A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean

Deborah K. Steinberg[1], Joseph S. Cope[1], Stephanie E. Wilson[1], and T. Kobari[2]

[1]Virginia Institute of Marine Science, 1208 Greate Rd., Gloucester Point, Virginia, 23062, USA. [2]Faculty of Fisheries, Kagoshima University, 4-50-20 Shimoarata, Kagoshima 890-0056, Japan.

Abstract

Mesopelagic mesozooplankton communities of an oligotrophic (Hawaii Ocean Time series-HOT station ALOHA) and a mesotrophic (Japanese time-series station K2) environment in the North Pacific Ocean are compared as part of a research program investigating the factors that control the efficiency of particle export to the deep sea (VERtical Transport In the Global Ocean -VERTIGO). We analyzed zooplankton (>350 μm) collected from net tows taken between 0-1000 m at each site to investigate the biomass size structure and the abundance of the major taxonomic groups in discrete depth intervals throughout the water column. Biomass of zooplankton at K2 over all depths was approximately an order of a magnitude higher than at ALOHA, with a significantly higher proportion of the biomass at K2 in the larger (>2 mm) size classes. This difference was mostly due to the abundance at K2 of the large calanoid copepods *Neocalanus* spp. and *Eucalanus bungii* which undergo ontogenetic (seasonal) vertical migration. The overall strength of diel vertical migration was higher at K2, with a mean night:day biomass ratio in the upper 150 m of 2.5, vs. a ratio of 1.7 at ALOHA. However, the amplitude of the diel migration (change in weighted mean depth between day and night) was higher at ALOHA for all biomass size classes, perhaps due to deeper light penetration causing deeper migration to avoid visual predators. A number of taxa known to feed on suspended or sinking detritus showed distinct peaks in the mesopelagic zone, which affects particle transport efficiency at both sites. These taxa include calanoid and poecilostomatoid (e.g., *Oncaea* spp.) copepods, salps, polychaetes, and phaeodarian radiolaria at K2, harpacticoid copepods at ALOHA, and ostracods at both sites. We found distinct layers of carnivores (mainly gelatinous zooplankton) in the mesopelagic at K2 including chaetognaths, hydrozoan medusae, polychaetes, and gymnosome pteropods, and, in the upper mesopelagic zone, of ctenophores and siphonophores; at both sites a

mesopelagic layer of hyperiid amphipods was found. The large population of ontogenetically migrating calanoid copepods is likely supporting large carnivorous populations at depth at K2. The contrasting zooplankton taxonomic structure at the two sites helps explain the higher efficiency of the biological pump at K2. Factors responsible for increased transport efficiency at K2 include rapid transport of POC via larger fecal pellets produced by zooplankton at K2, and enhanced active carbon export at K2 vs. ALOHA, due to the greater strength of diel vertical migration and to additional ontogenetic migration at K2.

Key Words: mesopelagic zone, zooplankton, diel vertical migration, particle flux, carnivore, gelatinous, North Pacific

1. Introduction

The structure of zooplankton communities plays a crucial role in determining the fate of primary production, the composition and sedimentation rate of sinking particles, and thus the flux of organic matter to the deep ocean. The majority of prior studies on the role of zooplankton in the ocean's biological pump have focused on carbon transfers and processes in the epipelagic zone, such as grazing and fecal pellet production (e.g., Dam et al., 1995; Roman et al., 2000; 2001). However, mid-water processes in the mesopelagic zone (the base of the euphotic zone to 1000m) also determine the efficiency by which particulate organic carbon (POC) is transported to the deep sea (Angel, 1989a; Banse, 1990; Steinberg et al., in press). Despite the presumed importance of this mid-water zooplankton community, we know comparatively little about its role in carbon cycling through mesopelagic food webs. This is partly due to the limited basic information available on the abundance, biomass, vertical structure, and behavior of the various component taxa in the mesopelagic zone (Robison, 2004), the stratum where sinking particle flux is rapidly attenuated (Martin et al., 1987; Berelson, 2001; Buesseler et al., 2007). Furthermore, while some detailed studies of multiple taxa in mesopelagic communities exist (Angel and Baker, 1982; Angel, 1989b; Andersen et al., 2001, 2004; Yamaguchi et al., 2002a), direct comparisons of mesopelagic zooplankton community structure between contrasting oceanic environments are scarce (Andersen et al., 1997; Yamaguchi et al., 2004).

The mesopelagic zooplankton community affects carbon flux in a variety of ways, including consuming (Gowing and Wishner, 1986, 1992; Uttal and Buck, 1996; Lampitt et al., 1993; Steinberg, 1995; Dilling et al., 1998; Schnetzer and Steinberg, 2002b), and metabolizing sinking detritus, fragmenting larger particles into smaller, non-sinking aggregates via their

58 feeding and swimming activities (Dilling and Alldredge, 2000; Goldthwait et al., 2004), and
59 producing new fecal pellet classes at depth as a result of feeding on detritus, or on other animals
60 (carnivory) (Wilson et al., this issue). Diel vertical migrators may also affect POC flux by
61 defecating surface-ingested POC after their descent to daytime mesopelagic residence depths
62 (Flint et al., 1991; Atkinson et al., 1996; Morales, 1999; Schnetzer and Steinberg, 2002a) or by
63 respiring and excreting this C in a dissolved form at depth (e.g., Longhurst et al., 1990; Zhang
64 and Dam, 1997; Steinberg et al., 2000). Similarly, seasonal or ontogenetic vertical migrators
65 may also contribute to C export (Longhurst and Williams, 1992; Kobari et al., 2003; Kobari et
66 al., this issue). This active transport by diel or seasonal migrators is a C flux that would bypass
67 sediment traps, so is not included in sediment trap-derived C export measurements.
68 Knowing the distribution and abundance of the various taxa involved in these processes
69 and behaviors provides a basis by which C transfers can be inferred. For example, some taxa,
70 such as oncaeid copepods, are known to feed on detritus (Ohtsuka et al., 1996) and may affect
71 POC flux where they occur. Filter feeders such as salps or larvaceans may repackage suspended
72 particles at depth into sinking particles (i.e., fecal pellets, or the abandoned mucous houses of
73 larvaceans), and carnivores, by repackaging their prey into fecal pellets, inject new particle types
74 into the mesopelagic zone (Wilson et al., this issue). Finally, taxa undergoing marked diel or
75 ontogenetic vertical migrations may have a significant impact on the 'active' C flux in a given
76 environment. When these types of data on zooplankton community structure are coupled with
77 feeding or metabolic rates and incorporated into mathematical models, C fluxes mediated by
78 different components of the mesopelagic food web can then be quantified (Angel, 1989b).
79 In this study we compare mesopelagic zooplankton communities between the subtropical
80 and the subarctic North Pacific Ocean as part of a research program investigating what controls

the efficiency of particle export to the deep sea (VERtical Transport In the Global Ocean - VERTIGO) (Buesseler et al., 2007; Buesseler et al., this issue). We analyzed meso- and macrozooplankton collected from net tows taken between 0-1000m at each site to investigate the biomass size structure and the abundance of the major taxonomic groups in discrete depth intervals throughout the water column. The magnitude and extent of diel vertical migration for various size fractions and taxa is also examined. We then discuss the implications of the contrasting zooplankton taxonomic structure at the two sites for carbon cycling and energy transfer in mesopelagic food webs, and on the efficiency of the biological pump.

2. Methods

2.1 Study sites

Zooplankton samples were collected from 0-1000m at two contrasting sites in the North Pacific Ocean. The first collections were made at the Hawaii Ocean Time series (HOT) station ALOHA in the oligotrophic subtropical gyre ($22^{o}45$'N, 158^{o}W) aboard the R/V *Kilo Moana* from June 22-July 9, 2004. The second collections were made at the Japan Agency for Marine-earth Science and Technology (JAMSTEC) time-series site K2, in a high nutrient, variable chlorophyll region of the subarctic gyre (47^{o}N, 160^{o}E) aboard the R/V *Roger Revelle* from July 22-August 11, 2005. An overview, plus detailed information on physical and particle properties, primary production, and particle flux at each site is presented in Buesseler et al. (2007, and this issue) and in other papers in this volume (Boyd et al., this issue; Lamborg et al., this issue). During our study period ALOHA was characterized by warm waters (26^{o}C at surface), mixed layer nutrients at nanomolar concentrations, low Chl a (~0.1 mg m^{-3} at surface), and a phytoplankton assemblage consisting of small diatoms, coccolithophorids, picoplankton and

104 cyanobacteria. K2 was characterized by colder waters (10°C at surface), higher surface nutrients
105 (12 μM mixed layer DIN), variable but higher Chl a (~0.8 mg m^{-3} at surface), and a
106 phytoplankton assemblage consisting of picoplankton and large diatoms.
107
108 *2.2 Zooplankton collection*
109 Meso- and macrozooplankton biomass and taxonomic composition were determined
110 using a 1 m^2, 335 μm mesh MOCNESS (Multiple Opening/Closing Net and Environmental
111 Sensing System, (Wiebe et al., 1985) at ALOHA and IONESS (Intelligent Operative Net
112 Sampling System) at K2. The following discrete depth intervals were sampled on the upcast: 0-
113 50, 50-100, 100-150, 150-200, 200-300, 300-400, 400-500, 500-750, and 750-1000 m. We
114 define 150 m as the boundary between the epipelagic and mesopelagic zones in this study (as 150
115 m was the depth of our shallowest sediment trap used for companion studies of
116 mesozooplankton effects on POC flux: Steinberg et al., in press; Kobari et al., this issue; Wilson
117 et al., this issue). The total duration of the net deployment was ~3.25-4 h at ALOHA, and 3.5-
118 4.5 h at K2- where a short second cast was required for the 3 shallowest depths as the IONESS
119 was equipped with 6 sampling nets. The average volume of water filtered by the net in a single
120 depth interval was 928 m^3 (range 266 m^3 - 3045 m^3). Paired tows during day (9:30-15:00 local
121 time) and night (21:30-03:00) were performed. A total of 4 day-night pairs of tows were
122 performed at each site (one day-night pair at the beginning and end of each of 2 sediment trap
123 deployment periods per site). Sensors on the net systems included a pressure sensor, Sea-Bird
124 temperature and conductivity probes, a flow meter, and an inclinometer. A GPS was available on
125 the ship, and environmental and flight data were available in real-time.

126 Upon recovery, nets were rinsed with seawater and the cod-ends were removed. Net tow
127 samples were then split using a Folsom plankton splitter and processed using protocols similar to
128 Landry et al. (2001) and Madin et al. (2001). Half of the sample was size-fractionated using
129 nested sieves of 0.35-, 0.5-, 1-, 2-, and 5 mm mesh. Zooplankton in each size class were
130 transferred onto pre-weighed 0.2 mm nitex mesh filters, rinsed with deionized water, and frozen
131 at -20^{o}C for biomass analysis. The other half sample was further split for additional analyses of
132 zooplankton lipid and gut content (Wilson et al. *in prep*.), and at K2, community structure of
133 ontogenetic migrating copepods (Kobari et al., this issue). The remainder was preserved in
134 sodium borate-buffered 4% formaldehyde for enumeration of major taxa. Larger gelatinous
135 zooplankton (especially at K2) and micronekton were removed from the tow prior to splitting
136 and were enumerated immediately. Biovolume of gelatinous zooplankton (e.g., ctenophores) was
137 determined by displacement in graduated cyclinders (see below). While larger scyphozoan
138 medusae were collected at both sites, they were usually rare and we exclude them from our
139 analysis as they were damaged and likely not sampled quantitatively. Similarly, a variety of
140 nekton such as myctophids, stomiiforms (*Cyclothone* spp. and hatchet fishes), *Bathylagus* sp.,
141 and juvenile squids were caught, but we do not quantify them here. We do, however, include
142 crustacean micronekton such as mysids and shrimps in our analyses, as they were sampled in
143 reasonable numbers and were relatively undamaged by the nets. Other larger crustacea such as
144 euphausiids are included as well, although they are likely also undersampled by our nets.
145 At K2, high numbers of phaeodarian radiolarians were also caught in the nets. These
146 large protozoans were clumped together and removed from the "biomass split" for separate
147 determination of their biomass (i.e., they are not included in the size-fractionated metazoan

biomass data).

2.3 Biomass analysis

Wet and dry weights for each size fraction were measured on a Sartorius BP211D or Mettler AE 160 balance. Wet weights were determined after sample filters were thawed on paper towels to remove excess water (~ 20 minutes). Samples were then dried for 24 h at 60 ºC and re-weighed. Wet and dry biomass (mg m^{-3}) were determined by dividing the biomass by the volume filtered through the net. Biomass of ctenophores was determined based our own measurements on beroid ctenophores (Condon and Steinberg, unpublished) and on previously established relationships of ctenophore biovolume vs. wet and dry weight (Purcell et al., 2001), assuming a specific gravity of 1ml (biovolume) = 1g (wet weight), and dry weight (g) = 0.01 x wet weight (g).

2.4 Taxonomic community structure analysis

Preserved samples were analyzed using an Olympus SZX12 stereo dissecting microscope under dark and light field illumination. Zooplankton were identified to major taxa (e.g., chaetognath, siphonophore, the 4 major orders of copepods) with abundant or conspicuous genera or species noted. The sample was rinsed through a series of nested sieves (200, 500, 1000, 2000, and 5000 µm). All animals collected on the 2000 and 5000 µm sieves were identified. Animals in the remaining fractions were subsampled with a Stempel pipette (5 - 15 ml) before identification. A minimum of 100 animals were identified from each of the smaller size fractions, resulting in examination of 1/1200-1/2 of each size fraction. We did not discriminate between copepod carcasses and those that were sampled live, as copepod carcasses were found

171 to be a minor fraction (<5%) of total copepods above depths of 1000m in the North Pacific
172 (Yamaguichi et al. 2002).
173
174 *2.5 Vertical structure*
175 In order to quantify the presence and extent of vertical migration in the various size
176 classes and taxa at each site, we calculated both night:day (N:D) ratios in the upper 150m and
177 weighted mean depth for zooplankton biomass and for abundance of major taxa. N:D ratio was
178 calculated by integrating zooplankton biomass (or abundance of a given taxon) over the upper
179 150 m (mg dry weight or number m^{-2}), and dividing the integrated night value by the day value
180 for each pair of tows. Weighted mean depth (m) was calculated as:
181 $$WMD = \Sigma(n_i \times z_i \times d_i) / \Sigma (n_i \times z_i)$$
182 where d_i is the depth of a sample i (center of the depth interval, m), z_i is the thickness of the
183 depth interval (m), and n_i is the biomass or abundance of individuals in the depth interval (mg or
184 no. m^{-3}) (Andersen et al., 2001; 2004). The amplitude of the migration (ΔWMD) was calculated
185 as day WMD minus night WMD (m). We did not determine WMD for taxa exhibiting a
186 pronounced bimodal vertical distribution.
187
188 *2.6 Statistical analyses*
189 WMD data were analyzed by paired t-tests. Biomass data were analyzed by 2- or 3-
190 factor repeated measures ANOVAs (see Results and table captions for individual factors used for
191 each ANOVA). Where data did not conform to the assumptions of the ANOVA (normality and
192 homogeneity of variance), data were either log- or inverse-square-root transformed.

193 Comparisons of interest were tested with specific contrasts using a Tukey adjustment (Neter et
194 al., 1996). We assumed a level of significance of alpha = 0.05 for all comparisons.
195
196 **3. Results**
197 *3.1 Size-fractionated biomass*
198 Depth profiles of size fractionated biomass at ALOHA and K2 illustrate some
199 fundamental differences between the two sites (Fig. 1). First, the biomass of zooplankton at K2
200 at all depths is approximately an order of a magnitude higher than at ALOHA. At ALOHA,
201 biomass of all size fractions combined (day or night) ranges from 1.3-9.2 mg m^{-3} in the surface
202 150 m, and 0.2-2.0 mg m^{-3} at mesopelagic depths (>150m). At K2 in comparison, biomass
203 ranges from 3.1-96.9 mg m^{-3} in the surface 150 m, and 2.9-20.2 mg m^{-3} at mesopelagic depths.
204 Both sites exhibit surface peaks in biomass, with a secondary biomass peak in the mesopelagic
205 zone. At ALOHA this secondary biomass peak occurs between ~400-750 m, while at K2 it lies
206 shallower, between ~200-500 m.
207 The distribution of the size classes is also different between the two sites, with a
208 significantly higher proportion of the 0-1000 m biomass in the larger (>2 mm) size classes at K2
209 (~48%) than at ALOHA (35%) (Figs.1, 2, Table 1). The difference is most pronounced in the
210 surface 150m, where at ALOHA, 14-21% (mean of 4 day and night tows, respectively) of the
211 biomass is in the larger size classes, and at K2 the proportion of larger sized organisms increases
212 significantly to 33-52%. At both sites, the proportion of biomass >2 mm generally increases
213 with depth. The difference between the two sites is less pronounced in the mesopelagic zone,
214 where approximately half to two-thirds of the biomass is >2 mm (Table 1, Fig. 2), with the

exception of the daytime upper mesopelagic (150-500 m) at ALOHA, where a smaller proportion (33%) of the biomass was >2mm (Table 1, Fig. 2).

At both sites, diel vertical migration of zooplankton was pronounced. This is indicated by the nighttime increase in zooplankton biomass in the surface 150 m, with a corresponding decrease in the mesopelagic zone (Fig.1, Table 1). This was particularly evident at ALOHA, where the lower mesopelagic daytime biomass peak diminished at night as organisms moved upwards (Fig. 1a, b, Table 1). Movements of larger size classes from mesopelagic residence depths into the surface waters at night was also evidenced by increasing proportions of these larger classes in the surface 150 m at night (Table 1, Fig. 2) at both sites. Increases in the proportion of larger size classes at night were also evident between 150-500 m at ALOHA (Table 1, Fig. 2), suggesting migration from deeper waters into the upper mesopelagic zone. This relative increase in strength of diel migration in the larger size classes vs. the smaller is also indicated by the higher N:D ratios of >2 mm size classes in the upper 150 m as compared to <2 mm size classes, and the steadily increasing amplitude of vertical migration (as indicated by ΔWMD) with increasing animal size at both sites (Table 2). The mean N:D ratio in the upper 150 m at ALOHA for all size classes combined was 1.7, while at K2 it was 2.5 (driven by the high N:D ratio in the 2-5mm size class), however the amplitude of vertical migration was higher at ALOHA than K2 (Table 2). The 0-1000m integrated biomass at both sites increased by ~ 20% at night at both sites (Table 1). The increase, although not statistically significant for either site (ANOVA, site x day/night x depth interval, $p>0.05$), is possibly due to daytime net avoidance, or vertical migration of deeper (>1000m) zooplankton into the mesopelagic zone at night as noted above (see Discussion).

3.2 Community structure

3.2.1 Copepods

As expected, copepods were the most abundant taxa of zooplankton and constituted 72 ±3% and 74 ±0.5% of the total abundance of zooplankton in the epipelagic (0-150m) and mesopelagic (150-1000) zones, respectively, at ALOHA, and 86 ±4% and 70 ±4% at K2 (mean ±standard deviation of day and night samples combined). Calanoids were the most abundant order at both sites (Figs. 3, 4), constituting 62-76% of the total copepod abundance in the epipelagic and 66-88% in the mesopelagic zone at ALOHA, and 98-99% (epipelagic) and 75-99% (mesopelagic) at K2 (Fig. 4). Calanoid copepods were an order of magnitude more abundant at K2 than ALOHA, and as a broad taxonomic category exhibited diel vertical migration, with N:D abundance ratios of 1.4 (ALOHA) and 1.8 (K2) (Fig. 3, Table 3). A number of individual calanoid taxa, such as *Pleurommama* spp., exhibited very strong migration and were not present at all in the surface 150m during the day at either site. Subsurface mesopelagic peaks in calanoid copepod abundance were present at both sites, occurring between 300-750m at ALOHA, and 200-400m at K2, mirroring the mesopelagic peaks in total zooplankton biomass (Section 3.1, Fig. 1). Calanoid diversity at ALOHA was high, as is typical for the north Pacific subtropical gyre (McGowan and Walker, 1979; Landry et al., 2001). The calanoid copepods at K2 were dominated by *Neocalanus* spp. and *Eucalanus bungii*. These ontogenetic vertical migrators were still in the surface waters and just beginning their seasonal descent to depth at the time of our sampling in August (Kobari et al., this issue).

The next most abundant order of copepods was the poecilostomatoids. This order consists of many small species that would usually not be sampled by our relatively large mesh (350 μm) net (Böttger-Schnack, 1996a; Nishibe and Ikeda, 2007), thus we undersampled many

261 of the smaller poecilostomatoid genera and life stages. These copepods exhibited remarkably
262 different depth distributions at each site, peaking in abundance in the surface waters at ALOHA,
263 vs. throughout the mesopelagic at K2 (Fig. 3). Abundance of poecilostomatoids was also
264 considerably higher in surface waters at ALOHA than at K2, but similar between the two sites in
265 the mesopelagic zone (~0.1-5 m^{-3} at both sites). Poecilostomatoids were mostly from the
266 families Oncaeidae and Corycaeidae at ALOHA (Oncaeidae: 1.1-15.7 m^{-3} in epipelagic, and 0.1-
267 2.5 m^{-3} in mesopelagic; Corycaeidae: 3.8-18.7 m^{-3} and <0.01-3.1 m^{-3}), and Oncaeidae at K2 (0-
268 0.4 m^{-3} in epipelagic, and 0.2-4.0 m^{-3} in mesopelagic). Smaller numbers of the genera *Copilla*
269 and *Sapphirina* (<2.5 m^{-3}) also occurred within the surface 200 m at ALOHA. As a major group,
270 the poecilostomatoids did not exhibit pronounced diel vertical migration, with 0-150 m N:D
271 ratios of 1.0 at ALOHA, but higher (1.4) at K2 (Fig. 3, Table 3).
272 The cyclopoid copepods were almost exclusively from the family Oithonidae at both
273 sites. Harpacticoid copepod abundance peaked both in the surface 50 m and in the mesopelagic
274 below 200 m at ALOHA, and in the mesopelagic 400-500 m at K2 (although their abundance at
275 K2 was low) (Fig.3). The mesopelagic harpacticoid copepods at ALOHA were dominated by
276 *Aegisthus* spp. As a group the harpacticoid copepods did not exhibit a strong diel migration.
277 Cyclopoid and harpacticoid copepods made up 0-25% of the copepod abundance at both sites
278 (Fig. 4). However, for reasons noted for the poecilostomatoids, our net under samples the
279 cyclopoid and harpacticoid copepods.
280
281 *3.2.2 Other crustacea*
282 After copepods, ostracods were the next most abundant taxa (Figs. 5, 8), constituting 0-
283 47% of the epipelagic and 21-59% of the mesopelagic non-copepod taxa (Fig. 8). Ostracods

284 exhibited pronounced diel vertical migration with N:D ratios in the upper 150 m of 2.5
285 (ALOHA) and 48.9 (K2), and ΔWMD of 77 m at ALOHA ($p<0.05$) and 38 m at K2 (Fig. 5,
286 Table 3). Thus, K2 ostracods were almost exclusively at mesopelagic depths during the day.
287 The diverse genus *Metaconchoecia* constituted 51% (ALOHA) and 22% (K2) of the mesopelagic
288 ostracod population. Strong diel vertical migrators such as *Mikroconchoecia* spp. were relatively
289 abundant in surface waters at ALOHA at night (up to 2.7 m^{-3} in top 50 m).
290 Euphausiids were the next most abundant crustacean and also exhibited some diel
291 migration, which was similar in magnitude at both sites, with N:D ratios in the upper 150 m of
292 1.4 (ALOHA) and 16.9 (K2), and ΔWMD of 73 m at ALOHA ($P<0.05$) and 77 m at K2 (Fig. 5,
293 Table 3).
294 Hyperiid and gammarid amphipods were also strong diel migrators, with hyperiid N:D
295 ratios in the upper 150 m of 2.4 (ALOHA) and 3.6 (K2) (Table 3). Migrating hyperiid
296 amphipods at ALOHA included members of the family Scinidae and *Phronima* spp. Hyperiids
297 in the genera *Phrosina* and *Primno* were almost exclusively found only in the mesopelagic
298 (>96%) at both sites. Gammarids were mostly found in low abundance in the surface waters
299 during day and night at ALOHA, but were relatively abundant at K2, where they resided solely
300 in the mesopelagic between 200-400m during the day and moved up into surface waters at night
301 (Fig. 5). These gammarids at K2 were almost exclusively *Cyphocaris* cf. *challengeri*; this
302 species underwent a pronounced diel vertical migration with a ΔWMD of 199 m.
303 The larger decapods and mysids were rarer than the other crustacean groups (Fig. 5, Fig.
304 8) but were significant contributors to biomass peaks, as seen in the large size classes (Fig. 1, 2).
305 At both sites, the abundance of decapods was highest in the surface waters. At ALOHA this was
306 dominated by decapod larvae and by *Lucifer* sp., and at K2 by decapod larvae and sergestids.

307 The large, red, caridean shrimp *Hymenodora* cf. *frontalis* also occurred solely in the mesopelagic
308 at K2. Mysids occurred in surface waters with lower abundances deeper at ALOHA, and almost
309 exclusively in the mesopelagic between 400-1000m at K2. While we did catch reasonable
310 numbers of mysids and decapods, our nets likely undersampled adult stages of these
311 micronekton.
312
313 *3.2.3 Gelatinous zooplankton*
314 Chaetognaths were the third most abundant taxon overall, and the most abundant of the
315 gelatinous taxa (Figs. 6, 7, 8). The vertical distribution of chaetognaths was different at the two
316 sites, with highest abundances in the surface waters at ALOHA (up to 11.2 m^{-3}) (Fig. 6a), and a
317 bimodal distribution at K2 (up to 28.5 m^{-3} in epipelagic, and 34.1 m^{-3} in mesopelagic) (Fig. 6b).
318 This distinct mesopelagic peak in chaetognaths at K2 occurred between 150-500 m. Diel vertical
319 migration in chaetognaths as a broad group was evident at K2 but not at ALOHA (Fig. 6, Table
320 3). Several individual species of chaetognaths at ALOHA, however, showed diel vertical
321 migration, such as *Pseudosagitta lyra*, which was only found in the surface 150m at night and
322 had a day and night WMD of 359m and 223m, respectively. Strong chaetognath migrators at K2
323 included *Flaccisagitta enflata*, with a day and night WMD of 127m and 74m, respectively.
324 Cnidarians such as siphonophores and hydrozoan medusae were relatively common in the
325 tows. Siphonophores were most abundant in surface waters at ALOHA, but interestingly did not
326 occur in the top 50 m at K2 (Fig. 6). At K2 a subsurface peak in siphonophores occurred
327 between 50-200m, and some animals were found deeper in the mesopelagic as well (Fig. 6b).
328 Most siphonophores sampled at ALOHA were calycophoran (families Abylidae and Diphyidae).
329 As a broad taxonomic group siphonophores did not exhibit diel vertical migration (Fig. 6, Table

330 3). Hydrozoan medusae were most common at ALOHA in the surface 0-50m at night, and good
331 evidence for their diel vertical migration includes a N:D ratio of 3, and a day to night change in
332 WMD of 177m (Fig. 6a, Table 3). A bimodal distribution of hydrozoan medusae occurred at K2,
333 with a population within the upper 150m, and between 200-500m (Fig. 6b). Diel migration of
334 hydrozoan medusae was not as evident at K2 (Table 3).

335 Pelagic tunicates (salps, doliolids, and larvaceans) were an important component of the
336 zooplankton community at both sites. While abundances of salps were comparable between the
337 two sites (on the order of <1 up to 3 m^{-3}), vertical distribution of salps was distinct. At ALOHA
338 salps occurred largely in the upper 150m, while at K2 a mesopelagic peak in salps occurred
339 between 200-500 m (Fig. 6). There is possible evidence for diel vertical migration of lower
340 mesopelagic or bathypelagic salps into the upper mesopelagic (200-300m) layer at night at K2,
341 although the standard deviation is high (Fig. 6b). Distribution of doliolids paralleled that of the
342 salps, with peaks in the epipelagic at ALOHA, and in the mesopelagic at K2. Larvacean
343 (appendicularian) abundance was higher in the epipelagic zone at K2 than ALOHA, with no
344 discernable day/night differences at either site (Fig.6). Although larvaceans were the second
345 most abundant gelatinous zooplankton in surface waters at the two sites (after chaetognaths), we
346 found few recognizable larvaceans in samples from >150m. Presumably larvaceans were present
347 in the mesopelagic zone, as we found mesopelagic peaks in larvacean fecal pellets in sediment
348 traps (Wilson et al., this issue), but they became damaged beyond recognition in our net tows.
349 Therefore we only report data from depths <150m.

350 The thecosome (shelled) pteropods mostly occurred in the epipelagic zone and decreased
351 with depth at ALOHA (Fig. 7a). Abundance of thecosome pteropods was about an order of
352 magnitude lower at K2, with abundance peaking in the lower mesopelagic zone between 400-

353 1000m (Fig. 7b). The gymnosome (shell-less) pteropods were very rare in our tows at ALOHA,
354 but were more abundant at K2 where they occurred mostly in the upper 300m (opposite to the
355 K2 thecosome distribution) at abundances up to 0.5 m^{-3}. As a broad taxonomic grouping the
356 pteropods exhibited weak diel migration at ALOHA, and none at K2 (Fig. 7, Table 3).
357 Heteropods (families Atlantidae and Pterotracheidae) were only sampled at ALOHA, and mostly
358 occurred in the top 200 m in low abundances (Fig. 7a).
359 Ctenophores did not occur in our tows at ALOHA, and at K2 were almost exclusively
360 *Beroe abyssicola*. These relatively large (up to 12 cm long), red/purple-tinged ctenophores were
361 conspicuous in tows between 50-300m in the day, and then spread out more throughout the water
362 column at night (Fig. 7b). Although they did move into the upper 50m at night (where they were
363 absent in the day) (Fig. 7b), there was not a discernable diel migration (Table 3). Although we
364 enumerated fresh, unpreserved ctenophores immediately after tows, we cannot rule out that the
365 more delicate lobate or cydippid ctenophores also occurred at either site, but became damaged
366 beyond recognition.
367 Polychaetes occurred in similar abundances (~1 m^{-3}) between the two sites in the
368 epipelagic zone, however, while at ALOHA abundance of polychaetes was reduced considerably
369 below 200m, at K2 their abundances remained at ~0.3-0.75 m^{-3} throughout much of the
370 mesopelagic zone (Fig. 7). The majority of the polychaetes in the epipelagic zone at the two
371 sites were phyllodocids– especially *Tomopteris* spp., and larval forms of benthic polychaetes. At
372 K2 *Poeobius* sp. was also present and occurred exclusively in the mesopelagic zone.
373
374 *3.2.4 Radiolaria*

In addition to the metazoan zooplankton described above, we sampled large protozoan zooplankton at K2. These were mostly phaeodarian radiolarians, mainly in the order Phaeosphaeria (Aulosphaeridae and Sagosphaeridae) and in the families Aulacanthidae and Coelodendridae, that occurred in the mesopelagic zone at K2 (Fig. 9). Throughout the mesopelagic zone, these radiolarians were equal to a mean of 5.5% (range 2.7-13.7%) of the metazoan biomass (for 150-1000m day and night samples combined). The peak biomass occurred between 200-300m and ranged from 1.0 mg m^{-3} (day mean) to 1.9 mg m^{-3} (night mean). These radiolarians were also found in our sediment traps.

4. Discussion

4.1 General vertical patterns in zooplankton biomass and community structure

A striking difference between the two sites was the order of magnitude higher biomass at K2 compared with ALOHA. This is perhaps not surprising in epipelagic waters, as K2 is a mesotrophic site with higher primary production than the oligotrophic ALOHA site (Karl et al., 1996; Buesseler et al., this issue). However, the same order of magnitude higher biomass occurred in the mesopelagic zone at K2 as well, indicating higher production in surface waters is also fueling significant secondary production at depth at K2. This contrast in deep biomass has interesting implications for the mesopelagic food webs at these sites, which are supported by sinking particles, diel vertical migration, and carnivory, as discussed below. In a comparative study of plankton biomass at several stations from the subarctic to the subtropical western N. Pacific Ocean, Yamaguchi et al. (2004) also found zooplankton biomass decreased from north to south. In their study 0-1000 m integrated 'metazooplankton' biomass (>90μm) was also an order of magnitude higher at 44°N (sampled in August) than at 25°N (sampled in September) (mean of

398 day and night 0-1000m integrated biomass, calculated from Table 4 in Yamaguchi et al. 2004).
399 While the biomass was higher and animal size was significantly larger in the mesopelagic at K2,
400 the percentage of biomass in the large size fractions (>2mm) was similar between the two sites in
401 the mesopelagic zone. This suggests a more uniform community size structure in the
402 mesopelagic between the two sites, as opposed to the larger disparity in both biomass and size
403 structure of zooplankton in the epipelagic zone.

404 There were many other distinct differences in the communities at the two sites. The most
405 conspicuous is the deep population of *Neocalanus* species copepods (*N. cristatus*, *N. plumchrus*,
406 and *N. flemingeri*) and *Eucalanus bungii* at K2. These large copepods dominate the zooplankton
407 community in the subarctic Pacific and its marginal seas (Miller et al., 1984; Vinogradov, 1997;
408 Mackas and Tsuda, 1999), where they also undergo extensive ontogenetic (seasonal) vertical
409 migration (Miller et al., 1984; Kobari and Ikeda, 1999, 2001a, b; Tsuda et al., 1999; Shoden et
410 al., 2005). During our study period ontogenetic migrating copepods on average comprised 62%
411 of the mean mesozooplankton biomass, and 31% of the mean mesozooplankton abundance,
412 integrated between 150-1000 m (Kobari et al., this issue). Much of the *Neocalanus* population
413 still resided in the epipelagic zone (i.e., 74% of the 0-1000 m integrated *Neocalanus* population,
414 by number was in the upper 150 m); however, *N. flemingeri* was already in dormancy at depth
415 (residing at 200-500 m) and *E. bungii* had begun its annual descent, forming a mesopelagic peak
416 at 200-400m (Kobari et al., this issue).

417 Along with the ontogenetic migrators, other species, most notably ostracods and
418 chaetognaths, contributed significantly to the 200-500m peak in zooplankton abundance and
419 biomass at K2. The subsurface peak at ALOHA extended further, down to 750m, and was also
420 largely comprised of copepods, ostracods, and chaetognaths (Fig. 3, 8). Although lower in

421 abundance, larger crustacea such as euphausiids, mysids, amphipods, and decapods, as well as
422 fish, also contributed to the mesopelagic biomass peak, particularly at ALOHA. Mesopelagic
423 peaks in micronekton have been studied extensively in the mesopelagic boundary community off
424 Hawaii, and are comprised mainly of myctophid fish, with shrimp being the second most
425 abundant taxa (Benoit-Bird and Au, 2006). Mesopelagic peaks in biomass of micronekton have
426 also been noted between 500-600 m during both day and night in the subarctic North Pacific
427 Ocean (Nishikawa et al., 2001). Some of the taxa exhibited a bimodal distribution (e.g., calanoid
428 copepods at both sites, chaetognaths and hydrozoan medusae at K2) with both a near-surface and
429 a mesopelagic population, some of the latter of which underwent diel migration into surface
430 waters at night.

431 Diel vertical migration was pronounced at both sites, but the strength of migration was
432 higher overall at K2, as indicated by the overall N:D ratio of 2.5 for combined size classes and
433 by the diel migration indices for many of the major taxa. The N:D ratio at ALOHA of 1.7 for all
434 size classes combined is the same as that reported for the HOT station ALOHA climatology (Al-
435 Mutairi and Landry, 2001). Although the overall strength of migration was higher at K2, we
436 found a greater migration amplitude for all biomass size classes at ALOHA vs. K2. These
437 results are similar to Anderson et al. (1997) who found higher migration amplitudes at an
438 oligotrophic site than at meso- and eutrophic sites in the northeastern tropical Atlantic Ocean.
439 They hypothesized this difference was due to sensitivity of migrators to different light
440 environments, with increased light penetration in the oligotrophic site causing zooplankton to
441 migrate deeper to avoid visual predators (Andersen et al., 1997).

442 There was a less consistent pattern between sites in migration amplitude of individual
443 taxa, presumably due to the myriad of environmental factors, including light, that interact to

affect diel vertical migrations (e.g., Sameoto, 1984; Pearre, 2003). For example, the depth of the chlorophyll maximum at K2 (50 m) was shallower than at ALOHA (125 m), possibly leading to variations in depth distributions of different taxa at the two sites, such as the surface peak in calanoid copepods (day and night) which was shallower and confined to 0-50 m at K2, vs. ALOHA where it was distributed 0-150 m. A subsurface chlorophyll layer has been shown experimentally to control the depth of ascent of diel migrating copepods (Bohrer 1980), and the abundance of many mesozooplankton taxa was enhanced at the depth of the seasonal deep chlorophyll maximum in the Northwestern Atlantic Ocean (Ortner et al., 1980). Shoaling of the vertical distribution of *Eucalanus bungii* and *Neocalanus cristatus* during a subarctic NE Pacific mesoscale iron addition induced diatom bloom also indicates these copepods can respond to changes in chlorophyll concentrations (Tsuda et al. 2006). In addition, a temperature minimum of <2°C occurred at K2 near 100m (Buesseler et al., this issue), which may have also acted as a boundary for the surface calanoid copepod peak, and affected vertical distributions of other taxa. Indeed, thermocline depth had the greatest influence of all physical factors on vertical distribution of copepods in the eastern tropical Pacific Ocean (Sameoto, 1986). Low sub-surface oxygen concentration can also act as a control on zooplankton vertical distribution, as seen in the oxygen minimum zone of the Arabian Sea where oxygen is <0.1 ml L^{-1} (Smith et al., 1998; Wishner et al., 1998). Mesopelagic zone oxygen concentration never reached this suboxic level at either site in our study, but began to fall below 1 ml L^{-1} at ~300 m at K2, and at ~600 m at ALOHA (Buesseler et al., this issue), which may have served as a refuge or barrier depending on taxon-specific differences in physiological tolerance to low oxygen; however our wide depth intervals make it difficult to correlate zooplankton vertical distributions with oxyclines (Wishner et al. 1998).

Some taxa were strong migrators, with a N:D ratio >2 or a large migration amplitude (as indicated by diel change in WMD); some were even absent (or nearly so) in surface waters during the day. These taxa included ostracods, hyperiid amphipods, and to some extent euphausiids at both sites, hydrozoan medusae at ALOHA, and gammarid amphipods (*Cyphocaris* sp.) at K2. We note that within some of the other migrating, or even apparently non-migrating, groups there were also a number of individual genera or species that were clearly strong migrators, but are not apparent because of the very broad taxonomic categories we present. For example, there are clearly a number of calanoid copepod genera at both sites, such as *Pleuromama* and *Metridia* spp., that were absent in the epipelagic zone during the day, and migrated considerable distances into the surface at night. Many of the same strongly migrating copepods and other taxa that we found at ALOHA have been noted previously (Al-Mutairi and Landry, 2001). Thus, like interacting environmental factors discussed above, behavior at the species level is important in shaping vertical distribution patterns between the sites, but not always resolvable in our data set.

4.2 Sampling considerations and limitations of the data set

The potential sources of error in estimating biomass and abundance of zooplankton and micronekton with nets, particularly from deeper depths, are discussed in Angel and Pugh (2000), and include underestimation of fragile gelatinous zooplankton, net avoidance, vertical migration to depths deeper than the lowest sampling depth, and the inherent patchiness of plankton communities–due to passive or active aggregation and rapid reproduction and growth. While gelatinous taxa were well represented in our tows, some of the more delicate groups such as larvaceans were unrecognizable in deeper samples. Other gelatinous groups, such as lobate

ctenophores, were not found in fresh samples, but have been observed in the mesopelagic with submersibles off Japan (Hunt and Lindsay, 1999) and other locations (Harbison et al., 2001). Some daytime net avoidance may have occurred at both sites, as illustrated by a ~20% increase in 0-1000m integrated biomass at night. This may also be due to vertical migration of deeper (>1000m) zooplankton into the mesopelagic zone at night. We may have evidence for the latter, as indicated by a slight increase in some larger taxa such as mysids between 750-1000m at night at K2 (Fig. 5b). Finally, patchiness can be a higher source of error for taxa that tend to form aggregations or 'swarms' such as salps, pteropods, and medusae (Angel et al., 1982; Angel and Pugh, 2000). Thus abundances of these organisms can fluctuate over small spatial and temporal scales (Angel and Pugh, 2000).

4.3 Trophic structure

4.3.1 Mesopelagic particle feeders

A number of taxa that are known to feed on particles of either suspended or sinking detritus showed distinct peaks in the mesopelagic zone. These include calanoid and poecilostomatoid copepods, salps, polychaetes, and radiolaria at K2, harpacticoid copepods at ALOHA, and ostracods at both sites.

As noted previously, the mesopelagic peak in calanoid copepod abundance at K2 was due to the ontogenetically migrating copepods *Neocalanus* spp. and *Eucalanus bungii* (Kobari et al., this issue). These species may feed on sinking particles or on microzooplankton at depth (Dagg, 1993; Gifford, 1993 ; Kobari et al., 2003; Kobari et al., this issue). A detailed study of calanoid copepods down to 4000 m in the western subarctic Pacific Ocean found that numerically, and in terms of biomass, suspension feeders dominated the surface waters (Yamaguchi et al., 2002b).

513 However below 200 m, detritivores (70% by abundance and 15% by biomass) and carnivores
514 (1% by abundance, 10% by biomass) increased, with suspension feeders in diapause making up
515 most of the meso- and bathypelagic biomass (63%) (Yamaguchi et al., 2002b).
516 Mesopelagic peaks in poecilostomatoid copepod species, particularly the family
517 Oncaeidae, have been observed previously in a number of environments including the western
518 subarctic Pacific Ocean (Nishibe and Ikeda, 2004), the Arctic Ocean (Richter, 1994), the Red
519 Sea (Böttger-Schnack, 1990a, b), the Mediterranean Sea (Böttger-Schnack, 1996a), and the
520 western Indian Ocean (Böttger-Schnack, 1996b). Although fewer studies have been carried out
521 on the less abundant harpacticoid copepods, some genera, such as *Aegisthus* seen in the
522 mesopelagic at ALOHA, concentrate in the meso- and bathypelagic zones (Böttger-Schnack,
523 1996a). Poecilostomatoid and harpacticoid copepods are known to associate with larvacean
524 houses in epipelagic (Alldredge, 1972; Shanks and Edmondson, 1990) and mesopelagic
525 (Steinberg et al., 1994) waters, and with other types of epipelagic marine snow aggregates
526 (Shanks and Edmondson, 1990; Bochdansky and Herndl, 1992). Poecilostomatoids such as
527 *Oncaea* feed on larvacean houses and other kinds of aggregates (Alldredge, 1972; Lampitt et al.,
528 1993; Ohtsuka et al., 1993,1996). The poecilostomatoids and harpacticoids are not strong
529 vertical migrators at ALOHA and K2, as has been shown elsewhere (Böttger-Schnack, 1990a),
530 thus sinking particles are likely an important food source for these taxa.
531 Ostracods showed peaks in the mesopelagic and were strong diel vertical migrators, as
532 reported in other studies (Angel, 1979; Kaeriyama and Ikeda, 2002). Ostracods consume marine
533 snow (Lampitt et al., 1993), thus it is likely some of the deep-living species also consume
534 sinking or suspended particles of detritus, in addition to feeding in surface waters on
535 phytoplankton or microzooplankton (Angel, 1972) during diel migrations. Some mesopelagic

ostracods are also considered to be predators (although it is unknown if they are feeding on dead or live animals), thus, mesopelagic ostracods overall appear to be opportunistic, omnivore-detritivores (Vannier et al., 1998).

As salps are non-discriminate filter feeders (Madin and Deibel, 1998), their presence almost exclusively in the mesopelagic at K2 indicates they must be feeding on suspended or sinking particles. It is notable that at ALOHA we saw some salps in the epipelagic, but not in the mesopelagic. This could be a sampling artifact due to the inherent patchiness of salps that tend to be found in aggregations when they occur (i.e., we hit a patch at K2, but not at ALOHA) (Madin et al., 2006). Alternatively, this may simply be due to species-specific ecological/behavioral differences within the broad 'salp' taxonomic grouping between the two sites (which may also apply to differences seen between sites for some other broad taxonomic groupings). Another alternative is the higher particle concentration in epipelagic waters at K2 may be enough to clog salp internal feeding filters (Harbison et al., 1986; Perissinotto and Pakhomov, 1997; Madin et al., 2006), thus at least some species of salps remain in deeper waters, while at ALOHA surface particle concentrations are lower and salps can continue to feed in the epipelagic. Although we were not able to sample them adequately at mesopelagic depths in this study, larvaceans are another particle feeding pelagic tunicate (Alldredge and Madin, 1982) found at mesopelagic depths (Gorsky et al., 1991; Hamner and Robison, 1992; Hopcroft and Robison, 2005) that would also affect particle concentrations, and thus sinking particle flux (see below).

Polychaetes may also consume detritus in the mesopelagic zone, and are found associated with marine snow (Alldredge, 1972, 1976; Shanks and Edmondson, 1990; Bochdansky and Herndl, 1992; Steinberg et al., 1994). Taxa such as *Poeobius* sp. that we found in the mesopelagic at K2 feed by passively collecting sinking particles on mucus attached to their

560 tentacles (Uttal and Buck, 1996). Other polychaetes sampled such as *Tomopteris* sp. are
561 carnivores (Fauchald and Jumars, 1979).
562 The abundance and relative importance of phaeodarian radiolarians in the mesopelagic
563 zone at K2 indicates these protozoa are key components of the food web, and may be affecting
564 flux. Phaeodarians have high abundances worldwide (Klaas, 2001; Okazaki et al., 2004), and
565 have long been hypothesized to be generalist feeders whose diet also includes sinking detrital
566 particles (Gowing, 1986, 1989). Phaeodarians store their food and wastes in their phaeodium
567 (vacuoles within the animal), thus a record of their diet and feeding can be obtained (Gowing,
568 1986; Gowing and Bentham, 1994). Prey found in their phaeodium include bacteria, large virus-
569 like particles, other protozoans, small crustaceans and organic aggregates (Gowing and Bentham,
570 1994). Some zooplankton species including gelatinous zooplankton have been observed with
571 phaeodarian radiolarians in their guts (Gowing and Coale, 1989) and large concentrations of
572 phaeodarians at depth may be a food source for omnivorous copepods (Vinogradov and Tseitlin,
573 1983). Living phaeodarians found in sediment traps can contribute a substantial amount of the
574 organic carbon fluxes in oligotrophic regions (Gowing, 1986). Phaeodarians are prone to
575 dissolution and thus mainly living cells are found in deep sediment traps (Gowing and Coale,
576 1989; Gowing and Wishner, 1992). The radiolaria found in our sediment traps, along with
577 diatom frustules, may contribute to the high particulate silica flux at K2 (Lamborg et al., this
578 issue).
579
580 *4.3.2. Carnivore layer*
581 For mesopelagic fauna, the alternative to obtaining nutrition by diel vertical migration or
582 by particle feeding at depth is carnivory. We found distinct carnivore layers in the mesopelagic,

583 especially gelatinous zooplankton at K2. At K2 mesopelagic peaks were observed of
584 chaetognaths, hydrozoan medusae, polychaetes, and gymnosome pteropods, and in the upper
585 mesopelagic zone, layers of ctenophores and siphonophores. At both ALOHA and K2 a layer of
586 hyperiid amphipods occurred in the mesopelagic as well. Peaks of chaetognaths in the
587 mesopelagic have also been observed in the Northeast Atlantic, with highest abundances
588 between 200-300 m or 100-400 m, depending on location (Angel and Baker, 1982; Angel,
589 1989b). Siphonophore peaks have been reported as well in the mesopelagic Northeast Atlantic
590 and North Pacific oceans, with some migrating into the epipelagic at night (Angel and Baker,
591 1982; Pugh, 1984; Silguero and Robison, 2000). Mesopelagic ctenophores have been observed
592 by submersibles in the Pacific Ocean (Hunt and Lindsay, 1999; Harbison et al., 2001). High
593 biomass and abundance of mesopelagic gelatinous zooplankton has been reported previously for
594 the subarctic Pacific Ocean, with cnidarians constituting 18-26% of the dry weight, and at some
595 stations. more than half of the abundance of micronekton in the 0-1000 m water column
596 (Nishikawa et al., 2001).

597 In general, the proportion of mesozooplankton biomass that is carnivorous increases with
598 depth down to about 3000 m, and can be significant below the euphotic zone (Vinogradov and
599 Tseitlin, 1983). In the northwestern subarctic Pacific Ocean carnivores (e.g., carnivorous
600 copepods, chaetognaths, amphipods, mysids, and decapod shrimps) comprised ~ 25% of the
601 mesozooplankton biomass between 200-500 m and over 50% of the biomass between 500-1000
602 m (Vinogradov and Tseitlin, 1983). Carnivorous zooplankton comprised 10-30% of the total
603 zooplankton biomass between 0-300m in the Southern Ocean (Pakhomov et al., 1999). And as
604 noted above, carnivorous copepods in the subarctic Pacific Ocean constituted ~10% of the total
605 meso- and bathypelagic copepod biomass (Yamaguchi et al., 2002a).

606 We suggest that high food availability in the mesopelagic, i.e., the large population of
607 ontogenetic migrators such as *Neocalanus* spp. and *Eucalanus bungii,* are supporting the large
608 carnivorous populations at depth at K2. These copepods, while too large for other copepods to
609 consume, are an important food source for small mesopelagic fishes such as myctophids (Moku
610 et al., 2000), and presumably some of the micronektonic crustacea (e.g., decapod shrimp,
611 mysids) (Nishida et al., 1988) and gelatinous zooplankton (Nishikawa et al., 2001). In fact, it is
612 estimated that one-third of the life-time mortality of *Neocalanus plumchrus* could be explained
613 by predation in the mesopelagic zone, most likely by micronekton and chaetognaths (Mackas and
614 Tsuda, 1999).
615
616 *4.4 Implications for the biological pump and the efficiency of particle export*
617 The different patterns in community structure of zooplankton at the two study sites has
618 important implications for the functioning of mesopelagic food webs and the transport of
619 particulate organic matter to depth, ultimately affecting the efficiency of organic carbon
620 sequestration in the deep ocean. Buesseler et al. (2007) show a higher transfer efficiency (ratio
621 of POC flux at 500 m to 150m) of 46-55% at K2 vs. 20% at ALOHA. Furthermore, Steinberg et
622 al. (in press) show sinking POC flux is inadequate to meet the metabolic demands of the
623 zooplankton and microbial communities at both sites, and suggest that diel vertical migration and
624 carnivory are supporting mesopelagic metabolism. Ultimately we need to know more about
625 mesopelagic food webs in order to fully reconcile the contrasting transfer efficiencies, given the
626 high C demand of the biological community.
627 We can begin to analyze this issue. First, the disparity in the size classes of organisms
628 between the two sites, with considerably larger animals at K2, likely expedites transfer of POC

629 to depth at K2, due to the larger fecal pellets produced by animals there. These significantly
630 larger fecal pellets (median POC content 2-5 times larger at K2 than ALOHA), most of which
631 were produced by *Neocalanus* spp. copepods, were collected in our sediment traps in high
632 numbers at K2 (Wilson et al., this issue). Sinking and suspended particle-feeders occurred at
633 depth (with some exclusively in the mesopelagic zone) at both sites, indicating the importance of
634 this community in intercepting flux. Clearly these zooplankton are also repackaging particles
635 into new classes of fecal pellets (Wilson et al., this issue). Some taxa, such as the salps or
636 larvaceans at K2, could expedite C flux to depth and increase transfer efficiency by repackaging
637 suspended or slower sinking particles into fast-sinking fecal pellets (Bruland and Silver, 1981;
638 Madin, 1982; Caron et al., 1989), and in the case of larvaceans, incorporating these particles into
639 their mucous 'houses' which are subsequently discarded and sink (Alldredge, 1976; Gorsky and
640 Fenaux, 1998). The layers of carnivores seen in the upper mesopelagic are likely the source of
641 red fecal pellets injected into mesopelagic, as sampled by our sediment traps (Wilson et al., this
642 issue).

643 Second, the higher degree of diel migration of zooplankton at K2 may also account for
644 the increased transfer efficiency there. Active transport of CO_2 and DOC by migrator respiration
645 and excretion, respectively, at depth was double to an order of magnitude higher at K2 (16-46
646 mg C m^{-2} d^{-1}; range of CO_2 + DOC transport for both deployments) than at ALOHA (2-8 mg C
647 m^{-2} d^{-1}; within the range previously reported for ALOHA, Al-Mutairi and Landry, 2001) (see
648 Table 1, Steinberg et al. in press). This active transport is equal to 11-44% of the sinking POC
649 flux across 150 m measured by our sediment traps at ALOHA (18 mg C m^{-2} d^{-1} for both
650 deployments), and 26-200% of the 150 m sinking POC flux at K2 (62 and 23 mg C m^{-2} d^{-1} for
651 deployments 1 and 2, respectively). Furthermore, the active transport of respiratory CO_2

652 accounted for a higher proportion of mesopelagic zooplankton respiratory C demand between
653 150-1000 m at K2 (30-88%; for both deployments) than at ALOHA (15-59%), indicating that
654 many of the mesopelagic zooplankton at K2 are relying on surface primary production to meet
655 their nutritional needs, rather than on sinking particles (Steinberg et al., in press). The large
656 population of ontogenetic migrators at K2 presents a pathway of C flux that is considerably
657 greater than at ALOHA. This large active seasonal flux of organic matter to depth in the
658 subarctic Pacific Ocean can exceed the flux of sinking particles (Kobari et al., 2003). Seasonal
659 differences in migratory active C flux generally follow patterns in total migrant biomass (Zhang
660 and Dam, 1997; Steinberg et al., 2000; Al Mutairi and Landry, 2001). Future studies will need to
661 address how the large seasonality in biological productivity at K2 versus ALOHA affects the role
662 of zooplankton in the biological pump, as our study took place during a season of relatively higher
663 productivity (summer) in the subarctic Pacific Ocean compared to the remainder of the year.
664 In conclusion, our current understanding of vertical particle flux in marine ecosystems is
665 dominated by studies that emphasize bottom-up control (i.e., nutrients regulate growth of
666 phytoplankton, which eventually die, aggregate, and sink). While this is undoubtedly a crucial
667 process, and phytoplankton community structure is a factor controlling transfer efficiency of
668 carbon to depth (Boyd et al., this issue), less attention has been paid to the role of consumers and
669 predators exerting top-down control on vertical particle flux through different trophic
670 interactions (Verity and Smetacek, 1996; Wassmann, 1998). Studying the role of higher trophic
671 levels in C flux is a challenging prospect, especially in the understudied mesopelagic zone, but is
672 key to making future strides in our understanding of C transport and sequestration.
673
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Table 1. Total (all size fractions combined) integrated dry weight biomass during day and night at ALOHA and K2, and the percentage of biomass in the larger (>2mm) fractions. Values are mean (±1 s.d.) of n=4. For all depth zones, day and night biomass was significantly higher at K2 than ALOHA (ANOVA, site x day/night x depth interval, $p<0.05$). The % biomass in the >2mm fraction was significantly higher at K2 for the 0-150 m (ANOVA, site x day/night x depth interval, $p<0.05$), and 0-1000m (ANOVA, site x day/night, $p<0.05$) depth intervals.

Site and Depth (m)	Day (mg m^{-2})	Night (mg m^{-2})	Day >2mm (%)	Night >2mm (%)
ALOHA				
0-150	507 *(148)*	814 *(185)*	14 *(1)*	21 *(4)*
150-500	214 *(34)*	284 *(66)*	33 *(9)*	57 *(10)*
500-1000	326 *(112)*	165 *(23)*	65 *(7)*	60 *(11)*
0-1000	1047 *(134)*	1264 *(173)*	35 *(5)*	35 *(5)*
K2				
0-150	1952 *(572)*	4972 *(2355)*	33 *(9)*	52 *(21)*
150-500	4929 *(572)*	3986 *(363)*	45 *(7)*	41 *(3)*
500-1000	1924 *(344)*	1896 *(288)*	66 *(7)*	62 *(10)*
0-1000	8805 *(754)*	10853 *(1896)*	47 *(3)*	48 *(12)*

Table 2. Diel vertical migration indices for size fractionated dry weight biomass at ALOHA and K2. Values are mean of n = 4, calculated separately for each of the five size classes, and for all size classes combined (Total). N:D ratio, Ratio of night:day biomass integrated over the surface 0-150m. Ratio was computed separately for each day/night pair and then averaged. WMD, weighted mean depth for day and night (see methods). ΔWMD, amplitude of the migration, calculated as day WMD minus night WMD. Asterisks (*) indicate a significant difference between WMD day and WMD night (ANOVA, site x day/night x individual size fractions; or paired t-test for Total, i.e., all size fractions combined, $p < 0.05$).

Site and Size Fraction	N:D ratio in surface150 m	WMD Day (m)	WMD Night (m)	ΔWMD (m)
ALOHA				
0.35- 0.5	1.5	201	181	20
0.5 - 1.0	1.1	182	136	46
1.0 - 2.0	2.1	260	131	129*
2.0 - 5.0	2.7	419	245	174*
> 5.0	2.6	542	361	181*
Total	1.7	311	197	114*
K2				
0.35- 0.5	1.3	293	304	-11
0.5 - 1.0	1.4	315	284	31
1.0 - 2.0	2.1	306	261	45
2.0 - 5.0	4.2	382	294	88*
> 5.0	2.5	440	294	146*
Total	2.5	348	270	78

Table 3. Diel vertical migration indices for major taxa of zooplankton at ALOHA and K2. Values are mean of n = 2, unless otherwise noted. N:D ratio- Ratio of night:day taxon abundance integrated over the surface 0-150m. The ratio was computed separately for each day/night pair and then averaged. WMD- weighted mean depth for day and night (see methods). ΔWMD- amplitude of the migration, calculated as day WMD minus night WMD. Dash (-) indicates not determined (see footnotes below table for explanation). Asterisks (*) indicate a significant difference between WMD day and WMD night (paired t-test, $p < 0.05$).

Site and taxon	N:D ratio in surface150 m	WMD Day (m)	WMD Night (m)	ΔWMD (m)
ALOHA				
Calanoid copepods	1.4	234	192	42
Poecilostomatoid copepods	1.0	125	107	18
Cyclopoid copepods	0.7	192	316	-124
Harpacticoid copepods	< 0.1 [a]	473	439	34
Ostracods	2.5	246	169	77 *
Euphausiids	1.4	157	84	73 *
Hyperiid amphipods	2.4	172	108	64
Gammarid amphipods	< 0.1 [a]	151	342	-191
Decapods	1.2	56	52	4
Mysids	- [b]	625 [a]	25 [a]	600 [a]
Chaetognaths	0.8	129	137	-8
Siphonophores	0.9	148	192	-44
Hydrozoan medusae	3.0	342	165	177
Salps	1.7	90	103	-13
Doliolids	1.3	96	106	-10 *
Larvaceans	0.8	- [c]	- [c]	- [c]
Polychaetes	1.0	120	115	5
Thecosome pteropods	1.2	181	299	-117
Heteropods	4.6	93	131	-38
K2				
Calanoid copepods	1.8	218	154	64
Poecilostomatoid copepods	1.4	541	498	43
Cyclopoid copepods	0.5	178	332	-154
Harpacticoid copepods	- [b]	450 [a]	- [e]	- [e]
Ostracods	48.9	351	313	38 *
Euphausiids	16.9	111	34	77
Hyperiid amphipods	3.6	194	134	60
Gammarid amphipods	- [b]	308	130	178
Decapods	0.7	356	410	-54
Mysids	- [b]	701	740	-39 *
Chaetognaths	1.6	- [d]	- [d]	- [d]
Siphonophores	1.1	205	261	-56
Hydrozoan medusae	0.8	- [d]	- [d]	- [d]
Pteropods	0.5	298	321	-23
Salps	- [b]	285	268	17
Doliolids	- [b]	426	431	-5
Larvaceans	1.4	- [c]	- [c]	- [c]
Polychaetes	2.5	480	429	51
Thecosome pteropods	0.7	- [d]	- [d]	- [d]
Gymnosome pteropods	< 0.1	196	98	98
Ctenophores	0.4	114	403	9

[a] n=1 (for second replicate N:D undefined as abundance=0 in 0-150m layer during day)
[b] each replicate either did not occur in 0-150 m layer in day (i.e., N:D undefined) or at night (i.e., N:D=0)

[c] no data available below 150m
[d] pronounced bimodal distribution, WMD not calculated
[e] did not occur

Figure captions

Figure 1. Day and night size-fractionated zooplankton biomass (mg m^{-3}) at stations ALOHA and K2 (redrawn from Steinberg et al., in press). Day or night biomass values are the mean of n=2 tows taken at the beginning and end of each of 2 sediment trap deployments (D1 and D2) at each station a) ALOHA D1, mean of tows taken 24 and 28 June 2004, b) ALOHA D2, mean of tows taken 3 and 8 July 2004, c) K2 D1, mean of tows taken 1 and 5 August 2005, d) K2 D2, mean of tows taken 12 and 16 August 2005. Note the biomass scale for K2 is an order of magnitude larger than for ALOHA, and the irregular depth intervals reflecting the actual sampling intervals.

Figure 2. Percent dry weight of zooplankton in different size fractions during day and night at stations ALOHA and K2. Day or night values are each the mean of n = 4 casts taken at each station.

Figure 3a. Day/night profiles of the four major orders of copepods at ALOHA. Values are mean of n=2, with error bars indicating the range. Note abundance scales vary, and the irregular depth intervals reflecting the actual sampling intervals.

Figure 3b. Day/night profiles of the four major orders of copepods at K2. Figure is as described in Fig. 3a.

Figure 4. Percent abundance of the four major orders of copepods during day and night at stations ALOHA and K2. Day or night values are each the mean of n = 2 casts analyzed for taxonomic composition at each station.

Figure 5a. Day/night profiles of crustacean zooplankton taxa (other than copepods) at ALOHA. Values are mean of n=2, with error bars indicating the range. Note abundance scales vary, and the irregular depth intervals reflecting the actual sampling intervals.

Figure 5b. Day/night profiles of crustacean zooplankton taxa (other than copepods) at K2. Figure is as described in Fig. 5a.

Figure 6a. Day/night profiles of gelatinous zooplankton (chaetognaths, hydrozoa, and pelagic tunicates) at ALOHA. Values are mean of n=2, with error bars indicating the range. Note abundance scales vary, and the irregular depth intervals reflecting the actual sampling intervals.

Figure 6b. Day/night profiles of gelatinous zooplankton (chaetognaths, hydrozoa, and pelagic tunicates) at K2. Figure is as described in Fig. 6a.

Figure 7a. Day/night profiles of gelatinous zooplankton (pelagic snails) and polychaete worms at ALOHA. Values are mean of n=2, with error bars indicating the range. Note abundance scales vary, and the irregular depth intervals reflecting the actual sampling intervals.

Figure 7b. Day/night profiles of gelatinous zooplankton (pelagic snails and ctenophores) and polychaete worms at K2. Figure is as described in Fig. 7a. Note biomass of ctenophores is also given.

Figure 8. Percent abundance of other crustacea (non-copepod), gelatinous zooplankton, and polychaetes during day and night at stations ALOHA and K2. Day or night values are each the mean of n=2 casts analyzed for taxonomic composition at each station. 'Other' category includes bivalve larvae, isopods, larval fish, and small squids. *Note: Larvacean data only included for 0-150m depth intervals (see text).

Figure 9. Abundance and biomass of phaeodarian radiolaria during day and night at station K2. Day or night values are each the mean of n=2 (error bars indicate the range) for abundance, and the mean of n=3 (error bars are ±1 s.d.) for biomass. Note the irregular depth intervals reflecting the actual sampling intervals.

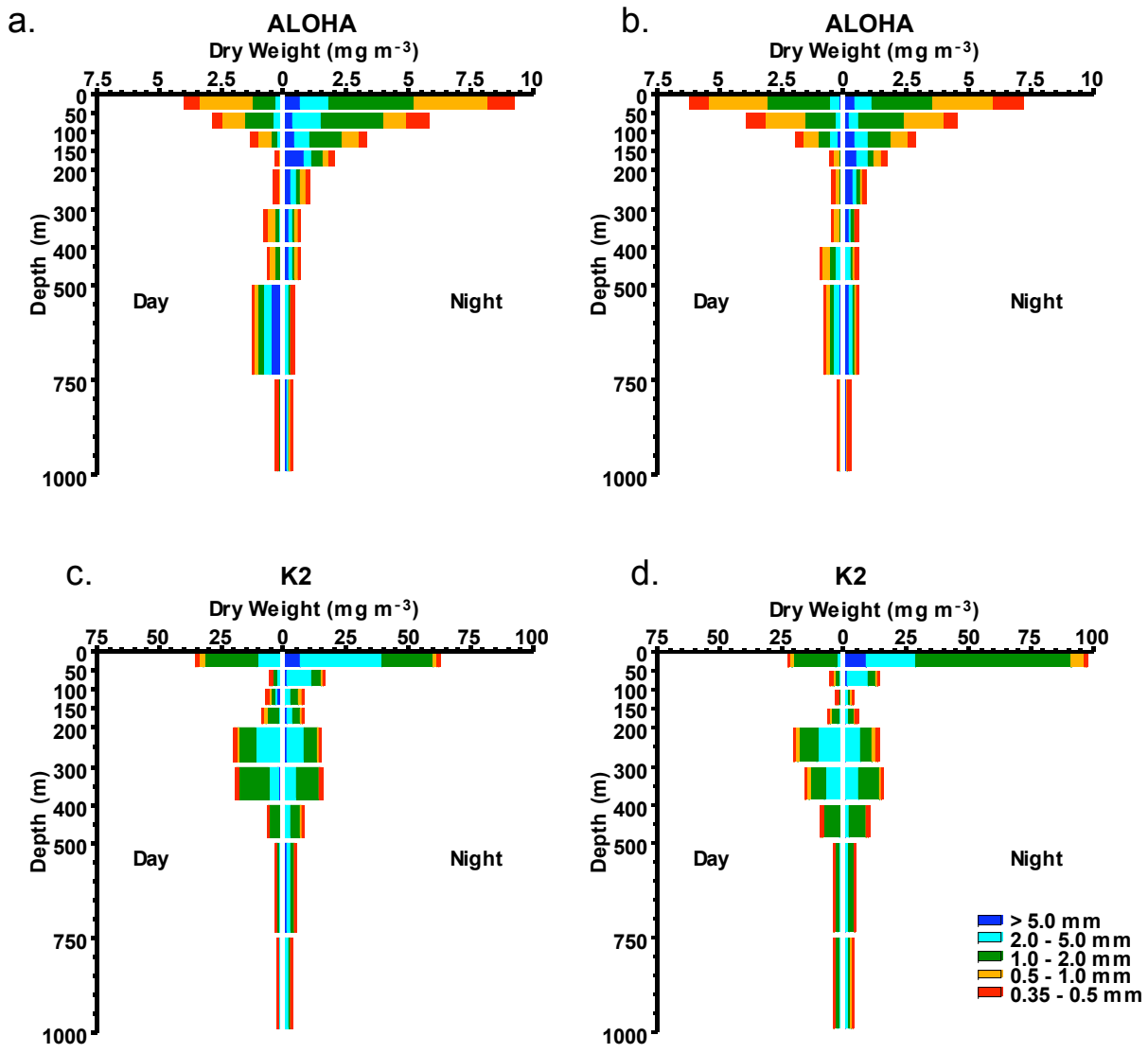

Fig. 1.
Steinberg et al.

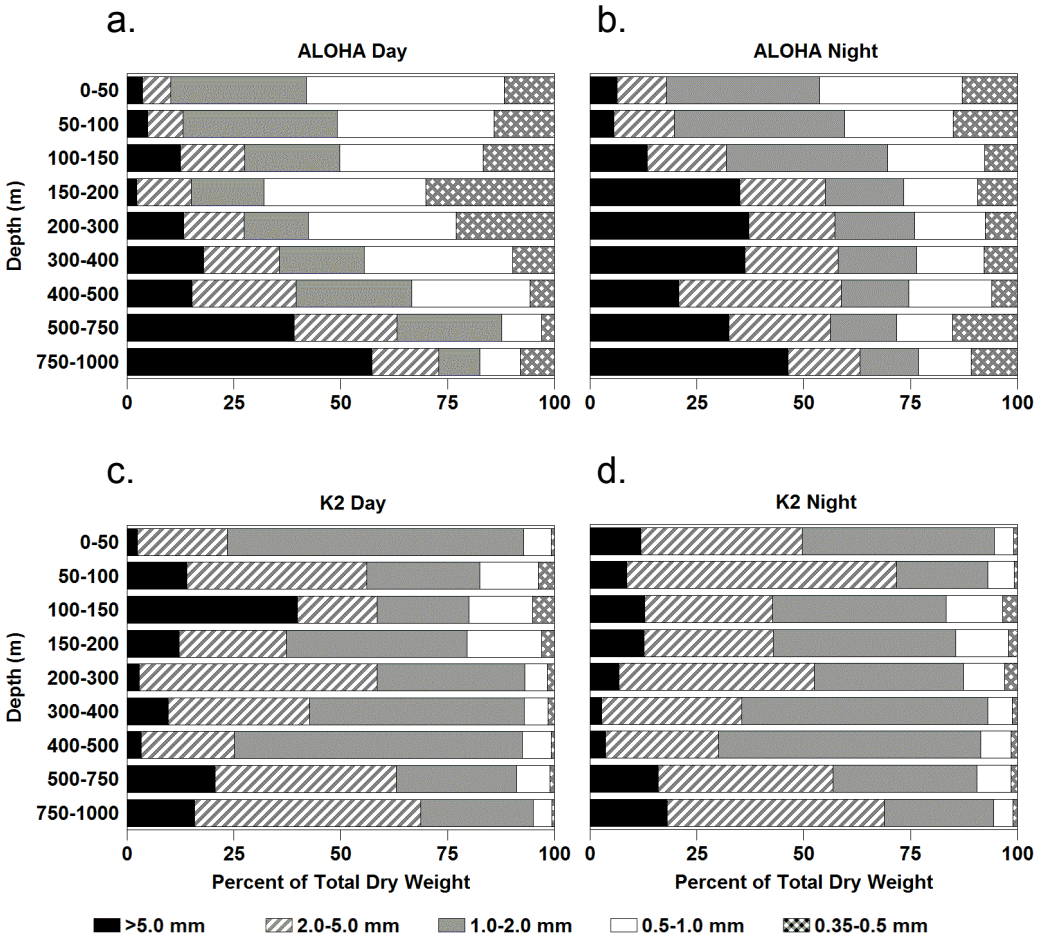

Fig. 2.
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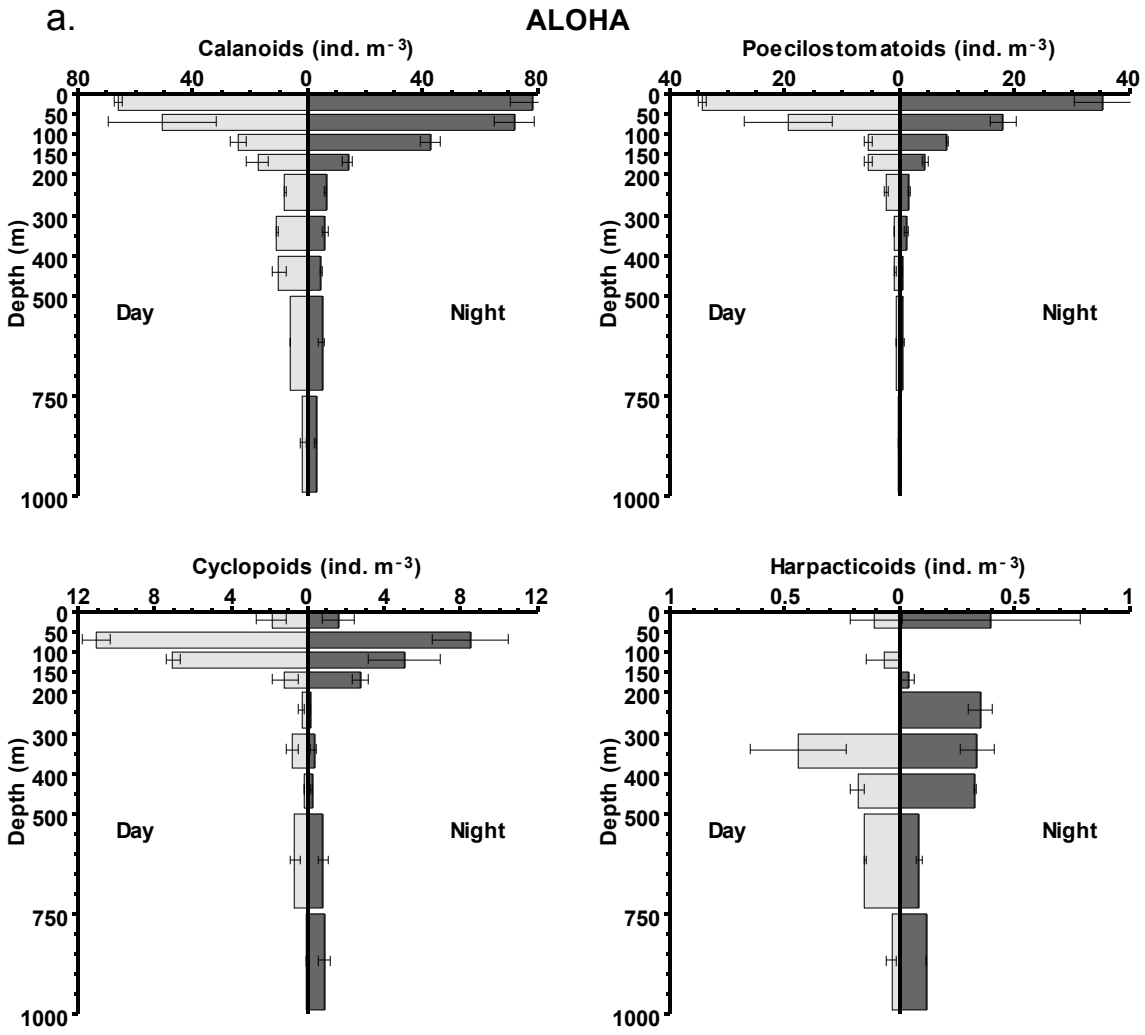

Fig. 3a.
Steinberg et al.

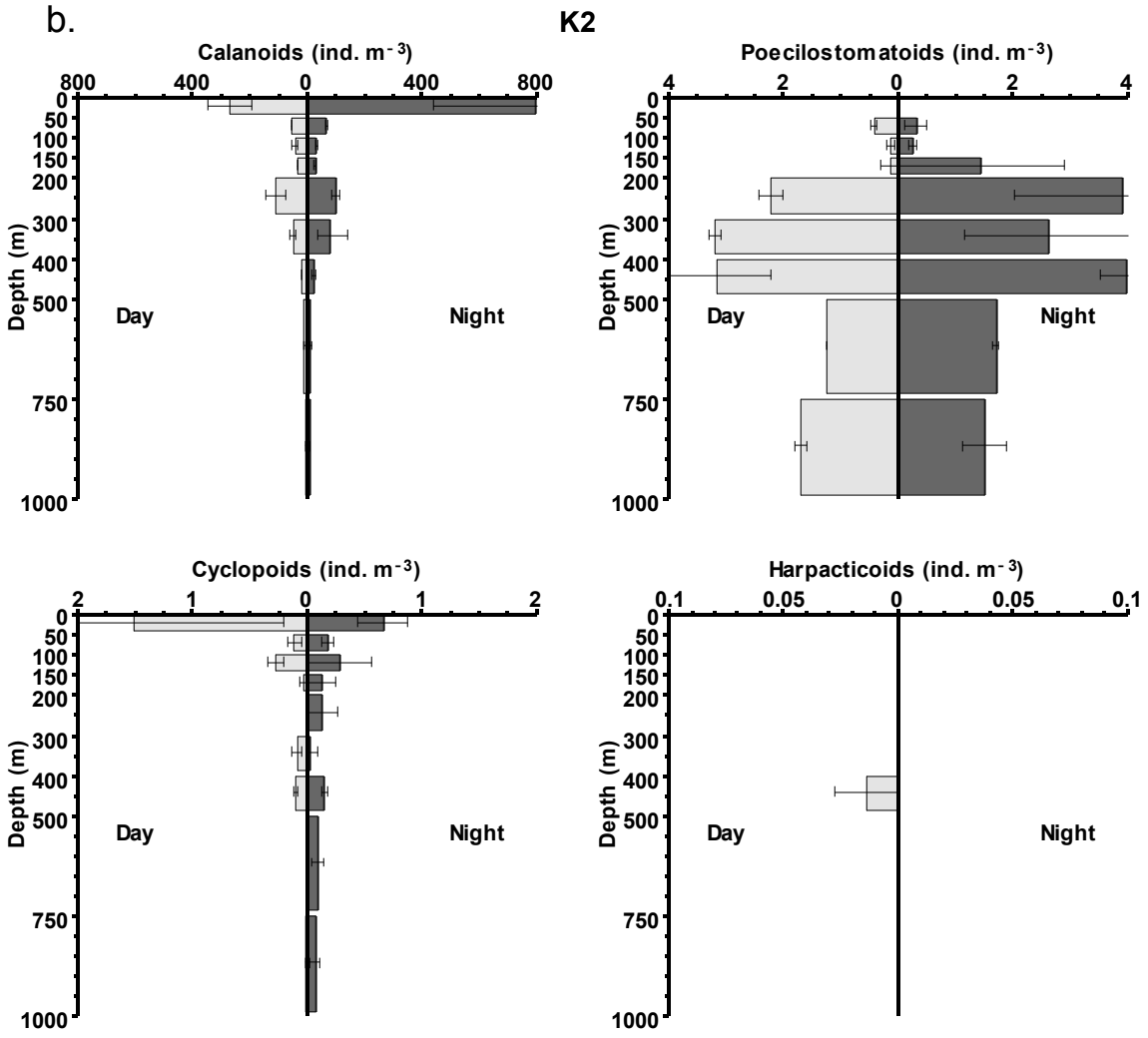

Fig. 3b.
Steinberg et al.

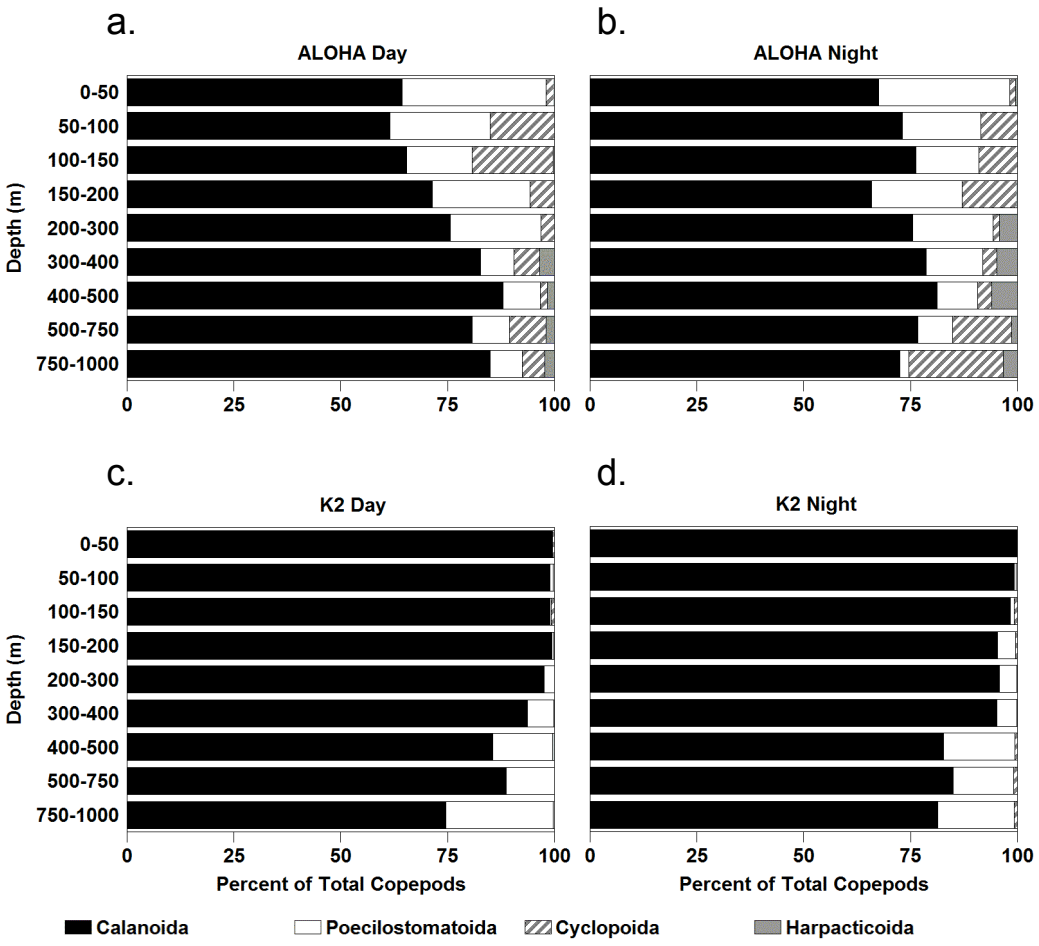

Fig. 4.
Steinberg et al.

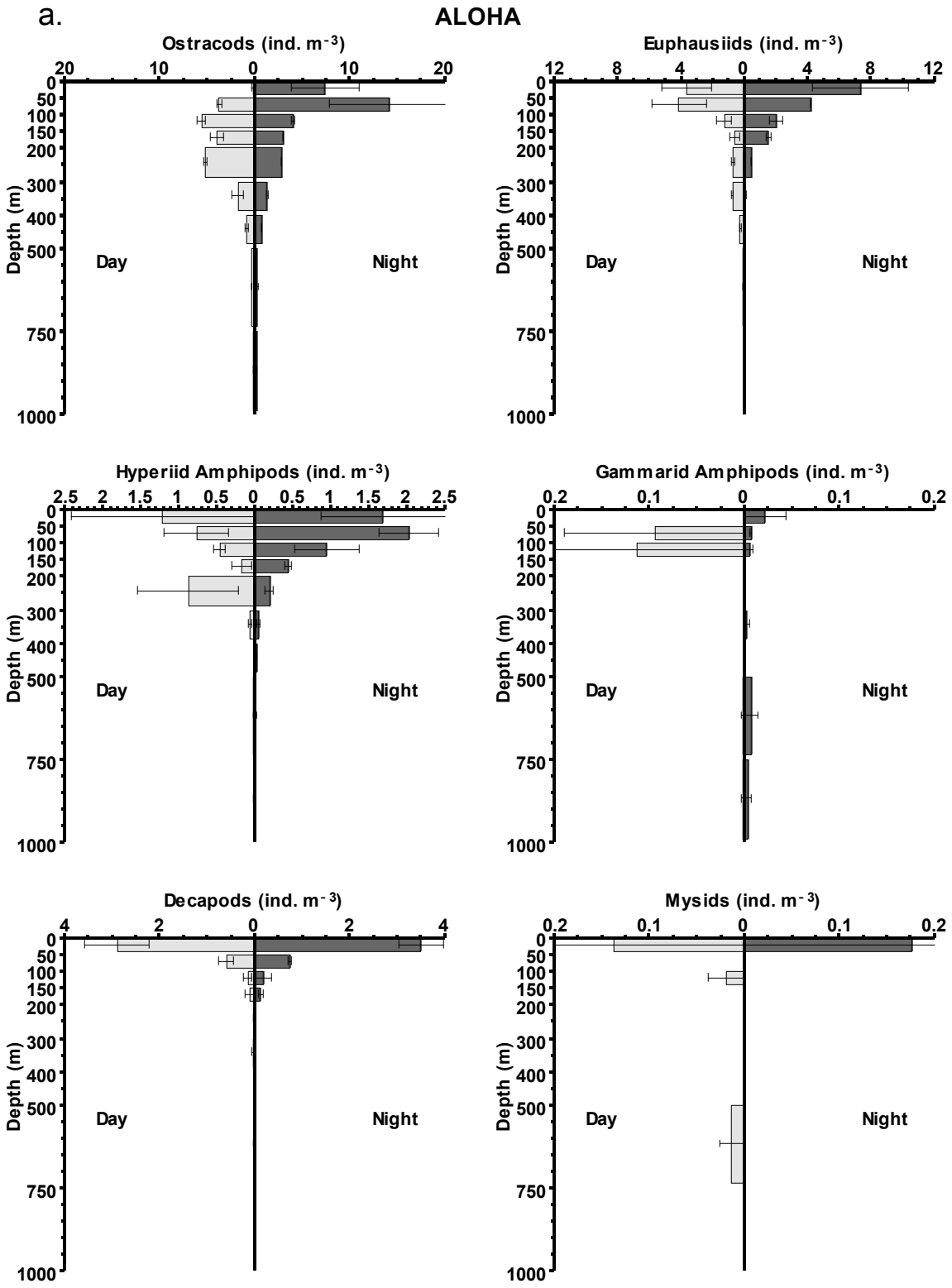

Fig. 5a.
Steinberg et al.

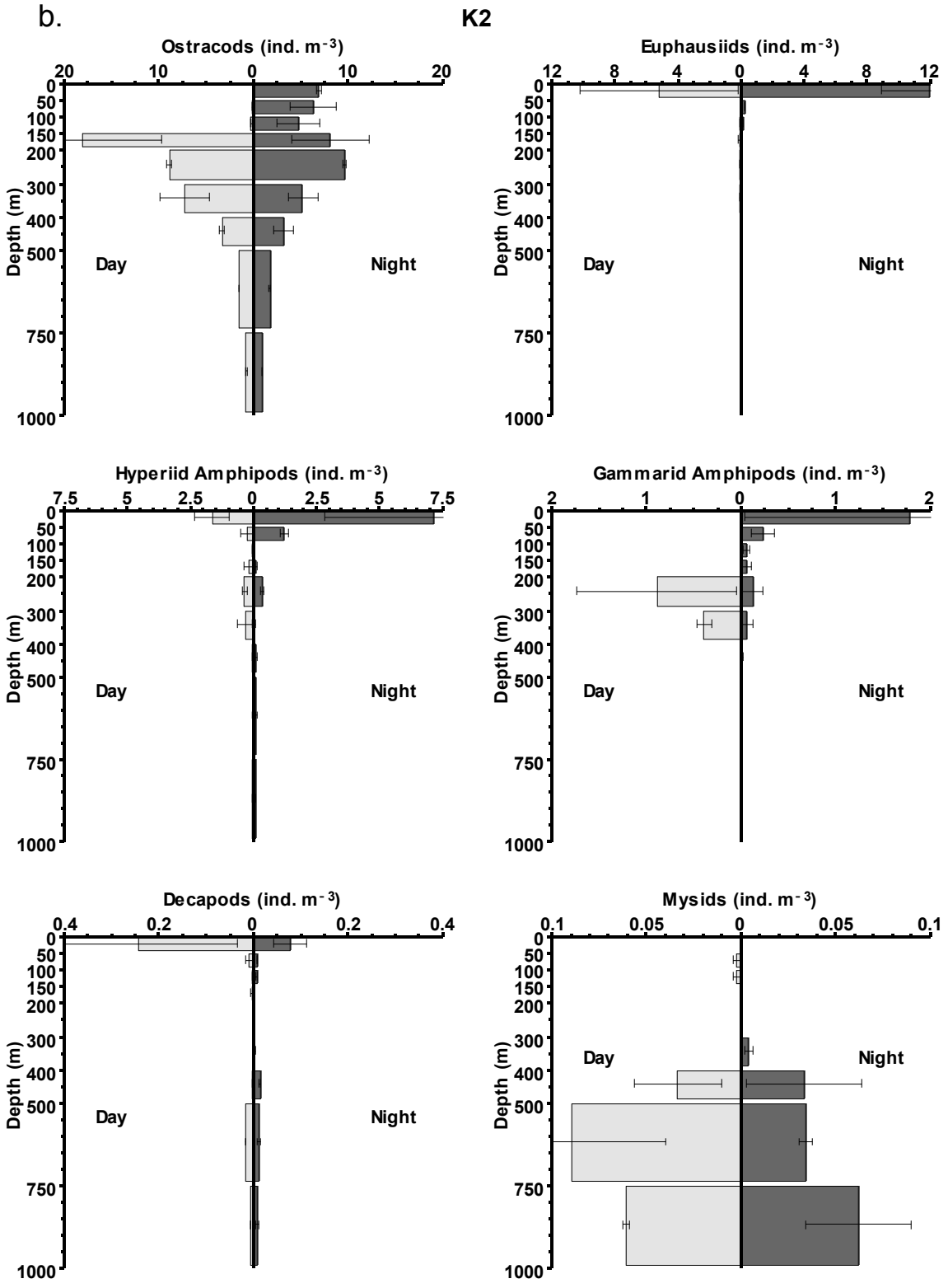

Fig. 5b.
Steinberg et al.

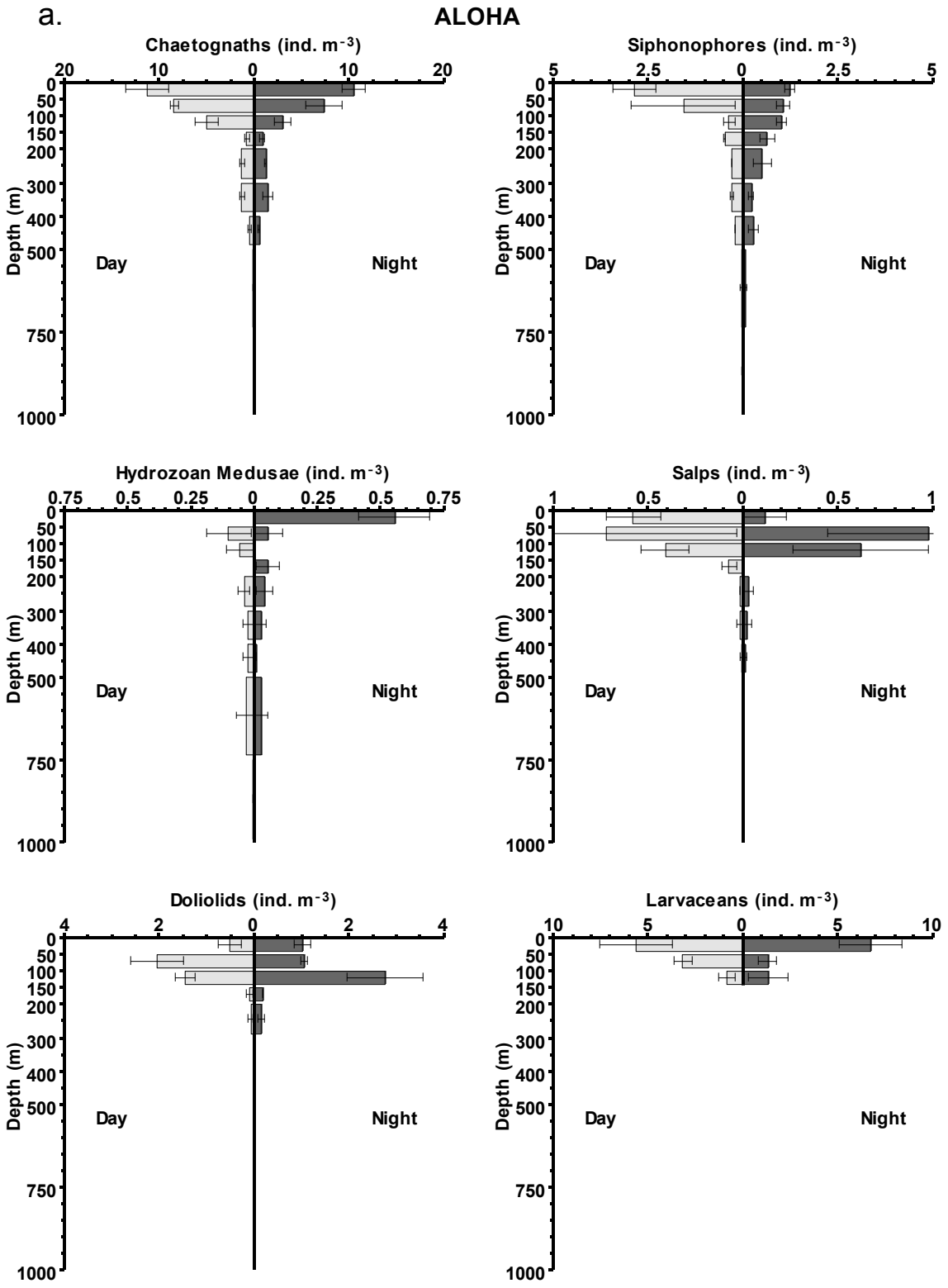

Fig. 6a.
Steinberg et al.

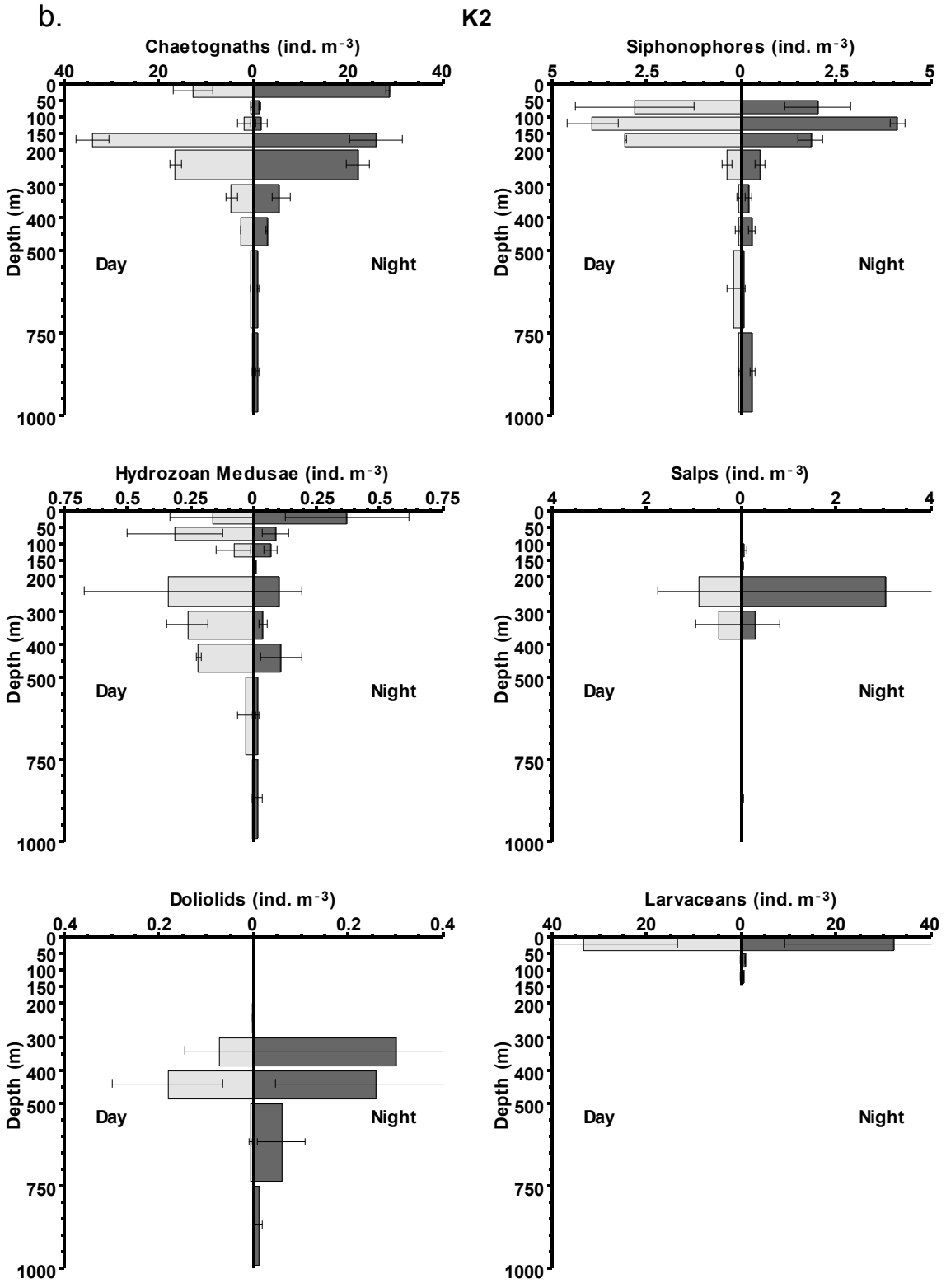

Fig. 6b.
Steinberg et al.

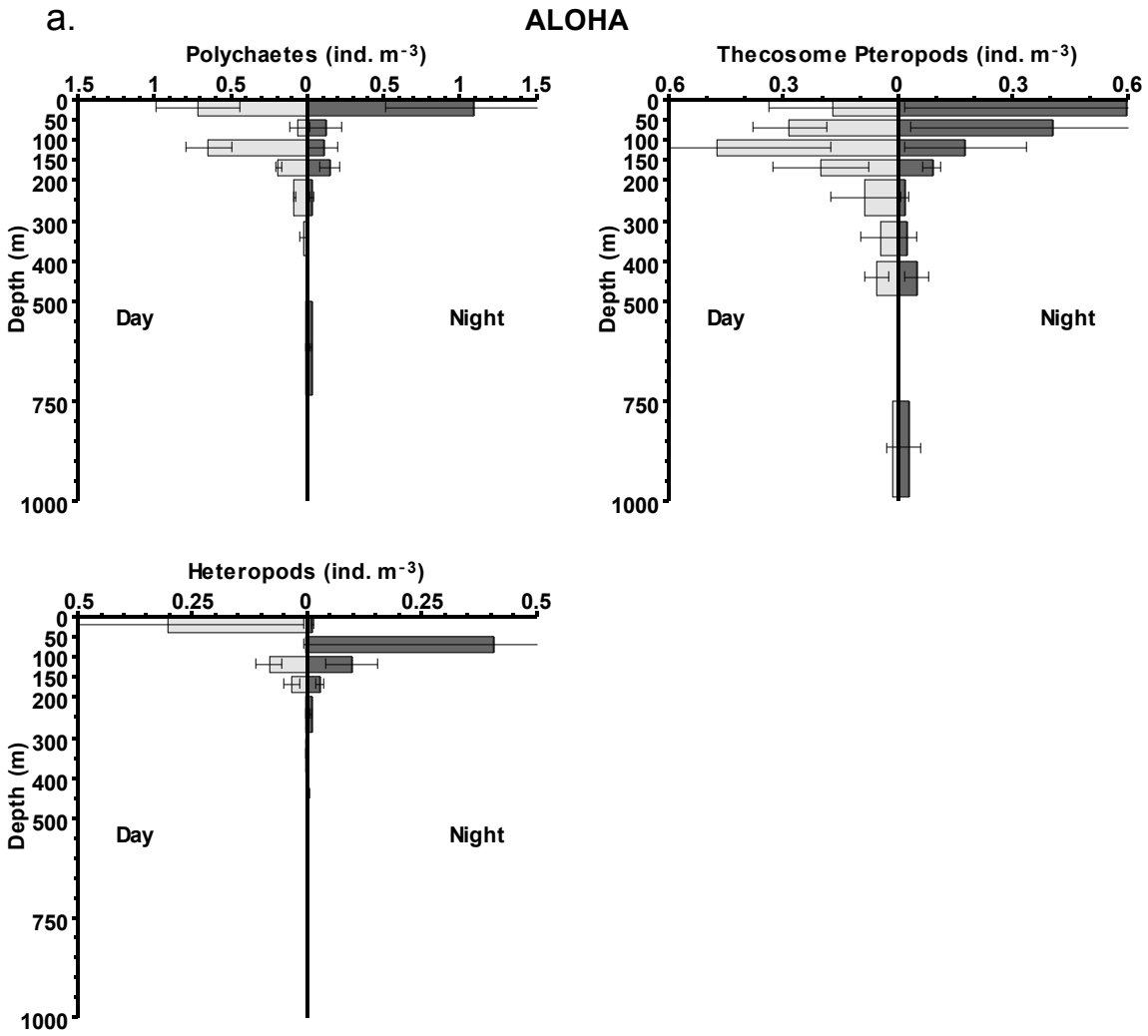

Fig. 7a.
Steinberg et al.

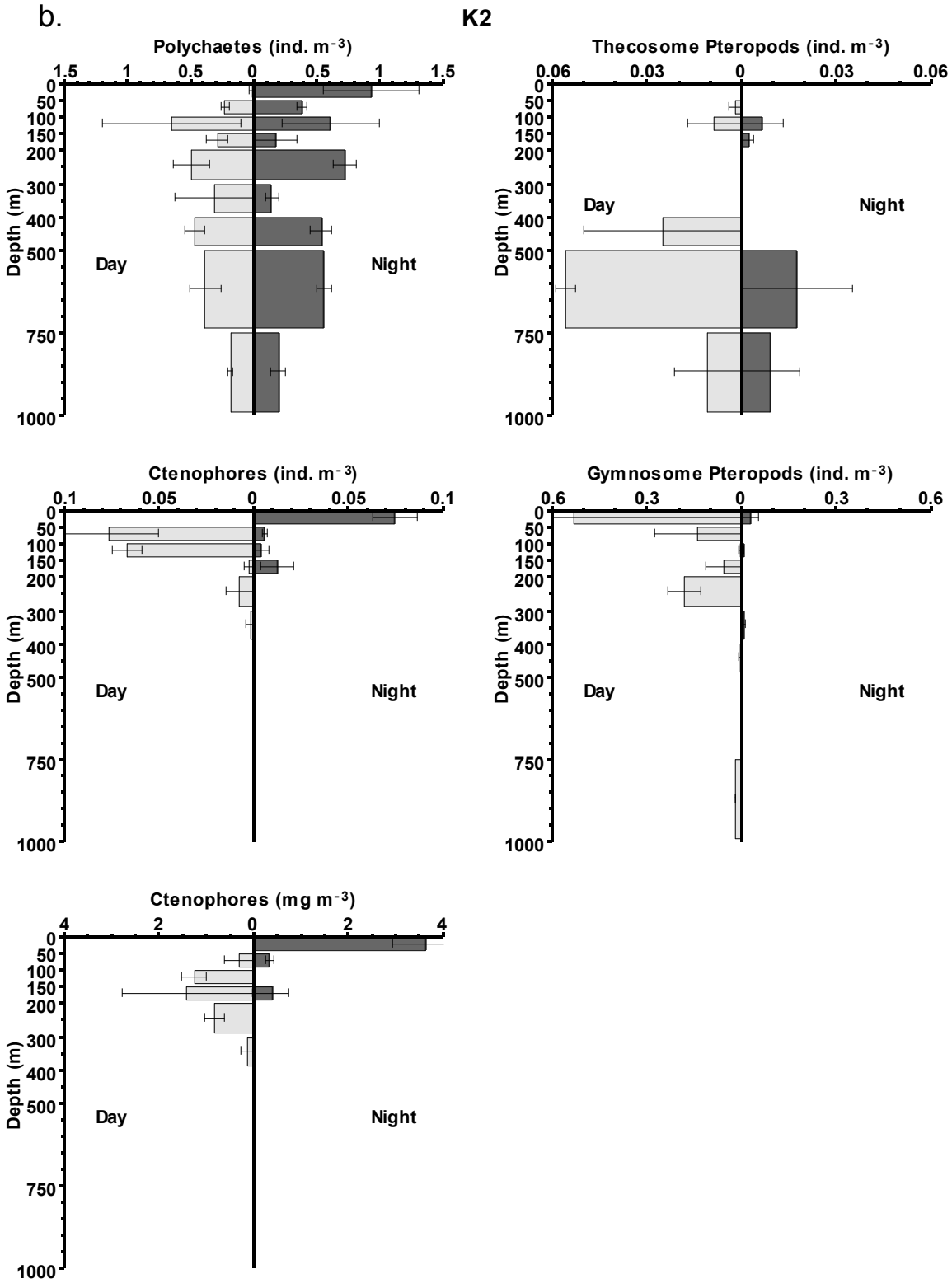

Fig. 7b.
Steinberg et al.

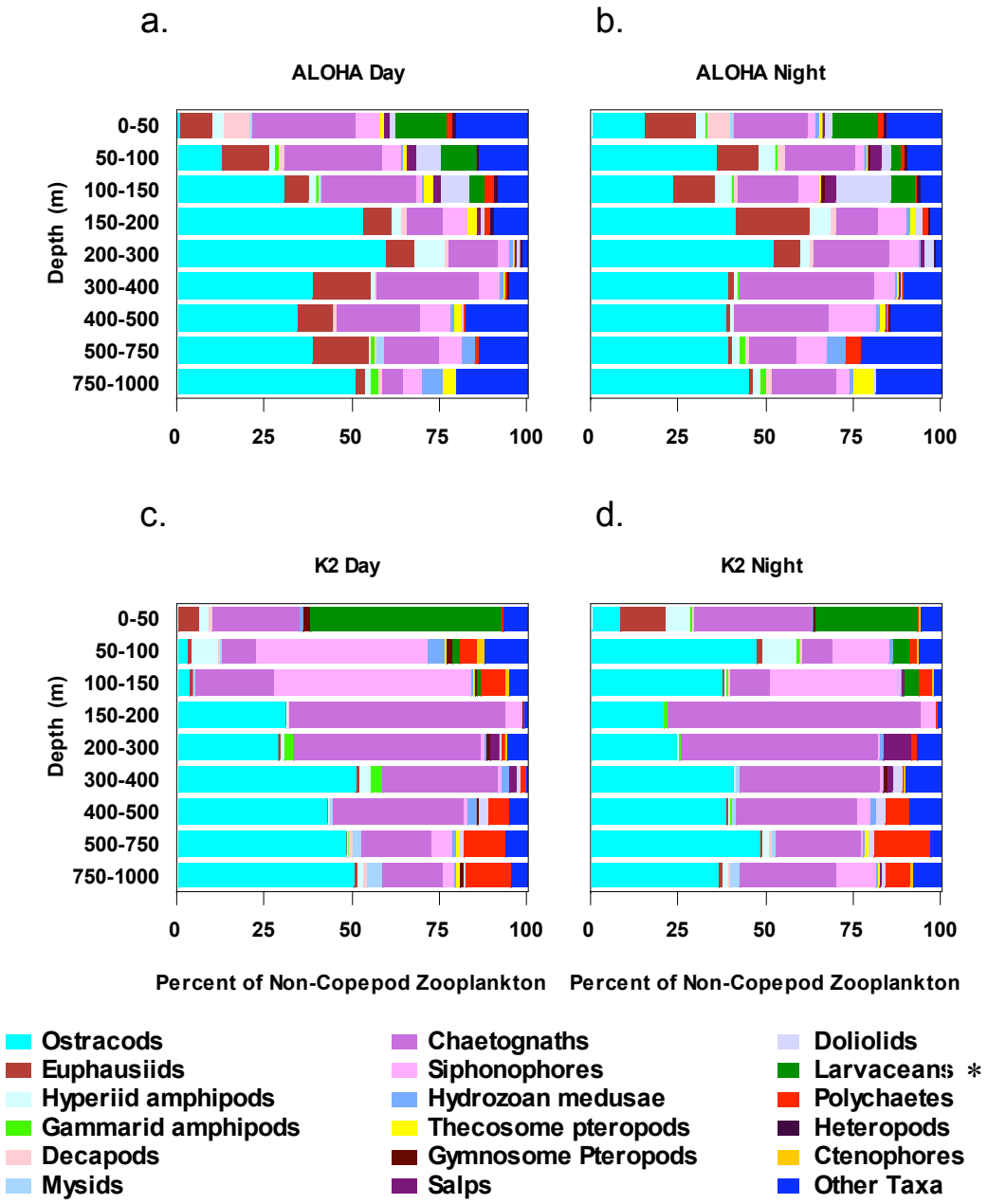

Fig. 8.
Steinberg et al.

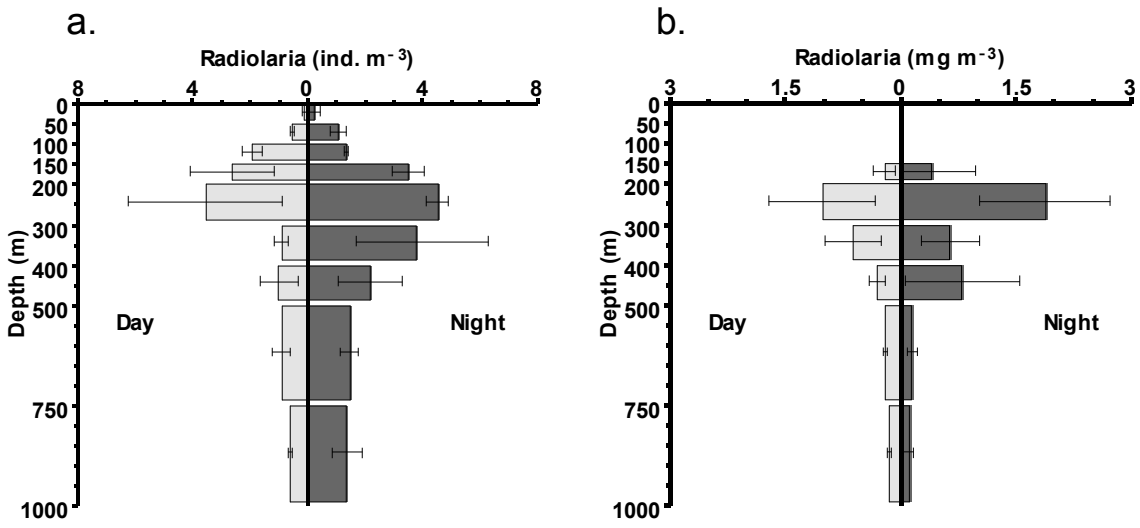

Fig 9.
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