

1 **High prey-predator size ratios and unselective feeding in**  
2 **copepods: a seasonal comparison of five species with**  
3 **contrasting feeding modes**

4 **ACCEPTED MANUSCRIPT**

5  
6  
7 **Nicolas Djeghri<sup>1</sup>, Angus Atkinson<sup>2\*</sup>, Elaine S. Fileman<sup>2</sup>, Rachel A. Harmer<sup>3</sup>,**  
8 **Claire E. Widdicombe<sup>2</sup>, Andrea J. McEvoy<sup>2</sup>, Louise Cornwell<sup>2</sup>, Daniel J. Mayor<sup>4</sup>**

9  
10  
11  
12 <sup>1</sup>Institut Universitaire Européen de la Mer, Rue Dumont d'Urville, 29280, Plouzané, France

13  
14 <sup>2</sup>Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth, PL1 3DH, United  
15 Kingdom

16  
17 <sup>3</sup>Institute of Hydrobiology and Fisheries Science, University of Hamburg, 22767 Hamburg,  
18 Germany

19  
20 <sup>4</sup>National Oceanography Centre, European Way, Southampton, SO14 3ZH, UK.

21  
22 \*Corresponding author: E-mail address [aat@pml.ac.uk](mailto:aat@pml.ac.uk)

25 Key words: Copepod; zooplankton biomass; feeding; selectivity; intraguild predation;  
26 predator-prey size ratio; Western Channel Observatory; sloppy feeding

27 **Abstract.**

28 There has been an upsurge of interest in trait-based approaches to zooplankton, modelling  
29 the seasonal changes in the feeding modes of zooplankton in relation to phytoplankton traits  
30 such as size or motility. We examined this link at two English Channel plankton monitoring  
31 sites south of Plymouth (L4 and E1). At L4 there was a general transition from diatoms in  
32 spring to motile microplankton in summer and autumn, but this was not mirrored in the  
33 succession of copepod feeding traits; for example the ambushing *Oithona similis* dominated  
34 during the spring diatom bloom. At nearby E1 we measured seasonality of food and grazers,  
35 finding strong variation between 2014 and 2015 but overall low mesozooplankton biomass  
36 (median 4.5 mg C m<sup>-3</sup>). We also made a seasonal grazing study of five copepods with  
37 contrasting feeding modes (*Calanus helgolandicus*, *Centropages typicus*, *Acartia clausi*,  
38 *Pseudocalanus elongatus* and *Oithona similis*), counting the larger prey items from the  
39 natural seston. All species of copepod fed on all food types and differences between their  
40 diets were only subtle; the overriding driver of diet was the composition of the prey field.  
41 Even the smaller copepods fed on copepod nauplii at significant rates, supporting previous  
42 suggestions of the importance of intra-guild predation. All copepods, including *O. similis*,  
43 were capable of tackling extremely long (>500 µm) diatom chains at clearance rates  
44 comparable to those on ciliates. Maximum observed prey:predator length ratios ranged from  
45 0.12 (*C. helgolandicus*) up to 0.52 (*O. similis*). Unselective feeding behaviour and the ability  
46 to remove highly elongated cells have implications for how copepod feeding is represented in  
47 ecological and biogeochemical models.

48

49

50

51

## 52 **1. Introduction**

53 Copepods play a central role in pelagic food webs. They form the link between  
54 microplankton and fish, and their feeding activities contribute to global biogeochemical  
55 cycles. Copepods can feed on a wide variety of food items, including phytoplankton,  
56 microzooplankton (Stoecker and Capuzzo, 1990; Calbet and Saiz, 2005), copepod eggs and  
57 nauplii (Boersma et al., 2014) and detritus (Roman, 1984; Iversen and Poulsen, 2007). Prey  
58 selection by copepods has been studied for decades (Brooks and Dodson, 1965; Steele and  
59 Frost, 1977) and recent studies (Kiørboe, 2011, 2016) have emphasised two broad types of  
60 feeding mechanisms: 1) ambush feeding, which is more effective on motile prey that alert  
61 predators to their presence via hydrodynamic disturbance; 2) more active feeding modes,  
62 such as cruise- and feeding-current feeding, thought to be more effective against non-motile  
63 prey that cannot detect and escape from the movement created by the copepod. The  
64 distinction between these modes is increasingly emphasised in “trait-based” modelling  
65 approaches (Kiørboe, 2011; Mariani et al., 2013; Litchman et al., 2013; Salliey et al., 2015;  
66 Kenitz et al., 2017), with implications for ecosystem function.

67 Alongside prey motility, prey size is considered to be a “master trait” for understanding  
68 food web dynamics, and an increasing number of studies are exploring the inter-relationships  
69 between size and feeding modes in predator-prey interactions (e.g. Fuchs and Franks, 2010;  
70 Wirtz, 2012; Visser and Fiksen, 2013; Kiørboe, 2016; Stamiesszkin et al., 2017). The  
71 component of the available prey size spectrum that is accessible to a predator, and the rate  
72 at which it can be ingested, can be represented numerically by a kernel function (Fuchs and  
73 Franks, 2010; Wirtz, 2014). These are important for modelling, but quantifying them is  
74 problematic, particularly when using data from grazing experiments in which predators are  
75 fed artificial prey assemblages that do not reflect the diversity of their normal prey (Wirtz,  
76 2014). Furthermore the size-based view of feeding is confounded by the other factors such  
77 as food motility, nutritional quality (e.g. essential fatty acid content), or stoichiometry, all of

78 which influence selection and in turn growth and egg production (Koski et al., 2010).

79         These interacting factors affecting selectivity are one reason for seemingly  
80 contradictory findings on the prey preferences of individual species derived from field  
81 experiments. For example, ecologically important copepods such as *Oithona similis* and  
82 *Calanus* spp. have been reported to select motile prey (Castellani et al., 2008; Zamora-Terol  
83 et al., 2013), non-motile prey (Hopkins, 1987; Atkinson, 1996), or show no clear feeding  
84 preference (Mayor et al., 2006, 2009). Differences in experimental methods further confuse  
85 the picture, making it problematic to parameterise zooplankton feeding in models (Mitra et al.,  
86 2014). This highlights the need for methodologically consistent studies that compare  
87 copepods with ambush and active feeding modes across the naturally occurring spectrum of  
88 food types.

89         Here we present data from copepod grazing experiments in which five biomass-  
90 dominant copepod taxa were fed natural prey assemblages. These species contrast both in  
91 size and feeding mode (Benedetti et al., 2016) and are well studied; Table 1 summarises  
92 some of the more recent work. We performed food removal experiments throughout one year  
93 from a stratifying shelf site to assess how copepod feeding behaviour differs according to  
94 feeding mode and the prey assemblage offered. Recent work near the site (Sailley et al.,  
95 2015; Kenitz et al., 2017) provides a central hypothesis: that seasonal changes in prey  
96 motility influence the feeding traits displayed by copepods. We examine firstly whether the  
97 classic pattern of succession from non-motile towards motile protists exists in our study area,  
98 and secondly, whether this leads to a seasonal pattern in copepods with feeding types that  
99 reflect their optimum prey motility, and thirdly, whether selectivity differs substantially between  
100 species. We focused attention on the large food items which also allowed us to examine  
101 maximum prey:predator ratios and the incidence of feeding on copepod nauplii.

## 102 **2. Material and Methods**

### 103 **2.1 Western Channel Observatory study location**

104 This study was made at a pair of neighbouring sites in the English Channel forming  
105 the “Western Channel Observatory” <http://www.westernchannelobservatory.org.uk/> (Smyth et  
106 al., 2015, Fig. 1). These seasonally stratifying sites have been sampled intermittently since  
107 1903 (Southward et al., 2005) and have comparable spring and autumn bloom dynamics.  
108 The most intensively sampled is L4, which is closest inshore (13 km from Plymouth) in ~54 m  
109 water depth. It has been visited weekly (weather permitting) since 1988 and is subject to a  
110 comprehensive suite of planktonic measurements.

111 The offshore site, E1, is 27 km further out in ~75 m water depth and sampled less  
112 regularly. This was selected as the main location for the present experimental study because,  
113 being further offshore and less subject to coastal influences, it forms a clearer comparison to  
114 the dynamics of other open shelf sites described within this Special Issue (Giering et al., in  
115 review). However, to test our hypothesis on seasonal succession we have used the much  
116 longer time series from nearby L4, which comprises sufficient sampling time points to provide  
117 robust generalisations.

## 118 **2.2 Micro- and mesozooplankton seasonality at E1 and L4**

119 The seasonal plankton cycle at site E1 has been estimated with near-monthly  
120 sampling during 2014 and 2015 (Fig. 2), while longer-term context has been provided by  
121 weekly sampling at site L4 from 1988—2015 (Fig. 3). Microplankton biomass data from both  
122 sites is based on CTD Niskin bottle water samples from 10m depth. This is within the upper  
123 mixed layer when a thermocline is present; typically from May to September.

124 At each sampling time-point from E1 and L4, an unfiltered 200 mL water sample was  
125 immediately preserved in acid Lugol’s iodine (2 % final concentration) for the subsequent  
126 enumeration of phyto- and microzooplankton species. A second 200 mL subsample was also  
127 preserved in neutral formaldehyde (1 % final concentration) for the enumeration of  
128 coccolithophore species. Cell counts were conducted following the European Standard  
129 protocol (EN 15204) “Water quality – Guidance standard on the enumeration of

130 phytoplankton using inverted microscopy” (Utermöhl, 1958) technique. Specifically, between  
131 50 mL and 100 mL sub-samples were settled and on average 897 cells were identified and  
132 enumerated in each weekly sample from L4; similar numbers of cells were counted from E1.  
133 This exceeds the abovementioned (EN 15204) protocol’s recommended limit of 400 cells to  
134 be counted for mixed natural samples to obtain a 95% confidence limit. Because of the high  
135 diversity in natural populations it is not possible (or recommended) to count 400 individuals  
136 for each species. Median abundance values for diatoms, dinoflagellates, ciliates,  
137 coccolithophores, flagellates from L4 were 17 mL<sup>-1</sup>, 17 mL<sup>-1</sup>, 5 mL<sup>-1</sup>, 10 mL<sup>-1</sup>, 1993 mL<sup>-1</sup>  
138 respectively. Further details of the light microscopy are provided in Widdicombe et al.,  
139 (2010). Cell biovolumes for each taxon were calculated assuming appropriate geometric  
140 shapes according to Kovalá and Larrance (1966) using average cell length, width and depth  
141 measurements of 10-50 individual cells. Carbon conversions were made using the  
142 conversions of Menden-Deuer and Lessard (2000). Median biomass values for diatoms,  
143 dinoflagellates, ciliates, coccolithophores, flagellates were 2.33 mgC m<sup>-3</sup>, 5.95 mgC m<sup>-3</sup>, 3.18  
144 mgC m<sup>-3</sup>, 0.18 mgC m<sup>-3</sup>, 11.48 mgC m<sup>-3</sup> respectively. Nauplii were under-sampled by the 200  
145 µm net and too rare in the Lugols volumes settled. Their biomass was derived from larger  
146 volume (2 L) water samples from 4 depths (surface, 10m, 25m and 50m) with the CTD.  
147 These were first pre-screened through 300 µm mesh, concentrated by reverse filtration and  
148 analysed on flowCAM to determine naupliar abundances and lengths. These lengths were  
149 then converted to biomass via the length-mass relationships in Supplementary Table 1.

150 Mesozooplankton were collected using a series of vertical net hauls with a UNESCO  
151 (1968) standard WP2 nets (57 cm diameter, 200 µm mesh) from either 70 m (E1) or from 50  
152 m depth (L4) to the surface at 0.2 m sec<sup>-1</sup>. Two net hauls from each site were preserved in 4  
153 % formalin for microscopic analysis, and one additional haul from E1 was filtered onto a 10  
154 cm square of 200 µm gauze and frozen on board for bulk zooplankton biomass estimates.  
155 Mesozooplankton from the formalin-preserved vertical net hauls were enumerated and  
156 identified by microscopy as detailed in Atkinson et al. (2015). Two sub-samples of different

157 size were analysed per sample. The smaller one was extracted with a Stempel pipette for the  
158 numerous taxa (including the 5 copepod species examined in this study). Typical subsamples  
159 ranged from 1-10ml from the 300 ml original sample. A second, larger aliquot was analysed  
160 for rarer and large taxa, typically either 12.5%, 25% or 50%. The number of copepods  
161 (excluding nauplii) counted in each weekly sub-sample ranged from 70 to 300 individuals,  
162 with a median of 194. Abundances across the two hauls were averaged and numbers  
163 expressed as individuals per m<sup>3</sup> allowing for a 95% net efficiency (UNESCO, 1968).

164 To estimate mesozooplankton carbon biomass from the abundance data we  
165 measured 3780 individuals of the more common taxa collected from L4 throughout the 2015  
166 season. Taxon-specific length-mass conversion factors obtained from the literature were  
167 applied to the seasonal lengths derived separately for the periods spring (March to May),  
168 summer (June to August), autumn (September to November) and winter (December to  
169 February). Supplementary Table 1 lists the source references for these conversion factors.  
170 We also obtained dry mass and carbon masses directly from bulk net catches from E1 during  
171 2014 and 2015. This provided an independent check on the method based on length-mass  
172 conversions described above. Frozen samples were defrosted, dried for 5 days at 60°C until  
173 reaching constant weight, removed from the oven and placed in a desiccator to weigh for dry  
174 mass, prior to CHN analysis of subsamples. For each sample the plankton was removed  
175 from the gauze, homogenised and four replicates weighed out for analysis using a  
176 Thermoquest FlashEA 1112 elemental analyser.

### 177 **2.3 Feeding experiments**

178 In total 11 experiments were run at E1, spanning March 2014 to March 2015. The  
179 complete experimental setup is summarised in Table 2 and the environmental conditions in  
180 Table 3. Sampling was conducted between mid-morning and midday on each visit, and  
181 comprised of first a CTD profile and collection of incubation water. This was collected from 10  
182 m depth and was gently drained from the 10m Niskin bottles into a large acid washed and

183 rinsed carboy via silicon tubing through a submerged 200 µm mesh bag, to exclude larger  
184 grazers. This water was kept cool and in darkness until return to the Plymouth laboratory  
185 within 3 hours of collection. It was then left overnight in the dark at ambient E1 surface  
186 temperature.

187           After the water collection, 0-70 m WP2 net hauls were used to collect zooplankton.  
188 The cod end contents were placed in lidded 5 L containers, topped up with surface seawater  
189 and maintained in a flowing water bath while in transit to the laboratory. Immediately on  
190 return to the laboratory, actively swimming representatives of the most common copepods  
191 were picked out. They were transferred to 0.2 µm filtered seawater and then left overnight to  
192 acclimate. In total, adult females of six species were incubated; *Oithona similis*, *Acartia*  
193 *clausi*, *Pseudocalanus elongatus*, *Centropages typicus*, *Calanus helgolandicus*, and *C.*  
194 *finmarchicus*, as well as *Calanus* spp. CV. Most of these *Calanus* incubations were with the  
195 dominant species *C. helgolandicus* (Table 2). However, all results for this genus are  
196 presented together simply as “*Calanus* spp”. because the two species and stages are of  
197 similar size and feeding types,

198           On the morning after sampling the incubation water was gently mixed and used to fill  
199 3 glass control bottles of 1.2 L and between 1 and 3 bottles of 0.6 L or 1.2 L, according to  
200 copepod size and availability (Table 2). The experimental animals were then checked and  
201 those that were intact and actively swimming were added to the bottles. Each bottle was  
202 spiked with ammonium chloride ( $15 \mu\text{mol L}^{-1} \text{NH}_4\text{Cl}$ ) and disodium hydrogen phosphate ( $1$   
203  $\mu\text{mol L}^{-1} \text{Na}_2\text{HPO}_4$ ), in order to counter potential artefacts arising from grazer excretion  
204 enhancing specific rates of prey growth in the grazed bottles (Båmstedt et al., 2000). All  
205 bottles were then filled to the top with mixed incubation water and sealed with Parafilm to  
206 exclude air bubbles. At  $T_{\text{zero}}$ , between 1 and 3 (according to the remaining E1 water volume)  
207 500 mL sub-samples were taken from the remaining incubation water and fixed in acid  
208 Lugol's iodine solution (2% final concentration). All experimental bottles were then incubated  
209 for 24 h on a plankton wheel ( $0.5 \text{ revolutions min}^{-1}$ ) in the laboratory maintained at ambient

210 E1 temperature and light conditions. Lighting was at estimated average ambient E1 10 m  
211 intensity and switched off at dusk and on at dawn.

212         After 24 h the copepods were first checked for mortality and then 450-500 mL from  
213 each bottle was fixed in acid Lugol's solution (2% final concentration) for microplankton  
214 community analysis. As an ongoing check on particle removal during the experiments (in  
215 order to adjust stocking densities if necessary between experiments) an additional 150 ml  
216 subsample from each bottle was filtered onto a GF/F filter and extracted in 90% aqueous  
217 acetone. This allowed fluorometric analysis to determine chlorophyll *a* (chl *a*) concentrations  
218 and the reduction in chl *a* due to grazing (Table 2). Removal of the copepods from the  
219 incubations for species verification was either by pipette from the abovementioned water  
220 sub-samples or by sieving them out of the remaining incubation water.

#### 221 **2.4 Analysis of feeding experiments**

222         Copepod feeding-induced changes within the microplankton community were  
223 estimated by comparing the abundance of large phytoplankton and microzooplankton among  
224 the treatments with and without added copepods. Because direct microscope counting of  
225 prey taxa is time consuming, we have channelled our resources into the larger end of their  
226 food size spectrum. This is because firstly, the rarity of these cells means that they are  
227 seldom enumerated in feeding studies, raising questions on the upper size limit of ingestable  
228 food (Kiørboe, 2016). Second, large prey are less prone to bottle incubation-induced "food  
229 chain effects" than the smaller cells (Båmstedt et al., 2000). These large cells are rarer so the  
230 lugols-preserved 450-500 ml sub-samples were concentrated by first passing the sample  
231 through a 63 µm mesh. The particles collected on the mesh were then washed into a  
232 counting chamber and examined and counted at x200 magnification using an Olympus IMT-2  
233 inverted microscope.

234         All ciliates, dinoflagellates, diatoms and nauplii > 32 µm in length were enumerated.  
235 Four taxonomic groups of prey were identified: diatoms, ciliates, dinoflagellates and nauplii.

236 Five size classes were used: 32 - 95  $\mu\text{m}$ , 95 - 220  $\mu\text{m}$ , 220 - 346  $\mu\text{m}$ , 346 - 472  $\mu\text{m}$  and 472 -  
237 598  $\mu\text{m}$ . Nauplii sizes ranged from 50 - 390  $\mu\text{m}$  but were not sufficiently numerous to be  
238 divided into different size classes. We acknowledge that the counted abundances of the  
239 larger and smaller end of this range are likely underestimates of their natural abundances  
240 because we screened the pre- and post-experimental seawater through 200 and 63  $\mu\text{m}$   
241 meshes, respectively. Our calculated total ingestion rates within the above size range are  
242 thus minimum estimates. However, we contend that since identical 63  $\mu\text{m}$  screening methods  
243 were used for all bottles, our clearance rate values on the 32-95  $\mu\text{m}$  spectrum are robust,  
244 with particles smaller than the screen size being retained due to their elongation.

## 245 **2.5 Calculation of feeding rates**

246 For consistency with previous studies of grazing in the Western English Channel  
247 (Fileman et al., 2010, 2014), clearance rates ( $\text{ml copepod}^{-1} \text{d}^{-1}$ ) for diatoms, ciliates and  
248 dinoflagellates were calculated according to Frost's (1972) equations incorporating the prey  
249 growth term:

$$250 \quad F = [\ln(C_{\text{cont}} / C_0) - \ln(C_{\text{exp}} / C_0)] \times (V / (n \times t)) \quad (1)$$

251 where  $C_{\text{exp}}$ ,  $C_{\text{cont}}$  and  $C_0$ , are respectively, the concentration ( $\text{prey. mL}^{-1}$ ) in the final  
252 experimental bottles, in the final control bottles and in the initial bottles.  $V$  is the volume of  
253 experimental bottles (ml),  $n$  the number of copepods in the incubation and  $t$  is the incubation  
254 duration in days. Following Fileman et al. (2014), we chose a threshold mean of 25 food  
255 items for each counted category (i.e. based on taxa and size-class), based on mean  
256 numbers counted in each of the final control bottles. If values for a food item were below this,  
257 then the results are not presented for the experiment. Rare instances where no cells were  
258 counted in the grazed bottles were likewise excluded, as these would provide infinite  
259 clearance rates.

260 Concentrations of nauplii tended to be low in the initial samples and higher in the final  
261 controls, likely due to hatching of eggs and the absence of predators in the control bottles.

262 Because low count numbers in the initial samples would introduce imprecision into the  
263 clearance rate calculations, we used the clearance rate equation in Båmstedt et al. (2000):

$$264 \quad F = \ln(C_{\text{cont}} / C_{\text{exp}}) \times (V / (n \times t)) \quad (2)$$

265 To calculate ingestion rates, the carbon contents for protistan preys were first  
266 calculated from the conversion factors given by Menden-Deuer and Lessard (2000)  
267 assuming appropriate geometric shapes (Kovalá and Larrance, 1966). For nauplii the lengths  
268 were measured and carbon contents were estimated from morphometric relationships.  
269 Average food concentrations in each bottle  $[C]$  were calculated according to the equation of  
270 Conover (1978), as presented in Båmstedt et al. (2000):

$$271 \quad [C] = C_0 \times (1 - e^g) \times (-g) \quad (3)$$

272 where  $g = \ln(C_{\text{exp}} / C_0)$  for experimental bottles and  $C_{\text{exp}}$ ,  $C_{\text{cont}}$  and  $C_0$ , are respectively,  
273 the concentration in carbon mass ( $\mu\text{g C mL}^{-1}$ ) in the final experimental bottles, in the final  
274 control bottles and in the initial bottles. In some instances there were more cells counted in  
275 the final experimental bottles than in the final controls. Those data were set to zero for  
276 calculations of average concentration and thence ingestion rate but are shown as negative in  
277 all calculations of clearance rates.

278 From these data ingestion rates ( $I$ ) were estimated using:

$$279 \quad I = F \times [C] \quad (4)$$

280 Selective feeding was evaluated using the electivity index  $E_i^*$  (Vanderploeg and  
281 Scavia, 1979) as follows:

$$282 \quad E_i^* = [(W_i - 1) / k] / [(W_i + 1) / k] \quad (5)$$

283 where  $k$  is the total number of prey types in a given experiment and  $W_i$  is defined as:

$$284 \quad W_i = F_i / \sum F_i \quad (6)$$

285  $F_i$  is the clearance rate on the  $i^{\text{th}}$  type of food and  $\Sigma F_i$  is the sum of clearance rates of all food  
286 types. The value of this index ranges from 1 to -1, positive values indicating selection and  
287 negative values indicating avoidance.

288

### 289 **3. Results**

#### 290 **3.1 Seasonality at E1 during 2015 and 2016**

291 Our experimental period at E1 spanned March 2014 to March 2015, while the nano-  
292 microplankton seasonality was also sampled throughout the rest of 2015 (Fig. 2). The nano-  
293 microplankton biomass at 10 m depth ranged from  $\sim 10 \text{ mg C m}^{-3}$  in winter to  $\sim 250 \text{ mg C m}^{-3}$   
294 in spring, and was typically dominated by small (2-6  $\mu\text{m}$ ) nanoflagellates. Both 2014 and  
295 2015 (and particularly the latter) diverged from the long-term average (Fig. 3), which supports  
296 the hypothesised succession of diatoms in the spring to dinoflagellates after the onset of  
297 seasonal thermal stratification (Widdicombe et al., 2010). Three diatoms blooms occurred in  
298 2014, one in spring (April-May), the second two in autumn (September and October). By  
299 contrast 2015 had no clear spring bloom but instead showed major autumn blooms  
300 dominated by autotrophic dinoflagellates.

301 Mesozooplankton abundance varied from  $276 \text{ ind. m}^{-3}$  to  $3744 \text{ ind. m}^{-3}$ , with an  
302 average of  $1490 \text{ ind. m}^{-3}$ . Our estimates of their seasonal median biomass based on length-  
303 mass relationships was  $4.5 \text{ mg.C m}^{-3}$ ; similar to the value of  $5.4 \text{ mg.C m}^{-3}$  based on CHN  
304 analysis of the bulk samples (Table 3). However, maximum values from bulk CHN analysis  
305 are unrealistically high, due to clogging of the  $200 \mu\text{m}$  nets with diatoms. Notwithstanding  
306 these uncertainties of determining biomass, either with length-mass relationships or with  
307 CHN, both methods agree that the values at E1 were noticeably less than at other English  
308 Channel/Celtic Sea sites sampled over the same time period (Table 4, see also Giering et al.,  
309 in review, this volume).

310 Mesozooplankton biomass was dominated by copepods (mean of 75 % of the total;  
311 Fig. 2c), and was not correlated with microplankton biomass (Linear regression,  $p = 0.34$ ).  
312 The 5 copepod taxa studied here represented, on average, 46 % of the total copepod  
313 biomass (Fig. 2d, Table 3).

### 314 **3.2 Average plankton seasonality at L4**

315 The long term average picture (Fig. 3) reveals the highest proportion of diatoms from  
316 March to June, with an increased proportion of motile cells thereafter. However, there is  
317 substantial inter-annual variation in plankton composition and phenology at this site (Atkinson  
318 et al., 2015). For example diatoms can bloom in autumn and ciliates also increase sharply in  
319 spring, and nanoflagellates persist at substantial levels throughout the season (Widdicombe  
320 et al., 2010; Atkinson et al., 2015).

321 The L4 and E1 time series do not provide strong support for the hypothesis (Sailley et  
322 al., 2013; Kenitz et al., 2017) that the seasonality of copepods is congruent with their feeding  
323 traits (i.e. that suspension feeders appear during the time of diatom blooms and ambush  
324 feeders appear when motile cells are most abundant). In accordance with this hypothesis,  
325 *Pseudocalanus elongatus* peaks during the spring diatom bloom whereas the more  
326 carnivorous *Centropages typicus* peaks in September, when its preferred motile prey is most  
327 abundant. By contrast, both the elevated abundance of ambush *Oithona similis* in spring and  
328 the summer abundance maximum of *Calanus* spp. are counter to the hypothesised  
329 relationship between prey motility and the predominant copepod feeding mode.

### 330 **3.3 Copepod feeding experiments: prey composition and potential for artefacts**

331 The larger prey studied in our experiments (nauplii excluded) ranged from 0.32-46%  
332 (median 2.8%) of the total microplankton biomass (Table 3), so given these low values we  
333 have not expressed our results in terms of total daily ration estimates. Ciliates and  
334 dinoflagellates comprised the smaller end of this large food spectrum, with the majority of  
335 ciliates belonging to the genera *Strombidium* spp., *Mesodinium* sp, and *Askenasia* sp. and

336 dinoflagellates consisting mainly of *Gyrodinium spp.*, *Dinophysis spp.* and *Protoperidinium*  
337 *spp.* Some larger ciliates and dinoflagellates were observed (e.g. *Ceratium spp.*) but they  
338 were never above our counting threshold for inclusion in calculations. Diatoms were the only  
339 prey category occurring across all our size-classes. These were mainly composed of large,  
340 elongated chain-forming diatoms such as *Rhizosolenia spp.* Their size categories refer to the  
341 chains lengths, not the individual cells. The concentrations of prey items sufficiently  
342 numerous to provide clearance rates are presented in [Supplementary Fig. 1](#).

343 The percentage removal of total chl *a* in our incubations was relatively low overall  
344 ([Table 2](#)), possibly reflecting the finding that some of the chl *a* resides within cells that are too  
345 small to be eaten. However in two of the incubations (of *Calanus* and *Oithona* in experiment  
346 4) the removal exceeded 50%. These two incubations are not presented here, due to their  
347 potential for unrealistic indications of grazing dynamics (Båmstedt et al., 2000). The median  
348 reduction of other cells was substantially greater, ranging from 25-41% ([Table 2](#)) and  
349 reflecting the high rates of removal of the largest cells.

### 350 **3.4 Copepod feeding selectivity**

351 For the large particle fraction examined, [Fig. 4](#) summarises the contribution of prey  
352 types to the available food and to the diets of the 5 copepod species. The available food  
353 varied greatly throughout the experiments with variable biomass dominance of long diatoms,  
354 ciliates or nauplii. The main feature of [Fig. 4](#) is that the diet of the species broadly reflected  
355 the composition of the available food, in other words the seasonal variation in prey field had  
356 a much clearer effect on diet than the identity of the grazer.

357 The estimated rates at which the five copepod species cleared each of the identified  
358 prey items are presented in detail in [Supplementary Fig. 2](#). Maximal significant clearance  
359 rates varied from 31 mL cop<sup>-1</sup> d<sup>-1</sup> for *Oithona similis* to 523 mL cop<sup>-1</sup> d<sup>-1</sup> for *Calanus spp.*  
360 These species tended to clear diatoms at the highest rates, with the exception of  
361 *Centropages typicus*, whose maximal clearance rates were on ciliates. For *Acartia clausi*,

362 *Oithona similis* and *Centropages typicus*, clearance rates on diatoms tended to be higher  
363 when the prey was large.

364 The feeding preferences of the 5 copepods are presented for each predator-prey  
365 combination in terms of electivity indices (Supplementary Fig. 3), and summarised by  
366 comparing the proportional contribution of available and ingested prey in each experiment  
367 (Fig. 5). The overall pattern was for predominantly unselective feeding, with copepod dietary  
368 composition tending to be proportional to prey availability. However, instances of significant,  
369 positive selection (t-test  $p < 0.05$ ) for both motile (dinoflagellates, ciliates or nauplii) and non-  
370 motile (diatoms) prey were identified (Supplementary Fig. 3). *Acartia clausi*, *Oithona similis*  
371 and *Centropages typicus* all showed a preference for ciliates and their selectivity towards  
372 diatoms typically increased as a function of cell size (Supplementary Fig. 3). These  
373 tendencies were less apparent in *Calanus* spp. and *Pseudocalanus elongatus*, both of which  
374 displayed instances both of positive and negative selection towards ciliates and diatoms.

375 Fig. 6 provides a summary overview of the differences in selectivity among the species.  
376 Overall, the contribution of non-motile cells (i.e. diatoms) to diets decreased from *Calanus*  
377 spp. (94%), *Pseudocalanus elongatus* (91 %), *Acartia clausi* (62 %), *Oithona similis* (57%),  
378 *Centropages typicus* (39 %) (Fig. 6a). However an ANOVA failed to identify significant ( $p <$   
379 0.05) inter-species differences, supporting the view depicted in Fig. 4 of a degree of  
380 unselective feeding, such that the diet strongly reflected the food composition offered. Fig. 6b  
381 shows that, for the prey cells enumerated, the maximum prey/predator length ratio ranged  
382 from 0.14 to 0.51. The order of species along this spectrum was similar to the contribution of  
383 non- motile diatoms to the diet (Fig. 6a); for example the suspension feeders *Pseudocalanus*  
384 *elongatus* and *Calanus* spp. had the lower maximum prey/predator ratio and the ambushing  
385 *Oithona similis* the highest ratio.

#### 386 4. Discussion

387 In combination, our findings provide little support for a clear, predictable seasonal  
388 succession of traits displayed by copepods in relation to their microplankton prey. First, we  
389 found highly variable patterns of plankton succession between years, with no clear link  
390 between the seasonality of ambush or feeding current copepods and the respective motile or  
391 non-motile preys. Second, we found reduced selectivity but considerable dietary diversity,  
392 including very high maximum prey sizes and ingestion of copepod nauplii. In combination,  
393 these factors blur the hypothesised coupling between microplankton motility and copepod  
394 feeding selectivity (Mariani et al., 2013; Sailley et al., 2015; Kenitz et al., 2017). Below we  
395 discuss our main feeding results, namely reduced feeding selectivity of copepods, their ability  
396 to eat or fragment even very large diatoms and the role of intra-guild predation.

#### 397 **4.1. Selection for motile and non-motile cells**

398 Ambush-feeding copepods such as *Oithona similis* locate their prey by detecting  
399 hydro mechanical signals, suggesting that they are best suited to catching motile prey  
400 (Paffenhöfer, 1993; Kiørboe, 2011). Conversely, those that can create feeding currents, such  
401 as *Calanus helgolandicus*, are considered to be more suited to catching the non-motile prey  
402 that cannot detect and escape from these currents. Our data broadly support these  
403 assertions, since the diet of *Oithona similis* contained the highest proportion of motile prey,  
404 and that of *Calanus* spp. contained the lowest (Fig. 6 a). However, both species also  
405 displayed statistically significant preference towards ciliates at times and conversely, all five  
406 species of copepods showed at least one significant instance of preference for diatoms in the  
407 experiments. Overall the diets were diverse, reflecting the composition of the available food  
408 (Figs. 4, 5). Our results thus provide only partial support for the generalisation that ambush  
409 feeders select for motile cells while more active feeding modes select for non-motile cells, so  
410 we investigate this further using the example of *Oithona similis*.

411 Previous studies have also reported the ingestion of diatoms by *Oithona similis*  
412 (Hopkins, 1987; Atkinson, 1996; Castellani et al., 2008), confirming that these ambush-

413 feeders are indeed capable of detecting and ingesting non-motile cells. Their positive  
414 selection for diatoms >300  $\mu\text{m}$  in length is consistent with the physics of fluid disturbance;  
415 *Oithona similis* is expected to be able to detect sinking, immobile phytoplankton cells  $\geq 80$   
416  $\mu\text{m}$  in diameter (Kjørboe and Visser, 1999). We therefore speculate that small, ambush-  
417 feeding copepods such as *Oithona* spp. have a bimodal distribution of clearance rates in  
418 relation to prey size, with the smaller peak reflecting the ingestion of motile prey that is not  
419 large enough to escape from the ambusher, and the larger peak occurring where larger, non-  
420 motile cells become detectable (e.g. Experiment 5 in [Supplementary Fig. 2](#)). Notwithstanding  
421 the mechanisms involved, the example of *Oithona* removing large diatoms will contribute to a  
422 blurring of the selectivity and enhance the generalist feeding abilities of copepods.

423         How does our suggestion of limited food selectivity fit with a multitude of studies  
424 showing clear selective abilities? Perhaps the method used is critical here, because the large  
425 majority of studies that find, like us, a degree of unselective feeding with respect to motility  
426 have all used the prey removal method in incubations with natural seston (e.g. Poulet, 1978;  
427 Huntley, 1981; Atkinson, 1995; Mayor et al., 2006; Castellani et al., 2008; Isari et al., 2013).  
428 This contrasts strongly with reductionist-type studies which, by offering formulated diets  
429 under controlled conditions, have indicated the presence of particle selection on the basis of  
430 motility, taste etc. (e.g. Marshall, 1973; Conover, 1978; Strickler, 1982). These conflicting  
431 findings may arise partly from differences in prey abundances; copepods feeding on highly  
432 diverse, but much diluted prey in the natural world cannot afford or do not need to be too  
433 selective.

434         This discrepancy raises some important issues for modelling zooplankton feeding.  
435 Trait-based models, for example, provide a mechanistic basis for understanding predator-  
436 prey interactions. They can address mechanisms behind the succession of zooplankton  
437 feeding mode and prey motility (Mariani et al. 2013; Sailley et al. 2015; Kenitz et al. 2017),  
438 and have provided the central hypothesis for this present study. However zooplankton  
439 feeding can also be interpreted and modelled in other ways, for instance according to prey

440 size or stoichiometry (e.g. Fuchs and Franks, 2010; Wirtz, 2012, 2014; Mitra et al., 2014;  
441 Stamieszkin et al., 2017). This makes it important to determine the degree of food selectivity  
442 that zooplankton show within natural food assemblages.

#### 443 **4.2 Selection according to cell size**

444 In a meta-analysis of predator-prey ratios in plankton, Hansen et al. (1994) found an  
445 optimal ratio for copepods of 18:1. However, our study suggests that even small copepods  
446 can display near maximal clearance rates on prey that are much longer relative to their body  
447 size. Our equivalent upper predator:prey length ratios range from 6:1 to 2:1 (depending on  
448 species). The ability of copepods to tackle large prey has also been found in previous studies  
449 (Lampitt, 1978; Atkinson, 1994; Calbet et al., 2007). The absolute maximum lengths of food  
450 items that the copepods can remove are likely to be even higher than those we present,  
451 because we only calculated values for prey items that decreased significantly in abundance  
452 over the experiments. Other, larger prey were present but were not sufficiently abundant to  
453 discern robustly the changes in their numbers. Our data add to the evidence (Kjørboe, 2016;  
454 Atkinson et al., 2014) that questions the use of single fixed predator:prey ratios.

455 While our experiments demonstrate that small copepods are capable of removing  
456 diatoms colonies 600  $\mu\text{m}$  long, it is unclear whether these are eaten intact or fragmented. For  
457 example, a brittle prey item, such as a diatom colony half of a copepod's body length, could  
458 easily break up during handling. Previous observations of copepod feeding have revealed  
459 that, whilst they can successfully feed on large, elongated diatom colonies, most is ultimately  
460 lost because of handling difficulties (Vanderploeg et al., 1988). Svensen and Vernet (2016)  
461 recently showed that sloppy feeding of *Oithona nana* on a dinoflagellate released 6-15% of  
462 carbon egested as DOC, so DOC release could also be substantial when copepods tackle  
463 large diatoms.

464 Overall, the capture and partial fragmentation of very large particles by copepods is  
465 increasingly becoming recognised for its consequences on nutrient fluxes (Noji et al., 1991,

466 Iversen and Poulsen, 2007; Mayor et al., 2014; Anderson et al., 2017). It seems likely that  
467 copepod feeding activities could also influence the size of phytoplankton colonies through  
468 fragmentation. Bergkvist et al. (2012) showed that diatom colonies tend to reduce their length  
469 when they are exposed to chemical cues derived from copepods, suggesting an evolutionary  
470 response to grazing pressure. Irrespective of the mechanisms involved, it is clear that large  
471 but rare food items can be important for copepods and represent an understudied aspect of  
472 their trophic ecology (Gifford, 1993).

### 473 **4.3 Importance of intraguild predation.**

474 The role of nauplii as prey items for copepods remains poorly understood, partly  
475 because few studies have quantified feeding rates on them and even fewer have offered  
476 them alongside the natural seston in feeding experiments (Sells et al., 2001; Bonnet et al.,  
477 2004; Boersma et al., 2014). In our experiments significant positive selection for nauplii was  
478 only observed for *Centropages typicus* and only in experiment 6. Given the size and  
479 suggested weak escape responses, this apparent lack of clear selection for nauplii was  
480 surprising.

481 All the copepod species investigated here were found to be capable of feeding on  
482 copepod nauplii, and in several experiments these formed important contributions to the  
483 large particle component of the diet. Given the biomass dominance of copepods (Fig 2c)  
484 these results support the view that copepods could be an important mortality agent for their  
485 own naupliar stages (Lampitt, 1978; Bonnet et al., 2004; Boersma et al. 2014). The fact that  
486 even the small copepods such as *Oithona similis* were feeding on nauplii emphasises that  
487 multiple trophic levels exist within relatively small increments of size.

### 488 **4.4 Concluding remarks**

489 This diversity of food types and sizes ingested by copepods reflects their wide range  
490 of ecological and biogeochemical roles. Irrespective of the subsequent fate (fragmentation or  
491 ingestion), the removal of particles larger than their own faecal pellets adds to the evidence

492 that copepods do not simply repackage small particles into larger, faster sinking pellets  
493 (Iversen and Poulsen, 2007). Reduced selectivity has other, fundamental, ramifications. For  
494 the grazers, it would increase resilience to highly unpredictable seasonality of prey resources  
495 (Fig. 2, Mazzocchi et al., 2012). Coincidental ingestion of non-food items also has a series of  
496 implications. For example copepods also consume lithogenic sediment particles (Paffenhöfer  
497 and Van Sant, 1985; Arendt et al., 2011) and acidic digestion in the gut can mobilise the  
498 attached iron to enhance productivity (Schmidt et al., 2016). Some studies have found that  
499 inert particles are selected against compared to nutritious ones (e.g. Paffenhöfer and Van  
500 Sant, 1985) whereas interestingly, recent microplastic studies emphasise the fact that  
501 copepods can and do ingest these inert particles (Cole et al., 2013). Overall, the natural  
502 diversity of possible prey needs to be taken into account when interpreting copepod feeding.

503         The variety of conclusions arising from zooplankton feeding studies over the last  
504 century raises some fundamental questions over how to incorporate this process into food-  
505 web models. On one hand, evidence of copepods feeding unselectively seems contrary to  
506 models stressing selection based on optimal size, motility or nutritional quality (Litchman et  
507 al., 2013; Mitra et al. 2014; Kenitz et al. 2017). On the other hand, size-based models can  
508 have difficulties with the parametrization of their kernel function (Wirtz, 2014), often  
509 emphasizing an “optimal” size of prey by characterising a unimodal kernel function. Our  
510 study shows that copepods are able to process very large prey with high clearance rates,  
511 questioning the extent of the unimodal feeding kernels. We speculate that, when large  
512 enough prey cells are available, this function could be bimodal, particularly for ambush  
513 feeders. Overall this study adds to the evidence that we should encapsulate the natural  
514 diversity of particle types, sizes and trophic levels into what we count as copepod food.

515

516 **Acknowledgements:**

517 We first thank the crews of the Plymouth Quest for the collection of samples at the E1 site  
518 during our field seasons, and Joanna Nunes and Sarah Dashfield for their help with sample  
519 collection in 2015. We are also indebted to the crews and scientists for supporting the ongo-  
520 ing L4 time series that provides the context for our seasonal observations. We are grateful to  
521 Denise Cummings who analysed the C and N contents of the zooplankton samples. This  
522 work was funded jointly through the NERC and Department for Environment, Food and  
523 Rural Affairs, Shelf Seas Biogeochemistry Programme and the Marine Ecosystems Re-  
524 search Programme (Grant nos. NE/K001833/1, NE/K001833/2, NE/L003279/1).

525

## 526 **References**

527 Arendt, K.E., Dutz, J, Jonasdottir, S.H., Jung-Madsen, S., Mortensen, J., Møller, E.F.,  
528 Nielsen, T.G., 2011. Effects of suspended sediments on copepods feeding in a glacial  
529 influenced sub-Arctic fjord. *Journal of Plankton Research* 33: 1526-1537

530 Atkinson, A., 1994. Diets and feeding selectivity among the epipelagic copepod community  
531 near South Georgia in summer. *Polar Biology* 14: 551-560

532

533 Atkinson, A., 1995. Omnivory and feeding selectivity in five copepod species during spring in  
534 Bellingshausen Sea, Antarctica. *ICES Journal of Marine Science* 52, 385-396.

535 Atkinson, A., 1996. Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate  
536 predation, food selectivity and impact on prey populations. *Marine Ecology Progress Series*  
537 130, 85-96.

538 Atkinson, A., Hill, S.H., Barange, M., Pakhomov, E.A., Raubenheimer, D., Schmidt, K.,  
539 Simpson, S.J., Reiss, C., 2014. Sardine cycles, krill declines and locust plagues: revisiting  
540 “wasp-waist” food webs. *Trends in Ecology and Evolution* 29: 309-316

541 Atkinson, A., Harmer, R.A., Widdicombe, C.E., McEvoy, A.J., Smyth, T.J., Cummings, D.G.,  
542 Somerfield, P.J., Maud, J.L., McConville, K., 2015. Questioning the role of phenology shifts  
543 and trophic mismatching in a planktonic food web. *Progress in Oceanography* 137, 498-512.

544 Anderson, T.R., Pond, D.W., Mayor, D.J., 2017. The role of microbes in the nutrition of  
545 detritivorous invertebrates: A stoichiometric analysis. *Frontiers in Microbiology* 7: 2113.

546 Båmstedt, U., Gifford, D.J., Irigoien, X., Atkinson, A., Roman, M., 2000. Chapter 8: Feeding.  
547 in: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M., (eds). ICES Zooplankton  
548 Methodology Manual. Academic Press, London. Pp 297-399.

549 Benedetti, F., Gasparini, S., Avata, S.-D., 2016. Identifying copepod functional groups from  
550 species functional traits. *Journal of Plankton Research* 38:159-166.

551 Bergkvist, J., Thor, P., Jakobsen, H.H., Wängberg, S.Å., Selander, E., 2012. Grazer-induced  
552 chain length plasticity reduces grazing risk in a marine diatom. *Limnology and Oceanography*  
553 57, 318-324.

554 Boersma, M., Wesche, A., Hirche, H.-J., 2014. Predation of calanoid copepods on their own  
555 and other copepods' offspring. *Marine Biology* 161, 733-743.

556 Bonnet, D., Titelman, J., Harris, R., 2004. *Calanus* the cannibal. *Journal of Plankton*  
557 *Research* 26, 937-948.

558 Brooks, J.L., Dodson, S.I., 1965. Predation, Body Size, and Composition of Plankton.  
559 *Science* 150, 28-35.

560 Calbet, A., Saiz, E., 2005. The ciliate-copepod link in marine ecosystems. *Aquatic Microbial*  
561 *Ecology* 38, 157-167.

562 Calbet, A., Carlotti, F., Gaudy, R., 2007. The feeding ecology of the copepod *Centropages*  
563 *typicus* (Krøyer). *Progress in Oceanography* 72, 137-150.

564 Castellani, C., Irigoien, X., Harris, R.P., Lampitt, R.S., 2005. Feeding and egg production of  
565 *Oithona similis* in the North Atlantic. *Marine Ecology Progress Series* 288, 173-182.

566 Castellani, C., Irigoien, X., Mayor, D.J., Harris, R.P., Wilson, D., 2008. Feeding of *Calanus*  
567 *finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea,  
568 North Atlantic. *Journal of Plankton Research* 30: 1095-1116.

569 Cleary, A.C., Durbin, E.G., Ryneerson, T.A., Bailey, J., 2016. Feeding by *Pseudocalanus*  
570 copepods in the Bering Sea: Trophic linkages and a potential mechanism of niche  
571 partitioning. *Deep Sea Research Part II: Topical Studies in Oceanography* 134, 181-189.

572 Cole, M., Lindeque, P., Fileman, E., Halsband, C., Goodhead, R., Moger, J., Galloway, T.S.,  
573 2013. Microplastic ingestion by zooplankton. *Environmental Science and Technology* 47 (12),  
574 6646-6655.

575 Conover, R.J., 1978. Transformation of organic matter. in *Marine ecology*, Vol. IV, pp. 221-  
576 499. Kinne, O., (ed), John Wiley, Chichester. (1), 106-115.

577 Conway, D. V. P. 2012. Marine Zooplankton of Southern Britain, Part 2: Arachnida,  
578 Pycnogonida, Cladocera, Facetotecta, Cirripedia and Copepoda, p. 1–164. Marine Biological  
579 Association Occasional Publication No. 26.

580 Cotonnec, G., Brunet, C., Sautour, B., Thoumelin, G., 2001. Nutritive value and selection of  
581 food particles by copepods during a spring bloom of *Phaeocystis* sp. In the English Channel,  
582 as determined by pigment and fatty acid analyses. Journal of Plankton Research 23 (7), 693-  
583 703.

584 Cowles, T.J., Strickler, J.R., 1983. Characterization of feeding activity patterns in the  
585 planktonic copepod *Centropages typicus* Kröyer under various food conditions. Limnology  
586 and Oceanography 28, 106-115

587 Fileman, E., Smith, T., Harris, R., 2007. Grazing by *Calanus helgolandicus* and *Para-*  
588 *Pseudocalanus* spp. on phytoplankton and protozooplankton during the spring bloom in the  
589 Celtic Sea. Journal of Experimental Marine Biology and Ecology 342, 70-84.

590 Fileman, E., Petropavlovsky, A., Harris, R., 2010. Grazing by the copepods *Calanus*  
591 *helgolandicus* and *Acartia clausi* on the protozooplankton community at station L4 in the  
592 western English Channel. Journal of Plankton Research 32, 709-724.

593 Fileman, E.S., Lindeque, P.K., Harmer, R.A., Halsband, C., Atkinson, A., 2014. Feeding rates  
594 and prey selectivity of planktonic decapod larvae in the Western English Channel. Marine  
595 Biology 161, 2479-2494.

596 Frost, B.W., 1972. Effects of size and concentration of food particles on the feeding of the  
597 marine planktonic copepod *Calanus pacificus*. Limnology and Oceanography 17, 805-815.

598 Fuchs, H.L., Franks, P.J.S., 2010. Plankton community properties determined by nutrients  
599 and size-selective feeding. Marine Ecology Progress Series 413, 1-15.

600 Giering, S.L.C., Wells S.R., Mayers, K.M.J., Schuster, H., Cornwell, L., Fileman, E.S.,  
601 Atkinson, A., Cook, K.B., Preece, C., Mayor, D.J. (in review, this issue) Seasonal variation of  
602 zooplankton community structure and trophic position in the Celtic Sea: a stable isotope and  
603 biovolume spectrum approach. Progress in Oceanography.

604 Gifford, D.J., 1993. Protozoa in the diets of *Neocalanus* spp. in the oceanic subarctic Pacific.  
605 Progress in Oceanography 32, 223-237.

606 Hansen, B., Bjørnsen, P.K., Hansen, P.J., 1994. The size ratio between planktonic predators  
607 and their prey. Limnology and Oceanography 39 (2), 395-403.

608 Hopkins, T.L., 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine*  
609 *Biology* 96, 93-106.

610 Huntley, M., 1981. Nonselective, nonsaturated feeding by three calanoid copepod species in  
611 the Labrador Sea. *Limnology and Oceanography* 26 (5), 831-842.

612 Irigoien, X., Head, R.N., Cummings, D., Harbour, D., 2000. Feeding selectivity and egg  
613 production of *Calanus helgolandicus* in the English Channel. *Limnology and Oceanography*  
614 45 (1), 44-54.

615 Isari, S., Anto, M., Saiz, E., 2013. Copepod foraging on the basis of food nutritional quality:  
616 can copepods really choose? *PloS ONE* 8 (12), e84742.

617 Iversen, M.H., Poulsen, L.K., 2007. Coprorhexy, coprophagy, and coprochaly in the  
618 copepods *Calanus helgolandicus*, *Pseudocalanus elongatus*, and *Oithona similis*. *Marine*  
619 *Ecology Progress Series* 350, 79-89.

620 Kenitz, K.M., Visser, A.W., Mariani, P., Andersen, K.H., 2017. Seasonal succession in  
621 zooplankton feeding traits reveals trophic trait coupling. *Limnology and Oceanography* 62,  
622 1184-1197.

623 Kiørboe, T., Saiz, E., Viitasalo, M., 1996. Prey switching behaviour in the planktonic copepod  
624 *Acartia tonsa*. *Marine Ecology Progress Series* 143, 65-75.

625 Kiørboe, T., Visser, A.W., 1999. Predator and prey perception in copepods due to  
626 hydromechanical signals. *Marine Ecology Progress Series* 179, 81-95.

627 Kiørboe, T., 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biological*  
628 *Reviews* 86, 311-339.

629 Kiørboe, T. 2016. Foraging mode and prey size spectra of suspension-feeding copepods and  
630 other zooplankton. *Marine Ecology Progress Series* 558, 15-20.

631 Koski, M., Dutz, J., Breteler, W.K., Rampen, S., Noordeloos, A. 2010. Seasonal changes in  
632 food quality of the common North Sea copepods *Temora longicornis* and *Pseudocalanus*  
633 *elongatus*: a bioassay approach. *Marine Ecology Progress Series* 399, 141-155

634 Kovala, P.E., Larrance, J.D., 1966. Computation of phytoplankton cell numbers, cell volume,  
635 cell surface area and plasma volume per litre, from microscopical counts. *Special Report*, vol.  
636 38, University of Washington, Seattle, 1-91.

637 Lampitt, R.S., 1978. Carnivorous feeding by a small marine copepod. *Limnology and*  
638 *Oceanography* 23, 1228-1231.

639 Leiknes, Ø., Striberny, A., Tokle, N.E., Olsen, Y., Vadstein, O., Sommer, U., 2014. Feeding  
640 selectivity of *Calanus finmarchicus* in the Trondheimsfjord. *Journal of Sea Research* 85, 292-  
641 299.

642 Litchman, E., Ohman, M.D., Kiørboe, T., 2013. Trait-based approaches to zooplankton  
643 communities. *Journal of Plankton Research* 35, 473-484.

644 Mariani, P., Andersen, K.H., Visser, A.W., Barton, A.D., Kiørboe, T., 2013. Control of plankton  
645 seasonal succession by adaptive grazing. *Limnology and Oceanography* 58, 173-184.

646 Marshall, S.M., 1973. Respiration and feeding in copepods. *Advances in Marine Biology* 11,  
647 57-120.

648 Mayor, D.J., Anderson, T.R., Irigoien, X., Harris, R., 2006. Feeding and reproduction of  
649 *Calanus finmarchicus* during non-bloom conditions in the Irminger Sea. *Journal of Plankton*  
650 *Research* 28: 1167-1179.

651 Mayor, D.J., Anderson, T.R., Pond, D.W., Irigoien, X., 2009. Egg production and associated  
652 losses of carbon, nitrogen and fatty acids from maternal biomass in *Calanus finmarchicus*  
653 before the spring bloom. *Journal of Marine Systems* 78, 505-510.

654 Mayor, J.D., Sanders, R., Giering, S.L.C., Anderson, T.R., 2014. Microbial gardening in the  
655 ocean's twilight zone: Detritivorous metazoans benefit from fragmenting, rather than  
656 ingesting, sinking detritus. *BioEssays* 36, 1132-1137.

657 Mazzocchi, M.G., Dubroca, L., García-Comas, C., Di Capua, I., Ribera d'Alcala, M., 2012.  
658 Stability and resilience in coastal copepod assemblages: the case of the Mediterranean long-  
659 term ecological research at Station MC (LTER-MC). *Progress in Oceanography* 97-100, 135-  
660 151.

661 Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates,  
662 diatoms, and other protist plankton. *Limnology and Oceanography* 45, 569-579.

663 Mitra, A., Castellani, C., Gentleman, W.C., Jónasdóttir, S.H., Flynn, K.J., Bode, A., Halsband,  
664 C., Kuhn, P. Licandro, P., agersted M.D., Calbet, A., Lindeque, P.K., Koppelman, R., Møller,  
665 E.F., Gislason, A., Nielsen, T.G., St.John, M., 2014. Bridging the gap between marine  
666 biogeochemical and fisheries sciences; configuring the zooplankton link. *Progress in*  
667 *Oceanography* 129, 176-199.

668 Nakamura, Y., Turner, J.T., 1997. Predation and respiration by the small cyclopoid copepod  
669 *Oithona similis*: How important is feeding on ciliates and heterotrophic flagellates? Journal of  
670 Plankton Research, 19, 1275-1288.

671

672 Noji, T.T., Estep, K.W., Macintyre, F., Norrbin, F., 1991. Image analysis of fecal material  
673 grazed upon by three species of copepods: evidence for coprorhexy, coprophagy and  
674 coprochaly. Journal of the Marine Biological Association of the United Kingdom 71, 465-480.

675 Paffenhöfer, G.-A., 1993. On the ecology of marine cyclopoid copepods (Crustacea,  
676 Copepoda). Journal of Plankton Research 15, 37-55.

677 Paffenhöfer, G.-A., Van Sant, K.B., 1985. The feeding response of a marine planktonic  
678 copepod to quantity and quality of particles. Marine Ecology Progress Series 27, 55-65.

679 Poulet, S.A., 1978. Comparison between five coexisting species of marine copepods feeding  
680 on naturally occurring particulate matter. Limnology and Oceanography 23 (6), 1126-1143.

681 Roman, M.R., 1984. Utilisation of detritus by a copepod, *Acartia tonsa*. Limnology and  
682 Oceanography 29, 949-959.

683 Saille, S., Polimene, L., Mitra, A., Atkinson, A., Allen, J.I., 2015. Impact of zooplankton food  
684 selectivity on plankton dynamics and nutrient cycling. Journal of Plankton Research 37, 519-  
685 529.

686 Sells, A.F., van Keuren, D., Madin, L.P., 2001. Predation by omnivorous copepods on early  
687 developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. Limnology and  
688 Oceanography, 46, 953-959.

689 Schmidt, K., Schlosser, C., Atkinson, A., Fielding, S., Venables, H.J., Waluda, C.M.,  
690 Achterberg, E.P., 2016. Zooplankton gut passage mobilises lithogenic iron for ocean  
691 productivity. Current Biology 26, 2667-2673.

692 Smyth, T., Atkinson, A., Widdicombe, S., Frost, M., Allen, I., Fishwick, J., Queiros, A., Sims,  
693 D., Barange, M., 2015. The Western Channel Observatory. Progress in Oceanography 137,  
694 335-341.

695 Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Dando,  
696 P.R., Genner, M.J., Joint, I., Kendall, M., Halliday, N.C., Harris, R.P., Leaper, R.,  
697 Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W.,  
698 Hawkins, S.J., 2005. Long-term oceanographic and ecological research in the western  
699 English Channel. Advances in Marine Biology 47, 1-105.

700 Stamieszkin, K., Poulton, N.J., Pershing, A.J., 2017. Zooplankton grazing and egestion shifts  
701 particle size distribution in natural communities. *Marine Ecology Progress Series* 573, 43-56.

702 Steele, J.H., Frost, B.W., 1977. The Structure of Plankton Communities. *Philosophical*  
703 *Transactions of the Royal Society B* 280, 185-534.

704 Stoecker, D.K., Capuzzo, J.M., 1990. Predation on Protozoa: its importance to zooplankton.  
705 *Journal of Plankton Research* 12, 891-908.

706 Strickler, J.R., 1982. Calanoid Copepods, Feeding Currents, and the Role of Gravity. *Science*  
707 218, 158-160.

708 Svensen, C., Vernet, M., 2016. Production of dissolved organic carbon by *Oithona nana*  
709 (Copepoda: Cyclopoida) grazing on two species of dinoflagellates. *Marine Biology* 163:237  
710 DOI 10.1007/s00227-016-3005-9

711 Tiselius, P., Saiz, E., Kjørboe, T., 2013. Sensory capabilities and food capture of two small  
712 copepods, *Paracalanus parvus* and *Pseudocalanus* sp. *Limnology and Oceanography* 58,  
713 1657-1666.

714 UNESCO (ed.) (1968) *Monographs on Oceanographic Methodology: Zooplankton Sampling*.  
715 United Nations, Paris

716 Utermöhl, H., 1958. Zur vervollkommnung der quantitativen phytoplankton methodik.  
717 *Mitteilung Internationale Vereinigung fuer Theoretische unde Amgewandte Limnologie* 9,1-  
718 38.

719 Vanderploeg, H.A., Scavia, D., 1979. Two electivity indices for feeding with special reference  
720 to zooplankton grazing. *Journal of the Fisheries Research Board of Canada* 36, 362-365.

721 Vanderploeg, H.A., Paffenhöfer G.-A., Liebig, J.R., 1988. *Diaptomus* vs. net phytoplankton:  
722 effects of algal size and morphology on selectivity of a behaviourally flexible, omnivorous  
723 copepod. *Bulletin of Marine Science* 43 (3), 377-394.

724 Visser, A.W., Fiksen, Ø., 2013. Optimal foraging in marine ecosystem models: selectivity,  
725 profitability and switching. *Marine Ecology Progress Series* 473, 91-101.

726 Wiadnyana, N.N., Rassoulzadegan, F., 1989. Selective feeding of *Acartia clausi* and  
727 *Centropages typicus* on microzooplankton. *Marine Ecology Progress Series* 53, 37-45.  
728

- 729 Widdicombe, C.E., Eloire, D., Harbour, D., Harris, R.P., Somerfield, P.J., 2010. Long-term  
730 phytoplankton community dynamics in the Western English Channel. *Journal of Plankton*  
731 *Research* 32, 643-655.
- 732 Wirtz, K.W., 2012. Who is eating whom? Morphology and feeding type determine the size  
733 relation between planktonic predators and their ideal prey. *Marine Ecology Progress Series*  
734 445, 1-12.
- 735 Wirtz, K.W., 2014. A biomechanical and optimality-based derivation of prey-size  
736 dependencies in planktonic prey selection and ingestion rates. *Marine Ecology Progress*  
737 *Series* 507, 81-94.
- 738 Zamora-Terol, S., Nielsen, T.,G., Saiz, E., 2013. Plankton community structure and role of  
739 *Oithona similis* on the western coast of Greenland during the winter-spring transition. *Marine*  
740 *Ecology Progress Series* 483, 85-102.

741 **Table1:** Size, feeding mode, and prey according to the literature for the five copepod genera studied  
 742 here. The third and fourth column are not an exhaustive reviews, but gives consensual findings for our  
 743 particular study species and then, when available, some different findings.

Genus	Female length (mm)*	Feeding mode	Prey
<i>Calanus</i>	2.4 - 3.9	Mainly feeding-current feeding?	Diatoms selected or omnivorous (Irigoien <i>et al.</i> , 2000; Fileman <i>et al.</i> , 2007, Leiknes <i>et al.</i> , 2014), but some records of selection for large motile prey (Fileman <i>et al.</i> , 2010).
<i>Pseudocalanus</i>	0.93 - 1.77	Feeding-current feeding (Tiselius <i>et al.</i> , 2013 )	Generally opportunistic eating on the most abundant food (Cottonnec <i>et al.</i> , 2001; Fileman <i>et al.</i> , 2007; Cleary <i>et al.</i> , 2016)
<i>Acartia</i>	0.81 – 1.47	Feeding-current and ambush feeding (Kiørboe <i>et al.</i> ,1996 )	Protozooplankton mainly (Wiadnyana and Rassoulzadegan, 1989; Fileman <i>et al.</i> , 2010) but records of feeding on phytoplankton (Cottonnec <i>et al.</i> , 2001)
<i>Oithona</i>	0.68 – 0.96	Strictly ambush feeding (Paffenhöfer, 1993 )	Ciliates mainly (Atkinson, 1995; Nakamura and Turner, 1997; Castellani <i>et al.</i> , 2005; Saiz <i>et al.</i> , 2007; Zamora-Terol <i>et al.</i> , 2013) But records of feeding on diatoms (Hopkins 1987; Atkinson, 1996)
<i>Centropages</i>	1.6 – 2.0	Feeding-current and ambush feeding (Cowles and Strickler, 1983)	Omnivorous with a preference for large and motile prey (Wiadnyana and Rassoulzadegan, 1989; Calbet <i>et al.</i> , 2007)

744 \*Maximum total body length based on the species used for the present study: data from Conway (2012)

745

746

**Table 2:** Summary of the bottle volume used and the copepod density (number L<sup>-1</sup>) of each species that has been incubated in each experiment. The numbers in brackets are the number of replicates. For *Calanus* spp. no star: *Calanus helgolandicus*, one star: *Calanus finmarchicus*, two stars copepodites V of *Calanus* spp..

Species	Volume incubated (L)	Percentage depletion*	Experiment number: copepod incubation L-1 (number of replicate grazer bottles)										
			1	2	3	4	5	6	7	8	9	10	11
<i>Calanus</i> spp.	1.2	37 (14)	4* (3)	6* (2)	6** (3)	6 (3)			6 (3)	6 (3)		5 (3)	5** (3)
<i>Pseudocalanus elongatus</i>	0.6	37 (9.6)	17 (3)	23 (2)	17 (3)							17 (3)	17 (3)
<i>Acartia clausi</i>	0.6-1.2	25 (0.2)		96 (2)		12 (2)	12 (3)	12 (3)	13 (3)	13 (3)	13 (3)		10 (3)
<i>Oithona similis</i>	0.6	41 (6.4)		83 (1)	83 (2)	83 (2)	83 (3)	83 (3)	83 (3)			75 (3)	
<i>Centropages typicus</i>	1.2	39 (6.7)				9 (3)	9 (3)	9 (3)	9 (3)	9 (3)			

\*Values refer to median percentage reduction in experimental bottles compared to final controls over all cell categories included in this analysis (Supplementary Figs 1-3). Values in brackets are percentage depletion of chl *a*.

**Table 3:** Environmental conditions at the site E1 at the time of our experiments.

Experiment number	1	2	3	4	5	6	7	8	9	10	11
Date	12/03/2014	24/04/2014	14/05/2014	17/06/2014	02/07/2014	22/07/2014	16/09/2014	14/10/2014	18/11/2014	10/02/2015	10/03/2015
Temperature (°C)	9.73	10.78	11.34	16.34	17.69	18.72	16.09	15.31	13.66	9.97	9.65
Biomass of microplankton *(mgC.m <sup>-3</sup> )	14.1	45.76	246.49	28.91	44.09	18.61	105.28	14.45	5.58	10.14	21.2
% of this biomass enumerated in the large food category	N/A	0.32	0.87	3.36	14.32	2.76	0.18	0.19	N/A	46.22	29.25
Biomass of mesozooplankton** (mgC.m <sup>-3</sup> )	1.03 (0.89)	1.47 (5.13)	4.74 (9.12)	4.93 (5.18)	3.24 (1.79)	4.5	8.01 (14.75)	6.12 (13.99)	0.75 (5.62)	4.01 (3.89)	7.26 <b>(31.16)</b>
% of this biomass represented in the experiments	17	19.43	52.9	27.81	29.18	32.71	25.47	12.16	9.19	13.8	12.66
Biomass copepods (mgC.m <sup>-3</sup> )	0.92	0.66	4.29	2.61	1.07	2.71	7.29	5.23	0.57	3.19	6.24
% of this biomass represented in the experiments	19.12	43.05	58.5	52.49	88.06	54.27	27.98	14.23	11.96	17.33	14.74

\* Biomasses have been obtained from lugols cell counts and conversion factors. Cell dimensions were converted to volumes based on Kovala and Larrance (1966) and thence to carbon using Menden-Deuer and Lessard (2000).

\*\* Biomasses obtained mainly from seasonal length measurements and conversions using literature length – mass relationships. Values in brackets refer to values derived from dry mass and carbon mass determination on a separate net haul, often including phytoplankton as well as zooplankton.

**Table 4.** Mesozooplankton biomasses during this study, as compared to 2014-2015 values reported during parallel, near full-depth sampling in the Celtic sea reported by Giering et al. (this issue)

Site	Median mesozooplankton biomass (mg C m <sup>-3</sup> )	Seasonal range of mesozooplankton biomass (mg C m <sup>-3</sup> )	Sampling depth (m)	Sampling period	Method Notes
E1	4.5	0.75-8.0	0-70	March 2014-March 2015: see Table 3	Use of length mass conversions derived for L4 site*
E1	5.4	0.89-32*	0-70	March 2014-March 2015: see Table 3	Weighing and C analysis of separate catches
L4	9.9	2.2-53**	0-50	45 sampling time-points spanning March 2014-March 2015	Use of length mass conversions derived for L4 site*
Central Celtic Sea: CCS site	16	5.5-28	0-120	Sampling spanning August 2014 to July 2015	Literature regressions based on Zooscan images***
Outer Celtic sea: CS2 site	6.7	1.2-14	0-120	Sampling spanning August 2014 to July 2015	Literature regressions based on Zooscan images***

\*High values represent clogging of WP2 with phytoplankton so are unrepresentative of mesozooplankton biomasses

\*\* Maximum value represents partly an exceptionally high abundance of *Centropages typicus*

\*\*\* Full details of sampling and methods in Giering et al. (this issue)

### Figure captions :

**Fig 1** Sampling sites of the Western Channel Observatory. Samplings for feeding experiments were conducted at station E1 in 2014-2015. Station L4 provided context for seasonality with its long time series of microplankton and mesozooplankton.

**Fig. 2.** Environmental conditions at E1 during the two year study including the times of the 11 feeding experiments as denoted by red arrows on the axes. (a) Temperature (°C) (b), biomass of microplankton from March 2014 to October 2015, (c) biomass of mesozooplankton, plus nauplii as determined from flowCAM from water samples taken at 10m depth denoted by red squares and red line ; (d) biomass of the copepod genera studied.

**Fig 3.** L4 station medians, quartiles and ranges of variation in nano-microplankton biomass and abundance of the five studied copepod species based on the weekly sampling (1993-2014 for nano-microplankton and 1988-2015 for copepods). Each box integrates 2 weeks (from the 1<sup>st</sup> to the 15<sup>th</sup> and from the 16<sup>th</sup> to the end of each month). Red line indicates the mean.

**Fig 4.** Proportion in terms of percentage biomass of available large food (top panel) and the corresponding biomass contribution to the diets of the five copepod species (expressed as carbon ingestion rate as a percentage of body carbon). Hatching signifies the various size classes. Experiments 1, 2, 8 and 9, are not presented since these had either one or no prey categories above our threshold for inclusion in feeding rate estimates.

**Fig 5** Numerical contribution of food to the diet plotted against its numerical proportion of available food (mean  $\pm$  S.D). Points near the  $y=x$  line indicate unselective behaviour. Points below the  $y=x$  line indicate avoidance of the prey. Points above the  $y=x$  line indicate selection

of the prey. Black stars indicate proportion in the available food significantly different from the proportion in the ingested food ( $t$ -test,  $p$ -value $<0.05$ ) Symbols are scaled according to the size of each food category, except for the nauplii.

**Fig. 6** Summary of copepod feeding selectivity across all available experiments. **a:** the “diatom index”, defined as the mean proportion of non-motile prey (diatoms) in the ingestion rate (number of prey  $\text{cop}^{-1}$  (mean  $\pm$  CI 95%). **b:** Maximum Prey/predator ratio (length of the largest prey on which we found a significant positive clearance rate ( $t$ -test,  $p<0.05$ ) divided by the length of the predator). Copepod lengths are from Conway (2012).

### Supplementary Fig 1

Concentration of food items that were above the threshold for inclusion in feeding rate calculations. Points are means, with bars representing 95% confidence intervals.

### Supplementary Fig. 2

Clearance rates ( $\text{mL.cop}^{-1}.\text{d}^{-1}$ , median  $\pm$  range across the replicate experimental bottles) versus prey length ( $\mu\text{m}$ ; horizontal bars show the range of the size-classes). Black stars indicate clearance rates significantly different from 0 ( $t$ -test  $p<0.05$ ). In experiments 1 and 9 none of our large food item categories reached the threshold so these experiments are omitted. Note that rarity of these large cells precludes precise estimates of the concentration in the incubation bottles, contributing to the sometimes large range in clearance rates between replicate bottles.

### Supplementary Fig 3

Median and range values for Electivity index (Vanderploeg and Scavia 1979) versus prey sizes (length ( $\mu\text{m}$ ), horizontal bars show the range of the size-classes). Black stars indicate

electivity index significantly different from 0 ( $t$ -test  $p < 0.05$ ). In experiments 1 and 9 none of our large food item categories reached the threshold so these experiments are omitted.

**Supplementary Table 1.** Literature sources used to convert linear dimensions of zooplankton to carbon masses. The characteristic lengths (e.g. copepod prosome lengths, medusa bell diameters) of 3780 individuals were measured, based on 25 daytime sampling time-points with the standard 57 cm diameter 200 $\mu$ m WP2 net at L4, during 2015 and 2016, supplemented by 7 day and night sampling occasions throughout 2015 using a 1 m square-sided frame net of 500  $\mu$ m mesh size. The formalin- preserved samples were measured with a calibrated eyepiece graticule under a binocular microscope, randomly selecting organisms to measure. We then applied length-mass regression based on the table below to estimate carbon mass of each individual. In the instances where several equations were available, we calculated the arithmetic mean carbon mass for each individual based on the available equations. For rarer taxa where we could not find taxon-specific relationships we measured characteristics lengths and applied volumetric appropriate conversions (Little and Copley 2003) then used an overall median carbon mass:wet mass conversion from the supplementary appendix of McConville et al. (2017) from which to estimate carbon mass.

Taxon	References used
<i>Calanus</i> spp.	McLaren 1969, Bottrell and Robins 1984, Hay et al. 1991 Uye 1991, Pond et al. 1996
<i>Centropages</i> spp.	McLaren 1969, Uye 1991
<i>Temora</i> spp.	Klein Breteler et al. 1982
<i>Clausocalanus</i> , <i>Ctenocalanus</i> , <i>Pseudocalanus</i> , <i>Paracalanus</i>	McLaren (1969), Uye 1991
<i>Acartia</i> spp.	Uye 1982, Cateleto and Fonda-Umani 1994, Landry 1978
<i>Oithona</i> spp.	Uye 1982, Uye and Sano 1998
<i>Oncaea</i> spp.	Satopoomin 1999
<i>Ditricocorycaeus</i> spp.	Satopoomin 1999
Copepod nauplii	Uye 1988, 1991, Liaing et al. 1996
Other copepod copepodites	McLaren (1969), Uye (1991)
Chaetognaths	McLaren 1969, Uye 1982, Little and Copley 2003,
<i>Noctiluca scintillans</i>	Kjørboe and Tittleman 1998
Appendicularians	Gorsky et al. 1988, Sato et al. 2001
Cladocerans	McLaren 1969, Uye 1982,
Pteropods	McConville et al. 2017
Cirripede larvae	Uye 1982, Berggeen et al. 1988, Sabatini and Kjørboe 1994, Hygum et al. 2000
Polychaete larvae	Uye 1982
Decapod larvae	Uye 1982
Bivalve larvae	Uye 1982
Echinoderm larvae	McConville et al. 2017
Euphausiids	Lindley 1978, Atkinson et al. 2006, 2012, Little and Copley 2003
Amphipods, mysids, cumaceans	Uye 1982
Eggs (mainly of fish and chaetognaths)	Conway (2012), McConville et al. 2017
Fish larvae	Uye 1982, Munk and Nielsen 1994
Ctenophores and Cnidarians	McLaren 1969, Larson 1986, Mizdalski 1988, Daan 1989, Clarke et al. 1992, Mutlu and Bingel 1999, Gibson and Paffenhöfer 2000, Båmstedt et al. 2001, Persad et al. 2003, Bastian et al. 2014
Other rarer, non-copepod taxa	Little and Copley 2003, McConville et al. 2017

### Supplementary Table 1 references

- Atkinson A, Shreeve RS, Tarling GA, Hirst AG, Rothery P, Pond D, Korb R, Murphy EJ, Watkins JL (2006) Natural growth rates of Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex, and maturity stage. *Limnology and Oceanography* 51: 973-987
- Atkinson A, Ward P, Hunt BPV, Pakhomov EA, Hosie GW (2012) An overview of Southern Ocean zooplankton data: abundance, biomass, feeding and functional relationships. *CCAMLR Science* 19: 171-218
- Båmstedt, U., B. Wild, and M. Martinussen. 2001. Significance of food type for growth of ephyrae *Aurelia aurita* (Scyphozoa). *Mar. Biol.* 139: 641-650. doi: 10.1007/s002270100623
- Bastian, T., M. K. S. Lilley, S. Beggs, G. C. Hays, and T. K. Doyle. 2014. Ecosystem relevance of variable jellyfish biomass in the Irish Sea between years, regions and water types. *Estuar. Coast. Shelf Sci.* 149: 302-312. doi: 10.1016/j.ecss.2014.08.018
- Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for the determination of copepod production. *Mar Biol* 99:341-352
- Bottrell HH, Robins DB (1984) Seasonal variations in length, dry weight, carbon and nitrogen of *Calanus helgolandicus* from the Celtic Sea. *Mar Ecol Progr Ser* 14:259-268
- Cateletto B, Fonda Umani S (1994) Seasonal variations in carbon and nitrogen content of *Acartia clausi* (Copepoda: Calanoida) in the Gulf of Trieste (Northern Adriatic Sea). *Hydrobiologia* 292/293: 283-288.
- Clarke, A., L. J. Holmes, and D. J. Gore. 1992. Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. *J. Exp. Mar. Biol. Ecol.* 155: 55-68. doi: 10.1016/0022-0981(92)90027-8
- Conway, D. V. P. 2012. Marine Zooplankton of Southern Britain, Part 2: Arachnida, Pycnogonida, Cladocera, Facetotecta, Cirripedia and Copepoda, p. 1–164. Marine Biological Association Occasional Publication No. 26.
- Daan, R. 1989. Factors controlling the summer development of copepod populations in the Southern Bight of the North Sea. *Neth. J. Sea Res.* 23: 305-322. doi: 10.1016/0077-7579(89)90051-3
- Gibson, D., and G.-A. Paffenhöfer. 2000. Feeding and growth rates of the doliolid, *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea). *J. Plankton Res.* 22: 1485-1500. doi: 10.1093/plankt/22.8.1485
- Gorsky G, Dallot S, Sardou J, Fenaux R, Carré C, Palazzoli I (1988) C and N composition of some northwestern Mediterranean zooplankton and micronekton species. *J Exp Mar Biol Ecol* 124:133-144

- Hay SJ, Kiørboe T, Matthews A (1991) Zooplankton biomass and production in the North Sea during the autumn circulation experiment, October 1987-March 1988. *Continental Shelf Res.* 11: 1453-1476
- Hygum, BH, Rey, C, Hansen BW, Tande K (2000) Importance of food quality to structural growth rate and neutral lipid reserves accumulated in *Calanus finmarchicus*. *Mar Biol* 136:1057-1073
- Kiørboe T, Titelman J (1998) Feeding, prey selection and prey encounter mechanisms in the heterotrophic dinoflagellate *Noctiluca scintillans*. *J Plankton Res* 20:1615-1636
- Klein Breteler WCM, Frasz HG, Gonzalez SR (1982) Growth and development of four calanoid copepod species under experimental and natural conditions. *Netherlands J Sea Res* 16:195-207
- Landry MR (1978) Population dynamics and production of a planktonic marine copepod, *Acartia clausi*, in a small temperate lagoon on San Juan Island, Washington. *Internationale Revue der gesamten Hydrobiologie* 63: 77-119.
- Larson, R. 1986. Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *J. Exp. Mar. Biol. Ecol.* 99: 107-120. doi: 10.1016/0022-0981(86)90231-5
- Liang D, Uye S, Onbé T (1996) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. I. *Centropages abdominalis*. *Mar Biol* 124:527-536.
- Little WS, Copley, NJ (2003) Silhouette DIGITIZER Version 1.0 Users Guide. Woods Hole Technical Report, 67 pp.
- Lindley JA (1978) Population-dynamics and production of Euphausiids. 1. *Thysanoessa longicaudata* in North Atlantic Ocean. *Mar Biol* 46: 121-130
- McLaren, I. A. 1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fiord on Baffin Island. *Journal of the Fisheries Board of Canada* 26: 1485-1559. doi: 10.1139/f69-139
- Mizdalski, E. 1988. Weight and length data of zooplankton in the Weddell Sea in austral spring 1986 (ANT V/3), p. 72. *Berichte zur Polarforschung (Reports on Polar Research)*. Alfred Wegener Institute.
- Mutlu, E., and F. Bingel. 1999. Distribution and abundance of ctenophores, and their zooplankton food in the Black Sea. I. *Pleurobrachia pileus*. *Mar. Biol.* 135: 589-601. doi: 10.1007/s002270050660
- McConville K, Atkinson A, Fileman ES, Spicer JI, Hirst AG (2017) Disentangling the counter-acting effects of water content and carbon mass on zooplankton growth. *J Plankton Res* 39:246-256
- Munk P, Nielsen T G (1994) Trophodynamics of the plankton community at Dogger Bank: predatory impact of larval fish. *J Plankton Res* 16:1225-1245
- Persad, G., R. R. Hopcroft, M. K. Webber, and J. C. Roff. 2003. Abundance, biomass and production of ctenophores and medusae off Kingston, Jamaica. *Bull. Mar. Sci.* 73: 379-396.
- Pond D, Harris R, Head R, Harbour D (1996) Environmental and nutritional factors determining seasonal variability in fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. *Mar Ecol Prog Ser* 143:45-63
- Sabatini M, Kiørboe T (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis*. *J Plankton Res* 16:1329-1351
- Satapoomin S (1999) Carbon content of some common tropical Andaman Sea copepods. *J Plankton Res.* 21:2117-2123

Sato R, Tanaka Y, Ishimaru T (2001) House production by *Oikopleura dioica* (Tunicata, Appendicularia) under laboratory conditions. J Plankton Res 23:415-423

Uye S (1982) Length-weight relationships of important zooplankton from the Inland Sea of Japan. J of the Oceanological Society of Japan 38:149-158

Uye S (1988) Temperature-dependent development and growth of *Calanus sinicus* (Copepoda, Calanoida) in the laboratory. Hydrobiologia 167: 285-293

Uye S (1991) Temperature-dependent development and growth of the planktonic copepod *Paracalanus* sp. in the laboratory. Bull Plankton Soc Japan. Spec. Vol: 627-636

Uye S, Sano K (1998) Seasonal variations in biomass, growth rate and production rate of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. Mar Ecol Prog Ser 163: 37-44