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. If and how these conditions affect the energy demand of the corals 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 scenarios: (1) live fjord zooplankton (100 – 2300 µm), (2) live fjord zooplankton plus krill (> 7 mm), 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). Additional feeding with 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, indicating a high assimilation and growth efficiency for the krill plus zooplankton 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). Notwithstanding, unfed corals 'lost' 2 % of their tissue-C and 1.2 % of their tissue-N per day in terms of metabolism and released particulate organic matter (likely mucus). To balance the C (N) losses, each *D. dianthus* polyp has to consume around 700 (400) zooplankters per day. The capture of a single,

large krill individual, however, provides enough C and N to compensate daily C and N losses and grow tissue reserves, 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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28 ## 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. If and how these conditions
31 affect the energy demand of the corals is so far unknown. In a laboratory experiment, we
32 investigated the carbon and nitrogen (C, N) budget of *D. dianthus* from Comau Fjord under three
33 feeding scenarios: (1) live fjord zooplankton (100 – 2300 µm), (2) live fjord zooplankton plus
34 krill (> 7 mm), and (3) four-day food deprivation. In closed incubations, C and N budgets were
35 derived 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). Additional feeding with krill significantly increased coral respiration (35 %),
38 excretion (131 %), and POC release (67 %) compared to feeding on zooplankton only.
39 Nevertheless, the higher C and N losses were overcompensated by the threefold higher C and N

40 uptake, indicating a high assimilation and growth efficiency for the krill plus zooplankton diet. In
41 contrast, short food deprivation caused a substantial reduction in respiration (59 %), excretion
42 (54 %), release of POC (73 %) and PON (87 %) compared to feeding on zooplankton, suggesting
43 a high potential to acclimatize to food scarcity (e.g. in winter). Notwithstanding, unfed corals
44 'lost' 2 % of their tissue-C and 1.2 % of their tissue-N per day in terms of metabolism and
45 released particulate organic matter (likely mucus). To balance the C (N) losses, each *D. dianthus*
46 polyp has to consume around 700 (400) zooplankters per day. The capture of a single, large krill
47 individual, however, provides enough C and N to compensate daily C and N losses and grow
48 tissue reserves, suggesting that krill plays an important nutritional role for the fjord corals.
49 Efficient krill and zooplankton capture, as well as dietary and metabolic flexibility, may enable
50 *D. dianthus* to thrive under adverse environmental conditions in its fjord habitat; however, it is
51 not known how combined anthropogenic warming, acidification and eutrophication jeopardize
52 the energy balance of this important habitat-building species.
53

Introduction

55 Corals are ecosystem engineers (Jones, Lawton & Shachak, 1994), forming reefs and other
56 'marine animal forests' (Rossi et al., 2017), that are amongst the most diverse ecosystems on
57 Earth (Jones & Endean, 1973; Henry & Roberts, 2016). As calcifying organisms, scleractinian
58 corals are vulnerable to anthropogenically-caused ocean acidification (Cohen & Holcomb, 2009).
59 Increased atmospheric carbon dioxide dissolves in seawater, where it decreases the pH (Caldeira
60 & Wickett, 2003) and the saturation state of aragonite, a crystal form of calcium carbonate
61 (Turley, Roberts & Guinotte, 2007). Since corals form aragonite skeletons, ocean acidification
62 affects their calcification and skeletal growth (Cohen & Holcomb, 2009; Hennige et al., 2015;
63 Büscher, Form & Riebesell, 2017). To maintain calcification under these conditions, the corals
64 may up-regulate their internal pH (Trotter et al., 2011; Anagnostou et al., 2012; McCulloch et al.,
65 2012), but this is an energy-costly process requiring a corresponding energy supply (Gattuso,
66 Allemand & Frankignoulle, 1999; Cohen & Holcomb, 2009). Accordingly, experimental studies
67 have suggested that enhanced heterotrophic feeding could partially counteract the negative
68 impact of ocean acidification on coral calcification (Cohen & Holcomb, 2009; Georgian, Shedd
69 & Cordes, 2014; Martínez-Dios et al., 2020).
70

71 Cold-water corals (CWCs) form one of the most structurally-complex habitats of the deep sea
72 (Roberts, Wheeler & Freiwald, 2006), but occur also in shallower waters of temperate fjords
73 (Freiwald et al., 2004). Since aragonite saturation is lower in the deep and cold (Chen, Feely &
74 Gendron, 1988; Jiang et al., 2015), scleractinian CWCs are considered particularly vulnerable to
75 ocean acidification (Turley, Roberts & Guinotte, 2007). Most CWC ecosystems are predicted to
76 experience aragonite undersaturation by 2100 (Guinotte et al., 2006; Zheng & Cao, 2014).
77 Nevertheless, in the North Patagonian Comau Fjord (Los Lagos Region, Chile; Fig. 1), the
78 scleractinian CWC species *Desmophyllum dianthus* thrives under low pH (7.4-8.4), near and
79 below aragonite saturation ($\Omega_{aragonite}$: 0.9 to 1.6; Fillinger & Richter, 2013; Jantzen et al., 2013a).

80   The low pH may relate to the high organic matter concentration from high productivity in the
81   area (Montero et al., 2011) and terrestrial run-off to the fjord (Försterra & Häussermann 2003,
82   Jantzen et al. 2013a). The naturally low aragonite saturation state provides a rare opportunity to
83   study the food demand of a CWC under geochemical conditions, which most CWCs will face by
84   the end of the century (Försterra, Häussermann & Laudien, 2016).
85
86   *Desmophyllum dianthus* is a solitary, ahermatypic (not reef-building) CWC species with a
87   cosmopolitan distribution (Försterra & Häussermann, 2003; Cairns, Häussermann & Försterra,
88   2005). In Comau Fjord, the species forms vast coral banks between 20 and 280 m water depth,
89   particularly on steep, partly overhanging walls (Försterra & Häussermann, 2003; Fillinger &
90   Richter, 2013; Försterra et al., 2016). Their sheltered occurrence, in an upside-down position
91   under overhangs, has been interpreted as avoidance to sedimentation (Försterra & Häussermann,
92   2003). Though ahermatypic, a diverse benthic community is (facultatively) associated with the
93   coral banks, including sponges, bryozoans, tube-forming polychaetes, anthozoans, and bivalves
94   (Försterra et al., 2005; Försterra, Häussermann & Laudien, 2016). Further, *D. dianthus* from the
95   shallow parts of Comau Fjord typically has live tissue only on the apical end of the corallum
96   (skeleton), while the basal end is bare and provides a settlement substrate (habitat) for various
97   epibiontic and endolithic organisms, e.g. foraminiferans, bio-eroding sponges, and
98   photoautotrophic microorganisms (Försterra et al., 2005; Hassenrück et al., 2013).
99
100   The natural conditions of low pH and relatively high turbidity in the fjord region are exacerbated
101   by climate change and intense salmon aquaculture (Buschmann et al., 2009; Mayr et al., 2014;
102   Iriarte, 2018). It is therefore important to (1) know the energetic costs involved in coping with
103   present and future fjord environments (low pH, high turbidity) and (2) estimate the resilience to
104   disturbance affecting the energy budget, growth and reproduction of these ecosystem engineers
105   (Melzner et al., 2009; Findlay et al., 2011; Vidal-Dupiol et al., 2013). The energy budget of the
106   fjord corals, i.e. their food supply against energetic costs, is presently unknown. The carbon and
107   nitrogen isotopic composition of *D. dianthus* from Comau Fjord indicates mostly consumption of
108   zooplankton (Mayr et al., 2011). With its large polyps (up to 6 cm in diameter, Försterra &
109   Häussermann 2003), *D. dianthus* is able to capture not only mesozooplankton (0.2-2 mm length),
110   such as copepods, but also larger micronekton, such as euphausiids (krill) (Sokol, 2012; Höfer et
111   al., 2018). To fuel its respiratory carbon demand, *D. dianthus* from the Mediterranean deep sea
112   requires the equivalent of three adult brine shrimps (*Artemia salina*) per day (Naumann et al.,
113   2011). However, *A. salina* does not occur in the coral habitat and feeding on natural prey may
114   entail a different carbon budget (Møller & Riisgård, 2007). In the North Patagonian fjord region,
115   the zooplankton abundance shows a pronounced seasonality, with a maximum following the
116   spring phytoplankton bloom and a minimum in Austral winter (Iriarte et al., 2007; González et
117   al., 2010). In experiments, increased availability of zooplankton food enhanced the skeletal
118   growth of the fjord corals (Martínez-Dios et al., 2020), but it is unknown whether food is
119   currently limiting coral growth in the fjord region.

120

121   Here, we investigate the carbon and nitrogen (C and N) budget of the CWC *D. dianthus* under
122   present-day low-pH conditions in Comau Fjord, Chile, i.e. the difference between C and N
123   uptake and C and N loss (Fig. 2). CWCs release the indigestible parts of their food and coral
124   mucus (Wild et al., 2008) as particulate and dissolved organic matter (POM, DOM), measurable
125   as particulate and dissolved organic carbon and nitrogen (POC, PON; DOC, DON). CWC
126   metabolism involves oxygen consumption and carbon dioxide production through respiration, as
127   well as ammonium production via excretion (Khripounoff et al., 2014; Maier et al., 2019). The
128   remaining, non-released C and N is available for growth of somatic and reproductive tissue and
129   therefore termed 'scope for growth' (Warren & Davis 1967). Since C and N uptake and loss
130   typically depend on meal size and quality (Secor, 2008), we determined the C and N budget
131   (uptake versus loss) of the fjord corals under three different feeding scenarios, simulating the
132   varying zooplankton availability in the fjord region (Iriarte et al., 2007; González et al., 2010):
133   (1) live fjord zooplankton (100-2300 μm), (2) live fjord zooplankton plus larger krill (>7 mm),
134   and (3) short-term food deprivation. From these budgets, we estimated the minimum C, N and
135   zooplankton demand of *D. dianthus* in the North Patagonian fjord region and evaluated the scope
136   for growth of this habitat-forming CWC species.

137

Materials & Methods

Coral collection and maintenance

140   Thirteen similar-sized *D. dianthus* specimens (calyx height: 3.4 ± 0.4 cm, calyx length:
141   1.4 ± 0.2 cm, calyx width: 2 ± 0.4 cm, Fig. 3A) were collected live from 20 m water depth in
142   Comau Fjord (Cross Huinay, Liliguapi, Fig. 1) in January 2012. The collection of *D. dianthus* for
143   scientific purposes was approved by the Chilean Ministry of Economy, Development & Tourism,
144   sub-secretariat of fisheries and farming (ref. 1742). The corals were chiseled off the substrate by
145   SCUBA divers and immediately placed into water-tight, sealed plastic containers, ensuring no
146   contact with either the brackish surface water layer or air during transport to the laboratory. To
147   remove epibiontic and endolithic organisms (Försterra & Häussermann, 2003), the bare corallum
148   was carefully cut off with a submerged diamond blade (3.2 mm thick), connected to an electric
149   grinder (Jantzen et al. 2013b). The fracture zone was sealed with cyano-acrylate gel (super flex
150   glue gel) and glued to a polyethylene screw (Jantzen et al., 2013b), which served to fix the corals
151   in their natural 'upside-down' growth position (Fig. 3A).

152

153   For maintenance before and during the experiment, corals were kept in three 28 L-maintenance
154   tanks (Fig. 3A, maximum seven corals per tank) with a flow-through of 10 μm- filtered fjord
155   water, continuously pumped from 25 m depth off Huinay (flow: 4.2 L h^{-1}; temperature: 11.9 °C;
156   salinity: 31.6; particulate organic matter concentration: 12.8 ± 4.2 μmol POC L^{-1}; 1.4 ± 1.2 μmol
157   PON L^{-1}). Before the start of the experiment, corals were fed for two hours per day with 1/4 of a
158   haul of live, freshly-collected fjord zooplankton (see next section). This corresponds to a
159   zooplankton concentration of 571 ± 203 zooplankton individuals L^{-1} (mean ± standard deviation),

160   equivalent to 85 ± 30 µmol C L^{-1} and 16 ± 6 µmol N L^{-1}, as analyzed in four additional aliquots
161   of 1/4 of a zooplankton haul (see section 'Sample analysis'). During feeding, water exchange
162   was interrupted.
163
164   Before the start of the experiment, all corals were weighed in seawater of ambient temperature
165   and salinity (density 1.026 g cm^{-3}) with an analytical balance equipped with an underfloor
166   weighing basket (Sartorius CPA225DOCE). Polyp dry mass was derived from buoyant weight
167   according to Davies (1989), using a species-specific aragonite density of 2.835 g cm^{-3} (Naumann
168   et al., 2011). Corals were given a recovery and acclimatization time of three weeks from
169   collection and preparation to the start of the experiment.
170
171   **Zooplankton and krill collection**
172   Live fjord zooplankton was collected ca. 1 km off the Huinay Scientific Field Station (Fig. 1)
173   every afternoon, by a single vertical haul from 20 m water depth with a 100 µm-Nansen net
174   (diameter 0.7 m). The size range of individual zooplankters (100-2300 μm maximum extension)
175   was measured under the binocular on three subsamples. To feed the corals in their maintenance
176   tanks (previous section), the zooplankton haul was split with a Motoda plankton sample splitter
177   into equal 1/4 portions. To feed the corals with zooplankton as part of the experimental feeding
178   treatments (see below), the respective zooplankton haul was split into equal 1/8 portions, which
179   were split again with measurement cylinders into ten equal portions (1/80 of the original haul).
180
181   Krill (euphausiids, i.e. *Euphausia vallentini*, adult and pre-adult stages) were collected at night in
182   Comau Fjord between 20 and 80 m water depth, in a 45-min horizontal trawl at 2 knots with a
183   ring trawl net (0.5 m diameter, 500 µm mesh size). Krill were drained on paper tissue, measured
184   (cephalo-thoracic length, ca. 7 mm), weighed (wet mass) and stored frozen (-13°C) until
185   utilization in the experiment (see below). Six euphausiids were dried (40 °C, three days),
186   weighed again (dry mass, 3.3 ± 1.5 mg) and used for C and N analysis (see below).
187
188   **Experimental design**
189   This section focuses on the experimental design, as shown in Fig. 4, while experimental set-up,
190   feeding and incubations are detailed in the following sections. A detailed chronology of the
191   experiment is provided in Supplemental Table 1.1.
192
193   To determine the C and N budget of *D. dianthus*, we designed a two-batch repeated-measures
194   laboratory experiment with in total three different feeding scenarios (Fig. 4). This experimental
195   design was chosen to simulate the temporally variable food availability in Comau Fjord (see
196   Introduction). Both coral batches were initially offered live fjord zooplankton (Fig. 4, feeding
197   scenario 'zooplankton'), which presumably corresponds to the natural 'baseline' food situation in
198   the field (Mayr et al., 2011). Batch I (n=6 corals) was subsequently offered a surplus of food, i.e.
199   zooplankton plus krill (feeding scenario 'zooplankton+krill', see below), while batch II (n=7

200 corals) remained unfed, mimicking food (zooplankton) shortage, e.g. in winter (feeding scenario
201 'unfed', see below). Within each batch, at least two C and N budgets were determined separately
202 for each individual coral, by repeated measurements on the same specimens (Fig. 4). To
203 determine the C and N budgets, we first measured the C and N uptake of each individual coral
204 from food during the respective feeding treatments (Fig. 4). Secondly, after each feeding
205 treatment, the corals were individually incubated without food for 9-11 h (Fig. 4), to measure
206 their C and N loss in terms of C respiration, ammonium excretion, and release of POC, PON,
207 DOC, DON (Fig. 2). In between the different feeding scenarios (Fig. 4), the corals were kept in
208 their maintenance tanks and fed daily with live fjord zooplankton (see section 'Coral collection
209 and maintenance'), for re-acclimatization to natural 'baseline' feeding conditions. Ideally,
210 experimental corals should have been kept separate throughout the entire experiment, to ensure
211 full independence of the replicates, but this was not possible for logistic reasons. Instead, each
212 coral batch was split into subsets of one to three corals, which were distributed over three
213 maintenance tanks. Different coral subsets within the batches were kept in different maintenance
214 tanks and tank position was shuffled during the experiment, to achieve a partial independence of
215 coral replicates within the batches (Supplemental Table 1.1) and to minimize the odds of a
216 differential tank effect between the batches. Experimental feeding treatments and incubations
217 (including measurements of C and N fluxes) were done in separate experimental bottles (see
218 section 'Experimental set-up') to ensure independence of the results.
219
220 In the 'zooplankton' feeding scenario (Fig. 4, both batches), the corals were fed with live fjord
221 zooplankton (1025 ± 332 zooplankters L⁻¹) in separate experimental bottles for 2 h (Fig. 3B; for
222 details, see section 'Feeding with zooplankton and krill'). Such short pulses of high zooplankton
223 availability may occur when a zooplankton swarm with high individual densities (Ambler, 2002)
224 is advected by local currents (3-11 cm s⁻¹, Jantzen et al. 2013b). Zooplankton swarms are
225 common in fjord boundaries (Hirche, Laudien & Buchholz, 2016). The 9-11 h-incubations in
226 separate experimental bottles (called 'zoopl') followed 2-3 h after feeding on zooplankton (for
227 details, see section 'Incubations'); hence, C and N losses were measured between 2-14 h after
228 feeding, covering the time it takes tropical scleractinian corals to digest zooplankton (Sebens et
229 al., 1996; digestion times of CWCs are unknown). In the 'zooplankton+krill' feeding scenario
230 (Fig. 4), the corals were additionally fed with one individual euphausiid, 3-4 h after receiving
231 live fjord zooplankton. Taking into account the larger food ration and the presumably prolonged
232 digestion time, we here carried out two 9-11 h-incubations, the first starting 1 h after feeding on
233 krill (covering the period between 1-12 h after feeding, called 'krill.d1'), the second starting 24 h
234 after feeding on krill (covering the period between 24-35 h after feeding, called 'krill.d2'). In
235 between the incubations 'krill.d1' and 'krill.d2', the corals remained unfed. In the 'unfed'
236 scenario (Fig. 4), corals remained unfed in their maintenance tank (10 μm-filtered seawater; all
237 corals in one tank) for four days. After this period, corals were incubated once for 9-11 h
238 (incubation called 'unfed').
239

Experimental set-up

240
241 Feeding with zooplankton and krill, and incubations, were carried out at 11°C (representing *in*
242 *situ* temperature) in separate experimental bottles with one coral each (Fig. 3B, C). As
243 experimental bottles, we used SCHOTT-DURAN® bottles of 0.5 L specified volume, which fit a
244 total volume of 0.8 L (including the bottleneck). The bottles were filled with 10 µm-filtered fjord
245 water, pumped from 25 m depth off Huinay. The coral was fixed in its natural 'upside-down'
246 position (Fig. 3B, C) in the custom-built bottle lid (Jantzen et al., 2013b). A magnetic stirring bar
247 at the bottle floor created a circular flow of ~1 cm s^{-1}; to estimate this flow, we filmed the
248 particle movement in unfiltered seawater from above, stopped the time that the circulating
249 particles needed to cross sections of known length at different orbits of the bottle, and averaged
250 the resulting flow velocities (distance/time). The flow was high enough to kept live zooplankton
251 in suspension, but low enough not to bend the coral tentacles (Sokol, 2012).
252

Feeding with zooplankton and krill

253
254 The feeding scenarios 'zooplankton' and 'zooplankton+krill' (Fig. 3B) were started by adding
255 one aliquot of live zooplankton food (1/80 of one zooplankton haul in 50 mL filtered seawater)
256 to each of the experimental bottles. For each zooplankton-fed coral subset (Supplemental Table
257 1.1), five additional aliquots of live zooplankton food were prepared the same way and analyzed
258 for the amount of POC and PON (n=3) and the number of zooplankton individuals (n=2) added
259 to each experimental bottle (Fig. 3B: 'start POC, PON, zooplankton'). In the feeding scenario
260 'zooplankton+krill', zooplankton food aliquots were analyzed for POC and PON (n=3), but not
261 for zooplankton. Start POC and PON concentrations in the feeding scenario 'zooplankton' were
262 164 ± 36 µmol C L^{-1} and 30 ± 7 µmol N L^{-1}, start POC and PON concentrations in the feeding
263 scenario 'zooplankton+krill' were 126 ± 0.3 µmol C L^{-1} and 24 ± 0.1 µmol N L^{-1}. The start
264 zooplankton concentration was 1025 ± 332 zooplankters L^{-1} in the feeding scenario
265 'zooplankton' (mean ± standard deviation; averaged over all replicates); the start zooplankton
266 concentration in the feeding scenario 'zooplankton+krill' was presumably similar. Per coral
267 subset (Supplemental Table 1.1), triplicate seawater controls were prepared (Fig. 3B: 'control');
268 these were experimental bottles without corals, but with zooplankton food, that served to
269 determine zooplankton loss from internal zooplankton predation and handling. During feeding,
270 polyp activity was closely monitored, to ensure that all corals had their tentacles expanded. To
271 end the feeding after 2 h, the corals were removed from the bottles and returned to the
272 maintenance tanks. Control incubations (seawater only) were ended with 0.5-1 h delay (i.e.
273 t=2.5-3 h), due to logistical limitations (handling time). Due to the low activity in the seawater-
274 only controls, we expect no significant bias related to the longer duration. End water samples for
275 the amount of POC and PON (290-370 mL) and for the number of zooplankton individuals (350-
276 490 mL; only in feeding scenario 'zooplankton') were taken from each experimental bottle after
277 thorough mixing (Fig. 3B, 'end POC, PON, zooplankton'). POC and PON samples were
278 collected on pre-combusted (24 h, 500 °C), pre-weighed 0.7 µm- glass-fiber filters (GF/F) by
279 vacuum filtration. Filters were frozen (-13 °C) and dried to constant mass at 40 °C. Zooplankton

280 samples were concentrated over a 55 µm-mesh and fixed in 4 %-borax-buffered formaldehyde.
281 For feeding with krill (in the feeding scenario 'zooplankton+krill'), the corals were returned to
282 the separate experimental bottles 3-4 h after feeding on zooplankton and received one thawed,
283 pre-measured euphausiid via tweezers (Fig. 3B).
284

Incubations

286 For the incubations (without food), the corals were placed into the experimental (SCHOTT)
287 bottles, that were filled with 10 µm-filtered fjord water and closed air bubble-free with a lid
288 (Fig. 3C). Per coral subset (Supplemental Table 1.1), we additionally prepared triplicate seawater
289 controls without corals (Fig. 3C: 'control') to determine the possible effect of nano- and
290 picoplankton oxygen (O_2), C and N fluxes on our results. At the start of the incubation, the start
291 O_2 concentration was measured with an optode (HQ40d; Hach, USA; resolution: 0.1 mg O_2 L^{-1})
292 in a separate experimental bottle B_o ('start O_2'). Start water samples were taken by syringe from
293 B_o for analysis of dissolved inorganic nitrogen (DIN, i.e. ammonium, nitrate, nitrite; 100 mL),
294 DOC, and DON (20 mL, in triplicates). The remaining water in B_o (300-600 mL) was used for
295 POC and PON analysis. During the incubation, coral polyps remained protruded with extended
296 tentacles. At the end of the incubation, the corals were removed and returned to their
297 maintenance tanks. In each experimental bottle, the end O_2 concentration was first measured,
298 before taking end water samples for DIN, DOC, DON, POC and PON. The end O_2 concentration
299 was never below 80 % of the start O_2 concentration, a conservative threshold to avoid effects of
300 low-oxygen concentration on coral physiology (Dodds et al., 2007). DIN samples were filtered
301 through GF/F-filters into glass vials and fixed with a concentrated mercury chloride solution
302 (0.105 g L^{-1}) to prevent microbial activity. Samples for DOC and DON were filtered through
303 GF/F-filters into glass vials (filters and vials pre-combusted, 450 °C, 12 h), acidified to pH=2
304 with 32 % hydrochloric acid to avoid microbial activity and stored dark at 4 °C. Sample
305 processing for POC and PON was described in the previous section ('Feeding').
306

Coral tissue sampling

308 At the end of the experiment, the coral tissue was removed from the skeleton with an airbrush
309 filled with 0.7 µm-filtered seawater and homogenized with an ultra turrax (Jantzen et al., 2013c).
310 The volume of the tissue-seawater suspension was measured. Subsamples of the tissue-seawater
311 suspension (1 mL, n=6 aliquots per coral) were collected on pre-combusted (500 °C, 24 h), pre-
312 weighed GF/F-filters and dried up to constant mass at 40 °C. Coral samples were transported to
313 Germany under CITES permit E-00427/12.
314

Sample analyses

316 Samples of coral tissue, krill, POC and PON were weighed for dry mass and subsequently
317 analyzed for organic carbon (OC) and organic nitrogen (ON) content on an elemental analyzer
318 (EuroEA3000, EuroVector) with acetanilide calibration (measurement precision >99 %, i.e.
319 <1 % relative standard deviation for triplicate measurement of acetanilide). To measure the OC

320   content of coral tissue (tissue-C), subsamples on GF/F filters (n=3 per coral) were vapor-
321   acidified with 12 N-hydrochloric acid prior to analysis, to remove remainders of skeletal
322   inorganic carbon (Hedges & Stern, 1984). The ON content of coral tissue (tissue-N) was
323   measured on separate subsamples (n=3) without acidification. The total tissue-C and -N content
324   of each coral was calculated by multiplying the OC and ON content measured in the subsamples
325   (1 mL) with the volume of the tissue-seawater suspension (see previous section). Samples of
326   krill, POC and PON (from feeding and incubations) were not acidified, as previous tests revealed
327   negligible amounts of inorganic carbon. POC concentration was determined as $POC\ [\frac{\mu mol\ C}{L}] =$
328   $\frac{POC\ content\ GF/F\ filter}{filtered\ volume}$; PON concentration was calculated accordingly. For krill, we determined the
329   relation between wet mass and C content (C content [μmol C euphausiid^{-1}] = 3.9 · wet mass [mg]
330   + 48.3; R^2 = 0.86) and the relation between wet mass and N content (N content [μmol N
331   euphausiid^{-1}] = 0.9 · wet mass [mg] + 11.4; R^2 = 0.87). Zooplankton samples were counted in a
332   Bogorov chamber under a stereo microscope. Only undamaged, non-gelatinous zooplankters
333   were counted.
334
335   Ammonium (NH_4^+), nitrate and nitrite concentration was analyzed spectrophotometrically at the
336   ICBM-Terramare Wilhelmshaven according to Grasshoff et al. (1983) (measurement resolution:
337   0.01 μmol N L^{-1}). DOC and total dissolved nitrogen (TDN) concentration was quantified via
338   high-temperature catalytic oxidation (HTCO, Sugimura & Suzuki 1988) on a Shimadzu TOC-
339   VcpH analyzer, equipped with a Total Nitrogen Measuring Unit (TNM-1), with L-arginine
340   calibration. Analytical accuracy and precision were determined by analyzing reference samples
341   (D. Hansell, University of Miami, USA) and were higher than 95 %. The datasets of DOC and
342   TDN concentrations contained a few extreme values, possibly due to sample contamination
343   during handling and processing. Therefore, outliers of DOC and TDN concentration were
344   identified as values < Q1 – IQR·1.5 and values > Q3 + IQR·1.5, where Q1 was the first quartile
345   of the data subset, Q3 the third quartile, and IQR the interquartile range between Q1 and Q3;
346   data subsets were end values of coral incubations, end values of control incubations, and start
347   values of coral and control incubations together. Outliers were excluded and the remaining start
348   and end values of each incubation (samples taken in triplicate) were averaged. DON
349   concentration was obtained as DON = TDN – DIN, with DIN = ammonium + nitrate + nitrite.
350
351   **Carbon and nitrogen budget**
352   For each feeding scenario, the C and N budgets of the corals were determined as the difference
353   between C and N uptake, measured during the feeding treatment, and C and N loss, measured in
354   the subsequent incubation (Fig. 2, 4). In the feeding scenario 'zooplankton+krill', two
355   incubations followed the feeding treatment, hence two C and N budgets were determined per
356   coral, one covering the period 1-12 h after feeding, called 'krill.d1', the second covering the
357   period 24-35 h after feeding, called 'krill.d2' (Fig. 4).
358

359   All C, N, and O_2 fluxes were calculated from the difference between the measurement at the start
360   of the feeding or incubation and the measurement at the end of the feeding or incubation, in coral
361   ('coral') and seawater-control ('control') trials. The (total) C uptake of the corals from
362   zooplankton (treatments 'zooplankton', 'zooplankton+krill', in µmol C) was determined as

363   $C\ uptake = \left[\dfrac{[POC]_{start,\ coral} - [POC]_{end,\ coral}}{t_{coral}} - \dfrac{[POC]_{start,\ control} - [POC]_{end,\ control}}{t_{control}} \right] \cdot V \cdot t_{coral},$

364   where [POC] is the POC concentration, t is the feeding time and V is the water volume of the
365   coral incubation (experimental bottle volume – coral volume). The N uptake of the corals from
366   zooplankton was determined similarly. In the feeding treatment 'zooplankton+krill', the total C
367   or N uptake is the sum of zooplankton-C or -N uptake and the C or N content of the krill
368   individual provided to the respective coral; the C and N content of the individual euphausiid was
369   estimated from its wet mass (see previous section). In the feeding treatment 'unfed', a zero C and
370   N uptake was assumed. In all feeding treatments, the C and N uptake was treated as daily rates
371   (i.e. µmol C and N d^{-1}), because the corals were fed once per day only. In treatment
372   'zooplankton', we additionally determined the zooplankton capture of the corals, as

373   $Zooplankton\ capture = \left[\dfrac{zoopl_{start,coral} - zoopl_{end,coral}}{t_{coral}} - \dfrac{zoopl_{start,control} - zoopl_{end,control}}{t_{control}} \right] \cdot V \cdot t_{coral},$

374   where zoopl is the number of zooplankton individuals.

375

376   Hourly respiration rates of the corals (in µmol O_2 h^{-1}) were derived as

377   $Respiration(O_2) = \left[\dfrac{[O_2]_{start,coral} - [O_2]_{end,coral}}{t_{coral}} - \dfrac{[O_2]_{start,control} - [O_2]_{end,control}}{t_{control}} \right] \cdot V,$

378   where [O_2] is the O_2 concentration. The C respiration rate was derived from the O_2 respiration
379   rate, assuming a respiratory quotient $CO_2:O_2 = 1$; this quotient was measured for CWCs *in situ*
380   (Khripounoff et al., 2014). Rates of NH_4^+ excretion and release of POC, PON, DOC, DON (in
381   µmol C or N h^{-1}) were obtained as

382   $C\ or\ N\ release = \left[\dfrac{[x]_{end,\ coral} - [x]_{start,\ coral}}{t_{coral}} - \dfrac{[x]_{end,control} - [x]_{start,control}}{t_{control}} \right] \cdot V,$

383   where [x] is the concentration of the respective substance. It should be noted that coral C and N
384   release may have been underestimated if coral-produced material was taken up by bacteria
385   during the incubations, i.e. by bacterioplankton passing the 10 μm-filter and/or by the coral
386   microbiome (Schöttner et al., 2009). Seawater control incubations without corals cannot control
387   for this bacterial uptake. Rates of respiration, ammonium excretion, release of POC, PON, DOC
388   and DON were extrapolated to 24 h and standardized to coral tissue organic carbon content
389   (tissue-C) as approximation of coral biomass. To facilitate comparability with other studies, we
390   additionally provide C and N fluxes standardized to polyp dry mass (determined via buoyant
391   weight) and skeletal dry mass (polyp dry mass – tissue dry mass) in Supplemental Table 1.2.

392

393   The daily C and N budget of the corals (Fig. 2) was derived as
394   $SfG_C = C\ uptake - C\ respiration - POC\ release,$
395   and
396   $SfG_N = N\ uptake - NH_4^+\ excretion - PON\ release,$

397   both in µmol C (mmol tissue-C d^{-1}). The term 'scope for growth' (SfG, Warren and Davis 1967)
398   denotes the net C or N gains of the corals, which remain from food uptake after subtraction of all
399   C and N losses. SfG > 0 indicates a C or N surplus, which can be invested in biomass growth
400   (somatic and/or reproductive), while SfG < 0 indicates a C or N deficit. It should be noted that
401   DOC and DON release were excluded from the C and N budgets, due to the high variability in
402   DOC and DON fluxes (see below). The summed C loss, i.e. C respiration + POC release, was
403   considered as minimum C demand of the corals, the summed N loss, i.e. NH$_4^+$ excretion + PON
404   release, as their minimum N demand.
405
406   **Data analysis**
407   Graphical and statistical analysis was performed with R (R Core Team, 2017). Values are given
408   as mean ± standard deviation. Firstly, we tested whether the feeding treatments (within the
409   different feeding scenarios, Fig. 4) had an effect on the C and N fluxes, i.e. on the total C and N
410   uptake and on rates of C respiration, NH$_4^+$ excretion, and release of POC, PON, DOC, DON. For
411   each flux, linear mixed effect (LME) models were fitted, separately for coral batch I and II
412   (Fig. 4), with the function lmer (R package lmerTest, Kuznetsova et al. 2017). The LME models
413   accounted for the repeated measures on the individual corals of the two batches, using coral
414   individuals as random effect and 'feeding treatment + incubation' (i.e. 'zoopl', 'krill.d1',
415   'krill.d2', 'unfed') as fixed effect (i.e. flux ~ treatment + (1|coral_individual)). In batch I, C and
416   N fluxes directly (i.e. within the first day) after feeding on zooplankton ('zoopl') were compared
417   with C and N fluxes directly after feeding on zooplankton+krill ('krill.d1'); and C and N fluxes
418   directly after feeding on zooplankton+krill ('krill.d1') were compared with C and N fluxes one
419   day later ('krill.d2'). In batch II, C and N fluxes after feeding on zooplankton ('zoopl') were
420   compared with C and N fluxes after four days of food deprivation ('unfed'). Detailed results of
421   the LME models are available as Supplemental Table 1.10. Secondly, C and N budgets were
422   visualized by plotting the total C and N loss over the total C and N uptake (for all C and N
423   budgets combined, i.e. 'zoopl', 'krill.d1', 'krill.d2', 'unfed'). The lines 'C loss = C uptake' and
424   'N loss = N uptake', i.e. 'SfG = 0', were interpreted as the minimum C and N demand of the
425   corals to balance their C and N loss, associated with each feeding treatment.
426
427   **Methodological limitations of this study**
428   *Ex situ* experiments, as presented here, allow the measurement of the total C and N fluxes of a
429   CWC, i.e. its C and N budget. This measurement proves difficult *in situ*, as it typically requires a
430   closed-off water volume. Nevertheless, *ex situ* experiments only provide specific simulations of
431   the dynamic fjord environment (González et al., 2010; Jantzen et al., 2013a; Iriarte, 2018). For
432   example, the *in situ* feeding rate of the corals is unknown. Addition of an 'artificial'
433   experimental amount of zooplankton in the feeding treatments may have led to higher or lower
434   than natural feeding rates. Furthermore, it cannot be excluded that *ex situ*, the corals were
435   exposed to higher stress than *in situ*. Stress can enhance the C and N loss of CWCs, e.g. through
436   increased *ex situ* respiration (Khripounoff et al., 2014) and stress-induced mucus production

437   (Zetsche et al., 2016). However, we minimized experimental stress, by maintaining the
438   experimental corals in natural fjord water to assure suitable water quality, and by minimum,
439   careful handling. Corals did not show visible signs of stress, such as visibly increased mucus
440   release, retracted tentacles or mortality. Measured DOC and DON fluxes were highly variable
441   (see below) and were therefore excluded from the C and N budgets, which likely caused an over-
442   or underestimate of the coral C and N demand. As noted above, bacteria may have taken up
443   coral-produced POC and PON (and DOC, DON) during the incubations, leading to a potential
444   underestimate of these loss terms and the coral C and N demand.
445

Results

Uptake of carbon and nitrogen

448   When fed with zooplankton (treatment 'zooplankton'), *D. dianthus* captured
449   156 ± 74 zooplankton individuals polyp^{-1} h^{-1}. Given the 2 h-feeding time per day, the total
450   zooplankton capture was 312 ± 148 zooplankton individuals d^{-1}, resulting in a C uptake of
451   18.8 ± 11.5 μmol C (mmol tissue-C)$^{-1}$ d^{-1} (Fig. 5A) and a N uptake of 4 ± 2.3 μmol N (mmol
452   tissue-C)$^{-1}$ d^{-1} (Fig. 5B). One euphausiid in addition to zooplankton increased the C and N uptake
453   of the corals (of batch I, treatment 'zooplankton+krill') by a factor of four (67.9 ± 6.7 μmol C
454   (mmol tissue-C)$^{-1}$ d^{-1}; 15.8 ± 1.8 μmol N (mmol tissue-C)$^{-1}$ d^{-1}).
455

Respiration and ammonium excretion

457   Increasing meal size enhanced the respiration and ammonium excretion rate of *D. dianthus*
458   (Fig. 5C, D), but relatively less compared to the increased C and N uptake. Within the first day
459   after feeding on zooplankton, *D. dianthus* respired on average 27.5 ± 5.8 μmol O$_2$ (mmol tissue-
460   C)$^{-1}$ d^{-1} and excreted 3.2 ± 1.3 μmol NH$_4^+$ (mmol tissue-C)$^{-1}$ d^{-1}. When the corals received krill in
461   addition to zooplankton, they showed an on average 35 % higher respiration rate than when they
462   were fed with zooplankton only (Fig. 5C: 'krill.d1' versus 'zoopl', blue colors). At the same
463   time, their ammonium excretion rate doubled (Fig. 5D). One day after feeding on zooplankton
464   plus krill, the corals showed a lower rate of respiration and ammonium excretion again (Fig. 5C,
465   D: 'krill.d2', corals were not fed between the incubations 'krill.d1' and 'krill.d2'). Four days of
466   food-deprivation reduced the respiration rate of the corals by 29 % and their ammonium
467   excretion rate by 54 %, relative to their metabolic activity after feeding on zooplankton (Fig. 5C,
468   D: 'unfed' versus 'zoopl', red colors).
469

Organic matter release

471   *Desmophyllum dianthus* showed a clear release of POC and PON in all feeding scenarios
472   (Fig. 5E, F). Directly after feeding on zooplankton, corals released 8.2 ± 6 μmol POC (mmol
473   tissue-C)$^{-1}$ d^{-1} and 1.7 ± 0.7 μmol PON (mmol tissue-C)$^{-1}$ d^{-1} (Fig. 5E, F: 'zooplankton').
474   Feeding on krill in addition to zooplankton increased the POC release by 67 % and the PON
475   release by 39 % compared to feeding on zooplankton only (Fig. 5E, F: 'krill.d1' versus 'zoopl',
476   blue colors). One day after feeding on zooplankton plus krill ('krill.d2'), POC and PON release

477   rates were low (1.8 ± 1.0 µmol POC (mmol tissue-C)$^{-1}$ d^{-1}, 0.6 ± 0.3 µmol PON (mmol tissue-C)$^{-1}$

478   ^{1} d^{-1}). Four days of food-deprivation reduced POC and PON release by 73 % and 87 % relative to

479   the POC and PON release after feeding on zooplankton (Fig. 5E, F: 'unfed' versus 'zoopl', red

480   colors).

481

482   DOC and DON fluxes ranged around zero with a high variability (Fig. 5G, H). Feeding

483   treatments had no detectable effect. In the seawater control incubations, DOC and DON fluxes

484   also showed a high variability with positive and negative values (Supplemental Table 1.8).

485

486   **Carbon and nitrogen budget**

487   Corals fed with zooplankton plus krill showed a positive scope for growth (SfG) for C and N

488   within the first day after feeding ('krill.d1', Fig. 6A, B), meaning that their C and N uptake

489   outweighed the combined losses via respiration, excretion, POC and PON release. Feeding on

490   zooplankton alone did, in most cases, not provide *D. dianthus* with enough C and N for a

491   positive SfG ('zoopl', Fig. 6A, B). The minimum C demand of *D. dianthus* in the experiment

492   increased with increasing meal size (Fig. 6A, Table 1), from 20 µmol C (mmol tissue-C)$^{-1}$ d^{-1} in

493   unfed corals to 44 µmol C (mmol tissue-C)$^{-1}$ d^{-1} in corals fed with zooplankton plus krill

494   ('krill.d1'), corresponding to 52.7 to 108.4 µmol C polyp^{-1} d^{-1}. Accordingly, the minimum N

495   demand of *D. dianthus* (Fig. 6B, Table 1) increased from 1.7 µmol N (mmol tissue-C)$^{-1}$ d^{-1} in

496   unfed corals to 9.4 µmol N (mmol tissue-C)$^{-1}$ d^{-1} in corals fed with zooplankton plus krill

497   (krill.d1), corresponding to 3.6 to 23.8 µmol N polyp^{-1} d^{-1}. This means that unfed corals lose 2 %

498   of their tissue-C per day to respiration and POC release and 1.2 % of their tissue-N per day to

499   ammonium excretion and PON release (Table 1). On a zooplankton diet, each polyp requires

500   687 zooplankters per day to balance the associated C loss (Table 1, 'zoopl'; 0.13 µmol C

501   zooplankter^{-1}, Supplemental Table 1.4) and 398 zooplankters per day to balance the associated N

502   loss (0.03 µmol N zooplankter^{-1}, Supplemental Table 1.4). On the other hand, less than one

503   euphausiid per polyp per day is enough to balance the total C and N loss associated with a

504   zooplankton plus krill diet (Table 1, 'krill.d1'; 129 µmol C euphausiid^{-1}, 31 µmol N euphausiid^{-1},

505   Supplemental Table 1.2). Please note that DOC and DON release were not considered in the

506   shown C and N budgets, since DOC and DON fluxes were highly variable and ranged around

507   zero (see above). Therefore, it cannot be ruled out that the C and N demand of *D. dianthus* is

508   higher (or lower) than indicated here.

509

510   **Discussion**

511   In this study, we report C and N budgets of the CWC *D. dianthus*, an important matrix species of

512   CWC banks in the fjords of the Los Lagos Region, under three different experimental feeding

513   regimes (fed with live fjord zooplankton, fed with zooplankton plus krill, four-day food-

514   deprived). We first discuss the metabolic flexibility (metabolic rate, organic matter release) of

515   the corals in response to varying food availability. Then, we evaluate how the corals could

516 sustain their C and N demand under the low-pH conditions in the fjord and speculate how their C
517 and N balance might change in the future.
518

519 **Metabolic rate**

520 The CWC *D. dianthus* shows a high metabolic flexibility in response to varying food
521 availability, indicated by increased respiration and ammonium excretion with increasing meal
522 size (from four-day unfed, over zooplankton, to zooplankton plus krill, Fig. 5C, D). The 1.5-fold
523 higher respiration rate within the first day after ingesting a large food ration (zooplankton plus
524 krill, incubation 'krill.d1') as compared to one day later (incubation 'krill.d2; corals not fed
525 between the two incubations) likely reflects the 'specific dynamic action of food' (SDA, Rubner
526 1902). The SDA describes the increased metabolic rate of animals after feeding, owing to the
527 energetic expenses of food capture and digestion (McCue, 2006; Secor, 2008). The SDA
528 typically increases with meal size, but also varies with meal type (Secor, 2008; present study).
529 Accordingly, krill in addition to zooplankton supplied the corals with four times more C and N
530 compared to zooplankton only, but only increased the respiration by a factor of 1.4, probably due
531 to higher energetic costs to capture and process many live, small zooplankters compared to one
532 large, dead euphausiid. Energy costs to process live krill might be higher than for dead krill;
533 however, we assume that the difference is minor, because in feeding trials with live krill, we
534 observed that the corals immobilized their prey within a fraction of a second.
535

536 *Desmophyllum dianthus* responds to short-term food deprivation with a reduction of metabolic
537 rates, likely to conserve energy (Naumann et al. 2011, present study). Corals from Comau Fjord
538 lowered their respiration by 40 % after four days of food deprivation (present study),
539 conspecifics from the Mediterranean deep-sea by 20 % after one week and by 50 % after three
540 weeks of food deprivation (Naumann et al., 2011). This fast, strong reduction of metabolic
541 activity stands in contrast to the closely related CWC *Lophelia pertusa*, which reduced oxygen
542 consumption only after several months of food deprivation (Larsson, Lundälv & van Oevelen,
543 2013; Maier et al., 2019). Overall, in the present study, the respiration rate of *D. dianthus* was
544 around 2.5 times lower (14 ± 5 µmol O_2 (g skeletal dry mass)$^{-1}$ d^{-1}) compared to the respiration
545 rate of Mediterranean *D. dianthus* (35 ± 8 µmol O_2 (g skeletal dry mass)$^{-1}$ d^{-1}; Naumann et al.
546 2011), in spite of a comparable feeding history (*Artemia salina*, krill, >24 h after feeding) and
547 temperature (12 ºC).
548

549 The metabolic flexibility of *D. dianthus* could allow colonization of different habitats, from
550 shallow areas of fjords with a high variability of food, temperature, salinity and pH, to the
551 environmentally more stable, deep CWC habitats (Freiwald et al., 2004). Global warming
552 increases the metabolic rate of CWCs (Dodds et al., 2007; Gori et al., 2016; Dorey et al., 2020),
553 which could cause severe energetical constraints for this and other CWC species.
554

555 **Organic matter release**

556   Cold- and warm-water corals release organic matter (POM, DOM), as feces egested from their
557   gastrovascular cavity (Yonge, 1930) and as coral mucus (Brown & Bythell, 2005; Naumann et
558   al., 2011). The high POC and PON release by *D. dianthus* within the first day after feeding
559   (Fig. 5E, F) suggests that fecal material accounts for most of its POM release. The CWC species
560   engulfs its prey whole; hence, sloppy feeding *sensu* Banse (1992), i.e. the loss of organic matter
561   in front of the mouth, can be ruled out. Krill are assimilated at a higher efficiency compared to
562   zooplankton (CN assimilation:CN uptake), due to the lower fecal loss in relation to the high C
563   and N uptake (Fig. 5).
564
565   Four-day-unfed corals continue to release smaller amounts of POM, likely as mucoid material.
566   Coral mucus consists of glycoproteins (Bythell & Wild, 2011) and serves as protection against
567   sediment smothering, biofouling and as feeding aid (Brown & Bythell, 2005). Wild et al. (2008)
568   reported that mucus of the CWC *L. pertusa* rapidly dissolved in seawater, hence, the DOC
569   release of this CWC species was >30 times higher than its POC release. This high DOC:POC
570   ratio was not confirmed for *D. dianthus* (present study); instead, rates of DOC release/uptake
571   were highly variable (Fig. 5G).
572
573   Four-day unfed *D. dianthus* from Comau Fjord released on average four times more total organic
574   carbon (7.1 µmol TOC (g skeletal dry mass)$^{-1}$ d^{-1}; POC plus DOC) than its Mediterranean
575   conspecifics (1.9 µmol TOC (g skeletal dry mass)$^{-1}$ d^{-1}, Naumann et al., 2011). Higher mucus
576   production in the shallow areas of the fjords may serve as protection against higher particle loads
577   (Larsson et al., 2013; Zetsche et al., 2016). In the Comau Fjord, the chlorophyll-a concentration
578   (up to >50 mg m^{-3}, Garcia-Herrera et al., 2021), and hence turbidity, is orders of magnitude
579   higher than in the deep parts of the oligotrophic Mediterranean (<2 mg m^{-3}; Lo Iacono et al.
580   2019).
581
582   Due to relatively high mucus and fecal loss, the TOC release already contributes 30-60 % to the
583   total C loss of the fjord corals (respiration plus organic matter release). Anthropogenically
584   increased sedimentation, e.g., from the extensive salmon farming in the Chilean fjords
585   (Häussermann et al., 2013; Försterra, Häussermann & Laudien, 2016), could further increase
586   mucus production and related energy expenditure.
587
588   On the steep, partly overhanging fjord walls, *D. dianthus* often co-occurs with other suspension
589   feeders, such as the bivalve *Acesta patagonica* and the sponge *Mycale thielei* (Försterra et al.,
590   2005). Like *D. dianthus*, these genera produce large amounts of detrital and/or fecal material
591   (Maier et al., 2020b). The organic matter 'waste' of the suspension feeding community may
592   serve as food for detritivores living underneath the vertical or overhanging walls, ensuring a
593   close material recycling, as suggested for *L. pertusa* reefs (Rix et al., 2016; Maier et al., 2020b).
594
595   **Carbon and nitrogen budget**

596   The CWC *D. dianthus* in Comau Fjord is characterized by a high C and N demand. To account
597   for their costs of respiration, ammonium excretion and POM (mucus) release, unfed corals have
598   to expend 2 % of their tissue-C and 1.2 % of their tissue-N per day. With growing meal size,
599   feeding-related costs and losses increase the total C and N loss to 4.4 % of the tissue-C and
600   6.4 % of the tissue-N. To grow somatic and reproductive tissue, the corals need additional
601   resources. Conspecifics from the Mediterranean show an even higher C demand, due to their
602   higher respiration rate (Naumann et al., 2011). In comparison, *L. pertusa* from a Norwegian fjord
603   has a ca. 10-times lower C demand, due to the lower respiration under the colder (8 °C), less-
604   acidic conditions, and due to the lower POC release (Maier et al., 2019). Higher temperatures
605   increase the respiration of CWCs and hence their energy demand (Dodds et al., 2007; Gori et al.,
606   2016; Dorey et al., 2020). Similarly, a low pH stimulates the production of respiratory-chain
607   enzymes in *D. dianthus*, likewise indicating an increased metabolic activity and energy demand
608   (Carreiro-Silva et al., 2014). Nevertheless, the comparatively high skeletal growth rate of
609   *D. dianthus* from Comau Fjord, in spite of (relatively) high temperatures and low pH (Jantzen et
610   al., 2013a,b), could indicate that the fjord corals are not food-limited.
611
612   To balance C (or N) losses, a medium-sized *D. dianthus* polyp in Comau Fjord has to capture
613   almost 700 (or 400) zooplankton individuals (>100 μm) per day. As a voracious zooplankton
614   predator, *D. dianthus* is capable to exploit high concentrations of zooplankton (Höfer et al.,
615   2018), which may occur in swarms at densities of >1000 zooplankters L^{-1} (Ambler, 2002).
616   Zooplankton aggregation was observed at pycnoclines (Tiselius, Nielsen & Nielsen, 1994), near
617   oceanographic fronts, and in the vicinity of abrupt topography like seamounts or coral reefs
618   (Genin et al., 1994). These aggregations form because zooplankton actively maintains its depth
619   by swimming against vertical currents (Genin et al., 2005). A surprising finding in our
620   experiments was that simulated zooplankton swarms of >1000 individuals L^{-1}, leading to the
621   capture of >300 zooplankters, were insufficient to balance the daily C and N losses of the fjord
622   corals.
623
624   This suggests that krill, or other larger prey, play a crucial role for the nutrition of *D. dianthus* in
625   Comau Fjord. The capture of one euphausiid alone boosts the C and N budget of the corals
626   (Fig. 6), firstly due to its ca. 1,000 times higher C and N content compared to small zooplankton.
627   Secondly, krill is processed more efficiently compared to zooplankton: On a krill plus
628   zooplankton diet, corals showed a higher assimilation efficiency (lower feeding-related POC and
629   PON release in relation to C and N uptake, see above) and growth efficiency (lower metabolic
630   costs, i.e. respiration, ammonium excretion in relation to C and N uptake, see above). We
631   observed dense krill swarms directly next to the corals during dives by remotely-operated vehicle
632   between 160 and 200 m depth (Fig. 7) and during SCUBA dives at 20 m depth. Likewise, the
633   recurrence of blue whales in Comau Fjord (Försterra & Häussermann, 2012) indicates krill
634   aggregations, which are known to attract the large mammals in the region (Buchan & Quiñones,

635   2016). In feeding experiments, *D. dianthus* captured live krill at a similar rate (18 % h^{-1}) as small
636   zooplankton (Höfer et al., 2018); *in situ*, krill capture remains to be quantified.
637
638   A maximized energy intake is crucial considering the pronounced seasonality in North Patagonia
639   (Pickard, 1971). The C and N budget of *D. dianthus* was assessed in austral summer, when high
640   abundances of zooplankton and krill follow the spring phytoplankton bloom (Iriarte et al., 2007;
641   González et al., 2010) and create feast conditions. The CWCs might invest the excess resources
642   in tissue reserves such as lipids (Maier et al., 2019) to overcome the less-productive winter
643   (Iriarte et al., 2007; González et al., 2010). In early spring (September), however, Patagonian
644   *D. dianthus* also starts to produce gametes, which is an energy-costly process (Feehan, Waller &
645   Häussermann, 2019). Reduced skeletal growth in summer could therefore indicate an energetic
646   trade-off between investment in reproductive tissue and growth (Hassenrück et al., 2013), as
647   suggested for *L. pertusa* from a Norwegian fjord (Maier et al., 2020a). In winter, when
648   zooplankton and krill abundance is reduced, the corals may benefit from their metabolic
649   flexibility. The fast downregulation of metabolic rate and POM release constrains C and N
650   losses. Further, after prolonged (3-week) zooplankton exclusion, *D. dianthus* was observed to
651   take up alternative resources, such as DOM and/or non-zooplankton POM (Naumann et al.,
652   2011). A potential diet shift to more degraded material in winter was also described for the CWC
653   *L. pertusa* (Maier et al., 2020a). Metabolic and dietary flexibility enable the fjord corals to
654   survive without particulate food for several months, as we recently observed.
655
656   By the end of the century, most CWC ecosystems are predicted to face ocean acidification with
657   anthropogenically lowered pH levels comparable to those occurring naturally in Comau Fjord at
658   present (Guinotte et al., 2006; Jantzen et al., 2013; Fillinger & Richter, 2013). Our study
659   indicates that a high energy supply is crucial for *D. dianthus* to grow in its low-pH fjord habitat.
660   Similarly, CWCs showed a higher (growth) resilience to experimentally acidified conditions
661   when their energy supply was high (Georgian et al., 2016; Martínez-Dios et al., 2020). On top of
662   food quantity (e.g. the amount of C and N), a high food quality increases assimilation and growth
663   efficiency of CWCs (present study) and hence their reserves to actively counteract adverse
664   conditions (Carreiro-Silva et al., 2014). Nevertheless, there are currently no indications that
665   zooplankton and krill supply to CWC may increase to offset a changing C and N budget in the
666   future. In contrast, on a global scale, climate change is decreasing the productivity at the ocean
667   surface, the efficiency of the biological pump and accordingly the food supply to deeper, benthic
668   ecosystems (Bopp et al., 2001, 2005; Gregg et al., 2003). A decreased energy supply, in
669   combination with an increased energy demand, could have a large, negative impact on the fitness
670   of the local population of *D. dianthus* we studied in particular, and global CWCs in general.
671

Conclusions

673   The CWC *D. dianthus* from the fjords of the Los Lagos Region in North Patagonia requires a
674   substantial supply of pelagic food to balance its daily C and N loss through respiration,

675   ammonium excretion and POM release. Experimental feeding on zooplankton alone was not
676   enough to balance their C and N loss, despite the high zooplankton food concentration. For a
677   balanced C (or N) budget, the solitary coral needs to capture a minimum of 700 (or 400)
678   zooplankton individuals per polyp and day, or one larger prey item such as one euphausiid.
679   Under experimental food deprivation, the corals swiftly reduced all C and N loss terms, likely to
680   conserve energy. We argue that the exploitation of zooplankton swarms and/or the consumption
681   of krill, combined with a high metabolic flexibility, are important in sustaining the energetic
682   requirements of *D. dianthus* in Comau Fjord under naturally low pH. The bulk of the population,
683   however, thrives in deeper waters under even lower pH, near or below aragonite saturation
684   (Fillinger & Richter, 2013; Jantzen et al., 2013a), which may further increase their energy
685   demand (Gattuso, Allemand & Frankignoulle, 1999; Cohen & Holcomb, 2009); this may be
686   evaluated in the future by carrying out similar measurements as presented here *in situ*, along the
687   pH depth gradient. Climate change, ocean acidification and the intense salmon aquaculture in the
688   Patagonian fjord region likely impact the energetic balance of *D. dianthus*. The species appears
689   particularly sensitive to a combination of stressors, such as high temperatures and acidification
690   (Gori et al., 2016) or hypoxia and elevated levels of sulfide/methane (Försterra et al., 2014). A
691   disrupted energy balance may have severe consequences for the growth, reproduction and hence
692   the distribution of this and other habitat-forming cold-water coral species.
693

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700

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Minimum C and N demand of *Desmophyllum dianthus*, under different feeding treatments.

Feeding treatments were 'zoopl': corals fed with zooplankton; 'krill.d1': corals fed with zooplankton+krill, within the first day after feeding; 'krill.d2': corals fed with zooplankton+krill, 24 h after feeding; 'unfed': corals 4-day unfed. The minimum C demand of the corals was derived from their C loss in terms of respiration and release of particulate organic carbon (POC); their minimum N demand was calculated from their N loss in terms of ammonium excretion and release of particulate organic nitrogen (PON). Release of dissolved organic carbon and nitrogen (DOC, DON) are excluded here. C and N demand are given in different units, as indicated.

Fee-ding treat-ment	Min. C demand (= C loss; excluding DOC release)			Min. N demand (= N loss; excluding DON release)		
	(μmol C polyp^{-1} d^{-1})	(μmol C mmol-tissue-C^{-1} d^{-1})	(% of tissue-C)	(μmol N polyp^{-1} d^{-1})	(μmol N mmol-tissue-C^{-1} d^{-1})	(% of tissue-N)
zoopl	89.3 ± 31.4	35.6 ± 10.3	3.6 ± 1.0	11.9 ± 3.4	4.9 ± 1.5	3.3 ± 0.9
krill.d1	108.4 ± 27.2	44.0 ± 5.0	4.4 ± 0.5	23.8 ± 8.9	9.4 ± 1.0	6.4 ± 1.0
krill.d2	61.6 ± 16.8	24.9 ± 2.9	2.5 ± 0.3	13.5 ± 7.5	5.2 ± 2.3	3.6 ± 1.9
unfed	52.7 ± 23.6	20.0 ± 4.9	2.0 ± 0.5	3.6 ± 4.1	1.7 ± 1.3	1.2 ± 0.9

Figure 1

Figure 1: Map of Comau Fjord, located in North Patagonia, Los Lagos Region, Chile.

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

Figure 2

Conceptual carbon (C) and nitrogen (N) budget of the cold-water coral *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 (CO_2) and ammonium (NH_4^+), 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).

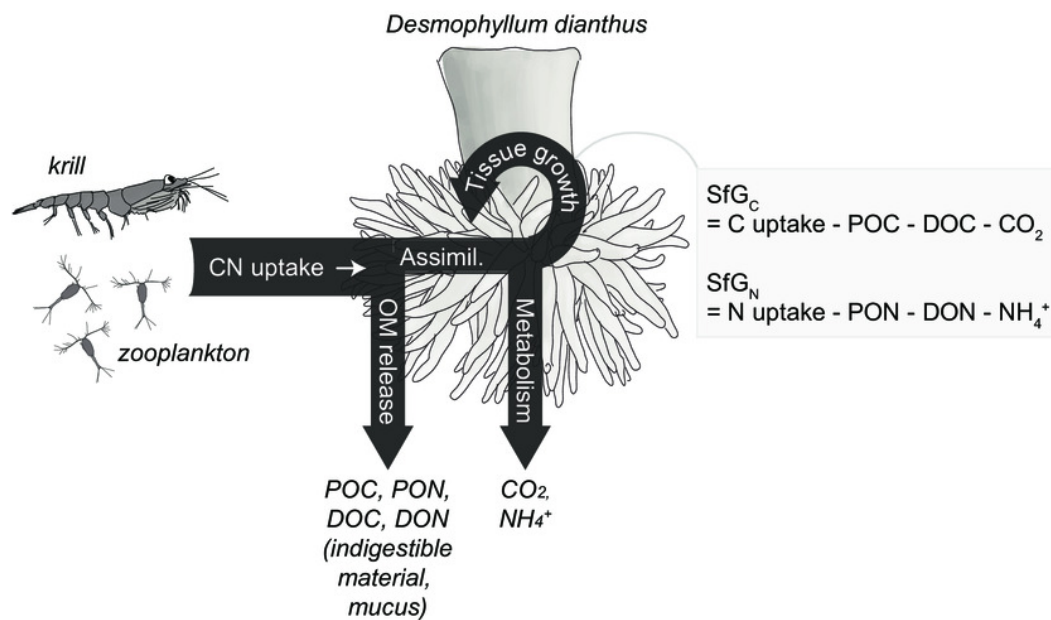
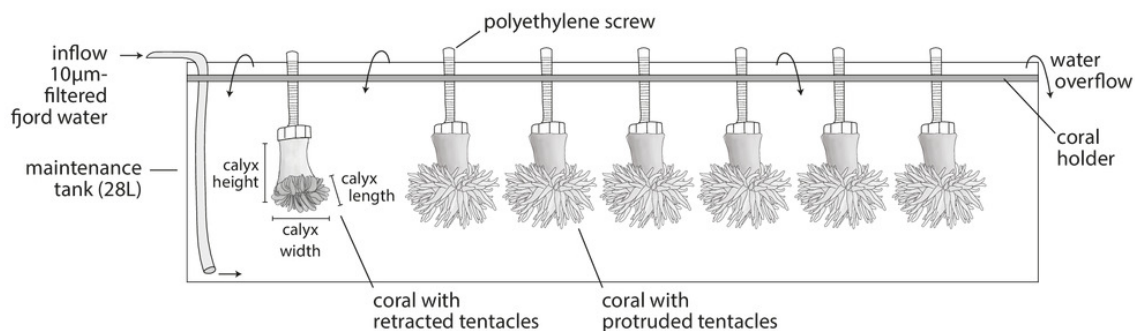
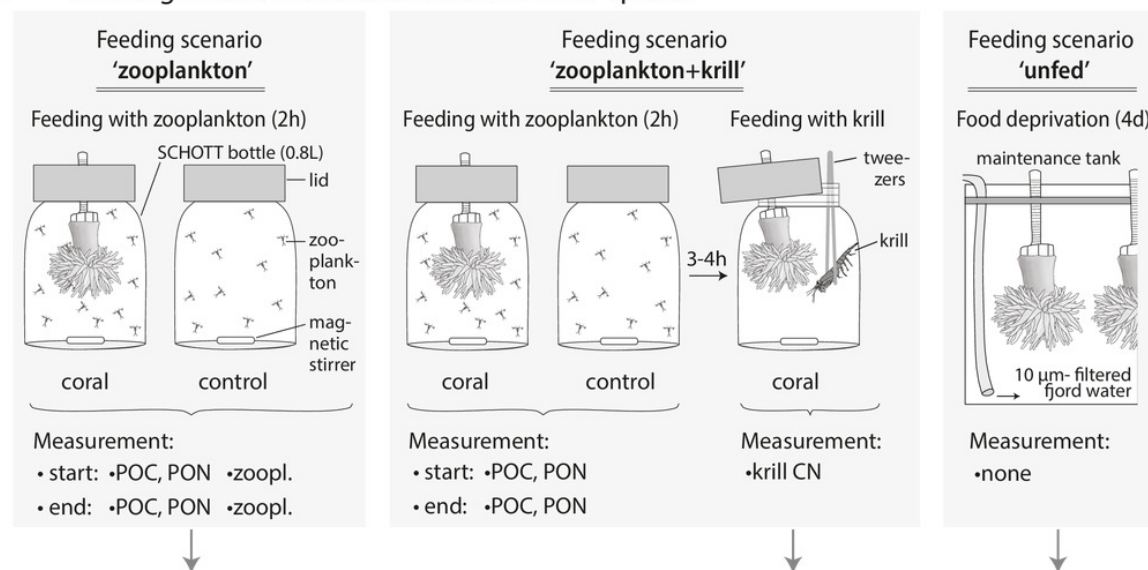



Figure 3

Coral maintenance, experimental set-up and measurements.

(A) Coral maintenance before and during the experiment. (B) Feeding treatments within the feeding scenarios 'zooplankton', 'zooplankton+krill', and 'unfed'. (C) Incubations following the feeding treatment in every feeding scenario. (B, C) Measurements at the start and end of the feeding/incubation are indicated. i.e. 'zoopl.': number of zooplankters in SCHOTT bottle; 'POC, PON': concentration of particulate organic carbon and nitrogen; 'krill CN': carbon and nitrogen content of krill; 'O$_2$': oxygen concentration; 'DIN': concentration of dissolved inorganic nitrogen (ammonium, nitrate, nitrite); 'DOC, DON': concentration of dissolved organic carbon and nitrogen.

a   Coral maintenance

b   Feeding treatments & measurement of CN uptake

c   Incubations to measure CN loss

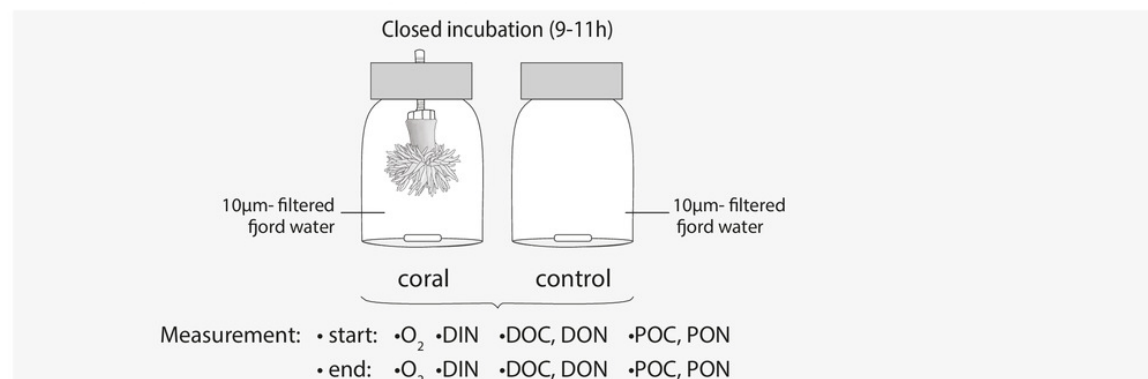



Figure 4

Experimental design.

The C and N budget of *Desmophyllum dianthus* was determined in a two-batch repeated-measures laboratory experiment. Each of the two coral batches was exposed to two subsequent feeding scenarios, simulating the temporally variable food availability in Comau Fjord. Each feeding scenario started with a feeding treatment, during which we determined the C and N uptake of the corals. In a subsequent incubation without food, the C and N loss of the corals was measured. In addition to the coral feeding treatments and incubations, we carried out seawater controls without corals, to account for planktonic C and N fluxes (see text). The C and N budget of the corals was calculated for each feeding scenario, as the difference between C and N uptake and C and N loss. For the feeding scenario 'zooplankton + krill', two incubations were carried out; accordingly two C and N budgets were calculated. In between the feeding scenarios, corals were fed daily with zooplankton.

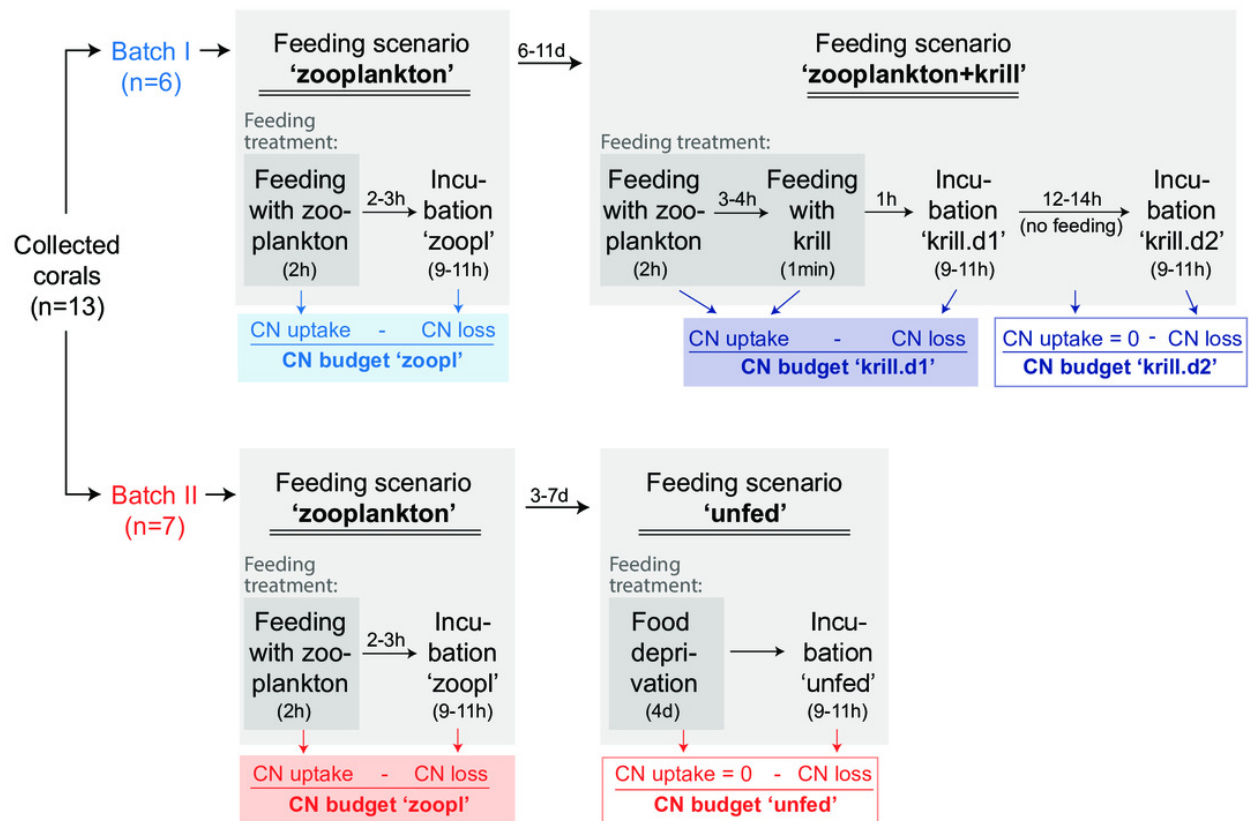



Figure 5

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

Feeding treatments were 'zoopl': fed with zooplankton; 'krill.d1': fed with zooplankton+krill, within the first day after feeding; 'krill.d2': fed with zooplankton+krill, 24 h after feeding; 'unfed': 4d-unfed. Blue colours: corals of batch I; red colours: corals of batch II. (A, B) C and N uptake during the feeding treatments; for 'unfed' and 'krill.d2', we assume no C and N uptake because corals were not fed for respectively four days and 24 hours; zero values represent six (open blue circles) and seven coral replicates (open red circles). (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). Bracket with *: linear mixed effect model found a significant difference between the indicated fluxes (see Supplemental Table 1.10 for details); ns: no significant difference.

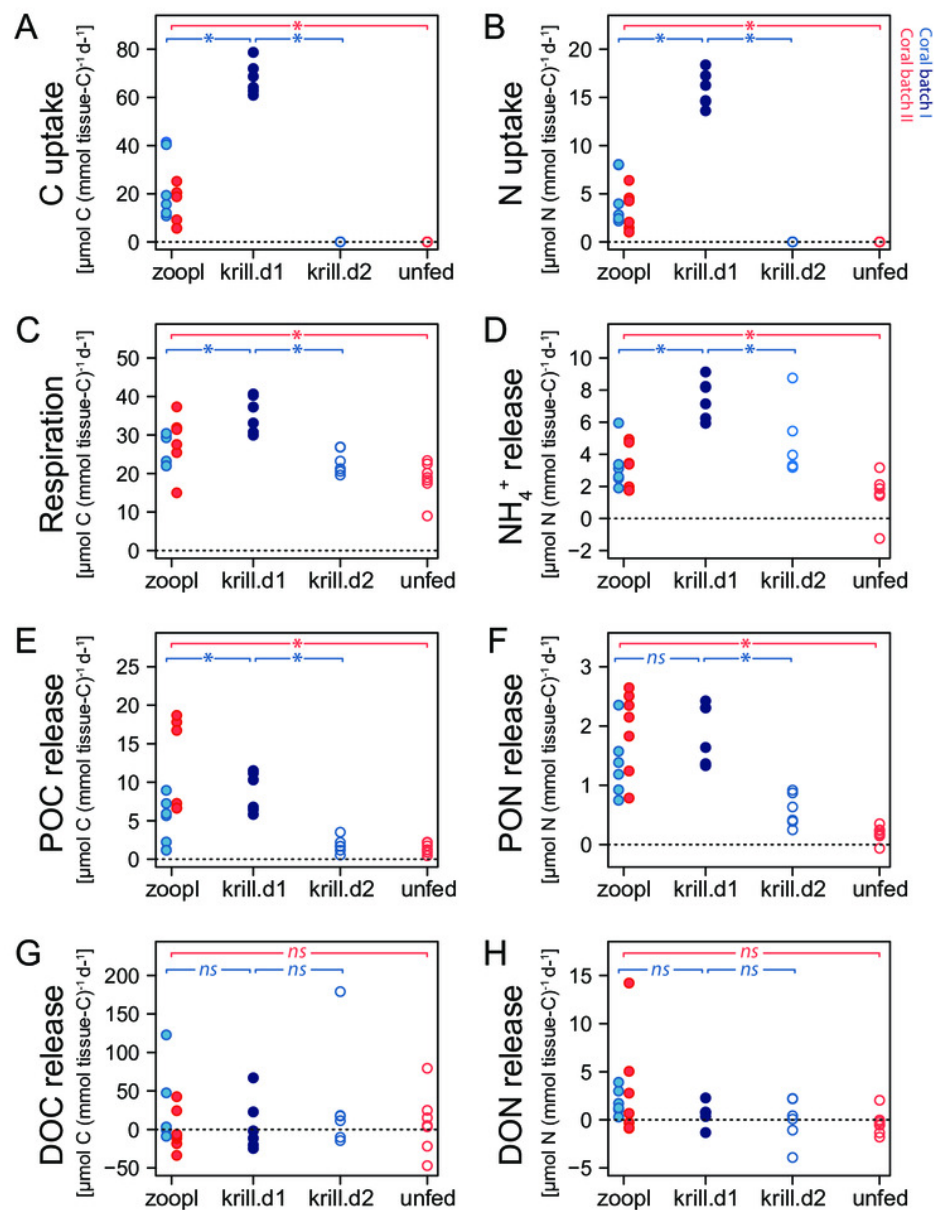



Figure 6

Carbon (C) and nitrogen (N) budget of *Desmophyllum dianthus* exposed to different feeding treatments, as C or N loss versus C or N uptake.

(A) C budget, (B) N budget. Dotted line: Scope for growth (SfG) = 0, i.e. C or N loss = C or N uptake. To the left of dotted line, marked in grey: SfG < 0, i.e. C or N deficit, to the right of dotted line: SfG > 0, i.e. C or N surplus. Blue colours: corals of batch I; red colours: corals of batch II. Different symbols represent the different feeding treatments, as indicated in the legend, i.e. 'zoopl': fed with zooplankton, 'krill.d1': fed with zooplankton+krill, within the first day after feeding, 'krill.d2': fed with zooplankton+krill, 24 h after feeding, 'unfed': 4d-unfed. C loss includes C respiration and release of particulate organic carbon; N loss encompasses ammonium excretion and release of particulate organic nitrogen.

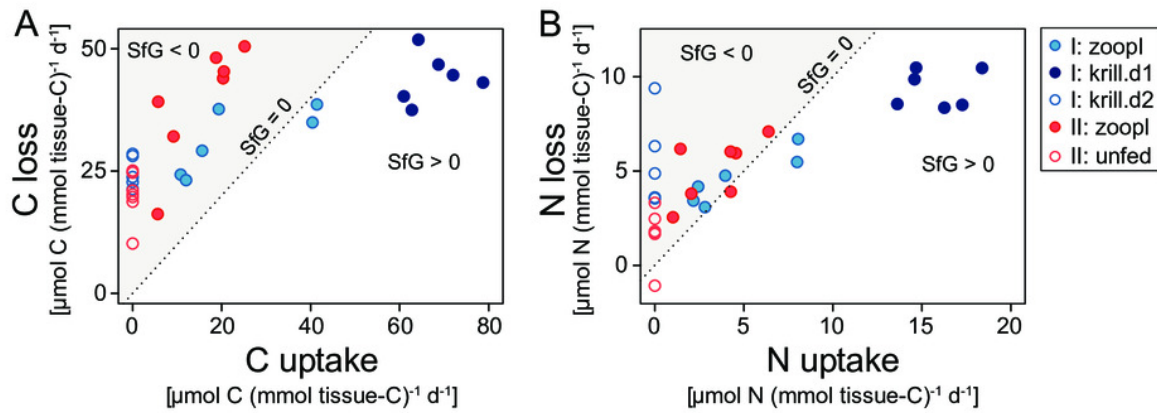



Figure 7

Dense swarms of krill and chaetognaths in Comau Fjord, directly above *Desmophyllum dianthus.*

Photo recorded by remotely-operated vehicle (C Richter) at 160 m depth. The arrow indicates one krill individual.