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The fossil record and palaeoenvironmental significance of

marine arthropod zooplankton

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Abstract.

Arthropods are a major component of the marine zooplankton, functioning as intermediates between primary producers and tertiary consumers in pelagic food webs. They have likely occupied the water column ecospace since the early Cambrian, co-evolving with several major plankton groups through the Phanerozoic. Analysis of the fossil record of arthropods indicates that a zooplanktonic lifestyle has arisen independently across several arthropod groups, and that the arthropod body plan has shown adaptability to fundamental environmental change. Key anatomical adaptations and reproductive strategies that are compatible with and/or facilitate a zooplanktonic lifestyle include well-developed swimming appendages, buoyancy, an active metabolism supported by efficient respiration, visual or photoreception organs for use in detecting mates, food and predators, and the nurturing of young within the exoskeleton. Many of these characters are apparent in the earliest record of arthropods. The development and diversification of arthropod zooplankton into the food chain helped enable large secondary and tertiary consumers to enter the water column and also contributed to the export of organic matter to the seabed via the faecal stream. Although the fossil record of arthropod zooplankton is extremely poor for most of the Phanerozoic, their position in marine food webs suggests they have been fundamental to rebuilding marine trophic structure following major extinction events, and to maintaining marine plankton diversity through Phanerozoic time.

1. Introduction

The global ocean fauna and flora is dominated in abundance and biomass by the drifting and swimming organisms collectively referred to as plankton, ranging from tiny picoplankton, just 2-3 μm in diameter, that are a significant component of ocean biomass (Buitenhuis et al., 2012), to macro-scale arthropod zooplankton predators (CMarZ, 2004). Plankton occurs at all depths within the oceans, and many species have wide biogeographical distribution. Zooplankton includes both animals and unicellular 'protistans' that are critical intermediaries (primary and secondary consumers) in the flow of energy and biomass through marine ecosystems.

In this paper we use the term 'zooplankton' to embrace organisms that have both a strictly planktonic (floating or drifting in the water column) and/or a nektonic lifestyle (able to swim and move independently of currents) as the difference between these lifestyles is often difficult to evaluate for fossil species. Zooplankton lives both in demersal (the zone close to the sea bed) and pelagic (the water column between the demersal zone and the surface) environments. Marine zooplankton diversity consists of about 7000 species, which includes eukaryotes such as rhizarians, actinopods, ciliophors, chaetognaths, rotifers, arthropods, ctenophores, cnidarians and chordates (CMarZ, 2004). Even given that this diversity is most likely an under-estimate relative to the physical area they occupy, it is by no means rich when compared, for example, to the more than 1 million insect species described from the terrestrial biosphere (Bucklin et al., 2010). The lower diversity of the zooplankton possibly in part reflects the environmental uniformity of pelagic habitats, with their relatively low physical heterogeneity compared to benthic or terrestrial niches. However, recent genetic studies have challenged previous assessments of biodiversity, and morphologically defined species might consist of complex, genetically distinct populations and cryptic

70   species, as it is well documented, for example, for foraminifera (see Darling et al.,

71   1996, 1999).

72   Among the Recent zooplankton, arthropods, with more than 4000 species living

73   permanently in the water column (holoplankton), are the most diverse group (Fig. 1).

74   In addition to these taxa, many arthropods are present in the plankton for only the first

75   part of their life cycle (meroplankton). Arthropods, at both adult and larval/juvenile

76   stages are primary and secondary consumers and frequently represent more than 50-

77   70% of the total plankton species diversity. Among the arthropods, copepods are by

78   far the dominant group, both in terms of species diversity (often more than 50% of

79   total plankton species diversity (CMarZ, 2004) and sheer abundance (e.g., Jivaluk,

80   2000), but other groups such as ostracods and eumalacostracans (both holo- and

81   meroplanktonic) can also be very diverse, constituting 2-10% of total plankton

82   diversity and abundance (Jivaluk, 2000; CMarZ, 2004).

83   This paper examines the key parameters of morphology that characterise arthropod

84   zooplankton. Many of these characteristics have been evident for over 500 million

85   years. We examine the veracity of the arthropod zooplankton fossil record through

86   time, focussing especially on the earliest evidence of arthropod zooplankton in the

87   Cambrian, where the fossil record is most complete, and also identifying major gaps

88   in the post-Carboniferous record of all arthropod groups. Lastly, we review the impact

89   of arthropod zooplankton on the evolution of marine ecosystems. Herein, the informal

90   terms 'early', 'mid' and 'late' Cambrian refer to the Terreneuvian Epoch and

91   unnamed Cambrian Epoch 2, the unnamed Cambrian Epoch 3, and the Furongian

92   Epoch respectively (for details of Cambrian stratigraphy see Peng and Babcock,

93   2011).

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2. Arthropod anatomies and zooplanktonic lifestyle

Arthropods possess several anatomical adaptations and reproductive strategies that are compatible with and/or facilitate a planktonic lifestyle (Figs 1, 2). These include well developed swimming appendages, buoyancy, an active metabolism supported by an efficient respiration, sensory organs (to find mates, or detect food or predators), and nurturing of young within the carapace (Figs 1, 2). Molecular clocks point to possible divergence times between major arthropod groups (e.g., Edgecombe and Legg, 2014), but with considerable uncertainties, sometimes tens of Myrs (see Rota-Stabelli et al., 2013). Nevertheless, they provide a general time frame for the appearance of key anatomical characteristics in arthropod evolutionary history (Figs 2, 3).

2.1. A basis for arthropod adaptability

The hypothetical ancestral Precambrian pan-arthropod was probably benthic and possessed a trunk of externally homonomous (essentially identical) segments, each bearing an undifferentiated pair of appendages (Edgecombe and Legg, 2013). Though the precise body plan organization of these arthropods is unknown, the hypothetical animal might be compared to living onychophorans and tardigrades, or to some early Cambrian lobopodian-like ecdysozoans (see review in Dzik, 2011) in which only the first head appendage is differentiated (e.g., *Jianshanopodia*; Vannier et al., 2014). The early Cambrian pan-arthropod body plan already represented an exceptional evolutionary basis for diversification and appendage specialisation, as exemplified by the wide range of arthropod morphologies observable from the early Cambrian onwards (Hou et al., 2004; Figs 2, 4).

119   Specialization in appendage structure along the antero-posterior axis commenced

120   with the first post-antennular appendage, the process of appendage specialization

121   being controlled by Hox genes (Pearson et al., 2005; Stansbury and Moczek, 2013).

122   Specialisation of the appendages is associated with feeding and locomotion strategies

123   (e.g., Budd, 2003; Chen et al., 2007; Waloszek et al., 2007). These adaptations, for

124   locomotion and feeding were already expressed in Cambrian free-living arthropod

125   larval stages such as *Wujicaris muelleri* Zhang et al., 2010 and *Rehbachiella*

126   *kinnekullensis* Waloszek and Mass, 2005. As feeding and locomotory strategies are of

127   the utmost importance for plankton and other types of colonization (see below), this

128   suggests that ancestral arthropods possessed an anatomical basis that allowed

129   colonization of the water column.

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131   ***2.2. Locomotion***

132   The morphology of numerous Cambrian arthropods suggests that they had

133   swimming abilities, pertinently in basal groups such as the Radiodonta (e.g.,

134   *Anomalocaris*, *Peytoia* and *Hurdia*; Fig. 2), gilled lobopodians (e.g., *Opabinia*) and

135   bivalved arthropods such as *Nereocaris* and *Isoxys* (see Legg et al., 2012, 2013;

136   Vannier and Chen, 2000; Fig. 4F, J). Radiodonta and gilled lobopodians swam in the

137   water column by synchronized movement of lateral flap-like structures (Figs 2, 4I).

138   *Anomalocaris* and related forms possibly waved their lateral lobes as a continuous

139   single flap, reminiscent of the swimming of Recent manta rays (Usami, 2006; Daley

140   et al., 2013). Among arthropods, this mode of swimming seems to be unique to the

141   Radiodonta and gilled lobopodians and as such is limited to the early Cambrian-Early

142   Devonian interval.

143   Unlike the majority of arthropods that swim using their appendages, some bivalved

144   arthropods may have used the posterior part of their body for propulsion, as in the

145   case of *Nereocaris* (Legg et al., 2012; Fig. 2). Propulsion may have been generated by

146   undulations of the elongate abdomen and telson. This swimming mechanism,

147   involving the abdomen and posterior paddle, recalls the caridoid escape reaction

148   observed in some Recent arthropods, such as euphausiaceans and decapods, that

149   allows animals to escape predators through rapid abdominal flexures that produce

150   powerful backwards swimming strokes (Waggett and Buskey, 2008). Several

151   Cambrian arthropods such as *Nereocaris* and *Waptia* possessed a flexible posterior

152   body (Legg et al., 2012; Vannier et al., 2012), implying that they might have

153   performed an escape reaction by fast contraction of the "abdomen". This kind of

154   locomotion could be performed by any arthropod in which at least part of the trunk

155   protrudes posteriorly from the carapace, as in malacostracans such as *Nebalia* (see

156   Vannier et al., 1997a).

157   These 'early' modes of locomotion are quite different from those of Recent and

158   more derived arthropod zooplankton in which movement mostly involves swimming

159   adaptations of various appendages (Fig. 2). The development of swimming

160   appendages was made possible by a rigid exoskeleton, allowing the attachment of the

161   musculature, and by arthrodization of appendages (Legg et al., 2012). The earliest

162   evidence of swimming appendages in arthropods comes from Cambrian forms, for

163   example bivalved arthropods such as *Isoxy* (Vannier and Chen, 2000), from some

164   'Orsten' taxa such as *Martinssonia*; Müller and Walossek, 1986, and from

165   marellomorphs and possibly trilobites (Fortey and Owens, 1999; Fig. 2) that probably

166   used synchronized short movements of several identical appendages. This mode of

167   swimming can be observed in living planktonic arthropods, as in some branchiopods

168   and remipeds (e.g., Kohlhage and Yager, 1994).

169   The first diect evidence, by comparison with Recent counterparts, of arthropod

170   appendages specifically adapted for swimming is identified in exceptionally well-

171   preserved Late Ordovician myodocope ostracods, which used their second antenna for

172   locomotion (Siveter et al., 2014; Figs 2, 4Q-S). A modified second appendage is used

173   for swimming by many Recent zooplanktonic arthropods including cladocerans and

174   copepods (Fig. 1A-B, D-F). In their evolutionary history, arthropods have developed

175   appendages specialized for swimming at several positions in their tagmosis. For

176   example, swimming eurypterids use a paddle-shaped 6th appendage (Fig. 4H), Recent

177   portunid crabs use the posteriormost (5th) thoracic appendage and euphausiaceans and

178   amphipods use five pairs of pleopods (Fig. 1L). Swimming appendages clearly

179   evolved independently in different groups of arthropods, and there are several

180   convergently acquired morphological features that replicate across arthropod groups.

181   Thus, a paddle-like posterior body is present in the Cambrian gilled lobopodian

182   *Opabinia*, some Radiodonta (*Anomalocaris*), some bivalved arthropods (e.g., *Waptia*),

183   some eurypterids and many malacostracans (e.g., *Caryocaris, Angustidontus*; Vannier

184   et al., 1997a; Rolf and Dzik, 2006; Fig. 4I-K). Specialized swimming appendages are

185   either paddle-shaped, as for example in eurypterids and decapods, or have numerous

186   ramifications and secondary setae as in ostracods and copepods (Fig. 2). All of these

187   modifications increased the surface area of the appendage for use in swimming and

188   demonstrate the ability of the arthropod body to advance various solutions for moving

189   efficiently through the water column.

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191   *2.3. Respiration and circulation*

192   Although not limited to planktonic forms, in order to enhance and/or sustain an

193   active metabolism for swimming, zooplanktonic arthropods need a higher oxygen

194   supply and have developed various respiratory strategies involving either a very thin

195   cuticle through which the oxygen enters the hemolymph by diffusion, or the

196   possession of a heart, circulatory system and in some cases also gills. Basal groups

197   present in the Cambrian, such as gilled lobopodians (e.g., *Opabinia*) and Radiodonta

198   (e.g., *Anomalocaris*), possessed a dorsal array of flexible blades attached to a

199   transverse rachis on the trunk segments that probably acted like gills (Van Roy and

200   Briggs, 2011; Fig. 2): though no heart or circulatory system has so far been identified

201   in these fossils, such structures would have been essential to carry the oxygen from

202   the gills to the rest of the large body. The benthic *Fuxianhuia protensa* bears a

203   complex heart and cardiovascular system (Ma et al., 2014) showing that these

204   structures were already present in early Cambrian stem euarthropods (see also

205   Vannier et al., 1997b). Some early Cambrian Orsten arthropods (*Yicaris* Zhang et al.,

206   2007), bivalved arthropods (*Isoxys*; Fu et al., 2011), and trilobites bear putative gill-

207   like structures on the exopods of their trunk appendages, a situation similar to that in

208   many extant arthropod groups such as branchiopods and malacostracans. In addition

209   to the presence of possible respiration-related flap-like exopods on their trunk

210   appendages, many early Cambrian bradoriid arthropods show the pattern of a complex

211   and well-developed putative circulatory system preserved as a trace on the carapace,

212   and comparable to that present in living and fossil myodocope ostracods (see Abe and

213   Vannier, 1995; Vannier et al., 1997b; Williams et al., 2011, and in press; compare

214   Fig. 1C and Fig. 4P). Although gill-like structures are present in Cambrian animals

215   such as *Waptia* and *Naraoia* (Williams et al., 2011, fig. 2; Briggs et al., 1994) and

216   Ordovician trilobites (Suzuki and Bergström, 2008; Suzuki et al., 2008), the first

217   undoubted gills in the arthropod fossil record are from exceptionally preserved

218   Silurian myodocope ostracods (Siveter et al., 2003, 2007, 2010, 2013; Fig. 4R) which

219 show posteriorly positioned book gills comparable to that of living cylindroleberids

220 (Abe and Vannier, 1995).

221   Not all planktonic arthropods require complex respiratory systems. Because of

222 their small size, most copepods have no need of a heart or circulatory system (the

223 members of the order Calanoida have a heart but no blood vessels; Howse et al.,

224 1975), and most also lack gills. Instead, they possess a very thin cuticle through which

225 the oxygen enters the hemolymph by diffusion, the hemolymph being kept in motion

226 by either a blood pump or rhythmic movements of the body, gut, or appendages.

227 Similarly, the small, benthic, podocope ostracods (Ordovician to Recent) have no

228 integumental circulatory system and simply take in oxygen through the cuticle

229 (Vannier and Abe, 1995).

230

231   *2.4. Buoyancy*

232   Most living zooplanktonic arthropods have developed near neutral buoyancy. The

233 smaller forms, for example copepods and branchiopods (Fig. 1), have virtually non-

234 calcified cuticles, whereas lipids are thought to play a key role in buoyancy control in

235 some larger arthropods (Campbell and Dower, 2003). A number of negatively

236 buoyant zooplankton species have developed a 'hop and sink' behaviour characterized

237 by repeated upward swimming for a short distance followed by passive sinking

238 (Haury and Weihs, 1976). This hop and sink behaviour may save energy relative to

239 continuous swimming at a fixed depth (Campbell and Dower, 2003). Buoyancy is

240 difficult to evaluate in the fossil record, as poorly calcified and fragile bodies will not,

241 in most cases, be preserved: this feature is, therefore, not plotted in Figure 2.

242 However, a possible rare example of these light carapaces may be evidenced in

243 Cambrian groups such as *Isoxys* that possibly had carapaces comparable to that of

244   Recent halocyprid ostracods (see Vannier and Chen, 2000). The presence of lipids

245   used for buoyancy in ancient fossil forms is difficult to assess, and these seem to have

246   left no specific biomarkers in sedimentary deposits. Some morphological

247   characteristics preserved in fossil zooplanktonic arthropods possibly functioned to aid

248   buoyancy and stability during swimming. For example, the external ornament such as

249   reticulation, corrugation and various flanges (compare Figs 1B and 4S) present on the

250   carapaces of several early Palaeozoic and Recent zooplanktonic taxa (e.g., some

251   bivalved arthropods [e.g., *Isoxys*, *Tuzoia*], ostracods, phyllocarids) probably represent

252   an adaptation for strengthening without adding to carapace mass (Benson, 1974,

253   1981). Some ornament may also have functioned to facilitate locomotion, reduce

254   turbulence or retard sinking in fossil and Recent arthropods (e.g., halocypridid

255   ostracods; Vannier and Chen, 2000; Vannier et al., 2007). Another feature shared by

256   several bivalved arthropods, planktonic ostracods, phyllocarids and decapod larval

257   stages are long cardinal spines at the dorsal margins of the carapace (compare Figs

258   1B, I, K, 4F). These and other carapace spines could clearly have an anti-predatory

259   defensive function, but they might also increase the drag and/or assist the stability of

260   the animal during swimming (Strathmann, 1993; Vannier and Chen, 2000).

261

262   *2.5. Feeding*

263   Arthropods have developed various strategies to feed in the water column, and

264   through their evolutionary history they have occupied all trophic levels from primary

265   consumers to top predators. These strategies and feeding modes involve various kinds

266   of specialized appendages. Although in Recent oceans most zooplanktonic arthropods

267   are primary or secondary consumers, as is the case of copepods, branchiopods and

268   cladocerans, the fossil evidence suggests that some early Cambrian arthropods swam

269   in the water column and were predators (Legg et al., 2012). Animals such as

270   Radiodonta, *Isoxys* and *Angustidontus* (Fig. 4F, K; Rolf and Dzik, 2006; Vannier et

271   al., 2009; Daley et al., 2013) were relatively large, about 5-50 cm long, and had robust

272   raptorial appendages armed with spines that were clearly designed to feed on other

273   organisms. However, some of these arthropods, such as the Radiodonta and gilled

274   lobopodians were possibly demersal rather than strictly pelagic and probably fed on

275   fauna present on or near the sea floor, as attested to by coprolites containing trilobite

276   fragments (Vannier and Chen, 2005) and also by trilobites with healed injuries

277   (Nedin, 1999) which have been attributed to anomalocaridid activity. Furthermore,

278   complex digestive structures in early Cambrian forms such as gilled lobopodians and

279   some basal arthropods (e.g., Radiodonta, bivalved arthropods) but absent in

280   onychophorans, tardigrades and many other Cambrian lobopodians, are 'arthropod-

281   specific' innovations interpreted as digestive glands that facilitated carnivory and

282   macrophagy (Vannier et al., 2014). Carnivory is an important step in the colonization

283   of the water column as it opens a route for secondary and tertiary predators to adapt to

284   new food sources. The large early Cambrian (Epoch 2) anomalocaridid *Tamisiocaris*

285   (40-70 cm long) had, as a possible secondary consumer, substantial frontal

286   appendages that probably functioned in filter-feeding on mesozooplankton in a

287   manner recalling Recent cetaceans (Vinther et al., 2014; Fig. 4E).

288   Small carbonaceous fossils from the early and mid Cambrian (Epochs 2 and 3;

289   Harvey and Butterfield, 2008) consist mainly of complex disarticulated feeding

290   appendages that are interpreted as mixed scraping and suspension-feeding apparatuses

291   possibly belonging to copepods and branchiopods (Butterfield, 1997; Harvey et al.,

292   2012; Fig. 4A-B). This, and the presence of coeval faecal pellets rich in acritarchs

293   (Harvey and Butterfield, 2011; Fig. 4C), suggests the presence of herbivorous or

294   omnivorous mesozooplankton in mid Cambrian Epoch 3 (Harvey et al., 2012; Harvey

295   and Pedder, 2013). Moreover, the diversification of unicellular phytoplankton, which

296   has been equated with increased predation, might imply that arthropods with

297   specialized appendages for feeding on phytoplankton were already present in the

298   latest Precambrian or earliest Cambrian (e.g., Butterfield, 1997).

299

300   *2.6. Vision*

301   Fossil evidence suggests that photoreception (i.e. vision) is a feature developed

302   already in basal arthropods (Legg et al., 2012; Fig. 2). Some early Cambrian

303   Radiodonta and gilled lobopodians such as *Opabinia* (Fig. 4I) bear very large and

304   complex pedunculate compound lateral eyes and are interpreted as having been highly

305   mobile visual predators in the water column (e.g., Paterson et al., 2011). The basal

306   euarthropods *Jugatacaris, Isoxys* and *Nereocaris* have well-developed pedunculate

307   eyes and a photoreceptor organ (Fu and Zhang, 2011; Legg et al., 2012; Vannier. et

308   al., 2009; Fig. 2, 4J). Most living pelagic arthropods have eyes (e.g., hyperiid

309   amphipods, cypridinid ostracods) or photoreceptor organs (e.g., halocyprid ostracods

310   and most copepods) for use, *inter alia*, in predation, defence, recognition of circadian

311   cycles, or detection of bioluminescence. Pelagic trilobites generally bear very large

312   compound eyes supposedly used, in part, to hunt smaller zooplankton (Fortey, 1985;

313   Fig. 4L-M). The known Silurian ostracods with preserved soft-parts possessed large

314   lateral eyes (Siveter et al., 2003, 2007, 2010, 2013; Fig. 4R) comparable to those of

315   the Recent zooplanktonic myodocopid ostracod *Macrocypridina*. If complex eyes in

316   the Radiodonta and trilobites had the same function as those of recent hyperiid

317   amphipods, they would have been capable of detecting small objects at low contrast in

318   dim-light conditions such as transparent prey against a dark background (Land, 1989).

319   The possession of lateral eyes is a symplesiomorphy of the euarthropods, but they

320   are not always present (Legg et al., 2012). Thus, most copepods only have a single

321   compound eye in the middle of their head (Fig. 1F) and some Recent zooplanktonic

322   groups such as remipeds and the halocyprid ostracods have secondarily lost their

323   lateral compound eyes. For such groups, chemical and/or tactile and other receptors

324   likely play a major role for detection and orientation (Fanenbruck et al., 2004). In

325   pelagic halocyprids the Bellonci organ, a mid-cephalic finger-like projection,

326   probably acts to detect changes in light and possibly pressure. The Bellonci organ is

327   already known from the Silurian, in the myodocope ostracod *Nasunaris* Siveter et al.,

328   2010.

329

330   *2.7. Bioluminescence*

331   Bioluminescence is generally more common in deep-marine living and planktonic

332   organisms than in benthic or shallow-water species. An estimated 90% of animals that

333   live below 500 m in the oceans are bioluminescent (Widder, 1999). Bioluminescence

334   is well represented in ctenophores and siphonophores, in which none of the benthic

335   species but more than 90% of planktonic genera are known to produce light (Haddock

336   and Case, 1995). Among zooplanktonic arthropods, copepods are also one of the most

337   prolific bioluminescent groups (Haddock et al., 2010). Bioluminescence serves an

338   important function in various Recent zooplanktonic arthropods such as copepods,

339   ostracods, euphausiaceans, decapods, mysids and amphipods. It is used, *inter alia*, to

340   lure prey, to attract mates and to aid defence; for example, to startle or misdirect

341   predators or to camouflage an otherwise dark silhouette (Haddock et al., 2010;

342   Nilsson et al., 2014). Based on the number of light-producing chemistries across

343   monophyletic lineages, bioluminescence is estimated to have evolved independently

344 at least 40 times across a range of groups from bacteria to vertebrates (Haddock et al.,

345 2010). Possible bioluminescent organs in fossil arthropods have been proposed for

346 one Ordovician trilobite genus, namely *Pricyclopyge* (Vassel et al., 2012), and for

347 some Silurian ostracods. The Silurian myodocope ostracod *Colymbosathon* possesses

348 tubercle-like processes at/near the margins of the labrum that resemble

349 bioluminescent-associated structures of living cypridinid ostracods (Siveter et al.,

350 2003) such as *Vargula hilgendorfii* (Vannier and Abe, 1993), and the Silurian

351 myodocope *Parabolbozoe* bears tubercles on its carapace, which are comparable to

352 those of Recent halocyprids that are interpreted as possible bioluminescent organs

353 (Perrier et al., 2011). Amongst ostracods, only Myodocopa have bioluminescence.

354 The two myodocope lineages, namely the Halocyprida and Myodocopida that possess

355 pelagic representatives have light emitting organs and produce different

356 bioluminescent chemicals (Haddock et al., 2010). These two groups may have

357 diverged around 460 Ma (Oakley et al., 2013), suggesting this as a maximum age for

358 at least one of the known luminescence systems (Haddock et al., 2010).

359

360 *2.8. Reproductive strategies and planktonic larval stages*

361 Zooplanktonic arthropods have developed various strategies for nurturing the

362 young within body parts and various protective extensions of the carapace. While

363 some mesozooplankton release their eggs, as in the case of some eucarids and

364 copepods (Ohman and Townsend, 1998), many arthropod species retain their eggs

365 until they hatch, either in egg sacs (e.g., copepods, Fig. 1F; Ohman and Townsend,

366 1998), in brood chambers (e.g., some ostracods, Fig. 4Q; Ikeda and Imamura, 1992)

367 or in a ventral marsupium derived from their appendages (e.g., peracarids; Poore and

368 Bruce, 2012). In Recent zooplanktonic copepods, brooding behaviour appears to be

369 more common in small species that produce only a limited number of small eggs

370 (Strathmann, 1993), as the predation risk associated with carrying eggs increases with

371 body size (Ohman and Townsend, 1998). This reproductive strategy was likely

372 present already in early benthic arthropods, as is evident in the early Cambrian (Epoch

373 2) bradoriid *Kunmingella douvillei*, which shows putative egg brooding within its

374 carapace (Shu et al., 1999; Duan et al., 2013). This strategy is also demonstrated for

375 Ordovician and Silurian nektobenthic myodocopid ostracods (Siveter et al., 2007,

376 2014; Fig. 4Q), which nurtured eggs and, in the case of *Nymphatelina* from the

377 Silurian, a first instar juvenile within their carapaces. Though a brooding strategy is

378 also common in benthic species (e.g., phyllocarids, a few podocope ostracods and

379 possibly trilobites; Vannier and Abe, 1993; Vannier et al., 1997; Fortey and Hughes,

380 1998; Cederstrom et al., 2011) and is not a prerequisite for a successful zooplanktonic

381 lifestyle, it was likely an important asset for protecting eggs from predation and thus

382 enhancing reproductive success within the water column.

383 A free-swimming larval phase is known from some species in most classes of

384 Recent marine arthropods for which developmental information is available. For

385 example, some Recent decapods (crabs, lobsters, Fig. 1I) and stomatopods (mantis

386 shrimp) are known to have several planktonic larval stages (protozoea, zoea,

387 megalopa; Harvey et al., 2002). There are naupliar stages of arthropods represented in

388 Cambrian 'Orsten' deposits (Zhang et al., 2010 and references therein), though these

389 fossils have mostly been interpreted as meiofauna (Waloszek et al., 2007). Trilobites

390 also possessed nauplius-like larvae (Fortey and Morris, 1978; Fig. 4N-O). A free-

391 swimming 'cyprid' larval stage is known from the crustacean *Rhamphoverritor*

392 (Cirripedia) from the Silurian Herefordshire Lagerstätte (Briggs et al., 2005).

393 Although malacostracans are known since the early Palaeozoic (Vannier et al., 2003),

394 the only evidence of possible decapod larvae in the fossil record is based on two

395 specimens from the Lower Cretaceous Santana Formation of Brazil that are

396 interpreted as planktonic protozoea of a branchyuran crab (Maisey and De Carvalho,

397 1995).

398   Orsten species provide evidence of various morphological stages of the arthropod

399 life cycle (i.e. nauplius, zoae, megalopa) in the Cambrian (Zhang et al., 2010). This

400 has important potential implications for the evolutionary and ecological success of

401 many arthropod lineages, especially for groups where the larval stages and adults

402 have distinct ecologies, such as trilobites, barnacles and crabs. Neoteny of planktonic

403 larval stages has been considered to be a long established route into the plankton

404 (Rigby and Milsom, 2000). This could be the case, for example, for some trilobites

405 that had a planktonic larval stage (protaspid; Fig. 4N-O) morphologically similar to

406 Recent crab zoea (Speyer and Chatterton, 1989). The colonisation of the water

407 column by some unrelated species of nine malacostracan higher taxa (see Table 1),

408 some also having a planktonic larval stage, may also have been the result of neotenic

409 processes.

410   All of these major innovations in arthropod design and morphology fundamentally

411 affected, *inter alia*, locomotion, vision, feeding and digestive systems, and

412 reproductive strategies, and they are beneficial to organisms living in the water

413 column.

414

415   *3. The fossil record of arthropod zooplankton*

416   Although diverse and abundant in Recent ecosystems, arthropod zooplankton are

417 rare in the fossil record, with virtually no occurrences from post-Carboniferous strata

418 (Fig. 3). In part, this reflects post-mortem buoyancy, scavenging of carcasses in the

419 water column, and reduction of skeletal material in response to lifestyle, meaning that

420 in many cases planktonic arthropods are small, fragile and have diminished

421 preservation potential (Rigby and Milsom, 2000; Fig. 5). In part, the record also

422 reflects the enhanced taphonomic window in the Cambrian, from where many early

423 arthropods are preserved, including forms with a non-mineralised exoskeleton. And

424 finally, it also reflects the record of pelagic arthropods that did possess a mineralised

425 exoskeleton – at least for part of their life cycle, and particularly including the

426 trilobites and ostracods (Fig. 3). Here we assess the veracity of the fossil record of

427 arthropod zooplankton and its potential to better interpret patterns of zooplankton

428 evolution through time.

429

430 *3.1. Taphonomy of arthropod zooplankton*

431 Studies comparing living plankton communities with fossil assemblages are mostly

432 restricted to groups which possess cysts or mineralized skeletons and therefore have a

433 better potential to become fossilized; for example, diatoms, dinoflagellates,

434 coccolithophores, radiolarians and foraminifers. Although many of these studies have

435 shown that surface productivity signals are transmitted to the sea bed (e.g., Billett et

436 al., 1983; Abelmann and Gersonde, 1991; Lampitt et al., 2001), several also report

437 that factors such as zooplankton grazing in upper waters, selective dissolution of

438 microfossils, and re-mobilization/re-deposition can distort or decouple this signal

439 entirely (e.g., Samtleben et al., 1995; Von Bodungen et al., 1995; Kohly, 1998).

440 Comparison of water column plankton diatom assemblages with those in core tops

441 demonstrates that a fundamental taphonomic change occurs in the surface sediment,

442 with sedimentary diatom accumulation rates being only about 1% of plankton

443 production rates (Ryves et al., 2003). Dissolution as well as bioturbation by the

444 zoobenthos has a significant impact on preservation. The same processes (post-

445 mortem transport, scavenging, decay and dissolution) are most likely involved in

446 arthropod zooplankton preservation but perhaps at an even more extensive scale, as

447 most of these animals are poorly or not mineralized (Fig. 5).

448   The absence of a zooplanktonic arthropod record for much of the Phanerozoic (Fig.

449 3) is explicable from an assessment of the likely preservation potential of arthropod

450 cuticle and soft tissues. Experimental taphonomy data are rare for planktonic

451 arthropods (Harding, 1973). However, several authors have noted that microbial

452 activity causes rapid (within days) disarticulation of crustacean (and insect) carcasses

453 left unburied in oxic conditions (Harding, 1973; Hof and Briggs, 1997; Duncan et al.,

454 2003). In addition, weakly calcified zooplanktonic arthropods are likely to endure

455 more or less long periods of post-mortem drift (Bengtson, 2002) and also scavenging

456 during their journey to the sea bottom. The rarity of arthropod zooplankton in early

457 Palaeozoic graptolite black shales (for an exception see Page et al., 2010) suggests

458 that, on the whole, arthropod cuticles were likely much less recalcitrant than the

459 organic skeletons of graptolites. As small, lightly mineralized pelagic or epipelagic

460 animals die and drift slowly down through the water column, a combination of

461 processes can break down and transport carcasses and component anatomy (Brett and

462 Baird, 1986). Small, flat and light parts that are weakly connected with the trunk, such

463 as appendages, are expected to travel farthest; partially articulated abdomens may

464 travel less distance than the lightest pieces, and carapaces might travel the least

465 distance (Collette and Hagadorn, 2010; Fig. 5). Support for this hypothesis is given by

466 sorting in death assemblages of other planktonic organisms, where heavier

467 components drop to the seafloor quickly, and lighter or complex-shaped components

468 may drift farther with even a weak current (Johnson, 1960; Kontrovitz, 1975).

469   Once partially decayed and disarticulated arthropods reach the sea floor,

470   bioturbation generally destroys the remains. More heavily mineralized or sclerotized

471   structures, such as carapaces of ostracods and trilobites and anomalocaridid grasping

472   appendages, are more likely to escape this process and this probably explains their

473   better fossil record. Experimental studies of arthropod carcasses that are buried under

474   less than 10 cm of sediment have shown rapid damage by scavenging and

475   bioturbation, whilst below 10 cm their preservation is largely undisrupted (Plotnick,

476   1986).

477   For small carbonaceous fossils (SCFs) the taphonomic pathways are probably

478   different than for whole animals, as these represent only disarticulated fragments of

479   sclerotized appendages and feeding structures that have the highest fossilization

480   potential of poorly biomineralized arthropods (Van Waveren, 1994; Figs 4A-B, 5).

481   Studies of modern marine sediment surfaces have identified various fragments of

482   zooplanktonic crustaceans that can, if the conditions are favourable, fossilise as SCFs

483   (Van Waveren, 1994). Indeed, analysis of the contents of copepod faecal pellets has

484   yielded an almost unaltered crustacean mandible (Turner, 1978, fig. 5J). Copepod

485   mandibles and sometimes appendages are also found in the guts of modern

486   zooplanktonic crustaceans such as euphausiaceans (e.g., Dalpadado et al., 2008) as

487   well as in chaetognaths (e.g., Baier and Terazaki, 2005). These suggest that some

488   SCF-type cuticular elements might represent the undigested remains of mid-water

489   predators that were originally wrapped in pellets and sunk to the bottom via the faecal

490   stream. So far, the study of SCFs has focussed on the Cambrian (e.g., Harvey et al.,

491   2012), but given the paucity of the arthropod zooplankton record (Fig. 3), future

492   analyses of other intervals of the Phanerozoic record may throw light on a largely

493   cryptic arthropod zooplankton story.

494

3.2. Is the fossil record sufficient to make inferences about arthropod zooplankton evolution through time?

It follows from consideration of taphonomic factors that except for those groups with mineralized skeletons, such as some bradoriids, trilobites, ostracods and malacostracans, most zooplanktonic arthropods are known almost exclusively from Konservat-Lagerstätten, and the majority of these in the Cambrian. This includes most of the Cambrian 'soft bodied' animals such as gilled lobopodians, Radiodonta, certain bivalved arthropods and marellomorphs, and also many groups present in Recent pelagic niches, such as branchiopods, copepods and most malacostracans. The (sparse) occurrence of these 'soft bodied' animals as fossils is the product of particular taphonomic windows. Thus, gilled lobopodians, radiodonts and marellomorphs have a very discontinuous record (see Fig. 3) in Cambrian (e.g., Sirius Passet, Chengjiang, Emu Bay, Burgess Shale), Ordovician (e.g., Fezouata), Silurian (e.g., Herefordshire) and Devonian (e.g., Hunsrück Slate) Lagerstätten.

Some SCFs (Harvey et al., 2012) in the Cambrian potentially represent groups such as branchiopods, copepods or ostracods, but they are known only from a few disarticulated appendages, which precludes a detailed reconstruction of their lifestyle. In addition, because studies of SCFs have mostly concentrated on Cambrian material, the Phanerozoic record of these arthropods is strongly biased, with virtually no record of copepods, for example, between the Cambrian and Recent (Selden et al., 2010; Fig. 3).

More strongly mineralized pelagic arthropods have a much higher fossilisation potential and thus a more continuous fossil record (see Figs 3, 5). These include representatives of such groups as ostracods (by far the most abundant and diverse

519 arthropod group in the fossil record) and trilobites that are common as fossil

520 specimens and species worldwide. However, usually the crucial soft anatomy is

521 missing, in part a result of post-mortem drifting of carcasses, making it more

522 circumspect to interpret the lifestyle of these organisms. The interpretation of a

523 pelagic lifestyle is then derived from skeletal morphology (which is not always

524 reliable; see Siveter et al., 2003, 2013) and from a set of indirect inferences that

525 include palaeogeographic distribution, depositional setting and associated faunas

526 (Fortey, 1974, 1975, 1985; Siveter et al., 1991).

527   Compared to other groups of arthropods, the fossil record of eumalacostracans is

528 notably incomplete (Fig. 3). Combined with the considerable range of variation in the

529 calibration of molecular data from this group (Jenner et al., 2009), this results in

530 fragile and imperfectly constrained phylogenetic trees (Wills et al., 2009). Porter et

531 al., (2005) place the first diversification of decapods in the early Silurian (437 Ma),

532 implying that the major diversification of malacostracans occurred between the late

533 Cambrian and the Ordovician (Fig. 3). Apart from putative phyllocarids (see Vannier

534 et al., 2003), no fossil zooplanktonic malacostracans are known before the Devonian.

535 Most of the record of possible zooplanktonic malacostracans (mainly decapods) from

536 the Devonian onwards comes from Lagerstätten such as the Sahel Alma (Late

537 Cretaceous, Santonian, Lebanon; Audo and Charbonnier, 2013). All other Recent

538 zooplanktonic eumalacostracans, for example Amphipoda (McMenamin et al., 2013),

539 Isopoda (Feldmann and Rust, 2006), Mysidia/Lophogastrida (Taylor et al., 2001) and

540 Cumacea (Schram et al., 2003) have a fossil record that is doubtful or absent (e.g.,

541 Euphausiacea, Amphionidacea). Apart from phyllocarids, the first convincing

542 evidence of malacostracans living in the water column comes from a genus that

543 cannot be assigned to a Recent higher taxon, the Late Devonian stem

544   Mysidia/Euphausiacea *Angustidontus* (Rolf and Dzik, 2006; Fig. 4K).

545   Despite the overall paucity of fossil data, some intervals of arthropod zooplankton

546   evolution are well constrained (Fig. 3), especially the record of soft-bodied forms in

547   the Cambrian, and forms with an exoskeleton in the Ordovician, Silurian and

548   Devonian. Therefore, inferences about the contribution of arthropods to early

549   Palaeozoic zooplankton ecologies can be made, and some of these inferences are

550   likely applicable to other parts of the geological column where data is wanting.

551

552   **4.** *The fossil record of Arthropod zooplankton colonization*

553   Herein, the definitions of plankton and zooplankton, especially the size categories

554   for the latter, follow Omori and Ikeda (1984; see Fig. 6).

555   Given the paucity of zooplankton arthropod fossils from much of the geological

556   record, the following discussion focuses on colonisation during the early Palaeozoic,

557   especially the Cambrian. There is sufficient evidence to suggest that the zooplankton

558   food web was already well developed by the early Cambrian, and arthropods are

559   likely to have been present in plankton ecospace from that time onwards (e.g., Signor

560   and Vermeij, 1994; Rigby and Milsom, 2000; Peterson et al., 2004; Vannier, 2007;

561   Vannier et al., 2009). Many of the major arthropod groups that have a supposed

562   record of water column colonization were already present during the Cambrian, albeit

563   not necessarily as zooplankton (Fig. 3).

564   A prerequisite for the development of heterotrophic zooplankton is the

565   development of primary productivity, the origins of which lie deep in the Precambrian

566   (Huntley et al., 2006; Knoll, 1994; Butterfield, 1997, 2007; Javaux et al., 2010).

567   Heterotrophic consumers of the phytoplankton developed much later, probably in the

568   terminal Precambrian or early Cambrian. In the absence of direct body fossil

569 evidence, the marked evolutionary radiation of rapidly evolving ornamented

570 acritarchs in the early Cambrian (Huntley et al., 2006) may signal an evolutionary

571 response to the evolution of small planktonic herbivorous metazoans (Butterfield,

572 1997, 2007). This is supported by phylogenetic reconstructions (e.g., Legg et al.,

573 2013; Edgecombe and Legg, 2014) suggesting that euarthropods were present in the

574 latest Precambrian (ca. 543 Ma; Rota-Stabelli et al., 2013).

575

576 *4.1. Mesozooplanktonic arthropods*

577 Mesozooplankton (size: 0.2-20 mm) is the essential link between the

578 phytoplankton and higher levels of the zooplankton food web (Fig. 6). Colonisation of

579 the water column by mesozooplankton must therefore have represented an important

580 step in the construction of higher trophic levels in marine food webs, and it follows

581 that they were essential for reconstructing food webs in the wake of major extinction

582 events. In Recent pelagic ecosystems, mesozooplankton is composed of essentially

583 primary consumers (e.g., copepods) but occasionally also of secondary consumers

584 (e.g., ostracods) preying on other mesozooplankton.

585 Apart from chaetognaths (Vannier et al., 2007), there is no fossil record of

586 mesozooplankton in the early Cambrian. Arthropod appendages that belong to three

587 extant crustacean groups, branchiopods, copepods and a putative ostracod (Harvey et

588 al., 2012), have been recorded from Cambrian deposits, but their appendage

589 morphology suggests grazing/scraping/filtering ecologies more consistent with a

590 benthic lifestyle. Nevertheless, some Cambrian (Epoch 3) copepod mandibles that are

591 strikingly similar to those of modern planktonic species (Harvey and Pedder, 2013)

592 suggest that copepods may have been present in the water column during the mid

593 Cambrian. The existence of an arthropod mesozooplankton is also supported by

594   evidence from faecal pellets rich with sphaeromorph acritarchs (Cambrian Epoch 3;

595   Harvey and Butterfield, 2011; Fig. 4C) that may be the product of arthropod grazers

596   among the Cambrian zooplankton. The high abundance of intact pellets in organic-

597   rich mudstones suggests that these were exported from an open water column

598   overlying an undisturbed, probably anoxic seabed. Furthermore, the appendages of

599   the large (up to 70 cm long) early Cambrian (Epoch 2) anomalocaridid *Tamisiocaris*

600   suggest that it was a microphagous suspension feeder (Vinther et al., 2014; Fig. 4E),

601   using its appendages for sweep-net capture of food items down to 0.5 mm, which is

602   within the size range of mesozooplankton such as copepods and branchiopods.

603   Other small putative mesozooplankton in the Cambrian include species of the

604   bradoriid *Anabarochilina* (Fig. 4P) that probably originated in benthic shelf settings in

605   the early and mid Cambrian (Siveter and Williams, 1997; Williams and Siveter,

606   1998), possibly migrating into the water column during intervals of widespread shelf

607   dysoxia in the Drumian and Guzhangian ages of Cambrian Epoch 3 (Collette et al.,

608   2011; Williams et al., in press). Species of *Anabarochilina* have a fossil distribution

609   that spans a trans-palaeolatitude distribution in the Cambrian, from the tropics to the

610   southern polar region (Williams et al., 2007) and between major palaeocontinents

611   separated by wide oceans (Hinz-Schallreuter, 1993; Colette et al., 2011). The size of

612   *Anabarochilina* species (about 5-10 mm long) is consistent with an animal feeding on

613   detritus or small mesozooplankton, as do Recent pelagic (myodocope) ostracods.

614   Post-Cambrian examples of mesozooplankton colonisations of the water column

615   are best exhibited by the Silurian radiation of ostracods (myodocopids) following the

616   mid-Homerian biotic crisis (Siveter et al., 1991; see Cramer et al., 2012 for context):

617   certain species developed a transoceanic distribution at this time, including *Richteria*

618   *migrans*, *Parabolbozoe bohemica* and *Silurocypridina calva* (Perrier et al., 2007,

619   2011; Perrier and Siveter, 2013; Fig. 4S). This colonisation event is associated with

620   the restoration of the planktonic ecosystem in general (including zooplankton such as

621   graptolites) post-dating the mid-Homerian extinction (Siveter et al., 1991; Porebska et

622   al., 2004; Cramer et al., 2012), though the precise factors that facilitated the radiation

623   of ostracods into the water column remain enigmatic (see Siveter et al., 1991 for a

624   review). During the Devonian and Carboniferous, the myodocopid Entomozoidae

625   with their weakly mineralized carapaces provide a continued, but rare, fossil record of

626   mesozooplankton (Gooday, 1983; Olempska, 1992; Fig. 3).

627

628   *4.2. Macrozooplanktonic arthropods*

629   Macrozooplanktonic (size: 20-200 mm) arthropods are primary or secondary

630   consumers and are represented in Recent pelagic ecosystems by groups such as

631   euphausiaceans (e.g., krill) and decapods (Fig. 6). Most of them are filter feeders

632   primarily on phytoplankton, although some species are predators on mesozooplankton

633   and other macrozooplankton (e.g., amphipods).

634   The record of arthropod macrozooplankton in the Cambrian is meager. *Isoxys*, with

635   its light carapace, appendages adapted for swimming, flap-like telson, powerful

636   prehensile frontal appendages, well-developed digestive system and large spherical

637   eyes, is probably one of the best candidates as a macrozooplankton predator (Vannier

638   and Chen, 2000; Vannier et al., 2009). Although *Isoxys* is not cosmopolitan at the

639   species level like some Cambrian bradoriids, evidence from functional morphology,

640   taphonomy and palaeogeographic distribution suggests that it may have been a

641   widespread visual predator living in the lower levels of the water column (Vannier et

642   al., 2009).

643   Although trilobites were already diverse during the Cambrian (Fortey and Owens,

644 1997), there are but a few adult forms that have been interpreted as pelagic (Table 1).

645 The Ordovician bears a wider range of what are generally agreed to be pelagic

646 trilobite species (Fortey, 1974, 1975, 1985). Some of these, such as *Carolinites*

647 *genacinaca*, display the most cosmopolitan distribution of any trilobite species

648 (McCormick and Fortey, 1999) and occur across inner and outer shelf facies.

649 Morphologically, pelagic trilobites are typically recognized, *inter alia*, by their large

650 or even hypertrophied downwards-pointing eyes, elongate exoskeletons with reduced

651 pleurae, and their downwards-directed genal spines (Fortey and Owens, 1999; Figs 2,

652 4L-M). Unfortunately, there is no preserved appendage morphology for supposed

653 pelagic trilobites. It is unknown, for example, whether the appendages were modified

654 for swimming or for feeding in the water column (Fortey and Owens, 1999). Based

655 mostly on functional morphology, small (20-40 mm) Ordovician trilobites such as the

656 Cyclopygidae and the Telephinidae have been interpreted as primary and/or

657 secondary consumers, whereas larger (up to 100 mm) and streamlined forms such as

658 *Degamella* were likely secondary consumers (predators) feeding on mesozooplankton

659 (Fortey and Owens, 1999; Table 1).

660   The first putative malacostracan crustaceans entered the water column during the

661 Early Ordovician (Fig. 3). Based on its cosmopolitan palaeogeographic distribution

662 and its associated faunas, the putative phyllocarid *Caryocaris*, recorded from the

663 Tremadocian onward, has been interpreted as a microphageous/opportunistic mid-

664 water zooplanktonic animal (Vannier et al., 2003). The fossil record of zooplanktonic

665 malacostracans, excluding phyllocarids, is poor (Fig. 3), especially compared to their

666 diverse and abundant benthic record and their ecological importance in Recent

667 oceans. The diversity of zooplanktonic malacostracan groups in the modern oceans,

668 represented *inter alia* by at least four families of Decapoda, and by Amphipoda,

669 Isopoda, Mysidia, Lophogastrida, Cumacea, Amphionidacea and Euphausiacea (Fig.

670 1L), suggests multiple zooplankton colonization events. However, it is difficult to

671 determine exactly when these events took place, as most of these groups also

672 comprise benthic representatives. The first definitive malacostracan (stem

673 Mysidia/Euphausiacea) recorded supposedly in the water column is from the Late

674 Devonian (*Angustidontus*, Rolf and Dzik, 2006; Fig. 4K)

675   Although Euphausiaceans have no known fossil record, their presence during the

676 mid Cenozoic can be inferred by indirect evidence. Significantly, baleen whales

677 (Mysticeti) evolved from the ancestors of toothed whales (Odontoceti) in the late

678 Eocene (at ca 35 Ma) and underwent a major adaptive radiation in the mid Oligocene

679 (30 Ma; Fordyce and Barnes, 1994; O'Leary and Uhen, 1999; Cavin, 2010). Many

680 modern Mysticeti are obligate krill predators (Matthews, 1978), so it is possible that

681 their radiation is associated with the exploitation of krill as a new food resource

682 (Jarman et al., 2002), linked to the reorganization of the Southern Ocean ecosystem at

683 this time (Houben et al., 2013).

684

685   *4.3. Large predators*

686   Although arthropods are absent from the highest trophic level in Recent pelagic

687 open-water ecosystems of the oceans, the presence of large (>200 mm) pan-arthropod

688 top predators (e.g., Radiodonta) in the early Cambrian (Epoch 2) water column is well

689 documented (Fig. 6 and Table 1). These animals reached metre-scale in length in the

690 Cambrian and Ordovician (Van Roy and Briggs, 2011) and were present until at least

691 the Early Devonian (Kühl et al., 2009). The functional morphology of the frontal

692 appendages suggests that some anomalocaridid taxa were durophagous predators,

693 whilst others fed on soft-bodied organisms (Daley et al., 2013; Fig. 4D), with one

694   early Cambrian species most probably a microphagous suspension feeder (Vinther et

695   al., 2014; Fig. 4E). The only other large arthropod predators of the early Palaeozoic

696   with a fossil record are the eurypterids, which were present from the Ordovician to the

697   Permian (Fig. 4H). The earliest (swimming) eurypterids are recorded from the Late

698   Ordovician (Hirnantian) but it is not until early Silurian (Llandovery) times that some

699   pterygotids possess a wide biogeographical distribution at the generic level (Tetlie,

700   2007). Selden (1981, 1984) suggested that some Silurian pterygotoid and

701   hughmillerioid eurypterids were slow but accomplished swimmers probably living in

702   the demersal zone. Provided with well-developed raptorial appendages, they almost

703   certainly occupied high trophic levels, as is also suggested by several pterygotoid

704   forms among the largest arthropods ever discovered (Miller, 2007; Braddy et al.,

705   2008). Some early Palaeozoic giant trilobites (up to 90 cm long), for example *Isoletus*

706   *and Hungioides*, were also probably tertiary predators/scavengers, but their

707   morphology and depositional setting suggest a strictly benthic lifestyle (Rudkin et al.,

708   2003; Gutiérrez-Marco et al., 2009).

709   The presence of such a diversity of lifestyles and feeding strategies in early

710   Palaeozoic arthropods suggests that the pelagic food web was already complex

711   perhaps as early as *circa* 521 Ma, implying that arthropods were present at several

712   trophic levels from primary consumer to tertiary predator (see Signor and Vermeij,

713   1994; Rigby and Milsom, 2000; Peterson et al., 2004; Vannier, 2007; Fig. 6).

714

715   *5. Arthropod zooplankton and their environment*

716   The Precambrian–Cambrian transition witnessed a succession of ecological

717   changes. Over a few tens of millions of years, the marine realm changed from

718   relatively simple ecosystems dominated by microorganisms and predominantly sessile

719   organisms, as occur in the Ediacaran biota, to complex ecosystems where many new

720   ecological interactions such as predation occupied a central position and exerted

721   feedback effects on the environment and evolutionary processes (Butterfield, 2011).

722   The adaptive radiation of arthropods during the Cambrian and their subsequent

723   evolution during the rest of the Phanerozoic played a central role in this process. The

724   arthropod colonisation of the water column provided a new food supply and enabled

725   large secondary and tertiary consumers to enter the water column. Planktonic

726   arthropods are also important consumers of phytoplankton and other organic matter,

727   repackaging carbon and delivering it to other parts of the water column, and as such

728   are integral to the efficient functioning of the biological pump (Butterfield, 1997).

729   They therefore provide a food source for organisms living in the water column as well

730   as in the benthos (Rigby and Milsom, 2000). The following review examines some of

731   the interactions of the arthropod zooplankton with the marine ecosystem.

732

733   *5.1. Predation and plankton*

734   The 'fast pelagic predator' niche was probably occupied since the early Cambrian

735   (Bambach et al., 2007). Indeed, some of the first arthropods were probably predators

736   (Legg et al., 2012). Until the Ordovician, with the diversification of the cephalopods

737   (Kröger et al., 2009), the 'fast pelagic predator' niche was mostly occupied by

738   arthropods such as gilled lobopodians, Radiodonta, some bivalved arthropods and

739   possibly trilobites, as well as non-arthropod conodonts and chaetognaths. The increase

740   in demersal predators in Cambrian epochs 2 and 3, such as gilled lobopodians,

741   Radiodonta and possibly some bivalved arthropods, coincides with the development

742   of specialised appendages designed for grasping prey (Vannier et al., 2009; Daley et

743   al., 2013; Vinther et al., 2014) and complex feeding appendages with which to

744   process food (Harvey et al., 2012). This also coincides with the development of

745   features that characterise predators such as well-developed vision (Paterson et al.,

746   2011), fast locomotion (Usami, 2006), and an efficient digestive system (Vannier et

747   al., 2014). Several authors (e.g., Signor and Vermeij, 1994; Peterson, 2005; Peterson

748   et al., 2005) have suggested that the Cambrian water column may have served as a

749   refuge for small animals from benthic and demersal predation pressure, and this might

750   have been one of the triggers of Cambrian plankton colonization events. According to

751   Verity and Smetacek (1996), amongst plankton, predator avoidance strategies fall into

752   four general categories that can be recognized in arthropods: chemical (e.g.,

753   bioluminescence), morphological (e.g., eyes, swimming appendages, spines),

754   behavioural (e.g., vertical migration, escape reaction) and life history (e.g., brooding).

755   Most of these predator avoidance strategies were already present in arthropods from

756   Cambrian epochs 2 and 3, as reviewed in section 2, and these strategies may have

757   facilitated colonisations of the water column multiple times during arthropod

758   evolutionary history. Assuming this hypothesis is correct, an initial high diversity in

759   the demersal zone (e.g., as witnessed in Chengjiang arthropods) was followed by a

760   radiation of some transitional demersal/nektonic organisms (e.g., some Bradoriida;

761   Williams et al., in press) and then finally by a nekton diversification (Klug et al.,

762   2010). Elements of these ecologies are clearly present in Cambrian arthropod faunas.

763   Klug et al., (2010) proposed that the Devonian nekton revolution (affecting, e.g.,

764   cephalopods and fishes) might have resulted from sea bottom predator pressure. An

765   important event in the history of the Palaeozoic nekton is the initial radiation of

766   gnathostomes in the Early Devonian (Emsian; Kröger, 2005), with the simultaneous

767   appearance of the Chondrichthyes, Placodermi, and Paleoniscides, the main late

768   Palaeozoic competitors and predators of cephalopods (Mapes et al., 1995; Mapes and

769   Chaffin, 2003). The radiation of gnathostomes may have increased predator pressure

770   on cephalopods, selecting for higher mobility forms (Klug and Korn, 2004) and

771   forcing an invasion of benthic or demersal organisms into the water column (Klug et

772   al., 2010).

773

774   *5.2. Impact on the phytoplankton*

775   The development of spiny acritarchs in the late Precambrian may have been a

776   reaction to mesozooplankton grazing pressure (Butterfield, 1997). Two earlier

777   radiation events of acanthomorphic acritarchs in the Proterozoic, one before the

778   Sturtian glaciation (750-700 Ma) and one immediately following (600-575 Ma) the

779   Marinoan glaciation, occured at a time when mesozooplankton probably did not exist

780   and could not have affected phytoplankton evolution (Vidal and Moczydłowska-

781   Vidal, 1997; Moczydłowska, 2002). Although zooplankton affects the growth of

782   phytoplankton populations (Berger et al., 1989; Brett et al., 1994), spines most likely

783   evolved to enhance buoyancy, and the best defense strategy of phytoplankton against

784   predation is mass occurrence, blooms, and the formation of colonies (Moczydłowska,

785   2002).

786   Nevertheless, the sharp increase in acritarch diversity and turnover during the

787   Cambrian and Ordovician coincide with a comparable evolutionary adaptive radiation

788   in animals (Servais et al., 2008, 2010). Multiple arthropod zooplankton colonisations

789   could have contributed in several ways to the complexity of environments occupied

790   by protistan-, nanno- and micro-plankton; for example, through predation (providing a

791   greater range of ecological niches and sub-environments, and trophic positions), and

792   the alteration of nutrient fluxes in marine platform and shelf waters (Butterfield,

793   2011).

794   In modern oceans, higher trophic levels, occupied by fish and marine mammals,

795   depend on short food chains driven by bloom-forming phytoplankton, which is

796   usually based on diatoms (Falkowski et al., 2004). The intermediaries in this energy

797   transfer are metazoan zooplankton, such as copepods and euphausiaceans: whilst both

798   of these groups have virtually no fossil record (Fig. 3), arthropods occupying this

799   position in the trophic structure, and being essential for this energy transfer, may have

800   existed since the Cambrian. It is possible that the rise of armoured phytoplankton

801   (coccolithophores, dinoflagellates and diatoms), from the Mesozoic onwards

802   represents a protective response to the diversification of primary and secondary

803   consumers. Though there is no direct fossil evidence to support this, it is possible that

804   armour developed in part in order to protect the phytoplankton from predation and/or

805   to prevent its digestion (Sarnelle, 2005; DeMott and Van Donk, 2013) by a newly

806   diversified arthropod zooplankton.

807

808   *5.3. Impact on the nekton*

809   The development and diversification of an arthropod zooplankton into the food

810   chain may have enabled the expansion of larger animals (macrozooplankon and

811   nekton) into this realm. The initial rise and rapid diversification of pelagic

812   cephalopods during the Early and Middle Ordovician indicate the establishment of a

813   food chain that could sustain a diverse fauna of large, active predators (Kröger et al.,

814   2009). This diversification in general was coeval with the diversification of two major

815   pelagic trilobite taxa, the Asaphida and Proetida (Adrain et al., 2004), and the

816   appearance of widespread phyllocarid malacostracans (Vannier et al., 2003). These

817   relatively large (up to about 5 cm long) zooplanktonic arthropods could have

818   represented an important food source for early cephalopods and possibly played an

819   important role in their Ordovician diversification. In turn, the presence of larger

820   predators indicates the likely presence of smaller meso- and microplankton as

821   intermediaries between the primary production and larger predators.

822   During the Silurian, vertebrates underwent an adaptive radiation into diverse

823   marine ecological niches (the nekton revolution of vertebrates *sensu* Blieck, 2009).

824   Agnathans and gnathostomes dominate these assemblages, and both include

825   representatives that were demersal or swimmers in the upper levels of the water

826   column (Blieck, 2011). The migration of fish into the water column during the late

827   Silurian (Ludlow and Prídolí; see Blieck, 2011, his Fig. 2) is associated with the first

828   ostracod zooplankton (Siveter et al., 1991), and as Recent pelagic fishes feed on

829   ostracods (e.g., Tanaka et al., 2006), there might be a putative link between these

830   events. The increase in diversity of marine vertebrate higher taxa during the Middle to

831   Late Devonian (Blieck, 2011) is also coeval with a contemporaneous radiation of

832   entomozoid ostracods, being the dominant (taphonomically preservable) component

833   of the Devonian-Carboniferous arthropod mesozooplankton. Thus, colonization

834   events across several animal groups may be linked, though the drivers of these events

835   remain speculative. Certainly the maintenance of an arthropod mesozooplankton may

836   have been an important component of sustaining fish stocks at higher trophic levels.

837   The lack of a detailed and continuous arthropod zooplankton fossil record for

838   much of the post-Carboniferous (Fig. 3) almost certainly reflects a taphonomic bias,

839   coupled with the likely dominance of zooplanktonic arthropods with unmineralised or

840   very weakly mineralized exoskeletons: this even pertains to pelagic ostracods, which

841   are known from the Carboniferous but are then absent until the Holocene (Fig. 3).

842   Likely, radiations of arthropod zooplankton were important for the reconstruction of

843   pelagic food webs following the major environmental crises marked by the Permian-

844   Triassic, Triassic-Jurassic and Cretaceous-Tertiary boundaries, though there is no

845   direct fossil record to support this. Nevertheless, the importance of the arthropod

846   zooplankton during the Cenozoic is evident for the evolution of the Southern Ocean

847   ecosystem at the transition between the warm Eocene and cooler Oligocene. The

848   major adaptive radiation of diatoms during the late Eocene (Falkowski et al., 2004)

849   and their ecological response to climate cooling produced by the development of an

850   Antarctic ice sheet in the early Oligocene (Houben et al., 2013) may have been an

851   important driver of niche differentiation in the oceans, affecting many biotic groups.

852   For example, baleen whales (Mysticeti) evolved from the ancestors of toothed whales

853   (Odontoceti) in the late Eocene (35 Ma) and underwent a major adaptive radiation in

854   the mid Oligocene (ca 30 Ma; Fordyce and Barnes, 1994; O'Leary and Uhen, 1999;

855   Cavin, 2010). This coincides with the origination of penguins in the Eocene and their

856   radiation during the Oligocene (Baker et al., 2006). Many modern Mysticeti

857   (Matthews, 1978) and penguins (Watanuki et al., 1994; Croxall et al., 1999) are krill

858   predators, and krill are filter feeders primarily on phytoplankton and in particular on

859   diatoms (Mauchline and Fisher, 1969). Though krill have no fossil record, it is

860   reasonable to infer that their evolution would have been influenced by diatom

861   abundances, and this in turn was possibly one of the triggers of baleen whale

862   diversification (Houben et al., 2013).

863

864   *5.4. Impact on the benthos*

865   Zooplankton plays a central role in the planktonic food web, both in terms of

866   biomass and energy fluxes. Grazing of phytoplankton by mesozooplankton provides

867   increased nutrient cycling, maintains autotroph populations in a state of more rapid

868   growth, and increases the food availability in the water column, allowing additional

869 trophic levels to be developed (Sterner and Elser, 2002). Furthermore, it

870 simultaneously increases the rain of organic matter to the benthos (Logan et al., 1995;

871 Tyson, 1995). Thus, the reorganization of biogeochemical cycles that occurred

872 between the latest Neoproterozoic and early Cambrian (Logan et al., 1995) has long

873 been attributed to the evolution of zooplanktonic metazoans whose faecal pellets

874 removed organic matter from the water column and delivered this to the benthos

875 (Butterfield, 1997). The increasing presence of meso- and microzooplankton in the

876 water column allowed the subsequent development of macrozooplankton and nekton,

877 whose faecal pellets are large enough to settle before they are consumed in the water

878 column (Turner, 2002). Possibly, these larger tertiary plankton consumers developed

879 mainly from the Ordovician onwards (e.g., trilobites, phyllocarids and cephalopods),

880 and the development of this enhanced faecal stream may have influenced

881 diversifications of various filter-feeding organisms such as crinoids and brachiopods

882 (Peterson et al., 2005). Within the water column, the Great Ordovician

883 Biodiversification Event involved a significant increase in the diversity of the

884 phytoplankton (e.g., protistan acritarchs; Servais et al., 2008, 2010), followed by the

885 development of a diverse zooplankton including arthropods such as trilobites and

886 phyllocarids. This revolution in the plankton may have enabled the establishment of a

887 diverse fauna of macrozooplankton and nekton, including vertebrates, molluscs and

888 arthropods (Kröger et al., 2009), and it may have promoted the rise of suspension

889 feeders in the benthos (Servais et al., 2009).

890

891 *6. Conclusions*

892 Analysis of the fossil record indicates that arthropods had already developed

893 morphologies during the Cambrian Period that facilitated a zooplanktonic lifestyle.

894   These anatomical adaptations, coupled with key reproductive strategies, included

895   well-developed swimming and feeding appendages, buoyancy, an active metabolism

896   supported by efficient circulatory systems, photoreception and bioluminescent organs

897   (to locate food or avoid being eaten, or to find mates), and the nurturing of young

898   within the carapace. Arthropods possess a unique evolutionary plasticity that has

899   allowed them to be a major force in marine planktonic ecosystems for over 500

900   million years.

901   Although diverse and abundant in recent ecosystems, zooplanktonic arthropods are

902   rare in the post-early Palaeozoic fossil record. Several factors diminish their

903   preservation potential, including a paucity of skeletal material, and post-mortem

904   transport damage and scavenging of carcasses in the water column. Nevertheless,

905   there is sufficient direct (fossil) and indirect (e.g., faecal pellets) evidence to suggest

906   that a complex zooplanktonic food web, involving primary to tertiary consumers, was

907   already well developed by the Cambrian, and that many of the major arthropod groups

908   that have a record of water column colonization were already present at that time,

909   albeit not necessarily as zooplankton.

910   As intermediates between the consumption of primary production and the

911   provision of food to higher trophic levels, mesozooplanktonic arthropods such as

912   copepods and ostracods are critical go-betweens in marine food webs. Although the

913   overall fossil record of arthropod zooplankton is very poor, their nascent ability to

914   colonise the water column was likely integral to the restructuring of the marine

915   trophic structure in post-extinction intervals, and to the long-term survival of

916   complexity in the marine ecosystem.

917

918   **Acknowledgements**

925

926   **References**

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1461 **Explanation of Tables**

1462

1463 **Table. 1. Summary of fossil and Recent arthropod zooplankton.** See main

1464 text for references.

1465

1466 **Explanation of figures**

1467

1468 **Fig. 1.** *Examples of Recent arthropod zooplankton.*

1469 (A) Myodocopid ostracod *Gigantocypris muelleri* (image from Creative

1470 Commons 3.0/M. Angel), frontal view, width about 15 mm.

1471 (B) Halocyprid ostracod *Conchoecia imbricata* (image courtesy of J. Vannier),

1472 lateral view, length 3.75 mm.

1473 (C) Detail of the integumental circulatory system of a myodocopid ostracod

1474 *Azygocypridina* sp., lateral view, length 4.05 mm.

1475 (D) Cladoceran branchiopod *Daphnia pulex* (image from Creative Commons

1476 2.5/P. Hebert), lateral view, length up to 4 mm.

1477 (E) Calanoid copepod *Calanus marshallae* (image from Creative Commons

1478 3.0/R. Hopcroft), dorsal view, length 4.10 mm.

1479 (F) Cyclopid copepod *Eucyclops speratus* (image from Creative Commons

1480 2.0/Proyecto Agua), dorsal view, length 0.65 mm.

1481 (G) Remiped *Speleonectes tanumekes* (image from Creative Commons 2.5/J.

1482 van der Ham, Nieber et al., 2011), dorsal view, length up to 27 mm.

1483 (H) Phyllocarid malacostraca *Nebaliopsis* sp. (image courtesy of D. Shale),

1484 lateral view, length up to 40 mm.

1485 (I) Decapod malacostraca Zoea larvae (image courtesy of N. le Bescot), oblique

1486   lateral view, length about 2 mm.

1487   (J) Hyperiid amphipod malacostraca *Hyperia macrocephala* (image from

1488   Creative Commons 3.0/U. Kils), lateral view, length up to 29 mm.

1489   (K) Lophogastrid malacostraca *Gnathophausia zoea* (image from Creative

1490   Commons 3.0/A. Semenov), lateral view, length up to 70 mm.

1491   (L) Euphausiid malacostraca *Euphausia superba* (image from Creative

1492   Commons 3.0/ U. Kils), lateral view, length up to 60 mm.

1493

1494   **Fig. 2.** *Possible timing of the origins of adaptations in arthropods.* Tree and

1495   taxa compiled from Legg et al. (2013) and Edgecombe and Legg (2014). Genera

1496   reconstructed   modified   as   follows*:   Anomalocaris*   after   J.   Meszaros

1497   (http://nocturnalsea.deviantart.com/); *Nereocaris* after Legg et al. (2012);

1498   *Opipeuterella*   and   its   swimming   appendages   after   N.   Jainschigg

1499   (http://www.nickjainschigg.org/Trilobite.html); *Parabolbozoe* after Perrier et al.

1500   (2011); reconstruction of swimming *Anomalocaris* after Usami (2006).

1501

1502   **Fig. 3.** *The fossil record and colonization events of arthropod zooplankton*

1503   *through the Phanerozoic and their relation to other major events in the evolution*

1504   *of the marine biosphere.* Tree and taxa compiled from Legg et al. (2013),

1505   Edgecombe and Legg (2014), Wills et al. (2009) and Porter et al. (2005). See main

1506   text for arthropod zooplankton fossil record. Radiations after the following authors:

1507   suspension feeders after Harper et al. (2009: brachiopods), Lefebvre et al. (2013:

1508   echinoderms) and Novack-Gottshall and Miller (2003: bivalves;); acritarchs after

1509   Servais et al. (2008, 2010); cephalopods after Kröger et al. (2009); pelagic fish

1510   after Blieck (2011); diatoms after Falkowski et al. (2004); baleen whales after

1511   Cavin (2010); penguins after Croxall et al. (1999).

1512

1513   **Fig. 4.** *Examples of fossil arthropod zooplankton.*

1514   (A-C) Small carbonaceous fossils. Fossil crustacean mandibles from the middle

1515   and upper Cambrian Deadwood Formation and carbonaceous faecal strings from

1516   the middle Cambrian Little Bear biota, Canada (images courtesy of T. Harvey and

1517   N. Butterfield; Harvey and Butterfield, 2011, 2012); (A) Branchiopod-type

1518   mandibles from the Riley Lake assemblage; length about 200 μm; (B) Copepod-

1519   type mandibles from the Riley Lake assemblage; length about 250 μm; (C)

1520   Carbonaceous faecal strings, length about 700 μm (inset: acritarchs, 5-6 μm

1521   diameter).

1522   (D) Radiodonta *Anomalocaris canadensis*, predatory frontal appendage (GSC

1523   45308), from the middle Cambrian Burgess Shale Lagerstätte, Canada (images

1524   courtesy of A. Daley); lateral view; length about 110 mm.

1525   (E) Radiodonta *Tamisiocaris borealis*, filtering frontal appendage (MGUH

1526   30500), from the lower Cambrian Sirius Passet Lagerstätte, North Greenland

1527   (images courtesy of J. Vinther; Vinther et al., 2014); lateral view; length about 115

1528   mm.

1529   (F) Bivalved arthropod *Isoxys actuangulus* (ROM 57898A) from the middle

1530   Cambrian Burgess Shale Lagerstätte, Canada (images courtesy of J. Vannier);

1531   lateral view; length about 50 mm.

1532   (G) Agnostid trilobite *Ptychagnostus gibbus* from the middle Cambrian

1533   Wheeler shale, Utah, USA, (image from Creative Commons 3.0 /Dwergenpaartje);

1534   dorsal view; length about 5 mm.

1535   (H) Eurypterid *Eurypterus remipes* from the Silurian Fiddlers Green Formation,

1536   New York, USA (image from Creative Commons 1.0 /Daderot); dorsal view;

1537   length up to 200 mm.

1538   (I) Reconstruction of the gilled lobopodian *Opabinia regalis* from the middle

1539   Cambrian Burgess Shales Lagerstätte, Canada (image from Creative Commons

1540   3.0/N. Tamura); oblique lateral view; length up to 100 mm.

1541   (J) Reconstruction of the bivalved arthropod *Nereocaris exilis* from the middle

1542   Cambrian Burgess Shales Lagerstätte, Canada (modified after Legg et al., 2012);

1543   lateral view; length up to 140 mm.

1544   (K) Reconstruction of the malacostracan *Angustidontus seriatus* from the Upper

1545   Devonian (Famennian) Woodruff Formation, Nevada, USA (modified after Rolf

1546   and Dzik, 2006); lateral view; length up to 100 mm.

1547   (L) Reconstruction of the trilobite *Telephina* from the Upper Ordovician

1548   (modified after Fortey, 1985); dorsal view; length up to 30 mm.

1549   (M) Hyperthrophied eyes of the trilobite *Pricyclopyge binodosa* (NHM I

1550   15232) from the Middle Ordovician Šárka Formation, Bohemia, Czech republic

1551   (modified after Fortey and Owens, 1999); frontal view; width about 15 mm.

1552   (N-O) Anaprotaspid larva of proetoid trilobite (UM2-RLA4) from the lower

1553   Carboniferous (Tournaisian) Griotte Formation, Montagne Noire, southern France

1554   (image courtesy of R. Lerosey-Aubril; Lerosey-Aubril and Feist, 2005); (N) dorsal

1555   view; (O) ventral view; length about 650 μm.

1556   (P) Bradoriid *Anabarochilina primordialis* (SGU 8622) from the middle

1557   Cambrian Alum Shale Formation, Sweden (Williams et al., *in press*); lateral view;

1558   length 8.9 mm.

1559   (Q) Myodocopid ostracod *Luprisca incuba* (YPM 237107) from the Upper

Ordovician (Katian) Beecher's Trilobite Bed, New York, USA (Siveter et al., 2014); latero-dorsal view; length 3.4 mm.

(R) Myodocopid ostracod *Pauline avibella* (OUMNH C.29613) from the Lower Silurian (Wenlock) Herefordshire Lagerstätte, UK (Siveter et al., 2012); lateral view of soft parts (carapace omitted), digital reconstruction with different colors corresponding to each appendage; length 10.2 mm.

(S) Myodocopid ostracod *Parabolbozoe armoricana* (FSL 710401) from the Silurian (Wenlock/Ludlow) Lande Murée Formation, France (Perrier et al., 2011); lateral view; length 8 mm.

Fig. 5. *Taphonomy of Recent and fossil arthropod zooplankton.* Based on literature on Recent and fossil arthropods (e.g., Collette and Hagadorn, 2010), as cited in the text.

Fig. 6. *Schematic comparison of the position of key arthropod zooplankton in simplified Recent and Early Palaeozoic pelagic food webs.* Both pyramids and drawings are based on a compilation of available data for the period of time considered and do not imply that these animals were co-occurring in the same horizons. Plankton sizes after Omori and Ikeda (1984).