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

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Abstract.

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

1. Introduction

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

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

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

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

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

2. Material and Methods

2.1 Western Channel Observatory study location

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

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

2.2 Micro- and mesozooplankton seasonality at E1 and L4

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

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

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

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

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

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

2.3 Feeding experiments

In total 11 experiments were run at E1, spanning March 2014 to March 2015. The complete experimental setup is summarised in Table 2 and the environmental conditions in Table 3. Sampling was conducted between mid-morning and midday on each visit, and comprised of first a CTD profile and collection of incubation water. This was collected from 10 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 µmol L^{-1} NH_4Cl) and disodium hydrogen phosphate (1
203 µmol L^{-1} Na_2HPO_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_{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 revolutions min^{-1}) in the laboratory maintained at ambient

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

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

2.4 Analysis of feeding experiments

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

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

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

2.5 Calculation of feeding rates

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

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

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

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

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

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

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

$$[C] = C_0 \times (1 - e^{g}) \times (-g) \qquad (3)$$

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

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

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

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

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

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

$$W_i = F_i / \Sigma F_i \qquad (6)$$

285 F_i is the clearance rate on the i^{th} type of food and ΣF_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 ~10 mg C m^{-3} in winter to ~250 mg C m^{-3}
294 in spring, and was typically dominated by small (2-6 µm) 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 ind. m^{-3} to 3744 ind. m^{-3}, with an
302 average of 1490 ind. m^{-3}. Our estimates of their seasonal median biomass based on length-
303 mass relationships was 4.5 mg.C m^{-3}; similar to the value of 5.4 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 µm 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

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

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

3.4 Copepod feeding selectivity

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

The estimated rates at which the five copepod species cleared each of the identified prey items are presented in detail in Supplementary Fig. 2. Maximal significant clearance rates varied from 31 mL cop^{-1} d^{-1} for *Oithona similis* to 523 mL cop^{-1} d^{-1} for *Calanus* spp. These species tended to clear diatoms at the highest rates, with the exception of *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**

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

4.1. Selection for motile and non-motile cells

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

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

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

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

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

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

4.2 Selection according to cell size

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

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

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

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

4.3 Importance of intraguild predation.

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

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

4.4 Concluding remarks

This diversity of food types and sizes ingested by copepods reflects their wide range of ecological and biogeochemical roles. Irrespective of the subsequent fate (fragmentation or 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

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

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

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Table 2: Summary of the bottle volume used and the copepod density (number L^{-1}) 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
Calanus spp.	1.2	37 (14)	4* (3)	6* (2)	6** (3)	6 (3)			6 (3)	6 (3)		5 (3)	5** (3)
Pseudocalanus elongatus	0.6	37 (9.6)	17 (3)	23 (2)	17 (3)						17 (3)	17 (3)	
Acartia clausi	0.6-1.2	25 (0.2)		96 (2)		12 (2)	12 (3)	12 (3)	13 (3)	13 (3)	13 (3)		10 (3)
Oithona similis	0.6	41 (6.4)		83 (1)	83 (2)	83 (2)	83 (3)	83 (3)	83 (3)		75 (3)		
Centropages typicus	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 *($mgC.m^{-3}$)	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** ($mgC.m^{-3}$)	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 **(31.16)**
% 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 ($mgC.m^{-3}$)	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^{-3})	Seasonal range of mesozooplankton biomass (mg C m^{-3})	Sampling depth (m)	Sampling period	Method Notes
E1	4.5	0.75-8.0	0-70	March2014-March 2015: see Table 3	Use of length mass conversions derived for L4 site*
E1	5.4	0.89-32*	0-70	March2014-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 1st to the 15th and from the 16th 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 ± 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 cop^{-1} (mean ± 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 ($mL.cop^{-1}.d^{-1}$, median ± range across the replicate experimental bottles) versus prey length (µm; 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 (µm), 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 200µm 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 µm 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**
Calanus spp.	McLaren 1969, Bottrell and Robins 1984, Hay et al. 1991 Uye 1991, Pond et al. 1996
Centropages spp.	McLaren 1969, Uye 1991
Temora spp.	Klein Breteler et al. 1982
Clausocalnus, Ctenocalanus, Pseudocalanus, Paracalanus	McLaren (1969), Uye 1991
Acartia spp.	Uye 1982, Cateleto and Fonda-Umani 1994, Landry 1978
Oithona spp.	Uye 1982, Uye and Sano 1998
Oncaea spp.	Satopoomin 1999
Ditricocorycaeus spp.	Satopoomin 1999
Copepod nauplii	Uye 1988, 1991, Liaing et al. 1996
Other copepod copepodites	McLaren (1969), Uye (1991)
Chaeotognaths	McLaren 1969, Uye 1982, Little and Copley 2003,
Noctiluca scintillans	Kiørboe and Titleman 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 Kiørboe 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, Daan1989, 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

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