Jantzen et al., 2013b). A magnetic stirring bar at the bottle floor created a circular flow of ~1 cm
- 172 s⁻¹, which kept live zooplankton in suspension without bending the coral tentacles (Sokol, 2012).
- 173 A detailed account of the feeding treatments and closed-cell incubations is provided in the
- 174 following two sections.

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Feeding

- 177 For the feeding treatment 'zooplankton', the corals were provided with live fjord zooplankton at
- 178 a concentration of 1025 ± 332 zooplankters L⁻¹ ($164 \pm 36 \mu mol C L^{-1}$, $30 \pm 7 \mu mol N L^{-1}$) for 2 h
- 179 (Fig. 3a). This feeding regime served to simulate a pulse of high zooplankton availability, which
- may occur when a zooplankton swarm with high individual densities (Ambler, 2002) is advected
- by local currents (3-11 cm s⁻¹, Jantzen et al. 2013b). Zooplankton swarms are common in fjord
- boundaries (Hirche, Laudien & Buchholz, 2016). Longer feeding times were avoided to prevent
- hypoxia in the closed chambers (Höfer et al., 2018; S Maier, 2012, unpublished data).

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- The 'zooplankton' treatment was carried out in subsequent subsets, each with three to four corals
- and triplicate seawater controls without corals, which served to determine zooplankton loss from
- internal zooplankton predation and handling. To start the feeding (at t₀), one aliquot of live
- zooplankton food (1/80 haul in 50 mL filtered seawater) was added to each of the experimental
- bottles. Five additional aliquots were analyzed for the number of zooplankton individuals (n=2)
- and for the concentration of POC and PON (n=3), to estimate the amount of food added to the
- experimental bottles. During feeding, polyp activity was closely monitored, to ensure that all
- 192 corals had their tentacles expanded. To end the feeding, the corals were removed from the bottles
- and returned to the maintenance tanks. End (t_1) water samples for number of zooplankton
- individuals (350-490 mL), POC and PON (290-370 mL) were taken from each bottle after
- 195 thorough mixing.

196

- 197 Zooplankton samples were concentrated over a 55 μm-mesh and fixed in 4%-borax-buffered
- 198 formaldehyde. POC and PON samples were collected on pre-combusted (24 h, 500 °C), pre-



199	weighed 0.7 μm- glass-fiber filters (GF/F) by vacuum filtration. Filters were frozen (-13 °C) and
200	dried to constant mass at 40 °C.
201	
202	For the feeding treatment 'zooplankton+krill', corals of batch I were first fed with live fjord
203	zooplankton, as described above, and received one thawed, pre-measured krill via tweezers 3.5 h
204	later (Fig. 3). All replicates of the 'zooplankton+krill' treatment were fed in one subset.
205	
206	For the feeding treatment 'unfed', corals of batch II were kept in their maintenance tank in
207	10 µm-filtered fjord water, without zooplankton food, for four days. The 'unfed' treatment was
208	carried out in two subsets, with three and four corals, respectively.
209	
210	Incubations
211	After each feeding treatment, the corals were incubated for 9-11 h in closed SCHOTT bottles
212	with 10 µm-filtered fjord water (Fig. 3c). Triplicate seawater controls per treatment subset
213	(3-7 corals, see 'Feeding') served to measure planktonic oxygen (O ₂), C and N fluxes. At the
214	start of the incubation (t_0) , the O_2 concentration was measured with an optode (HQ40d; Hach,
215	USA) in a separate SCHOTT bottle B_o . Start (t_0) water samples were taken by syringe from B_o
216	for analysis of dissolved inorganic nitrogen (DIN, i.e. ammonium, nitrate, nitrite; 100 mL), DOC
217	and DON (20 mL, in triplicates). The remaining water in B _o (300-600 mL) was used for POC
218	and PON analysis. During the incubation, coral polyps remained protruded with extended
219	tentacles. The O ₂ concentration remained above 80 % of the t ₀ -concentration, a conservative
220	threshold to avoid effects of low-oxygen concentration on coral physiology (Dodds et al., 2007).
221	At the end of the incubation (t ₁), the corals were removed and returned to their maintenance
222	tanks. In each bottle, the t_1 - O_2 concentration was first measured, before taking t_1 -water samples
223	as described above for the t ₀ -sampling.
224 225	DIN samples were filtered through GF/F-filters into glass vials and fixed with a concentrated
225 226	mercury chloride solution (0.105 g L ⁻¹) to prevent microbial activity. Samples for DOC and
227	DON were filtered through GF/F-filters into glass vials (filters and vials pre-combusted, 450 °C,
228	12 h), acidified to pH2 with 32% hydrochloric acid to avoid microbial activity and stored dark at
229	4 °C. Sample processing for POC and PON was described in the previous section ('Feeding').
230).
231	Coral dry mass and tissue sampling
232	At the end of the experiment, the coral tissue was removed from the skeleton with an airbrush
233	filled with 0.7 µm-filtered seawater and homogenized with an ultra turrax (Jantzen et al., 2013c).
234	The volume of the tissue-seawater suspension was measured. Subsamples of the tissue-seawater
235	suspension (1 mL, n=6 aliquots per coral) were collected on pre-combusted (500 °C, 24 h), pre-
236	weighed GF/F-filters and dried up to constant mass at 40 °C. Coral samples were transported to
237	Germany under CITES permit E-00427/12.

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239 Sample analyses

Zooplankton samples were enumerated in a Bogorov chamber under a stereo microscope. Only
 undamaged, non-gelatinous zooplankters were counted.

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- 243 Samples of coral tissue, krill, POC and PON were weighed (for dry mass) and subsequently
- analyzed for organic carbon (OC) and organic nitrogen (ON) content on an elemental analyzer
- 245 (EuroEA3000, EuroVector) with acetanilide calibration. To measure the OC content of coral
- 246 tissue (tissue-C), subsamples on GF/F filters (n=3 per coral) were vapor-acidified with 12 N-
- 247 hydrochloric acid prior to analysis, to remove remainders of skeletal inorganic carbon (Hedges &
- 248 Stern, 1984). The ON content of coral tissue (tissue-N) was measured on separate subsamples
- 249 (n=3) without acidification. The total tissue-OC and -ON content of each coral was calculated by
- 250 multiplying the OC and ON content measured in the subsamples (1 mL) with the volume of the
- 251 tissue-seawater suspension (see previous section).

252

- 253 Krill and GF/F filters with zooplankton (see 'Feeding') and POM (released by the corals, see
- 254 'Incubations') were not acidified, as previous tests revealed negligible amounts of inorganic
- 255 carbon. POC concentration was determined as
- 256 $POC\left[\frac{\mu mol\ C}{L}\right] = \frac{POC\ content\ GF/F\ filter}{filter\ d\ volume};$
- 257 PON concentration was calculated accordingly. For krill, we determined the relation between
- 258 wet mass and C content (C content [μ mol C krill⁻¹] = 3.9 · wet mass [mg] + 48.3; R² = 0.86) and
- 259 the relation between wet mass and N content (N content [μ mol N krill⁻¹] = 0.9 · wet mass [mg] +
- 260 11.4; $R^2 = 0.87$).

261

- Ammonium (NH₄⁺), nitrate and nitrite concentration was analyzed spectrophotometrically at the
- 263 ICBM-Terramare Wilhelmshaven according to Grasshoff et al. (1983). DOC and total dissolved
- 264 nitrogen (TDN) concentration was measured via high-temperature catalytic oxidation (HTCO,
- Sugimura & Suzuki 1988) on a Shimadzu TOC-VcpH analyzer, equipped with a Total Nitrogen
- Measuring Unit (TNM-1), with L-arginine calibration. The datasets of DOC and TDN
- 267 concentrations contained a few extreme values, possibly due to sample contamination during
- 268 handling and processing. Therefore, outliers of DOC and TDN concentration were identified as
- values $< Q1 IQR \cdot 1.5$ and values $> Q3 + IQR \cdot 1.5$, where Q1 was the first quartile of the data
- subset, Q3 the third quartile, and IQR the interquartile range between Q1 and Q3; data subsets
- were t_1 -values of coral incubations, t_1 -values of control incubations, and t_0 -values of coral and
- 272 control incubations together. Outliers were excluded and the remaining t_0 and t_1 -values of each
- incubation (samples taken in triplicate) were averaged. DON concentration was obtained as
- 274 DON = TDN DIN, with DIN = ammonium + nitrate + nitrite.

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Carbon and nitrogen budget

- 277 For each feeding treatment, the C and N budgets of the corals were determined; for the treatment
- 278 'zooplankton+krill', two C and N budgets were determined per coral, one directly after feeding

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- and one 24 h later. All fluxes (C, N, O₂) were calculated from the difference between a
- 280 measurement at t_0 (start of the feeding or incubation) and a second measurement at t_1 (end of the
- feeding or incubation) in coral ('coral') and seawater-control ('control') trials. The C uptake of
- 282 the corals from zooplankton (treatments 'zooplankton', 'zooplankton+krill', in μmol C) was
- 283 determined as

$$284 \quad \textit{Cuptake} = \frac{[\textit{POC}]_{t_{0,\textit{coral}}} - [\textit{POC}]_{t_{1,\textit{coral}}}}{t_{\textit{coral}}} - \frac{[\textit{POC}]_{t_{0,\textit{control}}} - [\textit{POC}]_{t_{1,\textit{control}}}}{t_{\textit{control}}}) \cdot \textit{V} \cdot t_{\textit{coral}},$$

- 285 where [POC] is the POC concentration, t is the feeding time and V is the water volume of the
- 286 coral incubation (SCHOTT bottle volume coral volume). The N uptake of the corals from
- 287 zooplankton was determined accordingly. In treatment 'zooplankton+krill', total C or N uptake is
- 288 the sum of zooplankton-C or -N uptake and the C or N content of the krill individual provided to
- 289 the respective coral; the C and N content of the krill individual was estimated from its wet mass
- 290 (see previous section). In treatment 'unfed', a zero C and N uptake was assumed. In all feeding
- 291 treatments, the C and N uptake was treated as daily rates (i.e. μmol C and N d⁻¹), because the
- 292 corals were fed once per day only. In treatment 'zooplankton', we additionally determined the
- 293 zooplankton capture of the corals, as

$$294 \quad Zooplankton \ capture = \frac{zoopl_{t_{0, \ coral}} - zoopl_{t_{1, \ coral}}}{t_{coral}} - \frac{zoopl_{t_{0, \ control}} - zoopl_{t_{1, \ control}}}{t_{control}}) \cdot V \cdot t_{coral},$$

- 295 where zoopl is the number of zooplankton individuals.
- 296
- 297 Coral respiration rates (in μmol O₂ h⁻¹) were derived as

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$$Respiration(O_2) = \frac{[O_2]_{t_0, coral} - [O_2]_{t_1, coral}}{t_{coral}} - \frac{[O_2]_{t_0, control} - [O_2]_{t_1, control}}{t_{control}}) \cdot V,$$

- 299 where $[O_2]$ is the O_2 concentration. The C respiration rate was derived from the O_2 respiration
- rate, assuming a respiratory coefficient $O_2:C = 1$ (Glud, Eyre & Patten, 2008). Rates of NH_4^+
- 301 excretion and release of POC, PON, DOC, DON (in μmol C or N h-1) were obtained as

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$$C \text{ or } N \text{ release} = \frac{[x]_{t_{1, coral}} - [x]_{t_{0, coral}}}{t_{coral}} - \frac{[x]_{t_{1, control}} - [x]_{t_{0, control}}}{t_{control}}) \cdot V,$$

- 303 where [x] is the concentration of the respective substance. Rates of respiration, ammonium
- excretion, release of POC, PON, DOC and DON were extrapolated to 24 h and standardized to
- 305 coral tissue organic carbon content (tissue-C) as approximation of coral biomass. To facilitate
- 306 comparability with other studies, we additionally provide C and N fluxes standardized to polyp
- 307 dry mass (determined via buoyant weight) and skeletal dry mass (polyp dry mass tissue dry
- 308 mass) in Supplemental Table 1.1.
- 309 The daily C and N budget of the corals (Fig. 2) was derived as
- 310 $SfG_C = C \text{ uptake} C \text{ respiration} POC \text{ release},$
- 311 and
- 312 $SfG_N = N \text{ uptake} NH_4^+ \text{ excretion} PON \text{ release},$
- both in umol C (mmol tissue-C d⁻¹). The term 'scope for growth' (SfG, Warren and Davis 1967)
- denotes the net C or N gains of the corals, which remain from food uptake after subtraction of all
- 315 C and N losses. SfG > 0 indicates a C or N surplus, which can be invested in biomass growth



(somatic and/or reproductive), while SfG < 0 indicates a C or N deficit. It should be noted that 316 DOC and DON release were excluded from the C and N budgets, due to the high variability in 317 DOC and DON fluxes (see below). 318

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Statistical analysis

320 321 Graphical and statistical analysis was performed with R (R Core Team, 2017). Values in text are given as mean \pm standard deviation. Firstly, we tested whether the feeding treatments had an 322 effect on the C and N fluxes, i.e. on the total C and N uptake and rates of C respiration, NH₄⁺ 323 excretion, and release of POC, PON, DOC, DON. For each flux, linear mixed effect (LME) 324 models were fitted, separately for coral batch I and II, with the function lmer (R package 325 326 lmerTest, Kuznetsova et al. 2017). The LME models accounted for the repeated measurements on the individual corals of the two batches, using coral individuals as random effect and feeding 327 treatment as fixed effect (i.e. flux ~ treatment + (1|coral individual)). In batch I, C and N fluxes 328 329 after feeding on zooplankton ('zoopl') were compared with C and N fluxes directly after feeding 330 on zooplankton+krill ('krill.d1'); and C and N fluxes directly after feeding on zooplankton+krill ('krill.d1') were compared with C and N fluxes 24 h later ('krill.d2'). In batch II, C and N fluxes 331 after feeding on zooplankton ('zoopl') were compared with C and N fluxes after four days of 332 333 food deprivation ('unfed'). Detailed results of the LME models are available as Supplementary

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Secondly, we analyzed the dependence of SfG_C and SfG_N on the respective C and N uptake by linear regression, for all feeding treatments combined (function lm, package stats, R Core Team 2017). The C uptake at $SfG_C = 0$ (x-axis intercept) was interpreted as minimum C demand of the corals, the N uptake at $SfG_N = 0$ as their minimum N demand.

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Results

Table 1.9.

Uptake of carbon and nitrogen

- 344 When fed with zooplankton (treatment 'zooplankton'), D. dianthus captured 156 \pm
- 74 zooplankton individuals polyp⁻¹ h⁻¹. Given the 2 h-feeding time per day, the total zooplankton 345
- 346 capture was 312 ± 148 zooplankton individuals d⁻¹, resulting in a C uptake of 18.8 ± 11.5 µmol C
- (mmol tissue-C)⁻¹ d⁻¹ (Fig. 4a) and a N uptake of 4 ± 2.3 µmol N (mmol tissue-C)⁻¹ d⁻¹ (Fig. 4b). 347
- 348 One krill in addition to zooplankton increased the C and N uptake of the corals (of batch I) by a
- factor of three $(67.9 \pm 6.7 \mu mol C \text{ (mmol tissue-C)}^{-1} \text{ d}^{-1}; 15.8 \pm 1.8 \mu mol N \text{ (mmol tissue-C)}^{-1}$ 349
- 350 d^{-1}).

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Respiration and ammonium excretion

- Increasing meal size increased the respiration and ammonium excretion rate of D. dianthus 354
- (Fig. 4c, d). Directly after feeding on zooplankton, D. dianthus respired on average 27.5 \pm 355



5.8 μ mol O₂ (mmol tissue-C)⁻¹ d⁻¹ and excreted 3.2 \pm 1.3 μ mol NH₄⁺ (mmol tissue-C)⁻¹ d⁻¹. When the corals received krill in addition to zooplankton, they showed an on average 35 % higher respiration rate than when they were fed with zooplankton only (Fig. 4c, 'krill.d1', versus 'zoopl', blue circles). At the same time, their ammonium excretion rate doubled (Fig. 4d). One day after feeding on krill plus zooplankton, the corals showed a lower rate of respiration and ammonium excretion again (Fig. 4c, d, 'krill.d2'). Four days of food-deprivation reduced the respiration rate of the corals by 29 % and their ammonium excretion rate by 54 %, relative to their metabolic activity after feeding on zooplankton (Fig. 4c, d, 'unfed' versus 'zoopl', red circles).

Organic matter release

Desmophyllum dianthus showed a clear release of POC and PON in all feeding treatments (Fig. 4e, f). Directly after feeding on zooplankton, corals released $8.2 \pm 6 \mu mol$ POC (mmol tissue-C)-1 d-1 and $1.7 \pm 0.7 \mu mol$ PON (mmol tissue-C)-1 d-1 (Fig. 4e, f, 'zooplankton'). Feeding on krill in addition to zooplankton increased POC release by 67 % and PON release by 39 % compared to feeding on zooplankton only (Fig. 4e, f, 'krill.d1' versus 'zoopl', blue circles). One day after feeding on krill plus zooplankton ('krill.d2'), POC and PON release rates were low (1.8 ± 1.0 μmol POC (mmol tissue-C)-1 d-1, 0.6 ± 0.3 μmol PON (mmol tissue-C)-1 d-1). Four days of food-deprivation reduced POC and PON release by 73 % and 87 % relative to the POC and PON release after feeding on zooplankton (Fig. 4e, f, 'unfed' versus 'zoopl', red circles).

DOC and DON fluxes ranged around zero with a high variability (Fig. 4g, h). Feeding treatments had no detectable effect. DOC and DON fluxes were likewise high and variable in the seawater control incubations (Supplemental Table 1.7).

Carbon and nitrogen budget

Corals fed with zooplankton plus krill showed a positive scope for growth for C and N (SfG_C, SfG_N) directly after feeding ('krill.d1', Fig. 5a, b), meaning that their C and N uptake outweighed the combined losses via respiration, excretion, POC and PON release. Feeding on zooplankton alone did, in most cases, not provide *D. dianthus* with enough C and N for a positive SfG (Fig. 5a, b). Linear regression revealed that *D. dianthus* in the experiment had a minimum C demand of 37.05 μ mol C (mmol tissue-C)⁻¹ d⁻¹ or 98.85 μ mol C polyp⁻¹ d⁻¹ to fully balance its C losses (i.e. SfG_C = 0). This corresponds to a daily consumption of 3.7 % of its total tissue-C content and ca. 760 zooplankters per polyp (0.13 μ mol C (zooplankton individual)⁻¹, Supplemental Table 1.3) or less than one krill per polyp (129 μ mol C krill⁻¹, Supplemental Table 1.1). Accordingly, the minimum N demand of *D. dianthus* was 5.38 μ mol N (mmol tissue-C)⁻¹ d⁻¹, which is 3.7 % of their tissue-N (tissue-C:tissue-N = 6.9). Please note that DOC and DON release were not considered in the shown C and N budgets, since DOC and DON fluxes were highly variable and ranged around zero (see above). Therefore, it cannot be ruled out that the C and N demand of *D. dianthus* is higher (or lower) than indicated here.



Discussion

In this study, we report C and N budgets of the CWC *D. dianthus*, an important matrix species of CWC banks in the fjords of the Los Lagos Region, under three different experimental feeding regimes (fed with live fjord zooplankton, fed with zooplankton plus krill, four-day food-deprived). We first discuss the metabolic flexibility (metabolic rate, organic matter release) of the corals in response to varying food availability. Then, we evaluate how and if the corals can sustain their C and N demand, today during different seasons and in the future.

Metabolic rate

The CWC *D. dianthus* shows a high metabolic flexibility in response to varying food availability, indicated by increased respiration and ammonium excretion with increasing meal size (from four-day unfed, over zooplankton, to zooplankton plus krill, Fig. 4c, d). The 1.5-fold higher respiration rate after ingesting a large food ration (zooplankton plus krill) as compared to one day later likely reflects the 'specific dynamic action of food' (SDA, Rubner 1902). The SDA describes the increased metabolic rate of animals after feeding, owing to the energetic expenses of food capture and digestion (McCue, 2006; Secor, 2008). The SDA typically increases with meal size, but also varies with meal type (Secor, 2008; present study). Accordingly, krill supplied the corals with four times more C compared to zooplankton, but only increased the respiration by a factor of 1.4, probably due to higher energetic costs to capture and process many live, small zooplankters compared to one large, dead krill. Energy costs to process live krill might be higher than for dead krill; however, we assume that the difference is minor, because in feeding trials with live krill (S Maier, C Jantzen, J Laudien and C Richter, 2012, unpublished data), the corals immobilized their prey within a fraction of a second.

Desmophyllum dianthus responds to short-term food deprivation with a reduction of metabolic rates, likely to conserve energy (Naumann et al. 2011, present study). Corals from Comau Fjord lowered their respiration by 40 % after four days of food deprivation (present study), conspecifics from the Mediterranean deep-sea by 20 % after one week and by 50 % after three weeks of food deprivation (Naumann et al., 2011). This fast, strong reduction of metabolic activity stands in contrast to the closely related CWC Lophelia pertusa, which reduced oxygen consumption only after several months of food deprivation (Larsson, Lundälv & van Oevelen, 2013; Maier et al., 2019). Overall, in the present study, the respiration rate of *D. dianthus* was around 2.5 times lower (14 ± 5 μmol O_2 (g skeletal dry mass)⁻¹ d⁻¹) compared to the respiration rate of Mediterranean *D. dianthus* (35 ± 8 μmol O_2 (g skeletal dry mass)⁻¹ d⁻¹; Naumann et al. 2011), in spite of a comparable feeding history (*Artemia salina*, krill, >24 h after feeding) and temperature (12 °C).

The metabolic flexibility of *D. dianthus* could allow colonization of different habitats, from shallow areas of fjords with a high variability of food, temperature, salinity and pH, to the



environmentally more stable, deep CWC habitats (Freiwald et al., 2004). Global warming increases the metabolic rate of CWCs (Dodds et al., 2007; Gori et al., 2016; Dorey et al., 2020), which could cause severe energetical constraints for this species.

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Organic matter release

Cold- and warm-water corals release organic matter (POM, DOM), as feces egested from their gastrovascular cavity (Yonge, 1930) and as coral mucus (Brown & Bythell, 2005; Naumann et al., 2011). The high POC and PON release by *D. dianthus* directly after feeding (Fig. 4e, f) suggests that fecal material accounts for most of its POM release. The CWC species engulfs its prey whole; hence, sloppy feeding *sensu* Banse (1992), i.e. the loss of organic matter in front of the mouth, can be ruled out. Krill is assimilated at a higher efficiency compared to zooplankton (CN assimilation:CN uptake), due to the lower fecal loss in relation to the high C and N uptake.

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- Four-day-starved corals continue to release smaller amounts of POM, likely as mucoid material. Coral mucus consists of glycoproteins (Bythell & Wild, 2011) and serves as protection against
- 451 sediment smothering, biofouling and as feeding aid (Brown & Bythell, 2005). Wild et al. (2008)
- 452 reported that mucus of the CWC L. pertusa rapidly dissolved in seawater, hence, the DOC
- release of this CWC species was >30 times higher than its POC release. This high DOC:POC
- ratio was not confirmed for *D. dianthus* (present study); instead, rates of DOC release/uptake
- were highly variable (Fig. 4g).

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- Unfed *D. dianthus* from Comau Fjord released on average four times more total organic carbon (7.1 μmol TOC (g skeletal dry mass)⁻¹ d⁻¹; POC plus DOC) than its Mediterranean conspecifics
- 459 (1.9 μmol TOC (g skeletal dry mass)⁻¹ d⁻¹, Naumann et al., 2011). Higher mucus production in
- 460 the shallow areas of the fjords may serve as protection against higher particle loads (Larsson et
- al., 2013; Zetsche et al., 2016). In the Comau Fjord, the chlorophyll-a concentration (up to
- 462 >40 mg m⁻³, Richter et al. unpubl.), and hence turbidity, is orders of magnitude higher than in the
- deep parts of the oligotrophic Mediterranean (<2 mg m⁻³; Lo Iacono et al. 2019).

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- Due to relatively high mucus and fecal loss, the TOC release already contributes 30-60 % to the
- 466 total C loss of the fjord corals (respiration plus organic matter release). Anthropogenically
- increased sedimentation, e.g., from the extensive salmon farming in the Chilean fjords
- 468 (Häussermann et al., 2013; Försterra, Häussermann & Laudien, 2016), could further increase
- 469 mucus production and related energy expenditure.

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- On the steep, partly overhanging fjord walls, *D. dianthus* often co-occurs with other suspension
- 472 feeders, such as the bivalve *Acesta patagonica* and the sponge *Mycale thielei* (Försterra et al.,
- 473 2005). Like D. dianthus, these genera produce large amounts of detrital and/or fecal material
- 474 (Maier et al., 2020b). The organic matter 'waste' of the suspension feeding community may



serve as food for detritivores living underneath the vertical or overhanging walls, ensuring a close material recycling, as suggested for *L. pertusa* reefs (Rix et al., 2016; Maier et al., 2020b).

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Carbon and nitrogen budget

fjord corals are not food-limited.

479 The CWC D. dianthus in Comau Fjord is characterized by a high C and N demand. To account for their costs of respiration, ammonium excretion and POM release, the corals require 4 % of 480 their tissue-C and -N per day; to grow somatic and reproductive tissue, they need additional 481 resources. Conspecifics from the Mediterranean showed an even higher C demand, due to their 482 higher respiration rate (Naumann et al., 2011). In comparison, L. pertusa from a Norwegian fjord 483 has a 10-times lower C demand, due to the lower respiration under the colder conditions (8 °C) 484 and a lower POC release (Maier et al., 2019). Nevertheless, the comparatively high skeletal 485 growth rate of D. dianthus from Comau Fjord (Jantzen et al., 2013a,b) could indicate that the 486

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the fjord corals.

To balance C and N losses, a medium-sized *D. dianthus* polyp in Comau Fjord has to capture almost 800 zooplankton individuals (>100 µm) per day. As a voracious zooplankton predator, *D. dianthus* is capable to exploit high concentrations of zooplankton (Höfer et al., 2018), which may occur in swarms at densities of >1000 zooplankters L-1 (Ambler, 2002). Zooplankton aggregation was observed at pycnoclines (Tiselius, Nielsen & Nielsen, 1994), near oceanographic fronts, and in the vicinity of abrupt topography like seamounts or coral reefs (Genin et al., 1994). These aggregations form because zooplankton actively maintains its depth by swimming against vertical currents (Genin et al., 2005). A surprising finding in our experiments was that simulated zooplankton swarms of >1000 individuals L-1, leading to the capture of >300 zooplankton individuals, were insufficient to balance the daily C and N losses of

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501 This suggests that krill, or other larger prey, play a crucial role for the nutrition of D. dianthus in Comau Fjord. The capture of one krill alone boosts the energy reserves of the corals (Fig. 5), due 502 to its 1,000 times higher C content compared to small zooplankton, the higher assimilation 503 efficiency and lower metabolic costs involved in food processing (i.e. higher growth efficiency). 504 505 Diver observations at 20 m depth (J Laudien, T Heran, 2017, 2021, unpublished data) and remotely-operated-vehicle footage between 160 and 200 m depth (Fig. 6; V Häussermann, 506 G Försterra, C Richter, 2012, unpublished data) revealed dense krill swarms directly next to the 507 corals. Likewise, the recurrence of blue whales in Comau Fjord (Försterra & Häussermann, 508 2012) indicates krill aggregations, which are known to attract the large mammals in the region 509 (Buchan & Quiñones, 2016). In feeding experiments, D. dianthus captured live krill at a similar 510 rate (18 % h⁻¹) as small zooplankton (Höfer et al., 2018); in situ, krill capture remains to be 511 quantified. 512

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514 A maximized energy intake is crucial considering the pronounced seasonality in North Patagonia (Pickard, 1971). The C and N budget of D. dianthus was assessed in austral summer, when high 515 abundances of zooplankton and krill follow the spring phytoplankton bloom (Iriarte et al., 2007; 516 González et al., 2010) and create feast conditions. The CWCs might invest the excess resources 517 518 in tissue reserves such as lipids (Maier et al., 2019) to overcome the less-productive winter (Iriarte et al., 2007; González et al., 2010). In early spring (September), however, Patagonian 519 D. dianthus also starts to produce gametes, which is an energy-costly process (Feehan, Waller & 520 Häussermann, 2019). Reduced skeletal growth in summer could therefore indicate an energetic 521 522 trade-off between investment in reproductive tissue and growth (Hassenrück et al., 2013), as 523 suggested for L. pertusa from a Norwegian fjord (Maier et al., 2020a). In winter, when zooplankton and krill abundance is reduced, the corals may benefit from their metabolic 524 flexibility. The fast downregulation of metabolic rate and POM release constrains C and N 525 losses; therefore, four-day unfed corals had a similar (negative) scope for growth as corals that 526 527 received 'too small' amounts of zooplankton (Fig. 5). Further, after prolonged (3-week) 528 zooplankton exclusion, D. dianthus was observed to take up alternative resources, such as DOM and/or non-zooplankton POM (Naumann et al., 2011). A potential diet shift to more degraded 529 material in winter was also described for L. pertusa (Maier et al., 2020a). Metabolic and dietary 530 flexibility enable the corals to survive without particulate food for several months (J Laudien, 531 532 2020, unpublished data).

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Ex situ experiments, as presented here, allow the measurement of the total C and N fluxes of a CWC, i.e. its C and N budget. This measurement proves difficult *in situ*, as it typically requires a closed-off water volume. Nevertheless, *ex situ* experiments only provide specific simulations of the dynamic fjord environment (González et al., 2010; Jantzen et al., 2013a; Iriarte, 2018). Furthermore, it cannot be excluded that *ex situ*, the corals were exposed to higher stress than *in situ*. Stress can enhance the C and N loss of CWCs, e.g. through increased *ex situ* respiration (Khripounoff et al., 2014), and stress-induced mucus production (Zetsche et al., 2016). However, we minimized experimental stress, by maintaining the experimental corals in natural fjord water to assure suitable water quality, and by minimum, careful handling. Corals did not show visible signs of stress such as visibly increased mucus release, retracted tentacles or mortality.

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Conclusions

The CWC *D. dianthus* from the fjords of the Los Lagos Region in North Patagonia requires a substantial supply of pelagic food to balance its daily C and N loss through respiration, ammonium excretion and POM release, amounting to 4 % of its tissue-C and -N. Experimental feeding on zooplankton alone was not enough to balance this C and N loss, despite the high zooplankton food concentration. For a balanced C and N budget, the solitary coral needs to capture a minimum of 800 zooplankton individuals per polyp and day, or one larger prey item such as krill. Under experimental food deprivation, the corals swiftly reduced all C and N loss terms, likely to conserve energy. We argue that the exploitation of zooplankton swarms and/or



- the consumption of krill, combined with a high metabolic flexibility, are important in sustaining the energetic requirements of *D. dianthus* in Comau Fjord. The bulk of the population thrives
- 556 near or below aragonite saturation in deeper waters (Fillinger & Richter, 2013; Jantzen et al.,
- 557 2013a), which may further increase their energy demand (Gattuso, Allemand & Frankignoulle,
- 558 1999; Cohen & Holcomb, 2009); hence, our findings from shallow water individuals are likely a
- 559 conservative estimate of their energetic requirements.

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- 561 Climate change, ocean acidification and the intense salmon aquaculture in the Patagonian fjord
- region likely impact the energetic balance of *D. dianthus*. The species appears particularly
- sensitive to a combination of stressors, such as high temperatures and acidification (Gori et al.,
- 564 2016) or hypoxia and elevated levels of sulfide/methane (Försterra et al., 2014). Yet, the Comau
- Fjord habitat already displays 'extreme' conditions, e.g. low aragonite saturation (Fillinger &
- Richter, 2013; Jantzen et al., 2013a). To sustain growth under the low aragonite saturation, high
- availability of zooplankton food is crucial for the fjord corals (Martínez-Dios et al., 2020). A
- disrupted energy balance may have severe consequences for the growth, reproduction and hence
- the distribution of this foundation species in the Patagonian fjord region.

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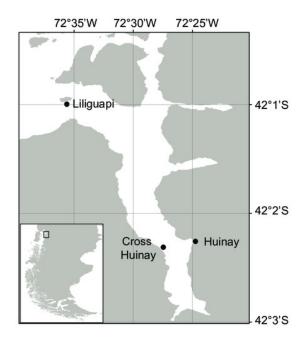
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Map of Comau Fjord, North Patagonia, Chile.

Shown are Huinay Scientific Field Station (Huinay) and the sampling sites Liliguapi and Cross Huinay.



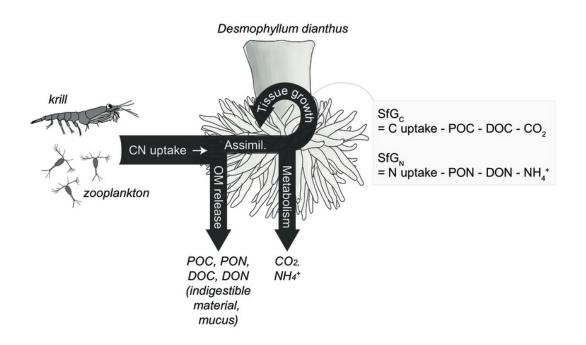




Conceptual carbon (C) and nitrogen (N) budget of Desmophyllum dianthus.

The corals release parts of the taken-up C and N as organic matter (OM), i.e. particulate and dissolved organic carbon and nitrogen (POC, PON, DOC, DON), the remainder is assimilated ('Assimil.'). Parts of the assimilated C and N are lost during metabolism as carbon dioxide (CO₂) and ammonium (NH₄⁺), the remainder is invested in the growth of somatic and reproductive tissue and is termed scope for growth (SfG). The figure is modified from Soetaert & van Oevelen (2009) and Warren & Davis (1967).



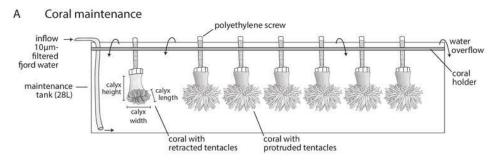




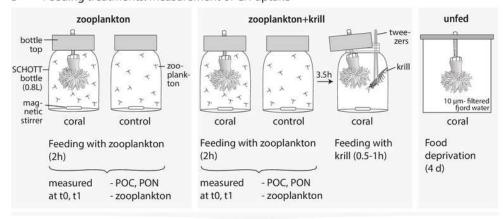
Maintenance and experimental set-up.

(A) Maintenance of *Desmophyllum dianthus* before and during the experiment. (B) Set-up of the feeding treatments. (C) Incubations following each feeding treatment. (B, C) Measurements and water samples taken at the beginning (t_0) and end (t_1) of the feeding/incubation are shown, i.e. 'zooplankton': number of zooplankton individuals; 'POC, PON', 'O₂', 'DIN', 'DOC, DON': concentration of particulate organic carbon and nitrogen, oxygen, dissolved inorganic nitrogen (ammonium, nitrate, nitrite), dissolved organic carbon and nitrogen.

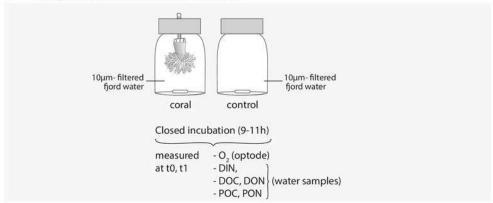




B Feeding treatments: Measurement of CN uptake



C Incubations: Measurement of CN losses

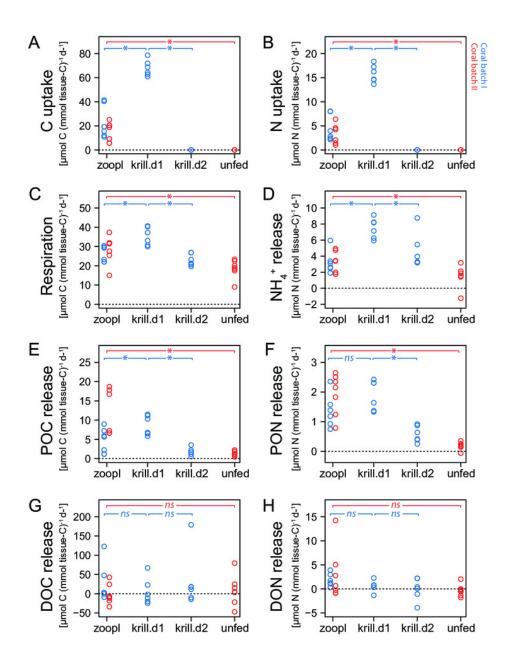




Carbon (C) and nitrogen (N) fluxes of *Desmophyllum dianthus* exposed to different feeding treatments

Feeding treatments were 'zoopl', i.e. fed with zooplankton; 'krill.d1', i.e. fed with zooplankton+krill; 'krill.d2', i.e. 24 h after feeding on zooplankton+krill; and 'unfed', i.e. 4 d-unfed. (A, B) C and N uptake during feeding; for 'unfed' and 'krill.d2', nil C and N uptake assumed. (C-H) C and N loss measured in incubations after feeding: (C) respiration, (D) ammonium excretion, (E, F) release of particulate organic carbon and nitrogen (POC, PON), (G, H) release of dissolved organic carbon and nitrogen (DOC, DON). Blue circles: corals of batch I, red circles: corals of batch II. Bracket with *: linear mixed effect model found a significant difference between the indicated fluxes (see Supplemental Table 1.9 for details); ns: no significant difference.





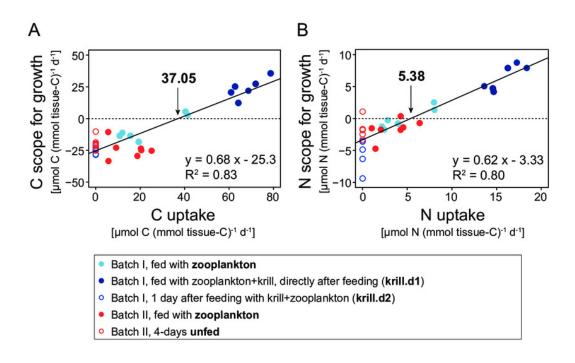


Carbon (C) and nitrogen (N) budget of *Desmophyllum dianthus*, as scope for growth (SfG), versus C and N uptake.

SfG: remaining C or N from food, after subtraction of C or N losses. SfG can be invested in tissue growth (Warren and Davies, 1967). (A) $SfG_C = C$ uptake – C respiration – POC release;

(B) $SfG_N = N$ uptake - NH_4^+ release - PON release; DOC and DON release neglected. Circle colors indicate coral batch and feeding treatment (see legend); for the treatment zooplankton+krill, two budgets are plotted, i.e. 'krill.d1' directly after feeding, and 'krill.d2' the day after feeding with CN uptake = 0. Black lines and equations show the results of the linear regression with adjusted R^2 ; the C or N uptake at which SfG = 0 (arrow) is interpreted as minimum C or N demand of the corals.





Dense swarms of krill and chaetognaths directly above *Desmophyllum dianthus*, recorded by remotely-operated vehicle at 160 m depth in Comau Fjord.

Arrow indicates one krill individual.

