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1 *Tang et al., Copepod carcasses in the Sargasso Sea*

2

3 **Copepod carcasses in the Subtropical Convergence Zone of the Sargasso Sea: Implications for**
4 **microbial community composition, system respiration and carbon flux**

5

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21 **Keywords:** Sargasso Sea; subtropical convergence zone; zooplankton; carcasses; carbon sinking
22 flux

23

24 **Abstract**

25 The oligotrophic subtropical gyre covers a vast area of the Atlantic Ocean. Decades of time-series
26 monitoring have generated detailed temporal information about zooplankton species and
27 abundances at fixed locations within the gyre, but their live/dead status is often omitted, especially
28 in the dynamic Subtropical Convergence Zone (STCZ) where the water column stratification
29 pattern can change considerably across the front as warm and cold water masses converge. We
30 conducted a detailed survey in the North Atlantic STCZ, and showed that over 85% of the copepods
31 were typically concentrated in the upper 200 m. Copepod carcasses were present in all samples and
32 their proportional numerical abundances increased with depth, reaching up to 91% at 300–400 m.
33 Overall, 14–19% of the copepods within the upper 200 m were carcasses. Shipboard experiments
34 showed that during carcass decomposition, microbial respiration increased, and the bacterial
35 community associated with the carcasses diverged from that in the ambient water. Combining field
36 and experimental data, we estimated that decomposing copepod carcasses constitute a negligible
37 oxygen sink in the STCZ, but sinking carcasses may represent an overlooked portion of the passive
38 carbon sinking flux, and should be incorporated in future studies of carbon flux in this area.

39

40 **INTRODUCTION**

41 About one-third of the world's ocean is classified as oligotrophic with low productivity and
42 nutrient concentrations (Carr et al., 2006), much of which is located in the subtropical gyres. Given
43 the vast area covered by the oligotrophic ocean, its biota and related ecological processes have far-
44 reaching ramifications for global biogeochemical cycles and O₂/CO₂ balance (Ducklow and Doney,
45 2013). Based on multi-year SeaWiFS ocean color data, oligotrophic subtropical gyres appear to be
46 expanding, and most rapidly in the North Atlantic (Polovina et al., 2008). As such, detailed
47 understanding of the pelagic food web in these regions becomes increasingly important.

48 A considerable amount of research effort has been focused on these large marine ecosystems,
49 as exemplified by long-running oceanographic time-series programs in the Sargasso Sea (BATS:
50 Michaels and Knap, 1996; Steinberg et al., 2001) and near Hawaii (HOT: Karl and Lukas, 1996).
51 While these time-series studies provide detailed temporal information of fixed locations, they do not
52 capture the spatial variabilities across the gyres, especially in the subtropical convergence zone
53 (STCZ) where the convergence of warm and cold waters creates complex frontal structures.
54 Detailed biological data of the North Atlantic STCZ are limited (Böttger, 1982), although some
55 studies have suggested that it is a key spawning and nursery ground for eel, presumably due to
56 localized enhanced biological productivity (Miller and McCleave, 1994; Munk et al., 2010). Recent
57 evidence also points to elevated copepod abundance and egg production (Andersen et al., 2011), but
58 not primary production (Riemann et al., 2011), within the STCZ.

59 Copepods are important drivers of carbon and nutrient fluxes in the Sargasso Sea (Deevey,
60 1971; Roman et al., 1993; Steinberg et al., 2000). Conventional sampling protocols often assume all
61 copepods are alive (e.g. Böttger, 1982; Steinberg et al., 2001). However, there has been increasing
62 recognition that a considerable fraction of *in situ* copepods are in fact carcasses (e.g. Weikert, 1977;
63 Geptner et al., 1990; Böttger-Schnack, 1996; Yamaguchi et al., 2002; Tang et al., 2006a), and
64 ignoring the live/dead status of the specimens could lead to considerable errors in understanding
65 their population dynamics and related ecological processes (Elliott and Tang, 2011). To our
66 knowledge, there has been only one report of copepod carcasses in the bathypelagic layer (2,000–
67 4,000 m) of the Sargasso Sea (Wheeler 1967), whereas the occurrence of copepod carcasses in the
68 upper layer has not been investigated. Upon death, the carcasses can become hotspots for microbial
69 activities (Tang et al., 2009; Bickel and Tang, 2010), be recycled in the upper layers, or transport
70 carbon to the deep waters via sinking (Sampei et al., 2009, 2012; Frangoulis et al., 2011). Hence,
71 knowledge on microbial colonization and rates of carcass degradation is critical for assessing the
72 fate and vertical distribution of carcass-associated carbon and nutrients.

73 In the present study, we investigated the copepod distributions as well as their live/dead
74 compositions across the North Atlantic STCZ. Recent studies have suggested elevated plankton
75 abundance in this dynamic region (Andersen et al., 2011; Riemann et al., 2011), but the live/dead
76 composition of the zooplankton community remains unknown. Furthermore, we tested how
77 copepod carcass decomposition influences microbial respiration and community succession using
78 shipboard experiments, which allowed us to examine the impacts of carcasses on the microbial
79 community and energy budget in this oligotrophic region (Williams, 1998). Finally, we combined
80 our field and experimental data to examine the influences of copepod carcasses on carbon flux
81 estimates, which we then compared against flux values in the literature to assess the contribution of
82 sinking carcasses to the overall carbon flux.

83

84 **METHOD**

85 **Cruise track and hydrography**

86 This study was conducted in March–April 2014 on board the RV Dana (National Institute of
87 Aquatic Resources, Denmark) in areas of the North Atlantic STCZ as a part of the larger
88 SARGASSO-EEL project (Fig. 1). Transects were positioned to cover the expected area of
89 European eel larvae distribution (Munk et al., 2018). At each station along the transects,
90 hydrographic vertical profiles were obtained by lowering a Seabird® 9/11 CTD from the surface to
91 400 m depth. Sea surface temperature (SST) information for a larger area of the North Atlantic was
92 obtained from the Operational Sea Surface Temperature and Sea Ice Analysis project (OSTIA,

93 <http://ghrsst-pp.metoffice.com>). Contours of water column temperatures and SST were generated by
94 an interpolation procedure using inverse distance method in the program Surfer[®].

95

96 **Copepod carbon biomass and live/dead composition**

97 Zooplankton were collected using an opening-closing MIDI Multinet[®] equipped with five nets
98 of 50- μ m mesh and a 0.125 m² opening. We used a smaller than usual mesh size to avoid under-
99 sampling small life stages and species (Tang et al., 2011) that are common in this region (Andersen
100 et al., 2011). The Multinet was lowered to 400 m, and hauled vertically to the surface at a speed of
101 10 m min⁻¹. Sampling was done at thirty-seven stations in five depth strata: 400–300 m, 300–200 m,
102 200–100 m, 100–50 m and 50–0 m. A total of 250 zooplankton samples were collected. Upon net
103 retrieval, a subsample (ca. 10%) from each cod-end was transferred to a container for live/dead
104 sorting using the Neutral Red staining method. This method, originally developed by Dressel et al.
105 (1972), later improved by Elliott and Tang (2009) and further evaluated by Zetsche and Meysman
106 (2012), allows researchers to quickly and easily distinguish between live and dead copepods. Each
107 subsample was incubated with Neutral Red solution for 20 min in the dark at room temperature.
108 Afterward, the stained subsamples were concentrated on a 50- μ m sieve and back-washed with
109 filtered seawater onto a petri dish. Under a stereomicroscope the copepods were counted as live
110 (stained red) or dead (unstained and without vital signs; some showing signs of decomposition).
111 Molts appeared completely transparent and were not counted. Species compositions were not
112 recorded for the live/dead counts due to time constraints. Only copepods were included in live/dead
113 counts because they were the majority of the mesozooplankton in our samples (ca. 75% of
114 estimated total zooplankton carbon biomass), and because the staining method works best on
115 copepods (Elliott and Tang, 2009).

116 After live/dead counting, the subsamples were added to the remainder of the corresponding
117 cod-end content and preserved in 4% buffered formaldehyde. The preserved samples were
118 identified and enumerated by the Arctic Agency (Poland). For each species and life stage, 10
119 individuals (when present) were sized and their body carbon contents were estimated from
120 published algorithms (Table 1). Carcass carbon biomasses were calculated as total copepod carbon
121 biomasses multiplied by the percentages of dead copepods. This is likely to overestimate the carcass
122 biomass as the carbon content of carcasses would be decreased by decomposition, and the carcasses
123 which had sunk farther from their depth of origin would have a lower carbon mass than new
124 carcasses. However, since the depth of origin of the carcasses was not known, it was not possible to
125 include a decomposition factor to the estimates of carcass biomass, particularly since the majority
126 of the zooplankton population at several stations appeared to be evenly distributed throughout the
127 0–200 m depth (see RESULTS), and the decomposition time of carcasses would thus be likely to

128 differ. Because most of the carcasses collected at depths appeared to be intact, we therefore
129 assumed that the majority of carcasses were collected close to their origin, and had a carbon content
130 equal to live copepods. To constrain the uncertainty associated with this assumption, we used our
131 experimental carcass decomposition rates (see next section) to estimate the expected depth
132 distributions of carcass carbon by assuming a maximum decomposition time in situ (i.e. assuming
133 all carcasses originated at 0 m; see DISCUSSION).

134 To better illustrate the spatial variations in total copepod carbon biomass (live + dead), we
135 binned the data based on longitudes (ca. every 3° West to East) and latitudes (every 2° North to
136 South).

137

138 **Copepod carcass decomposition experiments**

139 Carcass decomposition experiments were conducted at three locations (Fig. 1) with the
140 copepod *Oncaea* spp. They were the most numerically abundant in samples sorted for the
141 experiments, making up approximately one-third of the organisms in all samples. Copepods were
142 collected by towing a 45- μ m plankton net from just below the fluorescence maximum (FM; based
143 on CTD measurements) to the surface. Individuals of *Oncaea* spp. (size 200–500 μ m) were sorted
144 into 5-L bottles containing 0.2- μ m filtered seawater, and kept at *in situ* temperature for up to 24 h
145 before the experiments. Another subsample of ca. 100 copepods was measured under an inverted
146 microscope for body lengths (precision ± 20 μ m). To produce fresh carcasses for the experiments,
147 actively moving copepods were killed by brief exposure (a few seconds) to 10% HCl, then rinsed
148 with filtered seawater and added to the incubation bottles. Water for incubations was obtained from
149 5–10 m depth, immediately reverse filtered through a 20- μ m mesh and added to thirty-two 1-L
150 polypropylene bottles. To twenty of these bottles, 30–40 freshly killed copepods were added; the
151 other twelve bottles without carcasses were used as controls. Incubations were done on a slowly
152 rotating plankton wheel at 22 °C and *in situ* day-night cycles of 30 μ mol photons m⁻² s⁻¹ light
153 intensity. At 0, 6, 12 and 24 h, five replicates of carcass bottles and triplicate control bottles were
154 sacrificed for measurements of bacterial community composition and respiration.

155

156 **Bacterial community composition in carcass decomposition experiments**

157 In the following sections, the different bacterial samples are described as ‘carcass’ (bacteria
158 attached to the carcasses), ‘carcass water’ (free-living bacteria in water where carcasses were
159 incubated), or ‘control water’ (free-living bacteria in the controls).

160 At each time point of the carcass decomposition experiments, triplicate samples of carcasses
161 (10 each) were gently washed in 0.2 μ m-filtered seawater and transferred into Eppendorf tubes.

162 About 1 L of ‘carcass water’ (5 replicates) and ‘control water’ (3 replicates) taken at time 0 and 24
163 h were filtered onto Supor 0.2 μm filters and stored at $-80\text{ }^{\circ}\text{C}$ until processing.

164 DNA was extracted using the E.Z.N.A.[®] Tissue DNA Kit (Omega Bio-Tek, Inc.) and quantified
165 using Quant-IT PicoGreen (Invitrogen). Bacterial and Archaeal 16S rRNA genes were PCR
166 amplified using MyTag DNA polymerase (Saveen & Verner AB), 2 μL template, and Illumina
167 primers 515f (GCGTGCCAGCMGCCGCGGTAA) and 806r (GGACTACHV-GGGTWTCTAAT)
168 complemented with sample-specific barcodes (Bates et al., 2010) in 25 μl reaction volumes. In
169 addition, 10 $\mu\text{g } \mu\text{L}^{-1}$ bovine serum albumin (Sigma-Aldrich) and 5 mM MgCl_2 (DNA Diagnostic)
170 were added to the ‘carcass’ samples to facilitate PCR amplification. The PCR cycling condition
171 were: 95°C for 2 min, 29 cycles of: 95°C for 0.30 min, 54°C for 0.30 min, $72\text{ }^{\circ}\text{C}$ for 1.30 min. For
172 each sample, triplicate PCR products were pooled, purified using the Agencourt AMPure XP kit
173 (Beckman coulter Inc.), and quantified. The 84 samples were mixed in equimolar amounts and
174 sequenced (Illumina MiSeq, National High-throughput DNA sequencing Centre, University of
175 Copenhagen, Denmark). Sequence reads were assembled, trimmed to a mean length of 252
176 nucleotides, and de-multiplexed using the software QIIME v1.9 (Caporaso et al., 2010). Removal of
177 singletons and clustering at 97% similarity was done in USEARCH v1.8 (Edgar, 2010) using the
178 UPARSE-OTU algorithm (Edgar, 2013) with implicit chimera check. Taxonomy was assigned in
179 QIIME using UCLUST (Edgar, 2010) and the Greengenes v.13.8 reference database (McDonald et
180 al., 2012). Chloroplasts and mitochondrial reads were removed before subsequent analysis. The
181 total operational taxonomic units (OTU) were subsampled by randomly picked OTUs to
182 accommodate for the lowest number of sequences found in a sample (4401 sequences sample⁻¹) in
183 QIIME.

184 Phylogenetic similarity between samples was determined by principal component analyses
185 using square root transformed Bray-Curtis dissimilarity distances on OTUs relative abundance <
186 0.1% in Primer 6.1.7 (Primer-E). To identify the OTUs contributing to dissimilarity between 0 and
187 24 h old samples, a SIMPER analysis (Clarke and Warwick, 2001) was performed on the above
188 dissimilarity distances.

189

190 **Respiration during carcass decomposition**

191 Respiration rate was measured as decrease in dissolved oxygen over time in a gas-tight glass
192 chamber (2 mL) using a protected microsensor (Unisense), which registered the oxygen
193 concentration in 2 s intervals. The glass chamber was submerged in a 22°C water bath. Prior to
194 measurements, baseline was established using 0.2- μm filtered seawater. At each time point 4–5
195 carcasses were transferred from the incubation bottle to the chamber, and measurements were
196 carried out until the dissolved oxygen decreased at $<1\text{ mg L}^{-1}\text{ min}^{-1}$. Respiration rate ($\mu\text{g O}_2\text{ carcass}^{-1}$)

197 ¹ d⁻¹) was calculated from linear regression of the slope (significant at $p < 0.001$) after correction for
198 baseline drift. The daily total respiration was calculated as the sum of time-integrated respirations
199 over the three sampling intervals. Microbial oxygen consumption was then converted to microbial
200 carbon consumption (respiration + production) assuming 1: 1 O₂-to-C molar ratio and 30% bacterial
201 growth efficiency (Del Giorgio and Cole, 1998). The copepod's body volume was estimated from
202 its linear dimensions as $9.87 \times 10^7 \mu\text{m}^3$, which was then converted to a carbon content of 12.8 $\mu\text{g C}$
203 copepod⁻¹ (Hansen et al., 1997). Dividing the daily carbon consumption by the carcass carbon
204 content gave the daily carcass-carbon turnover.

205

206 **RESULTS**

207 **Hydrographical conditions**

208 The water column thermal structure showed distinct changes when crossing the frontal zone,
209 with a sharp incline of the isotherm from the thermocline depth (ca. 200 m) to the surface, most
210 noticeably in the southern sections of the transects (Fig. 2). The influence of colder water masses
211 was more conspicuous to the north of the front. Salinity ranged from about 36.6 at the surface to
212 36.4 at 400 m, with an intrusion of higher salinity water of up to 36.9 in the depth interval of 80–
213 180 m (Munk et al., 2018).

214

215 **Copepod carbon biomass and live/dead compositions**

216 Copepods were the most numerically abundant taxa at all stations. Copepod carbon biomasses
217 were highest within 0–200 m (up to 99 mg C m⁻²) and slightly higher in the northernmost stations
218 (Fig. 3). The carbon biomass at depths > 200 m was much lower, and was typically less than 15%
219 of that at depths < 200 m.

220 Neutral Red staining revealed that copepod carcasses were present in all samples (Fig. 4).
221 Longitudinally, the proportional abundances of dead copepods (as % dead) appeared to increase
222 toward the east; whereas latitudinally, it was slightly lower in the southern-most stations. The %
223 dead copepods increased with depth, most noticeably below 200 m. Nevertheless, the higher total
224 copepod carbon biomasses at 0–200 m resulted in considerably larger amounts of carcass carbon
225 biomass in the upper layer across the latitudes and longitudes (Fig. 5).

226

227 **Carcass decomposition experiments - Bacterial composition and respiration**

228 The bacterial communities were dominated by Gammaproteobacteria, Alphaproteobacteria and
229 Bacteroidetes (Supplementary materials Fig. S1). Bacterial community compositions in “control
230 water” and “carcass water” were similar, whereas “carcass” samples clearly differed from the other
231 two, apart from a small overlap (Supplementary material Fig. S2). A pronounced succession led to

232 an increasingly distinct carcass-associated bacterial community composition over time
233 (Supplementary materials Fig. S1).

234 SIMPER analysis showed that Rickettsiales and Pseudomonadales accounted for most of the
235 dissimilarity between 0 and 24 h in Exp. 1, but in opposite manner: Rickettsiales increased in
236 relative abundance over time, whereas Pseudomonadales decreased (Supplementary material Table
237 S1). On the contrary, Rickettsiales decreased over time in Exp. 2 and 3, whereas Pseudomonadales
238 increased in Exp. 2. In both Exp. 2 and 3, Vibrionales proliferated and contributed substantially to
239 the dissimilarity (Supplementary material Table S1).

240 Microbial respiration rates associated with carcass decomposition increased with time (Table
241 2). The integrated daily respiration rate was considerably lower in Exp. 2 than in the other two
242 experiments. The estimated carcass-carbon turnover varied from 18 to 93% per day, with an
243 average of 56.5% d⁻¹ (Table 2).

244

245 **DISCUSSION**

246 Zooplankton sampling at the Sargasso Sea BATS station has been on-going for nearly three
247 decades, generating detailed temporal information of the larger zooplankton (200- μ m net)
248 communities as influenced by the oceanographic conditions (Steinberg et al., 2001). However, like
249 many sampling programs, whether the zooplankton are live or dead upon collection has not been
250 taken into account. Here, we show that copepod carcasses were prevalent in the STCZ. Within the
251 upper 200 m, where zooplankton tend to exert the strongest grazing impacts (Roman et al., 1993;
252 Steinberg et al., 2001), 14–19 % of the copepod biomass was carcasses when assuming the same
253 carbon content for carcasses as for live copepods. Even if we assume an average decomposition
254 time of 24 h, hence ca. 57% of carbon loss to decomposition, carcasses would still account for 6–
255 8% of the biomass within the upper 200 m. In both cases, carcasses comprised a considerable
256 fraction of the total copepod biomass. Occurrence of carcasses implicates non-predation mortality
257 factors at work (Tang et al., 2014), although pin-pointing the actual cause(s) is beyond the scope of
258 this study. Nevertheless, the presence of carcasses can have important ramifications for the regional
259 biogeochemistry, as discussed below.

260 Similar to other detritus (e.g. marine snow, fecal pellets), copepod carcasses provide organic-
261 rich loci for bacteria in the otherwise oligotrophic Sargasso Sea (Carlson and Ducklow, 1996). In
262 our experiments, ambient bacteria rapidly colonized and exploited copepod carcasses leading to an
263 increase in microbial respiration. Concurrently, there was a shift in the carcass-associated bacterial
264 community composition, consistent with previous observations that carcass decomposition favors
265 certain bacterial groups (Tang et al., 2006b). In particular, members of Rickettsiales,
266 Pseudomonadales and Vibrionales—well adapted to high carbon concentrations—proliferated

267 substantially during carcass decomposition. It is noteworthy that the predominance of specific
268 OTUs (e.g. the lack of responsive Vibrionales in Experiment 1; Supplementary material Table S1)
269 and the estimated respiration rate (Table 2) varied considerably between experiments. Although the
270 incubations were done under the same temperature and light conditions, the copepods and the
271 incubation waters were taken from different locations for the different experiments, and they carried
272 different initial microbial communities (Supplementary material Fig. S1), which likely resulted in
273 different microbial successions and activity levels (Moisander et al., 2015). Similar to bacterial
274 communities on live copepods (e.g. Dziallas et al., 2013; De Corte et al., 2014; Shoemaker and
275 Moisander, 2015), communities associated with carcasses were distinct relative to those in the
276 seawater, although with an overlap for a few samples (Fig. S2). Interestingly, we noted the
277 appearance of several low-abundance anaerobic taxa towards the end of the incubations (data not
278 shown). Hence, it appears that carcasses were colonized by a subset of the free-living bacterial
279 community, which developed into a rather distinct assemblage over time as the carcass-associated
280 environmental conditions changed, including the potential development of micro-anoxic zones
281 (Glud et al., 2015).

282 Our calculations of microbial oxygen consumption and carcass-carbon turnover in the
283 decomposition experiments relied on a number of assumptions: We assumed that all carcass carbon
284 was equally labile, but the different organic fractions would likely degrade at different rates (Tang
285 et al., 2009; Bickel and Tang, 2010). We also assumed that decomposition was entirely aerobic, but
286 in reality anaerobic decomposition could occur (Glud et al., 2015). Nevertheless, the calculated
287 carcass-carbon turnover rates in Exp. 1 and 2 were comparable to those reported by others (Lee and
288 Fisher, 1992; Tang et al., 2009). The rate was considerably higher in Exp. 3, but similarly high
289 turnover rates have been observed for the protein fraction of copepod carcasses (Bickel and Tang,
290 2010), and carbon loss could also be accelerated by carcass fragmentation and leakage (Tang et al.,
291 2009).

292 Contributions of copepod carcasses to epipelagic respiration vs. sinking fluxes would depend
293 on their depths of origin and residence times above the thermocline. From the literature,
294 gravitational sinking velocity of copepod carcasses of comparable size in 25 °C seawater with a
295 salinity of 35 is ca. 90 m d⁻¹ (Elliott et al., 2010). If we conservatively assume that all copepod
296 deaths occurred at 0 m and the carcasses began their descent, based on our measured microbial
297 respiration rates, the carcasses could lose on average 57–100 % of their carbon to microbial
298 decomposition within 0–200 m, with the rest (0–43%; average 22%) potentially exported to below
299 the thermocline. Clearly, not all if any carcasses originated from 0 m, and 0% carcass export cannot
300 be correct because carcasses were present in 200–400 m. The fact that most of the carcasses
301 collected below the thermocline were intact suggests that many of them originated at depths and

302 that our calculation may have over-estimated carcass decomposition. Nevertheless, despite the
303 uncertainty in our calculations, the estimated average carcass carbon export (22%) is consistent with
304 our field data at least at the population level (Fig. 5): The estimated carcass carbon biomass in the
305 200–400 m layer was equal to 23–29% of that in the 0–200 m layer.

306 Carcass decomposition will add to the system's oxygen consumption, but it is ignored in
307 conventional bulk-water respiration measurements. We calculated the carcass-driven respiration as
308 *in situ* carcass carbon biomasses multiplied by the average carcass carbon-specific respiration rate
309 determined in the experiments (Table 3). The estimated carcass-driven respiration is at least 2–3
310 orders of magnitude lower than the ambient respiration rates reported in the literature (Table 3).
311 Therefore, copepod carcasses are a negligible oxygen sink, and their presence would not
312 significantly impact the overall autotrophy-heterotrophy balance in the Sargasso Sea.

313 In addition to being important trophic links within the pelagic food web, zooplankton can also
314 influence vertical transportation of material via vertical migration (active flux) and via sinking
315 carcasses and fecal pellets (passive flux). The contribution by migrating zooplankton to the active
316 carbon flux in the Sargasso Sea is of particular interest, as it has been proposed as an explanation
317 for the spring-fall carbon imbalance (Steinberg et al., 2000). In field studies, active flux is often
318 derived from the night/day differential in zooplankton biomass within the mixed layer, which
319 represents the zooplankton biomass that migrates downward, and which via respiration and
320 excretion releases carbon at depth (e.g. Dam et al., 1995; Steinberg et al., 2000). From this, Dam et
321 al. (1995) calculated a migratory carbon flux equivalent to an average of 34% of the gravitational
322 particulate carbon (POC) flux in the upper 150 m at BATS, whereas Steinberg et al. (2000)
323 estimated that migratory carbon flux accounts for 7.8–14.4 % (mean) of the POC flux within the
324 upper 300 m. The underlying assumption that all zooplankton in the mixed layer are alive (a pre-
325 requisite for “active” flux) was not verified in those studies, but violation to this assumption would
326 mean an overestimation of the active flux. Within the upper 300 m, we observed an average of 15%
327 (across latitudes) to 22% (across longitudes) dead copepods, and these percentages need to be taken
328 into account when calculating the active flux. It should be noted that the zooplankton community
329 compositions at BATS are different from our observations in the STCZ partly due to the use of
330 different mesh sizes (200 μm vs. 50 μm), and we did not identify migratory vs. non-migratory
331 species in our live/dead sorting. Nevertheless, the percentages of dead copepods (15–22%) are of
332 similar magnitude as the migratory flux percentage estimate by Dam et al. (1995) and Steinberg et
333 al. (2000). Therefore, the migratory flux could have been overestimated in the previous studies
334 when the zooplankton live/dead status in the mixed layer was not considered.

335 Instead of the active flux, carcasses can be a part of the passive detrital flux. In our study,
336 carcasses were concentrated in the upper 200 m, but some intact carcasses were still present below

337 the thermocline (Fig. 5), which could readily contribute to the passive POC flux to depth. Although
338 there are no available POC flux data for the STCZ, we may use data from BATS to speculate on the
339 importance of carcass carbon flux. We estimated an average carcass carbon biomass of 0.82–1.44
340 mg C m⁻² in the 200–300 m layer, and 0.87–1.05 mg C m⁻² in the 300–400 m layer in the STCZ
341 (Fig. 5). According to an earlier study, POC flux at BATS was 13.9 mg C m⁻² d⁻¹ at 300 m, and 8.7
342 mg C m⁻² d⁻¹ at 600 m (Steinberg et al., 2000). Carcass sinking rate is unknown and is highly
343 influenced by decomposition state and turbulence (Kirillin et al., 2012). Assuming a carcass sinking
344 rate of 90 m d⁻¹ for our hydrographical conditions (Elliott et al., 2010), the carcasses could
345 contribute ca. 6–10 % of the POC flux at 300 m, and 5–6 % at 600 m. These, coincidentally, are
346 comparable to the estimated migratory active flux at similar depths at BATS (Steinberg et al.,
347 2000).

348 Other researchers, using different methods, have also shown significant contributions of
349 zooplankton carcasses to passive carbon flux elsewhere. For example, copepod carcasses
350 contributed on average 36% of the annual total passive carbon flux in the Beaufort Sea (Sampei et
351 al., 2009), and up to 91% in the Amundsen Gulf during the post-bloom period (Sampei et al., 2012).
352 Copepod carcass carbon flux exceeded even the fecal pellet carbon flux on most occasions in the
353 Bay of Calvi (Frangoulis et al., 2011). While our simple calculations ignore the effects of
354 decomposition and necrophagy in the mesopelagic layer (Elliott et al. 2010), our study as well as
355 others show that knowledge of the zooplankton live/dead composition may reveal an unexpected
356 carbon flow pathway via passively sinking zooplankton carcasses, instead of or in addition to active
357 transport by vertical migrators.

358

359 CONCLUSIONS

360 The dynamic nature of the STCZ was illustrated by the distinct latitudinal variations in the
361 water column thermal structure across the front. Within the STCZ, copepod carcasses were
362 ubiquitous and their biomass was concentrated in the upper 200 m. Our experiments showed that
363 copepod carcasses were colonized by specialized bacterial taxa and rapidly degraded by microbial
364 activity. While decomposing carcasses overall constitute a negligible oxygen sink in the STCZ,
365 sinking copepod carcasses provide an alternative carbon transport pathway comparable in
366 magnitude to conventional zooplankton migratory flux. Inclusion of data on *in situ* live/dead
367 compositions of copepods and other zooplankton may therefore lead to a different understanding of
368 active (migratory zooplankton) vs. passive (sinking carcasses) carbon flux to the deep waters, as
369 well as other zooplankton-driven biogeochemical processes in the STCZ.

370

371 **ACKNOWLEDGEMENTS**

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376 the manuscript.

377

378 **Authors' contributions:** All authors contributed to conceiving the idea, collecting the data, and
379 analyzing the data. KWT wrote the manuscript with input from co-authors.

380

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- 530

531 **TABLE LEGENDS**

532

533 Table 1. Algorithms used for size-carbon conversation in this study. L is prosome length; TL is total
534 length; Dry weight (DW) is converted to carbon assuming a C:DW ratio of 0.45.

535

536 Table 2. Microbial respiration during carcass decomposition measured in three time intervals and
537 integrated over 24 hours, as well as the microbial carbon consumption of carcasses and carcass
538 turnover.

539

540 Table 3. Biological oxygen demand reported for Sargasso Sea and the nearby regions. Where
541 necessary, published carbon respiration rates are converted to oxygen consumption rates assuming
542 1:1 C-to-O₂ molar ratio.

543

544 **FIGURE LEGENDS**

545

546 Fig. 1. Chart of SST contoured from satellite observations on 1st April 2014. Isotherms are
547 illustrated in 0.5°C intervals. Transects of sampling stations (dots) are numbered 1–9. Larger circles
548 indicate locations of carcass decomposition experiments.

549

550 Fig. 2. Vertical temperature profiles for transects 1-9 (see Fig. 1) with isotherm interval at 0.5°C.

551

552 Fig. 3. Total copepod carbon biomass (mean + s.d.) in different strata across latitudes (A-E; 31.50°
553 to 24.67°; binned every 2°) and longitudes (F-J; -68.50° to -37.67°; binned every 3°) along the cruise
554 track (see Fig. 1). Note the different y-axis scale for panels D, E, I and J.

555

556 Fig. 4. Proportional abundances of dead copepods (mean + s.d.) in different strata across latitudes
557 (A-E) and longitudes (F-J) along the cruise tracks. Data are binned in the same manner as in Fig. 3.

558

559 Fig. 5. Copepod carcass carbon biomass (mg C m⁻²; mean + s.d.) for the different strata averaged
560 across latitudes 31.50° to 24.67° (A) and longitudes -68.50° to -37.67° (B), assuming the same
561 carcass carbon content as for live copepods.

562

563

Table 1. Algorithms used for size-carbon conversion in this study. L is prosome length; TL is total length; Dry weight (DW) is converted to carbon assuming a C:DW ratio of 0.45.

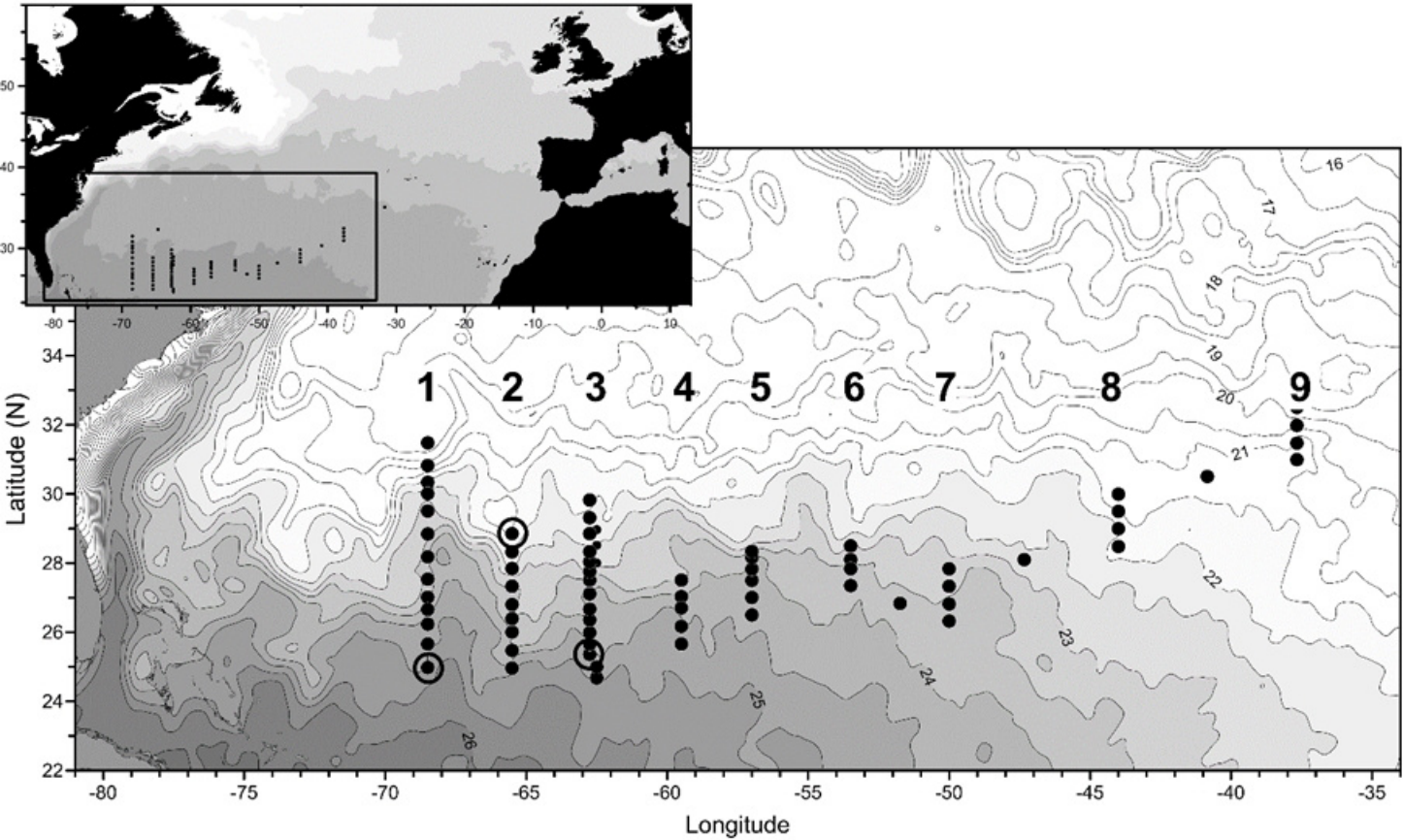
Taxa	Stage	Equation	Reference
Copepoda	Nauplii	$\text{mg C} = 3.18 \times 10^{-12} \times L_{\mu\text{m}}^{3.31}$	Berggreen et al. (1988)
<i>Paracalanus</i> , <i>Clausocalanus</i> and <i>Calocalanus</i>	Copepodites	$\ln(\mu\text{g DW}) = 3.25 \times \ln(L_{\mu\text{m}}) - 19.65$	Chisholm and Roff (1990)
<i>Oithona</i>	Copepodites	$\log(\mu\text{g DW}) = 3.16 \times \log(L_{\text{mm}}) - 8.18$	Hopcroft et al. (1998)
All other Calanoida	Copepodites	$\ln(\mu\text{g DW}) = 2.74 \times \ln(L_{\mu\text{m}}) - 16.41$	Chisholm and Roff (1990)
All other Cyclopoida (incl. <i>Oncaea</i>)	Copepodites	$\ln(\mu\text{g DW}) = 1.96 \times \ln(L_{\mu\text{m}}) - 11.64$	Chisholm and Roff (1990)
Harpacticoida	Copepodites	$\ln(\mu\text{g C}) = 1.15 \times \ln(\text{TL}_{\mu\text{m}}) - 7.79$	Satapoomin (1999)

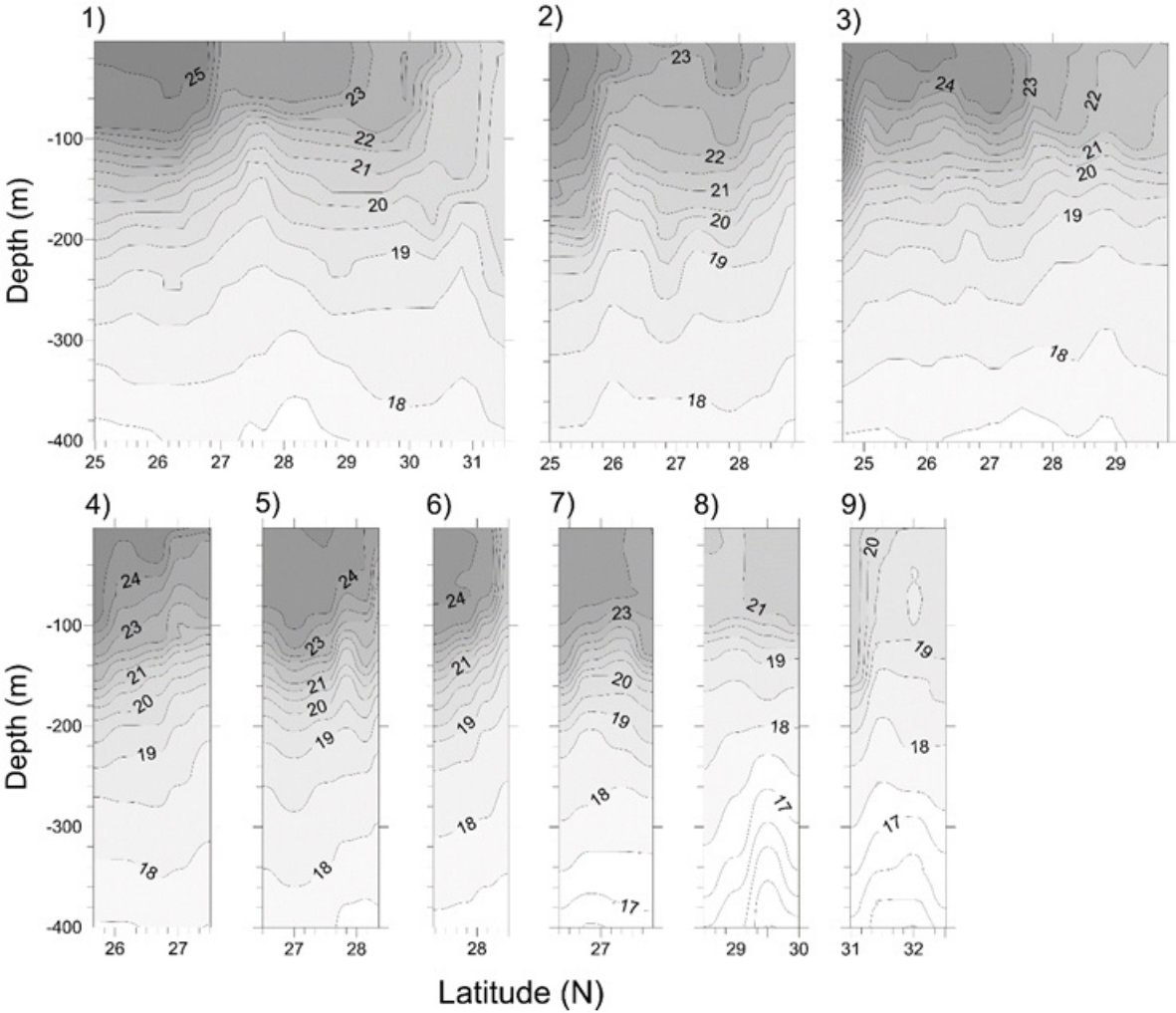
Table 2. Microbial respiration during carcass decomposition measured in three time intervals and integrated over 24 hours, as well as the microbial carbon consumption of carcasses and carcass turnover.

	Respiration ($\mu\text{g O}_2 \text{ carcass}^{-1}$)			Integrated respiration ($\mu\text{g O}_2 \text{ carcass}^{-1} \text{ d}^{-1}$)	Carcass-C consumption ($\mu\text{g C carcass}^{-1} \text{ d}^{-1}$)	O ₂ consumption ($\mu\text{gO}_2 \mu\text{g}^{-1} \text{ C d}^{-1}$)	Carcass-C turnover (% d^{-1})
	0-0.25 d	0.25-0.5 d	0.5-1 d				
Exp 1	1.66	2.13	5.13	8.92	7.43	0.70	57.9
Exp 2	0.27	0.58	1.97	2.82	2.35	0.22	18.3
Exp 3	2.66	4.05	7.63	14.34	11.95	1.12	93.2
			Mean	8.70	7.25	0.68	56.5
			S.D.	5.76	4.80	0.45	37.4

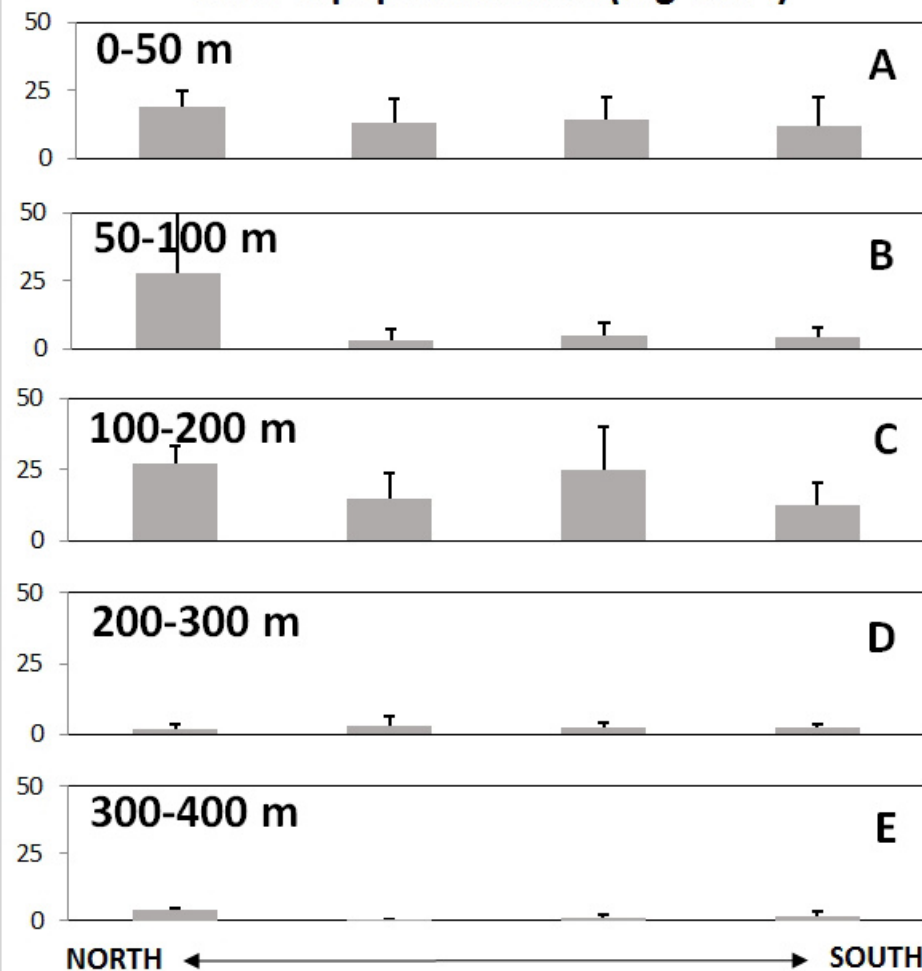
Table 3. Biological oxygen demand reported for Sargasso Sea and the nearby regions. Where necessary, published carbon respiration rates are converted to oxygen consumption rates assuming 1:1 C-to-O₂ molar ratio.

Depth (m)	Respiration ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ d}^{-1}$)	Note	Reference
20	$8.8\text{-}9.0 \times 10^3$	24-h incubation	Hansell et al. (1995)
0-75	9.8×10^4 in surface mixed layer; 8.2×10^4	BOD bottle incubation	Obernosterer et al. (2003)
200-1000	4.1×10^3	ETS method	Aristegui et al. (2005a)
Epipelagic	$6.4\text{-}9.7 \times 10^4$	Cited N. Navarro pers. comm.	Aristegui et al. (2005b)
Epipelagic	$8.9\text{-}13.6 \times 10^4$	Cited Duarte et al. (2001)	Aristegui et al. (2005b)
Mesopelagic (600 and 1000)	350 at 600 m; 80 at 1000 m	Dark bottle incubation + Winkler titration	Aristegui et al. (2005b)
0-100	$2\text{-}11 \times 10^4$	Mesoscale eddies; Winkler titration	Mourino-Carballido & McGillicuddy (2006)
0-400	17.5-73.1 (North-South) 18.5-116.5 (West-East)	Estimated carcass-driven respiration	This study

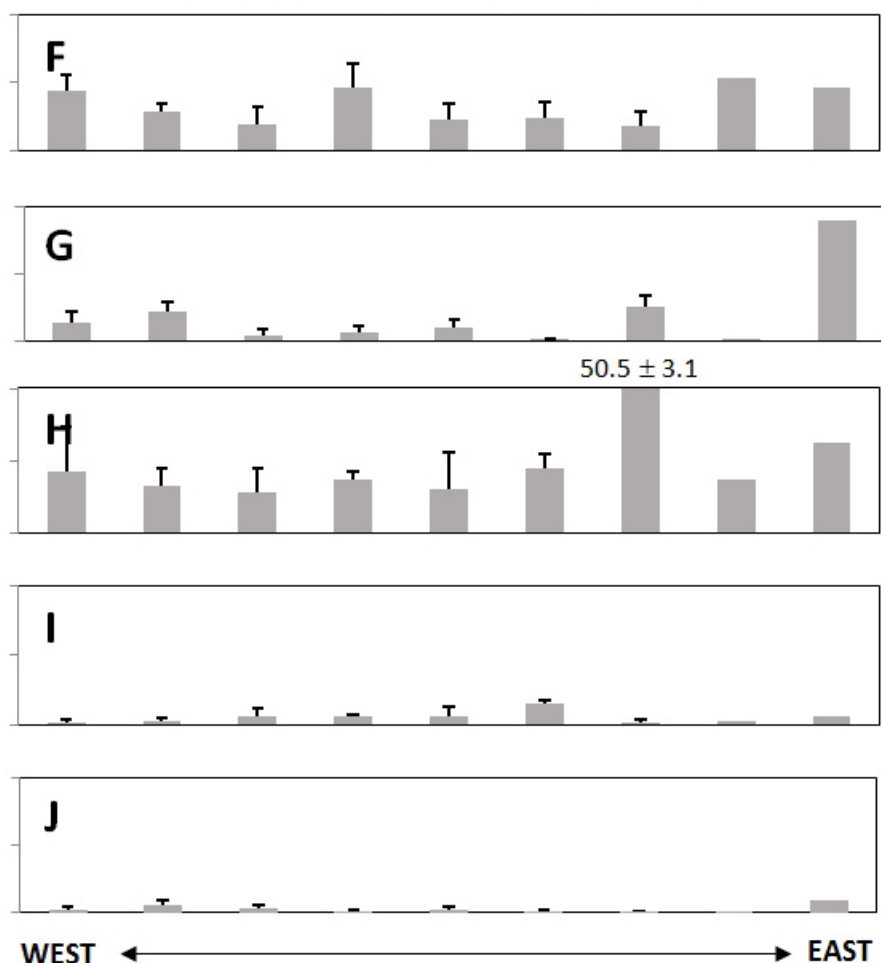




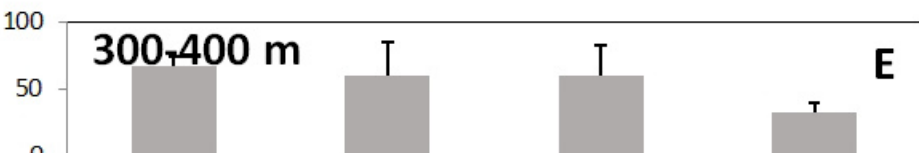
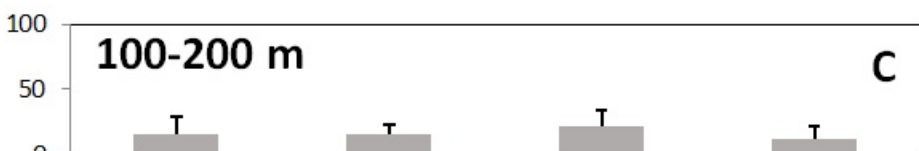
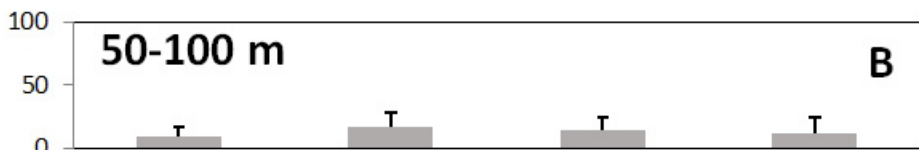
Total copepod biomass (mg C m⁻²)



Total copepod biomass (mg C m⁻²)

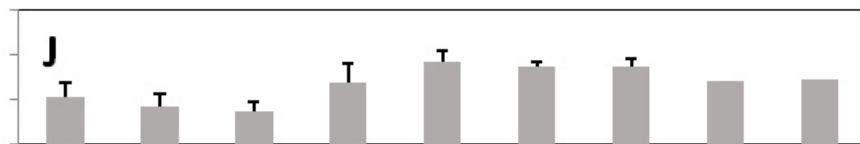
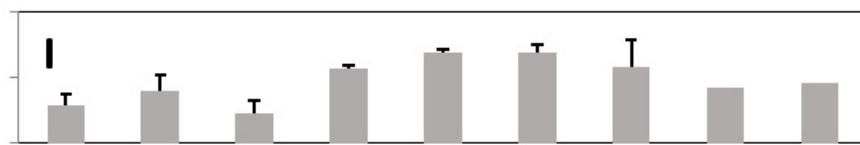
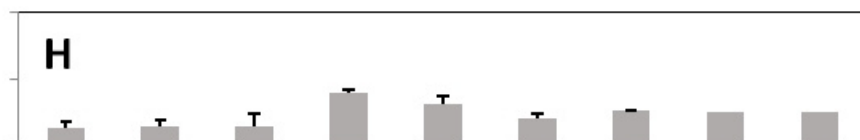
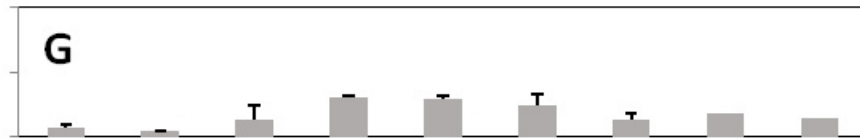
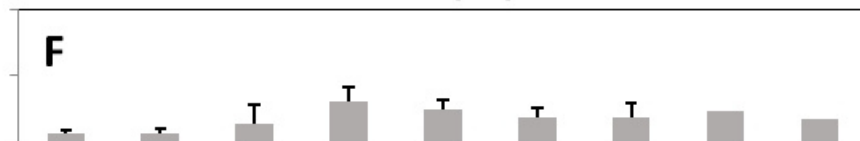


% dead copepods

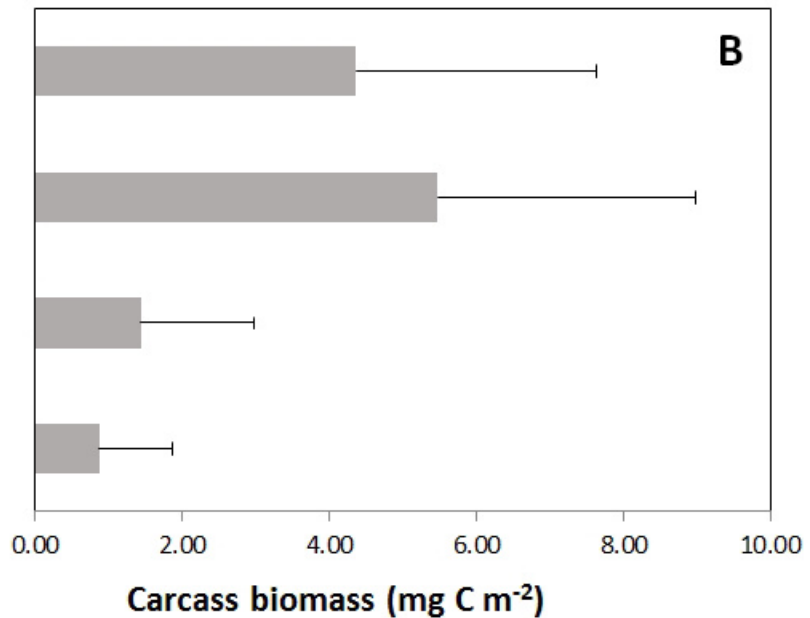
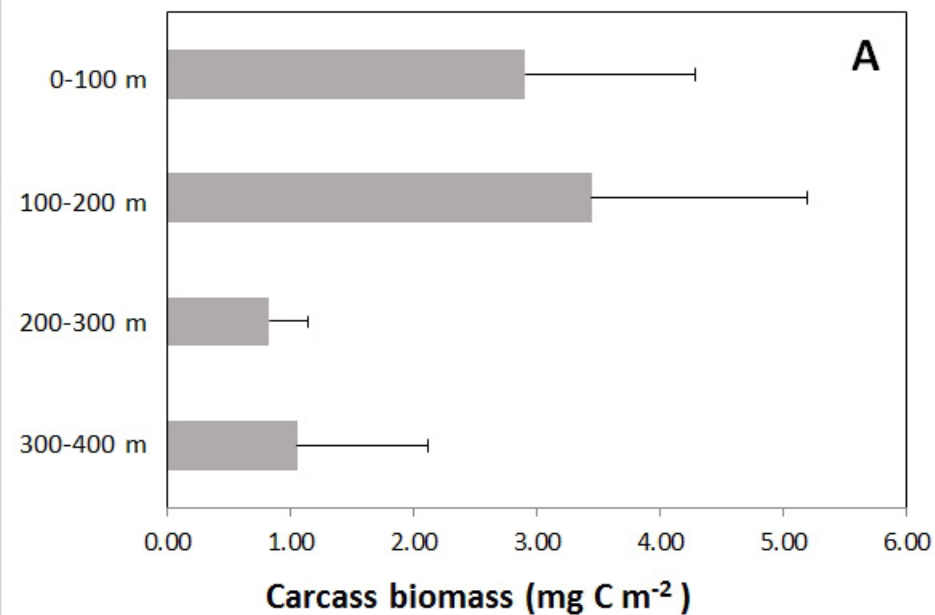


NORTH ← → SOUTH

% dead copepods



WEST ← → EAST



1 **SUPPLEMENTARY MATERIALS**

2

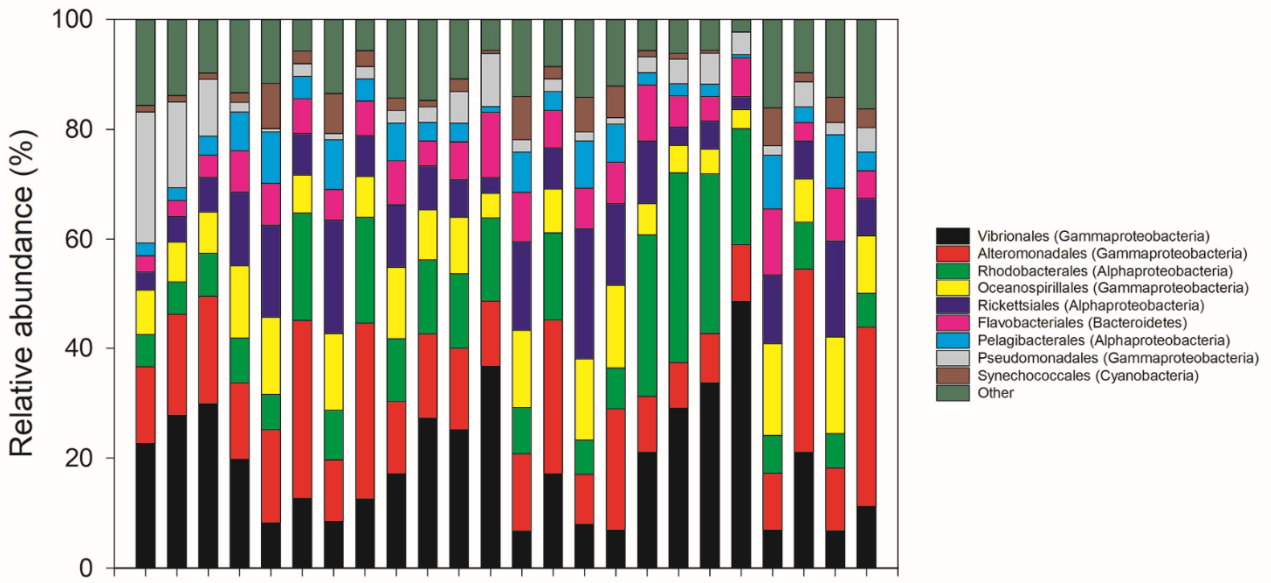
3 Table S1. SIMPER (similarity percentage) analysis showing the main operational taxonomic units
 4 (OTUs) explaining the dissimilarity between carcass-associated bacterial communities at 0 h and 24
 5 h of the three carcass decomposition experiments.

Experiment 1	Average relative abundance (%)	Average relative abundance (%)	Contribution to dissimilarity (%)
OTU closest relative	at t ₀	at t ₂₄	
Pseudomonadales	23.1	2.0	17.6
Rickettsiales	3.5	12.7	8.8
Pelagibacterales	2.4	7.1	5.8
Flavobacteriales	2.9	7.3	5.2
Thiotrichales	3.0	0.6	5.0
Oceanospirillales	7.7	13.2	4.5
Acidimicrobiales	0.7	2.7	4.0
Total	43.2	45.5	51.0
Experiment 2	Average relative abundance (%)	Average relative abundance (%)	Contribution to dissimilarity (%)
OTU closest relative	at t ₀	at t ₂₄	
Vibrionales	16.8	36.3	10.6
Rickettsiales	11.0	3.1	8.5
Pseudomonadales	2.8	9.5	7.8
Oceanospirillales	12.6	4.9	7.3
Pelagibacterales	7.2	1.8	7.3
Acidimicrobiales	2.8	0.5	5.5
Synechococcales	2.6	0.5	4.8
Total	55.6	56.6	52.0
Experiment 3	Average relative abundance (%)	Average relative abundance (%)	Contribution to dissimilarity (%)
OTU closest relative	at t ₀	at t ₂₄	
Vibrionales	20.6	46.3	22.4
Rickettsiales	11.2	2.2	18.3
Rhodobacterales	29.3	21.4	7.8
Pelagibacterales	2.7	1.0	6.1
Total	63.7	70.9	54.6

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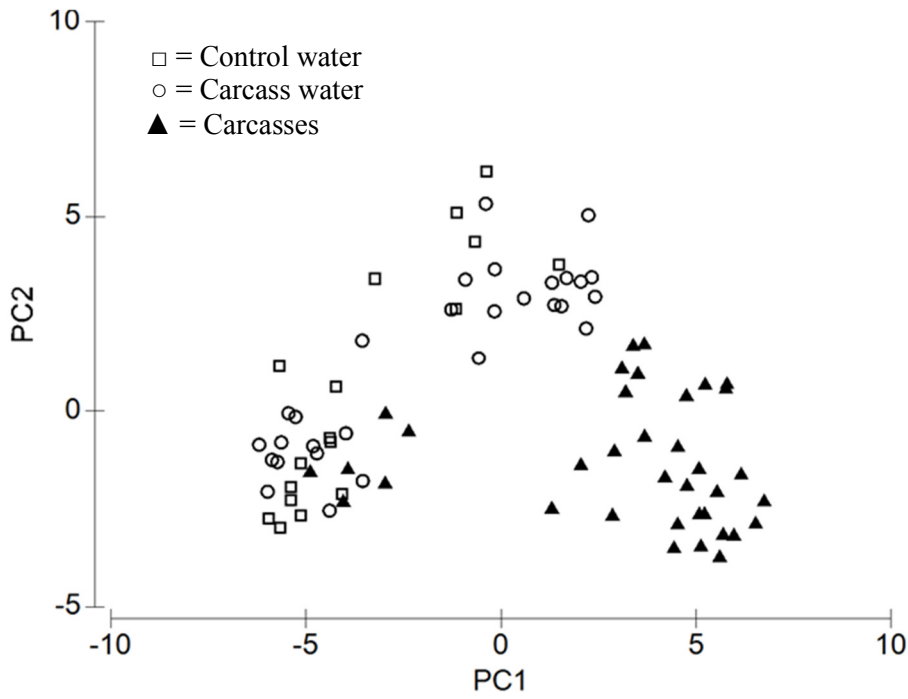
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10 Fig. S1. Relative bacterial abundance (class) expressed as % of total sequences obtained in Exp. 1,
11 2 and 3 for “carcass” (triplicates), “carcass water” (five replicates) and “control water” (triplicates).
12 “Other” includes taxa accounting for less than 0.3% of the relative abundance in a single sample.
13 Bars represent sequence reads pooled from replicate samples.

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15

16 Fig. S2. Bacterial community composition and succession in carcass decomposition experiments.

17 Principal coordinates comparison of carcass-associated (triangles) microbial community

18 composition and those in carcass water (circles) and control water (squares), where PC1 and PC2

19 explain 52.1 and 18.5 % variations, respectively.

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