

1 Running head: SCAVENGING AMPHIPODS OF THE ANGOLAN DEEP-SEA HABITAT

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4 SCAVENGING AMPHIPODS OF THE ANGOLAN DEEP-SEA HABITAT, WITH A

5 FOCUS ON ABYSSORCHOMENE DISTINCTUS (BIRSTEIN & VINOGRADOV, 1955)

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18 **ABSTRACT**

1
2 19 Owing to its vast natural resources and the influence of the Congo River and
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4 20 associated submarine canyon, the Angolan continental margin is of both
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7 21 socioeconomic and ecological interest. The deep-sea ecosystems of the region are,
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9 22 however, understudied, and much of the deep-sea fauna remains undescribed. Here,
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11 23 we document the scavenging amphipods of the the Angolan deep-sea habitat, which
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13 24 provides valuable new insight into the ecology of Angolan deep-sea scavengers. This
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15 25 can be used as an ecological baseline, against which resource-extraction impacts can
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17 26 be measured. 7 996 scavenging amphipods, representing 10 species, were identified.
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19 27 At least four species were new to science. The relatively low scavenger diversity of
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21 28 the region, combined with the large sample sizes, may be indicative of abundant food-
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23 29 falls in the region due to the presence of the submarine canyon system.
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29 30 The dominant species across all samples, *Abyssorchomene distinctus* (Birstein
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31 & Vinogradov, 1955), was the focus of a population-level study, which was used to
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33 32 describe the population structure of this species and identify species traits. Of the 826
34
35 33 *A. distinctus* dissected and measured, 533 were unsexed juveniles, 149 were male, and
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37 34 144 were female. Females were significantly larger than males, which is indicative of
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39 35 non-mate-guarding pre-copulatory behaviour, but had significantly shorter antennae,
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41 36 which may indicate that males use chemical cues during mate-searching. Two, three,
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43 37 and five discrete size-based cohorts were identified for juveniles, males, and females
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45 38 respectively. No ovigerous females were caught but brood size of *A. distinctus* was
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47 39 estimated to be 10 – 38 offspring based on ovary contents.
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56 41 **Keywords:** Amphipoda, Angola, Congo Submarine Canyon, continental margin,
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58 42 necrophage, population ecology
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44 INTRODUCTION

1
2 45 In general, the continental margin environment is of great ecological
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4 46 importance owing to its role in connecting terrestrial and shallow-water habitats to
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7 47 deep-sea ocean basins. The continental margin region off the coast of Angola is of
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9 48 particular socioeconomic and ecological interest due to its abundant natural resources
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11 49 and large, deeply incised, submarine canyon (Heezen et al., 1964), which is directly
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13 50 linked to the second largest river system in the world, the Congo (Eisma & Van
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15 51 Bennekom, 1978; Savoye et al., 2009). The deep-sea ecosystems of the Angolan
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17 52 continental margin are, however, relatively understudied. Chemosynthetic systems
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19 53 have received some attention but bathyal habitats on the margin are underrepresented,
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21 54 though unpublished environmental assessments by industry scientists do exist (Jones
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23 55 et al., 2014). Therefore, study of the bathyal habitat of the Angolan continental
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25 56 margin presents the opportunity to identify and describe novel deep-sea assemblages
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27 57 and species that are new to science. Furthermore, ecological assessments can be used
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29 58 as a baseline against which the potential impacts of expanding resource extraction
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31 59 activities in the region can be measured.
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39 60 Previous assessments of the deep-sea fauna of the Angola continental margin
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41 61 and basin have identified a large number of species that are new to science. Of the
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43 62 682 Harpacticoida copepod species recently identified by George et al. (2014) only
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45 63 five were formally described with the remainder new to science. This is despite past
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47 64 research programmes (e.g. BIOZAIRE, Sibuet & Vangriesheim, 2009) and
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49 65 expeditions to the region that resulted in first description of many peracarid species
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51 66 (Brandt et al., 2005, and references therein). Other, previously undescribed,
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53 67 crustaceans (e.g. isopods, Brix et al., 2014; amphipods, Horton, 2004; Horton &
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55 68 Thurston, 2014) and loriciferans (Gad, 2005) have also been recently described from
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69 the region. While these advances have no doubt furthered our understanding of
70 Angolan deep-sea communities, the scavenging fauna of the region remains
71 understudied, especially in comparison to studies on legacy study areas in the North
72 Atlantic (e.g. the Porcupine Abyssal Plain and Seabight, Billett et al., 2001; Hartman
73 et al., 2012). Records of invertebrate scavengers in the Angolan continental margin
74 region are particularly lacking.

75 Scavenging organisms play an integral role in deep-sea communities,
76 dispersing and reintegrating organic carbon from food-falls into the wider ecosystem
77 (Stockton & DeLaca, 1982; Britton & Morton, 1994; Payne & Moore, 2006; Higgs et
78 al., 2014). These food-falls provide a localised and concentrated input of nutrients
79 into the generally nutrient poor deep-sea habitat and their assimilation by scavengers
80 forms the foundation of deep-sea food chains driven by secondary production (Payne
81 & Moore, 2006). The Angola basin has been identified as a region with frequent large
82 food-falls (Higgs et al., 2014), possibly due to the presence of the Congo Submarine
83 Canyon, one of the largest submarine canyons in the world (Heezen et al., 1964;
84 Shepard & Emery 1973). Traces from the plume produced by the Congo River and its
85 interaction with the canyon system can be detected up to 800 km from the river mouth,
86 where nutrient-rich effluent enhances the primary productivity of surface waters (Van
87 Bennekom & Berger, 1984). Nutrient-rich waters are also found in deep marine
88 environments owing to the active canyon system (Van Bennekom & Berger, 1984;
89 Khrifounoff et al., 2003; Vangriesheim et al., 2009). The effects of the nutrient-rich
90 environments generated by the Congo River plume are reflected in high-density
91 assemblages of sipunculans and echiurans in the Angola basin (Saiz-Salinas, 2007).
92 Nutrient-rich areas are also expected to have scavenging assemblages dominated by a

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93 few specialist scavenger species (Stefanescu et al., 1994; King et al., 2008; Duffy et
94 al., 2012).

95 This study aims to document the scavenging amphipods (Crustacea:
96 Lysianassoidea) that attend large food-falls in the Angolan deep-sea habitat and
97 provide new insight into the life history and population structure of the dominant
98 scavenging amphipod species in the region.

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102 MATERIALS & METHODS

103 Sample collection and processing

104 Samples were collected as part of baseline benthic surveys on behalf of the oil
105 company BP Exploration (Angola) Limited. Five samples of scavenging amphipods
106 were collected in 2005, with a further five samples collected in 2014 (Table 1; Figure
107 1). All samples were collected using simple traps (a Perspex tube with single funnel
108 opening) baited with bigeye tuna (*Thunnus obesus* (Lowe, 1839)) and attached to the
109 frame of the ROBust BIODiversity lander (ROBIO; OceanLab, Aberdeen, UK), a free-
110 fall lander equipped with two acoustic releases, current meter, digital stills camera,
111 flashgun, and battery pack (Jamieson & Bagley, 2005). The ROBIO lander was
112 deployed in 'tripod mode' off the coast of Angola from the Gardline operated *Ocean*
113 *Endeavour* in water 482 - 2073 m deep. On retrieval, amphipod samples were fixed in
114 100 % ethanol and returned to the laboratory where they were sorted, identified to
115 species level, and counted. A non-metric multidimensional scaling plot was used to
116 visualise Bray-Curtis dissimilarity amongst deep-water sites after species counts were
117 converted to proportions. Sample B19-ROBIO was excluded from this analysis as the
118 only sample taken from < 500 m water depth. A PERMANOVA test with 999
119 permutations was used to compare the composition variance of samples collected in
120 2005 and 2014.

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122 [FIGURE 1 / TABLE 1]

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124 The most abundant species was selected for a detailed population-level analysis. A
125 random number generator was used to select a random subset of 826 individuals
126 identified as *Abyssorhomene distinctus* (Birstein & Vinogradov, 1960) from sample

127 56761#1. Selected *A. distinctus* individuals were dissected and measured under a
128 stereo-dissecting microscope. Organisms were sexed using primary and secondary
129 sexual characteristics and diagonal length of coxal plate 4 (C4L; as described in Duffy
130 et al., 2015) was measured for all individuals using a stage graticule. Oostegite and
131 gill length were also measured for all females. Prior to dissection, the total body
132 length (TBL; distance along the dorsal margin between the anterior margin of the
133 head and the tip of the telson) of 50 randomly selected individuals was measured
134 using a digital graphics tablet and HTML-assisted Measuring System (HaMS; Duffy
135 et al., 2013). A linear model was used to correlate total body length to coxal plate 4
136 measurements so that the latter could be used a proxy for the former in all individuals.
137 This reduces error that may arise from the variable posture of specimens and allows
138 damaged specimens to be included in analyses.

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140 **Population characterisation**

141 Characterisation analyses can be performed on either the total body length
142 measured for all individuals or a correlated proxy (Duffy et al., 2013; Duffy et al.,
143 2015). Therefore, the diagonal length of coxal plate 4 was used for this analysis as a
144 proxy for total body length. Growth stages, or cohorts, of the *A. distinctus* population
145 were identified from the length-frequency distribution of all measured specimens,
146 with each discrete Gaussian component representing a successive moult. Oostegite
147 stages were identified from a frequency distribution of the oostegite length:gill length
148 ratio, where each discrete Gaussian component represented an oostegite stage.

149 Probability density histograms of coxal plate 4 measurements were plotted by
150 sex (male, female, unsexed juveniles). Oostegite:gill ratios for all females were also
151 plotted as probability density histograms. Gaussian components were identified from

152 these plots initially by eye and then confirmed using the probability paper method
153 (Cassie, 1954; Harding, 2009). The ‘mixdist’ package (Macdonald & Pitcher, 1979;
154 Macdonald & Du, 2011) in R statistical software (R Development Core Team 2015)
155 was used to confirm and refine the parameters of each identified component. The
156 ANOVA function of this package was used to test if the identified Gaussian
157 components differed significantly from the original data.

158 RESULTS

159 A total of 7 996 lysianassoid amphipods were identified from the 10 sampling
160 sites. Ten species were identified, representing seven genera (Table 1). Of these, at
161 least four species were new to science at the time of collection, though *Cyclocaris*
162 *franki* Horton & Thurston, 2014, has now been described. *Abyssorchomene distinctus*
163 or *Paracallisoma* sp. 6 were the dominant species in all but one (B19-ROBIO) sample
164 (5.0 - 94.7 %, 5.0 - 87.5 % relative abundance respectively). *Podoprion ruffoi* Lowry
165 & Stoddart, 1996 was the only species found in sample B19-ROBIO, which was the
166 shallowest trap deployment (482 m), and was represented by only three individuals.
167 Species richness of each sample was low and ranged from one (B19-ROBIO) to six
168 (B18-ROR1). A multidimensional scaling plot visualising Bray-Curtis dissimilarity
169 amongst sites > 1000 m water depth (Figure 2), in combination with a PERMANOVA
170 test ($n = 9$, $F_1 = 1.5258$, $R^2 = 0.1790$, $p = 0.0550$), indicated that the compositions of
171 samples taken in 2005 and 2014 were not significantly different.

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173 [FIGURE 2]

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175 Of the 826 *A. distinctus* specimens from sample 56761#1 that were dissected
176 and measured for population analyses 149 males, 144 females, and 533 unsexed
177 juveniles of varying size were identified. No ovigerous females were identified. There
178 was a positive correlation between total body length and coxal plate 4 length ($n = 50$,
179 $TBL = 6.8743 C4L + 2.0486$, $R^2 = 0.8878$). This allowed for coxal plate 4
180 measurements to be used as a proxy to estimate total body length. Estimated total
181 body length for *A. distinctus* studied ranged from 5.46 to 19.12 mm (9.04 - 13.91 mm
182 and 9.49 - 19.12 mm for specimens identified as males and females respectively).

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184 Sexual dimorphism

185 The size distributions of males and females were significantly different from
186 each other (Figure 3A; Mann-Whitney U-test: $U = 3911.5$, $p < 0.001$). Coxal plate 4
187 measurements of females were on average larger than males and had greater
188 maximum size (males, $Q1 = 0.900$, $Q2 = 1.200$, $Q3 = 1.300$; females, $Q1 = 1.300$, $Q2$
189 $= 1.500$, $Q3 = 2.000$). Males had significantly longer antennae relative to total body
190 length (Figure 3B; MWU: $U = 1\ 733$, $p = 0.003$; males, $Q1 = 1.363$, $Q2 = 1.775$, $Q3 =$
191 2.000 ; females, $Q1 = 1.613$, $Q2 = 1.900$ $Q3 = 2.387$).

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193 [FIGURE 3]

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195 Sexual development

196 Oostegites were visible in females as small as 5.46 mm body length. It should
197 be noted that *A. distinctus* possesses an accessory gill that may be mistaken for an
198 oostegite, however it is present in both males and females and close examination
199 confirms it is part of the primary gill structure. An oostegite:gill ratio frequency
200 histogram and 'mixdist' model (ANOVA: $d.f. = 12$, $\chi^2 = 12.26$, $p = 0.4250$) identified
201 three distinct oostegite stages (OS). All but one of the females with OS3 oostegites
202 possessed setose oostegites, which indicates sexual maturity. Only one individual
203 with OS2 oostegites had setae and no OS1 oostegites were setose. Ovaries were
204 recoverable from 11 individuals and oocytes were arranged linearly. The total number
205 of oocytes within recovered ovaries ranged from 5 to 19 with a median of 15 oocytes
206 per ovary. Author observations, coupled with knowledge of a congener species (Duffy
207 et al., 2013), indicate that both ovaries contain approximately equal numbers of

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208 oocytes and therefore brood size estimates lie between 10 and 38 individuals. Penal
209 papillae in this species were pronounced and easily identified on examination of
210 section 7 of the carapace.

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212 **Population characterisation**

213 Gaussian components, each representing a cohort or growth stage, were
214 identified for juveniles, males, and females (Table 2). Individuals that could not be
215 sexed were assigned to one of two juvenile stages (Figure 4). There was minimal
216 overlap between the distribution of the largest juveniles (J2) and the smallest sexed
217 individuals (M3, F3; Figure 4). Males fitted into three distinct cohorts (M3, M4, and
218 M5; Figure 4A). The presence and number of these was confirmed using the
219 probability paper method and the parameters were further refined using the ‘mixdist’
220 package. The fitted model did not differ significantly from the data (ANOVA: *d.f.* = 5,
221 $\chi^2 = 4.10$, $p = 0.5348$).

222 Five cohorts were identified for females (F3 – F7; Figure 4B). The parameters
223 of these cohorts were confirmed using the probability paper method combined with a
224 ‘mixdist’ model fitted to the data (ANOVA: *d.f.* = 2, $\chi^2 = 0.2728$, $p = 0.8725$). Linear
225 growth factors between cohorts ranged from 1.18 to 1.36 with juvenile growth factors
226 at the higher end of this range. These growth factors are comparable to those
227 previously reported for *Abyssorhomene abyssorum* (Stebbing, 1888) (Duffy et al.,
228 2013).

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230 [FIGURE 4 / TABLE 2]

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232 **DISCUSSION**

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2 233 Two of the species identified, *Abyssorchomene distinctus* and *Paracallisoma*
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5 234 sp. 6, featured in all but the shallowest sample, frequently in high relative abundances.
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7 235 *Abyssorchomene distinctus* has been previously found at depths ranging from 2635–
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9 236 5173 m (Barnard & Ingram, 1990; Jamieson et al., 2011). Sampled at 1157 m deep,
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11 237 the four *A. distinctus* in sample B18-ROR2 represent the shallowest confirmed record
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13 238 of this species to date (though it should be noted that the species was described by
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15 239 Birstein & Vinogradov, 1960, from a specimen taken in a non-closing net operating
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17 240 between 2000 m deep and the surface, thus the actual depth of capture of the original
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19 241 record cannot be confirmed). The low abundance, relative to deeper samples, in this
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21 242 sample and sample B18-ROR1 (1461 m depth) suggests that this represents the
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23 243 uppermost limits of the depth-range of this species. *Abyssorchomene distinctus* is
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25 244 reported from the type locality in the Pacific Ocean, Near Palau (Birstein &
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27 245 Vinogradov, 1960), the East Pacific vent region (Barnard & Ingram, 1990), the
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29 246 Loyalty Islands (Lowry & Stoddart, 1994), the Kermadec Trench (Jamieson et al.,
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31 247 2011), the Cape Verde Plain, North Atlantic (Thurston, 1990), and Mid-Atlantic
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33 248 Ridge (Horton et al., 2013). The finding of this species in both the Pacific and
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35 249 Atlantic Oceans warrants further investigation to determine whether or not the
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37 250 populations are conspecific.
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46 251 *Paracallisoma* sp. 7 is similar in appearance to a species of *Paracallisoma*
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48 252 Chevreux, 1903, yet to be described from the Faroe-Shetland Channel (*Paracallisoma*
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50 253 sp. 2; Horton, 2006), but individuals are outside the known size range for that species
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52 254 and it is therefore likely to be new to science. Only 34 individuals were found from
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54 255 six samples (Table 1). All new species of *Paracallisoma* are being described
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256 elsewhere as part of a series of revisions of the family Scopelocheiridae (first revision,
257 Horton & Thurston, 2015).

258 *Cyclocaris franki* Horton & Thurston, 2014, was described in a recent revision
259 of the genus *Cyclocaris*, from the material reported herein. The species is only known
260 from the Atlantic Ocean, from the Angolan continental margin, 1850–2059 m, the
261 Sierra Leone Rise, 1203 m, and the Cape Verde Islands, 1477 m (Chevreux, 1903;
262 1935). All known material of *C. franki* has been obtained from baited benthic traps
263 (Horton & Thurston, 2014).

264 The entity reported here as *Valettiopsis macrodactyla* Chevreux, 1909 and as
265 redescribed in Horton (2004) is likely also a new species. *Valettiopsis macrodactyla*
266 was first described by Chevreux (1909) and the description repeated with different
267 illustrations and further material in 1935 (Chevreux, 1935). A further specimen was
268 attributed to *V. macrodactyla* by Lincoln & Thurston (1983). This entity is now
269 recognised as *V. lincolni* Horton, 2004. The key to *Valettiopsis* provided by
270 Hendrycks (2007) indicates that the description of the palm of Gnathopod 2 for *V.*
271 *macrodactyla sensu strictu* does not match that of the illustrations of *V. macrodactyla*
272 *sensu* Horton 2004. The type of *V. macrodactyla* Chevreux, 1909 thus warrants a full
273 redescription to distinguish it from the Angolan species and to prevent further errors
274 in identification.

275 The species *Valettiopsis longidactyla* Horton, 2004, was originally described
276 from material collected off the coast of Angola from two male type specimens. This
277 study adds a further four specimens to those known and extends the known depth of
278 occurrence of this species from 1252 m to 1850 m (Horton, 2004). *Valettiopsis*
279 *lincolni* Horton, 2004 was described from material taken from the Bay of Biscay

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280 Abyssal Plain, at 4300 m and has also been recorded from the Gulf of Mexico at 1326
281 m. This study adds a further four specimens from 1850 m off the Angolan coast.

282 *Podoprion ruffoi* is the sole species collected from the shallowest sample at
283 482 m. There is only one other specimen known, described from the stomach of a fish
284 taken off the coast of Namibia in 410–460m depth (Lowry & Stoddart, 1996). The
285 samples collected as part of this study add three specimens and provide a significant
286 range extension, indicating that members of the genus *Podoprion* appear to be
287 specialist scavengers occurring shallower than 1200m. This second finding of *P.*
288 *ruffoi* in the 400–500m depth range off the coast of West Africa suggests the species
289 is constrained to this depth-range but may have a broad geographic distribution along
290 the African continental slope.

291 The absence of species of the genus *Eurythenes* Smith in Scudder, 1882 from
292 all samples described here is notable. *Eurythenes* is a ubiquitous genus of scavenging
293 amphipod with a pan-oceanic distribution (Stoddart & Lowry, 2004; Brandt et al.,
294 2012). With the recent resolution of the *E. gryllus* (Lichtenstein in Mandt, 1822)
295 species-complex, it is now understood that the genus is comprised of at least seven
296 species. (D'Udekem D'Acoz & Havermans, 2015). Members of the genus are almost
297 always recovered from baited traps deployed at bathyal, abyssal, and hadal depths
298 (e.g. Thurston, 1990; Duffy et al., 2012; Horton et al., 2013). There are two potential
299 explanations for its apparent absence from samples from the Angolan slope, either
300 sampling bias or true absence of *Eurythenes*. Although the former cannot be wholly
301 ruled out, 10 localised samples across a 1500 m depth range represents relatively
302 good sampling effort for deep-sea scavenging amphipods and one would expect to
303 catch at least one *Eurythenes* specimen if they are present in the environment (e.g.
304 Horton et al., 2013 described the contents of 12 baited trap deployments on the Mid-

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305 Atlantic Ridge and all contained *Eurythenes*; of the eight trap deployments on the
306 Iberian margin described by Duffy et al., 2012, all but two contained *Eurythenes*).
307 The diameter of the trap opening may have prevented large individuals from entering,
308 but an identical trap has previously caught multiple *Eurythenes* specimens (Cousins et
309 al., 2013). It is, therefore, likely that the genus is absent from the Angolan continental
310 margin at the studied depths. The distribution of *E. gryllus sensu lato* suggests that the
311 upper thermal tolerance of *Eurythenes* is ~ 4 °C (Thurston, 1990, and references
312 therein) and, as the water temperature recorded at all sites is near to or in excess of
313 this temperature (Table 1), the environment of the Angolan deep sea may be
314 inhospitable to this species.

315

316 **Angolan scavenging amphipod assemblages**

317 The identification of four species not previously described, and unexpected
318 absence of *Eurythenes*, highlights how little is currently known of deep-sea
319 scavenging guilds in the Angola region. Despite multiple sample sites, a broad depth-
320 range of sampling (482 – 2073 m deep), and the large number of individuals collected
321 in this study, only ten in species in total were found. A regional species richness (γ -
322 diversity) of ten is similar to the regional diversity reported for the bathyal depths of
323 the Bay of Biscay (22 deployments, 2080 – 2225 m water depth, $\gamma = 8$; Thurston,
324 1990), although the sampling depth-range and sample-size of these samples was much
325 smaller. The richness of the Angolan continental margin scavenging amphipod
326 community is lower than the lysianassoid richness reported from large catches from
327 bathyal depths at the Mid-Atlantic Ridge (12 deployments, 2340 – 2628 m water
328 depth, $\gamma = 31$; Horton et al., 2013) despite sampling efforts at the Mid-Atlantic Ridge
329 covering a narrow depth-range of 288 m compared to the 1591 m depth-range of this

1 330 study. The Mid-Atlantic ridge may, however, be acting as a biogeographic boundary
2 331 in this region (Alt et al., 2013; Horton et al., 2013) meaning that the high regional
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4 332 diversity is an artefact of sampling across multiple biogeographic regions. Regardless,
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7 333 the species richness values reported by Horton et al. (2013) for each of the discrete
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10 334 sampling areas around the Mid-Atlantic ridge (NW = 15, NE = 18, SE = 23, SW = 18)
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12 335 were all higher than the total richness of the Angolan continental margin.

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14 336 The relatively low diversity and large sample sizes reported here are
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17 337 comparable to scavenging amphipod assemblages described from submarine canyons
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19 338 on the Iberian Peninsula (Duffy et al., 2012). The finding of high numbers of only a
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21 339 few amphipod species in samples between 6.0 and 6.5 ° S (Figure 1) is particularly
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23 340 interesting. The large sample sizes suggest that there is a large background
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26 341 scavenging population in the sampling area (Blankenship et al., 2006) and this may be
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29 342 indicative of a high nutrient deep-sea habitat in the region, a result of the Congo
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31 343 submarine canyon system (Figure 1). Submarine canyons, especially large canyons
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34 344 like Congo that deeply incise the continental shelf (Heezen et al., 1964), capture
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36 345 sediments and channel them into the deep sea (van Weering et al., 2002; Cúrdia et al.,
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39 346 2004). This makes submarine canyons hotspots of secondary production (Soliman &
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41 347 Rowe, 2008; De Leo et al., 2010; van Oevelen et al., 2011), with active canyon
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44 348 systems enriching surrounding deep-sea environments (Van Bennekom & Berger,
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46 349 1984; Khripounoff et al., 2003; Vangriesheim et al., 2009). Cúrdia et al. (2004)
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49 350 identified estuarine input as a primary source of the large quantities of terrigenous
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51 351 organic matter that enter canyon systems. As Congo Submarine Canyon is directly
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54 352 linked to the second largest river system in the world (Eisma & Van Bennekom, 1978;
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56 353 Savoye et al., 2009), the terrigenous input is expected to be sizeable. Nutrient-rich
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58 354 river effluent also enhances primary productivity of surface waters up to 800 km from
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355 the coast (Van Bennekom & Berger, 1984). Surface productivity is closely linked to
356 deep-sea nutrient availability via particulate organic carbon flux and benthic-pelagic
357 coupling processes (Lutz et al., 2002; Drazen et al., 2012).

358 The combination of enhanced primary production of surface waters,
359 terrigenous and shelf-material input, and enhanced secondary production that is
360 driven by the Congo submarine canyon and river systems results in deep-sea habitats
361 that are relatively rich in nutrients. These nutrient-rich environments have been shown
362 to support dense sipunculan and echiuran assemblages in the Angola Basin (Saiz-
363 Salinas, 2007). The effects of the river and canyon systems on the frequency of large
364 food-falls for scavenging organisms are difficult to accurately ascertain. However,
365 increased primary and secondary productivity are expected to increase overall
366 ecosystem biomass including the number of larger organisms that become food-falls
367 when they die. This theory is supported by the finding of three large food-falls in the
368 vicinity of the Congo Canyon (Higgs et al., 2014), a remarkably high number given
369 the infrequent occurrence of naturally occurring deep-sea food-falls recorded globally
370 (Stockton & DeLaca, 1982; Smith et al., 2015), though this may be reflective of
371 sampling effort. Turbidity currents in the canyon system may also increase food-fall
372 occurrence through direct mortality of megafauna (Angel & Rice, 1996).

373

374 **Potential impacts of oil-extraction**

375 Generally, scavenging species are thought to benefit from disturbances as
376 mortality of less motile organisms (Jones et al., 2006) would increase food-fall
377 availability. Scavenging amphipods are relatively motile (Laver et al., 1985; Bluhm,
378 2001) and are therefore able to quickly respond to disturbance events. The
379 pervasiveness of scavenging amphipods in disturbed environments may mean that

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380 physical disturbance from oil-extraction activity will benefit scavenging communities
381 as a result of increased food-fall availability. Coupled with the findings of Neff &
382 Durell, (2012) that concentrations of contaminants associated with deep-sea oil
383 extraction (polycyclic aromatic hydrocarbons, saturated hydrocarbons, sterane
384 triterpane petroleum biomarkers) were not significantly different in amphipods found
385 near extraction sites before and after well commission, it is unlikely that the short-
386 term effects of oil-extraction activities will be detrimental to deep-sea scavenging
387 amphipods. Regardless, this study of the deep-sea scavenging amphipod community
388 in the early stages of extraction activity provides a valuable baseline for studying any
389 long-term effects that may occur.

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391 **Population ecology of *Abyssorhomene distinctus***

392 The large number of *A. distinctus* recovered in this study provided the opportunity of
393 a population-level study of this poorly understood deep-sea amphipod. This provides
394 further population-level baseline data for any future studies examining the effect of
395 prospecting and extraction activity. The sexual dimorphism observed in *A. distinctus*
396 is very similar to that documented for its congener *A. abyssorum* (Duffy et al., 2013).
397 Lysianassoid females are often larger than males (Sainte-Marie, 1991), which may
398 reflect the non-mate-guarding pre-copulatory behaviour (Bousfield & Shih, 1994;
399 Bousfield 2001) that is characteristic of lysianssoid amphipods (Conlan, 1991). The
400 significantly longer antennae possessed by male *A. distinctus* is another sexual
401 dimorphic trait also observed in *A. abyssorum* (Duffy et al., 2013). Elongated
402 antennae are hypothesised to enhance tactile detection (Steele, 1995) and
403 chemosensing ability (Kaufmann, 1994) during mate searching activity.

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405 Five female cohorts were identified with larger, sexually mature females, possessing
406 large setose oostegites (OS3), indicating their ability to form a brood-pouch and carry
407 a brood (Steele, 1991). The estimated brood size of *A. distinctus* (10-38 eggs) is much
408 lower than that reported for *A. abyssorum* (36-78 eggs; Duffy et al., 2013). Sainte-
409 Marie (1991) identified a generally positive correlation between brood size and
410 female body length in other lysianassoid species but noted that this relationship is
411 variable. As such, the brood size relative to female body size is within expectations
412 for lysianassoid amphipods.

413 No ovigerous female *A. distinctus* were identified from individuals examined
414 in this study. Brooding deep-sea scavenging amphipods are rarely observed at food-
415 falls (Duffy et al., 2015), although there are a handful of exceptions (e.g. Blankenship
416 et al., 2006; Horton & Thurston, 2011; Horton et al., 2013). The rarity of brooding
417 females at food-falls is attributed to reduced mobility when carrying a brood,
418 vulnerability owing to a softened cuticle (Ingram & Hessler, 1987; Thurston & Bett,
419 1995), and general increase in predation risk at food-falls (Lampitt et al., 1985;
420 Jamieson et al., 2011). Due to the sampling methods used in this study, a bias in
421 population structure is unavoidable. Openings of all traps used were wide enough so
422 as to not prohibit entry of any *A. distinctus* regardless of their size. The possibility that
423 local hydrographic conditions influence the population structure (e.g. strong currents
424 prevent smaller individuals with reduced mobility reaching the trap) should also be
425 noted.

426 Owing to its position, linking coastal waters to abyssal basins, the deep-sea
427 ecosystem on the Angolan continental margin houses a unique, interesting, and newly
428 described scavenging amphipod community. The presence and influence of the Congo
429 Submarine Canyon further adds to the complexity and connectivity of the margin

1 430 region, providing a pathway for the estuarine system to affect deep-sea organisms.

2 431 The study of this region will allow for comparisons to be made with other deep-sea

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4 432 scavenging assemblages and populations around the world and provide an important

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7 433 ecological baseline to monitor the effects of resource extraction activities.

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698 Figure 1: Bathymetric map of the continental margin off the coasts of the Republic of
699 Angola and the Democratic Republic of the Congo (DRC). Contours indicate depth in
700 metres. Sampling sites used in this study indicated by stars.

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702 Figure 2: Non-metric multidimensional scaling plot of Bray-Curtis similarity amongst
703 deep (> 1000 m water depth) sites used in this study. Triangles and circles represent
704 samples taken in 2005 and 2014 respectively, stress = 4.1144. See Table 1 for site
705 specific environmental data and location.

706

707 Figure 3: Estimated body-size (A) and corrected antennal length relative to body size
708 (B) of antenna 1 (grey) and antenna 2 (white) of male and female *Abyssorhomene*
709 *distinctus*. Median and interquartile ranges shown.

710

711 Figure 4: Probability density histogram for coxal plate 4 measurements for juveniles
712 (A, B; grey), males (A; white), and females (B; white). Normal distributions,
713 identified using 'mixdist' package of R statistical software, indicated.

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715

716 Table 1: Sampling site location and environmental data, and scavenging amphipod composition of each baited-trap analysed from deployments
 717 on the Angolan continental margin in 2005 and 2014. Samples ordered by depth. Four species were new to science at the time of collection, and
 718 *Cyclocaris franki* has since been described.

	B19-ROBIO	B18-ROR2	B18-ROR1	B31-ROR2	56770#1	56734#1	56741#2	56755#2	56761#1	B31-ROR1
Latitude (°)	-9.2320	-7.7550	-7.9170	-6.1790	-6.2147	-6.1690	-6.1529	-6.3034	-6.3113	-6.4110
Longitude (°)	12.6090	12.0850	12.0840	10.821	10.7857	10.7770	10.7179	10.6877	10.7476	10.7500
Depth (m)	482	1157	1461	1760	1850	1859	1965	2002	2059	2073
Date (dd/mm/yy)	02/09/14	26/08/14	27/08/14	23/08/14	01/11/05	26/10/05	27/10/05	02/10/05	30/10/05	18/08/14
Soak time (hh:mm)	18:58	20:50	12:23	13:03	27:47	22:14	15:14	15:00	23:15	20:55
Temperature (° C)	7.94	4.29	4.10	3.88	3.87	4.08	3.72	3.81	3.69	3.33
Current velocity (cm s⁻¹)	2.9	1.8	2.7	1.9	1.90	4.80	2.50	2.70	3.30	2.6
<i>Abyssorchomene distinctus</i> (Birstein & Vinogradov, 1960)	0	4	3	17	160	86	162	147	2991	738
<i>Cyclocaris franki</i> Horton & Thurston, 2014	0	0	0	2	1	6	0	1	41	0
<i>Cyphocaris bouvieri</i> Chevreux, 1916	0	0	1	0	0	0	0	0	0	0
<i>Hirondellea</i> sp. 1	0	0	41	5	0	0	0	0	0	1
<i>Paracallisoma</i> sp. 6	0	28	13	94	125	223	395	67	2562	39
<i>Paracallisoma</i> sp. 7	0	0	1	1	0	10	6	0	15	1
<i>Podoprion ruffoi</i> Lowry & Stoddart, 1996	3	0	0	0	0	0	0	0	0	0
<i>Valettioopsis lincolni</i> Horton, 2004	0	0	0	0	4	0	0	1	0	0
<i>Valettioopsis longidactyla</i> Horton, 2004	0	0	0	0	4	0	0	0	0	0
<i>Valettioopsis macrodactyla</i> Chevreux, 1909	0	0	1	0	0	0	0	0	0	0
Combined abundance	3	32	60	119	290	325	563	216	5609	779
Species richness	1	2	6	5	4	4	3	3	4	4

719 Table 2: Mean coxal plate 4 measurement (C4L) and estimated total body length
 720 (TBL) for all *Abyssorhynchone distinctus* cohorts identified in this study. Linear
 721 growth factor between successive cohorts in parentheses.

Juvenile	C4L	TBL	Male	C4L	TBL	Female	C4L	TBL
J1	0.65	6.52						
		(1.31)						
J2	0.85	7.89						
			M3	1.02	9.04	F3	1.08	9.49
					(1.25)			(1.25)
			M4	1.27	10.75	F4	1.35	11.32
					(1.36)			(1.25)
			M5	1.73	13.91	F5	1.68	13.57
								(1.26)
						F6	2.11	16.57
								(1.17)
						F7	2.48	19.12

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