

1 **Comparative morphology of Southern Ocean *Euphausia* species: ecological**
2 **significance of sexual dimorphic features**

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13

14 **Abstract**

15 Species of the genus *Euphausia* dominate the euphausiid biomass of the Southern Ocean, the three
16 largest being *Euphausia superba*, *E. triacantha* and *E. crystallorophias*. We measured a number of
17 morphological features to identify differences between, and within, these species to obtain
18 ecological insights. Interspecifically, the greatest difference was carapace size, with that of *E.*
19 *superba* being by far the largest and most variable. This likely reflects its prolific spawning capacity
20 compared with other euphausiid species. *E. triacantha* exhibited an extended sixth abdominal
21 segment that could facilitate greater levels of thrust in the tail flip escape response. The pleopods,
22 which provide propulsion in forward swimming, were more than 50% larger in *E. superba*, indicating
23 a greater capacity for directional movement at high velocities. *E. crystallorophias* had eyes that were

24 almost double the size of those in *E. superba* and *E. triacantha*, which may help retain visual
25 resolution within its under-ice habitat. Intraspecifically, we found the above morphological features
26 differed little between sexes and developmental stages in *E. crystallophias* and *E. triacantha*, but
27 differed significantly in *E. superba*. Compared to females and juveniles, male *E. superba* had
28 significantly larger eyes and pleopods, while the carapace in males became shorter as a proportion
29 of body length during growth. These features indicate a greater capacity for searching and swimming
30 in males, which, we hypothesise, increases their ability to locate and fertilise females. This
31 morphological specialisation in male *E. superba* is indicative of comparatively greater inter-male
32 competition resulting from its tendency to form large, dense swarms.

33

34 **Key Words:** Antarctic krill, euphausiids, swarm, reproduction, swimming, mating

35 **Declarations**

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38 **Conflicts of interest/Competing interests** We declare no conflicts of interest in the production of
39 this work

40 **Ethics approval** All work was completed in compliance with British Antarctic Survey (BAS)
41 procedures, following the Antarctic Treaty Environmental Protocol (1996), which requires the prior
42 assessment of all activities in the Antarctic Treaty Area, and is applied by BAS with equal rigour to
43 South Georgia. Work on Antarctic krill (*Euphausia superba*) and other euphausiid species is exempt
44 from the UK Animals (Scientific Procedures) Act 1986, but all work was compliant with
45 recommended procedures in the handling and treatment of specimens.

46 **Availability of data and material** All raw data on which this study is based are published as an
47 appendix (Appendix 1) to the present manuscript.

48 **Consent to participate** We declare all relevant parties consented to participate in this study.

49 **Consent for publication** We declare all relevant parties have consented to the publication of this
50 work.

51 **Code availability** Not applicable.

52 **Authors' contributions** CH, MLJ and GAT devised this study with supporting ideas from JFL. All
53 measurements were performed by CH. GAT wrote the manuscript with support from all authors.

54 **Introduction**

55 The genus *Euphausia* is the most species rich of the Euphausiacea, accounting for 31 of the 85
56 known species (Baker et al. 1990). The genus dominates the biomass of the Southern Ocean
57 euphausiid community, where three of the largest *Euphausia* species are found, *E. superba*, *E.*
58 *crystallorophias* and *E. triacantha* (Cuzin-Roudy et al. 2014). These species are a major part of the
59 diet of a large number of Southern Ocean higher predators, including penguins, seals and baleen
60 whales (Croxall et al. 1999; Santora et al. 2010). They are also important in biogeochemical cycles,
61 particularly with regards the biological carbon pump, where their activity provides a major route for
62 carbon sequestration to depth (Tarling and Johnson 2006; Belcher et al. 2017; Liszka 2018).

63 Despite all three species being located in the Southern Ocean, the distributions of *E. superba*, *E.*
64 *crystallorophias* and *E. triacantha* only partially overlap (Baker 1959; Cuzin-Roudy et al. 2014). *E.*
65 *triacantha* has a distribution that spans across the Polar Front, penetrating part way into the
66 Antarctic water masses to the south and covering much of the sub-Antarctic water mass to the
67 north. *E. superba* is found between the Polar Front and the continental land mass, but particularly
68 concentrates in the seasonal ice zone. *E. crystallorophias* has an even greater affiliation to sea-ice
69 but is mainly restricted to regions where this overlaps with the continental shelf. These differing
70 distributions are accompanied by differences in lifestyle. *E. triacantha* are mostly found in diffuse
71 aggregations or layers and are capable of making extensive diel vertical migrations, ranging over 400
72 m in depth (Baker 1959). *E. superba* are obligate swimmers, and can form swarms that are both
73 densely packed and spatially extensive (Tarling et al. 2009). Less is known about the under-ice
74 behaviour of *E. crystallorophias* but there have been limited observations of them forming small
75 swarms and dispersing within sea-ice through maintaining a location close to the underside of the
76 ice and moving within ice crevices and channels (O'Brien 1987).

77 All euphausiids have a body composed of a cephalothorax, which includes the carapace, two pairs of
78 antennae, the eyes, mouthparts, thoracic limbs and external gills, and an abdomen, with six

79 articulating segments, each bearing a pair of pleopods (swimming legs), and a terminating segment
80 containing a telson and a pair of uropods (Fig. 1). Major morphological variations among genera and
81 species principally occur in the thoracic legs, the shape and relative length of the carapace and in the
82 eyes, which can be round or bilobed and variable in size. Within the genus *Euphausia*, interspecific
83 variations in morphology are relatively conservative compared to other euphausiid genera. The eyes
84 are always round (never bilobed), the carapace only really varies in the comparative length of the
85 rostrum and the presence or absence of small spines at its margins, and the thoracic legs are all
86 similar, often directed forward (Baker et al. 1990). Indeed, the most notable morphological variation
87 between *Euphausia* species is in overall body size, which can span almost an order of magnitude in
88 total body length (7 to 65 mm). Nevertheless, morphological similarity between species does not
89 imply similarity in lifestyle, with the genus containing a mix of herbivorous, omnivorous and
90 carnivorous species (Suh and Choi 1998; Sogawa et al. 2017)

91 Like all other euphausiid species, *Euphausia* species reproduce through the transfer of
92 spermatophores from males to females. During secondary sexual development, males modify the
93 first two pairs of pleopods to grasp and transfer the spermatophore during mating. The first pair of
94 pleopods becoming particularly transformed with various lobes, hooks and processes into structures
95 called petasma. In the females, variously shaped outgrowths from the ventral body wall and the
96 coxae of the limbs develop into a cup shaped structure called the thelycum, which receives the
97 spermatophore. The process of mating has been little observed, but is believed to follow a particular
98 behavioural sequence in which the male first chases the female before an embrace and then the
99 transfer of a spermatophore (Ross and Quetin 2000; Kawaguchi et al. 2011a; Kawaguchi et al.
100 2011b). Females themselves are only receptive to receiving new spermatophores for small windows
101 of time, just subsequent to moulting, although a number of moults may take place over the
102 productive season (Cuzin-Roudy and Amsler 1991; Cuzin-Roudy and Buchholz 1999).

103 Beyond the development of sexual organs, a number of sexually dimorphic features have been
104 noted in several euphausiid genera. In the genus *Thysanoessa*, there is sexual dimorphism in the
105 shape of the eyes and antennular flagellae, the breadth of the rostrum, the ratio of abdominal
106 segments and the arrangement and shape of pre-anal spines (Nemoto 1966). Färber-Lorda (1990)
107 also found a significant difference between males and females (as well as juveniles) in the regression
108 slope of carapace to total length in *Thysanoessa macrura*. In *Euphausia vallentini*, *Nematobrachion*
109 *flexipes* and *Nematoscelis difficilis*, sexual dimorphism has been found in the preanal spines (Boden
110 et al. 1955; McLaughlin 1965; Nemoto 1966) while several species of *Nematoscelis* exhibit great
111 enlargement of certain photophores in the males (Einarsson 1942; James 1973). In *Stylocheiron*
112 *indicum*, the proportion of length to depth of the sixth abdominal segment, and the proportion of
113 the width of the upper part of the eye to the width of the lower part of the eye were found to be
114 significantly different between the sexes (Mathew 1980).

115 In *Euphausia superba*, sexual dimorphism has been reported in the size of the carapace and length of
116 the abdomen (Siegel 1982; Miller 1983; Färber-Lorda 1990; Färber-Lorda 1991; Amakasu et al. 2011;
117 Färber-Lorda and Ceccaldi 2020). In female *E. superba*, an increase in carapace to total body length
118 occurs whereas, in males, the reverse is apparent. Färber-Lorda (1990) further identified two sub-
119 groups of males (Males I and II) that could be distinguished according to a Differentiation Index (DI),
120 which is the ratio between total length and the difference between abdominal length and carapace
121 length. Males II (the older subgroup) were found to have a proportionally larger abdomen and larger
122 pleopods than Males I, although supporting data for the latter was not published. Färber-Lorda and
123 Ceccaldi (2020) also reported Males II to have more total carotenoids and a lower lipid content than
124 other sex-stage categories. Behaviourally, it has been shown that male and female *E. superba* have
125 different swimming capacities, with the swimming strokes of males being slower and more powerful
126 than those of females (Johnson and Tarling 2008). However, it remains unclear whether such
127 differences are also reflected in the morphology.

128 In this study, we compare a number of morphological features in juvenile, sub-adult, male and
129 female specimens of *E. superba*, *E. crystallophias* and *E. triacantha*. Our objectives are, firstly, to
130 identify morphological variations that may reflect known differences in life-style and behaviour of
131 the three species. Secondly, we will test the hypothesis that all three *Euphausia* species show similar
132 levels of sexual dimorphism. For *E. superba*, this will provide a more thorough examination of the
133 number of features that potentially show dimorphism in adult stages. For *E. crystallophias* and *E.*
134 *triacantha*, this will be the first examination of whether there is any sexual dimorphism akin to that
135 observed in *E. superba*. Our results will be considered in terms of the ecological and evolutionary
136 pressures on Southern Ocean *Euphausia* and how the morphology of each species has adapted in
137 response.

138 **Materials and Methods**

139 Specimen acquisition

140 Specimens were collected during cruises to South Georgia and to Deception Island (Table 1) using
141 either MIK nets (1m² mouth area) or Rectangular Midwater trawls (8m² or 25 m² mouth area). Such
142 sampling techniques are considered to obtain relatively representative population samples despite
143 patchiness in distributions (Watkins et al. 1990; Dalpadado et al. 2016).

144 Measurement and categorisation of specimens

145 Specimens were preserved in 99% Ethanol and were rinsed with distilled water before examination.
146 Each was placed under the viewing lens of an Olympus ZSX7 binocular dissecting microscope with a
147 calibrated eyepiece graticule, from which unit measurements were taken (Figs. 1 and 2, Table 2). All
148 specimens were orientated to the left and laid flat on their side to ensure measurements were
149 consistent. Samples of *E. superba* and *E. triacantha* were measured using a magnification of 1x
150 whereas *E. crystallorophias* required a 1.6x magnification. The unit measurements were converted to
151 millimetres. Note that the telson (TS) measurement was not included in subsequent statistical
152 analyses since it was frequently damaged.

153 Specimens were categorised by sex and maturity stage according to the guidelines of Makarov and
154 Denys (1980) for the classification of preserved specimens. Initially the presence or absence of the
155 thelycum was determined by examining the ventral surface of the specimen's cephalothorax.
156 Presence of the thelycum meant the specimen was sexed as female and categorised further according
157 to the level of development; specimens with tri-lobed structures were considered adult and specimens
158 with less developed structures considered sub-adult. Where the thelycum was absent, examination of
159 the inner paddle of pleopod 1 (p1I) for signs of male differentiation was carried out. At higher
160 magnification, the paddle was inspected for presence of the petasma; the term sub-adult was applied
161 to specimens with single or bi-lobed petasmae whereas specimens that had spermatophores or

162 greater petasmal differentiation were considered adult. Specimens which showed none of the above
163 characteristics were considered juveniles. As a result of difficulties in assessing the maturity stages of
164 the thelycum and petasma in *E. crystallorophias*, sex-stage categories in this species were reduced to
165 male, female and juvenile only. For that species, females were any specimens with evidence of a
166 thelycum, males with any level of development in the petasma, and juveniles, with an absence of
167 either of those characters. All measurements across all species and sex stage categories are provided
168 in [Appendix 1](#).

169 Statistical analysis

170 The size structure of the population of each species was examined through determining the frequency
171 of individuals within 1 mm intervals of reference length, plotted as histograms, onto which the
172 respective sex-stage categories were superimposed. The relationship between reference length (rl)
173 and carapace length (s6) was explored through the fitting of a least-squares regression, performed in
174 Sigmaplot v14 (Systat Software Inc., Build 14.0.3.192).

175 Principal Component Analysis (PCA) was performed on (1) the entire dataset and (2) each species
176 separately. PCA analysis is an ordination method where plots are generated in which the placement
177 of samples reflects the dissimilarity of their variables i.e. those samples where variables have dissimilar
178 values lie far part from each other and vice versa. PCA reduces the many dimensional space in which
179 samples vary from each other into a small number of dimensions, or principal components. The first
180 principal component explains the largest amount of variance, with each subsequent component
181 explaining less in turn. In the present study, PCA was used to analyse data matrices containing 7
182 different morphometric variables (s6, as6, p1u, p4u, p1l, p4l and d0; see [Fig. 1](#) and [Table 2](#)) as variables
183 and individual specimens as samples. Only specimens for which it was possible to measure all 7
184 morphometric variables were included in the final matrix, such that the total number of specimens
185 was 97 for *E. crystallorophias*, 136 for *E. superba* and 93 for *E. triacantha*, giving an N for the entire
186 dataset of 326 specimens. Prior to analysis, all data were standardised through dividing the variable

187 value by the corresponding value of standard length (s_3). The PCA was run to identify 5 principal
188 components, of which the first 2 principal components (PC1 and PC2) were projected onto 2-
189 dimensional plots. All PCAs were performed in Primer 7 (Primer-e) version 7.0.13.

190 Sexual dimorphism within species was initially examined through consideration of the Differentiation
191 Index (DI; Farber-Lorda 1990) for each individual, calculated as:

192

$$DI = \frac{s_3}{(s_3 - s_6) - s_6} \quad (1)$$

194

195 where s_3 is total standard length and s_6 , carapace length as defined in [Table 2](#). The term $(s_3 - s_6)$ is
196 equivalent to abdominal length (i.e. end of carapace to end of the 6th of abdominal segment, so
197 excluding the telson). The DI of individuals were grouped according to species and sex-stage category
198 for subsequent ANOVA tests (see below).

199 A further analysis to assess levels of dissimilarity between different sex-stage categories was
200 performed using the ANOSIM test in Primer 7 which included the 7 standardised morphometric
201 variables mentioned above. ANOSIM is a permutation test built on a non-parametric procedure
202 applied to a rank similarity matrix. The test generates a statistic that assesses the significance of levels
203 of dissimilarity between samples. In the present study, we generated a matrix where the samples were
204 sex-stage categories of all three species and the variables were the 7 standardised morphometric
205 variables detailed above. This data was initially used to generate a resemblance matrix using Euclidean
206 distance. A 1-way unordered ANOSIM was run on the resemblance matrix using sex-stage category as
207 a factor and with 13 levels, representing each of the different sex-stage categories. The significance
208 level was set at 0.1%. The output was a table detailing the level of dissimilarity between each pair of
209 sex-stage categories, making comparisons both within and between species.

210 Comparisons between individual variables were carried out using 1-way ANOVA tests, first
211 performing tests for normality (Shapiro-Wilk) and equal variance (Brown-Forsythe) and using a non-
212 parametric Kruskal-Wallis 1-way Analysis of Variance on Ranks test when either of these tests were
213 failed. Where significant differences were found, either a Holk-Sidak (parametric) or Dunn's Method
214 (non-parametric) post-hoc test was performed to identify the pairs of sex-stage categories that were
215 significantly different from each other at $p < 0.05$ level. All 1-way ANOVA tests were performed in
216 Sigmaplot v14.

217 Functions relating the growth of an individual morphometric variables to growth in standard body
218 length (s_3) for *E. superba* were examined in RStudio (RStudio Inc., Version 1.2.5001). Competing
219 linear models were fitted, one where the sex of the individual was included as an interaction term
220 and the other where it was not. The best fitting model was determined through running 1-way
221 ANOVAs followed by Akaike information criterion (AIC) analyses. Sex was considered to have an
222 influence on the growth trajectory of a morphometric variable if the model with sex as an
223 interaction term had the lowest AIC score. Linear models, including 95% confidence bands, were
224 subsequently plotted in Sigmaplot v14.

225 **Results**

226 Interspecific differences in morphology

227 Within the study populations, there was some degree of overlap in body lengths, particularly within
228 the region of 20 to 30 mm reference length (Fig. 3). *E. crystallorophias* was the smallest of the three
229 species, with the study population spanning 17 to 28 mm reference length and a single modal peak
230 at 22 mm. *E. triacantha* was, on average, 8 mm longer than *E. crystallorophias*, with a single modal
231 peak at 30 mm and a range of 23 to 37 mm. *E. superba* spanned a large range of lengths, from 25
232 mm to 62 mm, with several overlapping modes indicating a number of year classes. There was a
233 clear trend of juvenile and sub-adult specimens dominating the smaller size classes and adults
234 dominating the larger size classes, with the transition occurring around 45 mm.

235 The relationship between Reference length (*rl*) and Carapace length (*s6*) was similar between all 3
236 species and could be adequately described by a single linear regression ($s6 = 0.361rl - 2.4802$, $t_{slope,319}$
237 $= 59.85$, $p < 0.0001$, $r^2 = 0.9187$; Fig. 4). *E. superba* exhibited the greatest level of deviation from this
238 relationship, particularly in the upper size classes.

239 A Principal Component Analysis including 7 standardised morphometric variables (*s6*, *as6*, *p1u*, *p4u*,
240 *p1l*, *p4l* and *d0*) found there to be a clear separation of *E. superba* from *E. crystallorophias* and *E.*
241 *triacantha* in the first two principal components (PC1 and PC2), which explained 80% of the variance
242 in the dataset (Fig. 5). *E. superba* had a strong negative loading in both PC1 and PC2 while *E.*
243 *crystallorophias* and *E. triacantha* had mostly positive loadings on PC1 and a range of loadings on
244 PC2, spanning both the positive and negative domains. Although there was considerable overlap
245 between *E. crystallorophias* and *E. triacantha*, it was also clear that only *E. triacantha* specimens had
246 highly positive loadings on PC2 while *E. crystallorophias* were the only specimens with highly
247 negative loadings on PC2. The superimposed morphometric vectors indicated that variability along
248 PC1 was mainly driven by carapace length (*s6*), while variability along PC2 was strongly influenced by
249 the length of abdominal segment 6 (*as6*).

250 Considering individual morphometric variables, standardised carapace length (s_6) was significantly
251 longer in *E. superba* than the other two species (Kruskal-Wallis 1-way ANOVA [KW], $H_2 = 178.97$, $p <$
252 0.001), accounting for around 40% of body length in the former as opposed to around 30% in the
253 latter (Fig. 6). The standardised 6th abdominal segment in *E. triacantha* was significantly longer than
254 the other two species (KW, $H_2 = 231.88$, $p < 0.001$). Other differences were found (i) in the
255 standardised lengths of the lower pleopods (p_{1l} and p_{4l}), which were significantly longer in *E.*
256 *superba* (p_{1l} : KW, $H_2 = 140.87$, $p < 0.001$; p_{4l} : KW, $H_2 = 174.45$, $p < 0.001$), and (ii) in standardised
257 eye diameter (d_0), which was significantly larger in *E. crystallorophias* (KW, $H_2 = 154.72$, $p < 0.001$).

258 Intraspecific differences in morphology

259 An initial indication of sexual dimorphism was apparent from considering levels of variability in the
260 Differentiation Index (DI), which determines the relative sizes of the carapace and abdomen (larger
261 values indicating a comparatively larger carapace; Fig. 7). Although no significant differences in DI
262 were found between sex-stage categories in *E. crystallorophias* and *E. triacantha* (*E. crystallorophias*:
263 KW, $H_2 = 0.587$, $p = 0.746$; *E. triacantha*: KW, $H_4 = 6.367$, $p = 0.173$), significant differences were
264 found between adult females and both adult and subadult males in *E. superba* (KW, $H_4 = 21.599$, $p <$
265 0.001). The DI of adult female *E. superba* was particularly wide ranging, with a value of 8.6 for the
266 75th percentile and 3.9 for the 25th percentile (Fig. 7). These values minimally overlap with those of
267 adult males (4.0 for the 75th percentile, 3.1 for the 25th percentile). DI values in the present study are
268 similar to those of Farber-Lorda (1990) for adult females while, for males, our values spread across
269 both age categories identified by Farber-Lorda (1990), namely Males I (DI ~ 4.1) and Males II (DI ~
270 3.2). Nevertheless, it is to be noted that differences in measuring technique may be a source of
271 variance between studies.

272 Sexual dimorphism was further explored by ANOSIM, which considered levels of dissimilarities
273 between sex-stage categories across the same 7 standardised morphometric variables mentioned
274 above. As expected, significant levels of dissimilarity ($\leq 0.1\%$) were seen when comparing between

275 species (Table 3). The only exception was the comparison of *E. triacantha* juveniles with male,
276 female and juvenile *E. crystallorophias*, where levels of similarity were low (0.3 to 1.4%) but not
277 significantly dissimilar. When considering dissimilarity within species, it was apparent that male,
278 female and juvenile *E. crystallorophias* were not significantly dissimilar from each other (1.4 to
279 45.5%). This was also found in *E. triacantha*, with the exception of the juveniles, which were
280 significantly different to the majority of other sex-stage categories, suggesting an ontogenetic effect.
281 The only species in which there were significant levels of dissimilarity between males and females
282 was *E. superba*, observed between adult females and adult males, as well as between adult females
283 and sub-adult females. Nevertheless, significant dissimilarity was not found between other *E.*
284 *superba* sex-stage categories, indicating that morphological differences between sexes increased
285 with maturity in this species.

286 Species-specific PCA analyses further clarified the above patterns (Fig. 8). The first two principal
287 components, PC1 and PC2, did not separate out clusters according to sex-stage categories in *E.*
288 *triacantha* and *E. crystallorophias*. However, clustering was more coherent in *E. superba*, where
289 adult female and, to a certain extent, sub-adult females, separated out from the other stages. In *E.*
290 *superba*, the superimposed morphometric vectors indicated that this separation was being driven
291 mainly by carapace length (*s6*), which showed a high loading on PC1. However, there was also a
292 separation of females from males and juveniles on PC2, for which there was an especially strong
293 influence of the lower pleopod segments (*p1l* and *p4l*). Pleopod parameters did not show a strong
294 influence in the PCA analyses in the other two species, indicating that a differentiation in pleopod
295 length between sex-stage categories is comparatively unique to *E. superba*.

296 In Fig. 9, standardised morphometric variables were normalised according to average values per
297 species to allow them all to be plotted on a single scale. The figure shows variability between stages
298 to be more evident in *E. superba* than the other two species in the majority of morphometric
299 variables (note *s6* is excluded from Fig. 9 as it broadly repeats the pattern in Fig. 7). Fig. 9 also

300 provides further detail on the intraspecific differences between sex-stage categories. In *E. superba*,
301 all pleopod segments in adult male *E. superba* were significantly longer, in standardised terms, than
302 all other sex-stage categories (*p1u*: 1-way ANOVA, $F_{4,132} = 5.83$, $p < 0.001$; *p4u*: KW, $H_4 = 27.24$, $p <$
303 0.001 ; *p4l*: 1-way ANOVA, $F_{4,132} = 4.413$, $p = 0.002$). The exception was *p1l*, which was not
304 significantly different from the other categories (*p1l*: 1-way ANOVA, $F_{4,132} = 2.20$, $p = 0.072$), probably
305 as a result of the secondary sexual development of *p1l* into the petasma. Also, standardised eye
306 diameter in male *E. superba* was significantly larger than all other sex-stage categories (KW, $H_4 =$
307 42.226 , $p < 0.001$). Standardised eye-diameters were not significantly different between sex-stage
308 categories in the other two species.

309 Morphological growth trajectories in *E. superba*

310 Male-female differences in the size of pleopods and diameter of the eyes in *E. superba* were further
311 examined in relation to growth in body length (Fig. 10). For the pleopods, we focussed on pleopod 4
312 to avoid the effects of petasma development on pleopod 1, and on the lower pleopod section,
313 where we observed the greatest variability between sex-stage categories. It was apparent that
314 pleopod growth in the two sexes showed very different trajectories, with that in males being
315 significantly steeper ($F_2 = 4.41$, $p = 0.014$). From a similar origin at around 25 mm standard length
316 (*s3*), male pleopods became 50% longer than those of females by the time 60 mm standard length
317 was reached. In terms of eye-diameter (*d0*), there was also a significant difference between the male
318 and female growth trajectories ($F_2 = 10.16$, $p < 0.001$), with males always having larger diameters
319 than females from standard lengths of 25 mm onwards. This separation became gradually wider
320 during growth.

321 **Discussion**

322 This study has highlighted that, despite the relatively uniform body plan within the genus *Euphausia*,
323 significant variations in certain morphological characters were apparent between the three largest
324 Southern Ocean species of *Euphausia*. We further demonstrated that sexual dimorphic features
325 were only apparent in *E. superba* and were not detectable in *E. triacantha* or *E. crystallorophias*.
326 Comparison of these variations provides important insights into the ecological drivers of *Euphausia*
327 populations that has influenced their morphology over evolutionary timescales. Furthermore, the
328 unique types of sexual dimorphism apparent in *E. superba* suggests that lifestyle and behaviour
329 differs between the sexes and that a strong selective pressure is optimising their morphology to fulfil
330 these differing roles. The uniqueness of such sexual dimorphic features in *E. superba* indicates that
331 similar selective pressures to alter morphology according to sex are less acute in other euphausiid
332 species.

333 Carapace size

334 Between species, *E. superba* had the largest relative carapace length, making up around 40% of total
335 body length, whereas it was closer to 30% in the other two species. The major organs within the
336 carapace are the hepatopancreas, gut, heart and, in females, the ovary. Of these, the ovary takes up
337 the majority of space when developed, which can be up to 43% of the total wet mass of the body
338 (Tarling et al. 2007). The size of the ovary ultimately dictates the size of the spawned brood, which
339 can vary significantly both within and between species (Ross and Quetin 2000). Mauchline (1988)
340 found that the relationship between brood volume and body volume for 13 species of brooding
341 euphausiids (including *E. superba* and *E. triacantha*) was logarithmic. The slope was slightly greater
342 than 1, implying the size of brood increased faster than the corresponding increase in body size.
343 Accordingly, Ross and Quetin (2000) reported that the average number of eggs per spawning
344 episode was 187 for *E. crystallorophias* (the smallest of the three species considered in the present
345 study), and between 1300 and 2900 for *E. superba* (the largest species) despite adult length differing

346 only by a factor of around 2. The relative increase in carapace size in *E. superba* is therefore a means
347 of facilitating this logarithmic increase in brood size. Assuming stable population sizes in these
348 species (meaning that each individual on average only ever replaces itself), the high brood size in *E.*
349 *superba* implies that mortality over the course of the life-cycle must be far greater in *E. superba* than
350 in *E. crystallorophias* or *E. triacantha*. *E. superba* swarms are the target for many mid- and higher
351 trophic levels in the Southern Ocean (Croxall et al. 1999) and large brood size in *E. superba* may be
352 the product of overcoming comparatively higher levels of predation mortality. However, much less is
353 known about predator consumption of *E. crystallorophias* and *E. triacantha* and further work on this
354 aspect is required if this is to be considered a driver of brood size in *Euphausia* species.

355 Within species, PCA analysis identified carapace size as the main trait separating out adult, and to
356 some extent, subadult female *E. superba* from other conspecific stages. Such dimorphism between
357 sexes and stages was not seen in *E. crystallorophias* and *E. triacantha*. The fact that carapace size
358 separates out adult female *E. superba* from other stages supports what is already known for this
359 species. First mention of this sexual dimorphic character was by Bargmann (1937), who noted that
360 the carapace was 4.5 mm shorter and 2 mm less wide in male *E. superba* compared to females of
361 equivalent length. The relationship between body length and carapace length for different sexes of
362 *E. superba* was formalised by Siegel (1982) and Miller (1983) through deriving sex-specific linear
363 relationships for the two characters, mainly for the purpose of population dynamic studies.

364 However, whereas the female carapace increases in relative size as it grows, Färber-Lorda (1990)
365 demonstrated that growth in males is accompanied by a decrease in carapace size, while the relative
366 length of the abdomen increases. While the functional attributes of increasing carapace size in
367 females can be clearly related to enhanced brood size (see above), the function of the morphological
368 changes observed in males is less certain. Färber-Lorda (1990) considered that the smaller carapace
369 might be a remnant of shrinkage in body length during periods of over-wintering starvation.

370 Nevertheless, although shrinkage has been demonstrated in laboratory situations (Thomas and
371 Ikeda 1987), in field data, Tarling et al. (2016) found that shrinkage was far more common in females

372 than in males during the overwintering period. Therefore, the dimorphism is more likely to be driven
373 by other factors, such as locomotory capabilities and levels of activity (Färber-Lorda and Ceccaldi
374 2020), which we consider further below.

375 6th Abdominal segment

376 The 6th abdominal segment of *E. triacantha* was almost double the length of that of *E. superba*, with
377 *E. crystallophias* being midway between the two. The function of this particular segment is
378 uncertain. The abdomen is where the majority of thrust is generated, both in forward swimming and
379 in tail-flipping (a rapid escape response). A longer 6th abdominal segment may enhance the strength
380 of the tail-flipping response through increasing the total length of the abdomen in its function as a
381 paddle. Such an escape response may be more important in euphausiids in dispersed aggregations
382 where they are more likely to have individual encounters with potential predators. Baker (1959)
383 reports that “*E. triacantha* displays none of the shoaling habit found in *E. superba*”, with adults being
384 “sparsely but evenly distributed”. *E. triacantha* are also noted for their prolific diel vertical migration
385 (DVM; Baker 1959; Liszka 2018), avoiding predation through occupying deeper layers during
386 daytime. For *E. crystallophias*, an alternative refuge is sought under pack-ice, although they do
387 exhibit some degree of swarming in certain situations (Everson 1987; O'Brien 1987). *E. superba* rely
388 far more on swarming as an anti-predation strategy (Hamner and Hamner 2000; Tarling et al. 2018),
389 in which the close vicinity of conspecific neighbours and higher chance of collision may make tail-
390 flipping a less effective escape strategy.

391 Pleopod length

392 Pleopod length differed significantly between species, being close to 10% of body length in *E.*
393 *superba* but around 6% in the other two species. The pleopods generate the thrust for forward
394 swimming through synchronised backward strokes. Murphy et al. (2009) examined the kinematics
395 of swimming in *E. superba* and determined that they stroke their pleopods in a metachronistic
396 fashion, where the swimming beat starts with the rearmost pair of pleopods and then moves

397 forwards sequentially through the other four pairs. This pattern of swimming is affected by the
398 distance between pleopods (B) relative to the pleopod length (L), with B/L falling between 0.2 and
399 0.65. The disadvantage of L being small is that short appendages yield small amounts of forward
400 thrust. However, larger values of L require greater limb rigidity and musculature to compensate for
401 the higher hydrodynamic loads experienced by the longer limb moving through the water. Making
402 the pleopods as long as possible will generate greater thrust for forward swimming, so long as they
403 do not interfere with adjacent pleopods. *E. superba* is capable of sustained forward swimming
404 speeds in excess of 2 body lengths per second (Kils 1979) and can perform directional horizontal
405 migrations, even against prevailing flows (Hamner 1984; Tarling and Thorpe 2014). The swimming
406 capabilities of *E. crystallophias* and *E. triacantha* are less well known, but their comparatively
407 shorter pleopods suggest that directional horizontal migrations are less important to their
408 behavioural ecology.

409 The only species to show significant differences in pleopod length between sexes and stages was *E.*
410 *superba*. In some of the largest specimens (60 mm), we found pleopods to be 50% longer in males
411 compared to females, although this proportional difference is less in smaller specimens. Endo
412 (1989), who found that the pleopods in males were better developed in more mature specimens,
413 was first to report this phenomenon and it was subsequently noted by Färber-Lorda (1990). In
414 tethering experiments carried out by Johnson and Tarling (2008), male *E. superba* were found to
415 have stronger but slower pleopod beats compared to equivalently sized females. As mentioned
416 above, greater limb rigidity is required in larger pleopods to withstand the higher hydrodynamic
417 loads (Murphy et al. 2009). Euphausiids lose rigidity during the premoult and postmoult periods of
418 their moult cycle, which repeatedly occur every 10 to 30 days in *E. superba*. Compared to females,
419 Tarling et al. (2006) found that the moult cycle lasted around twice as long in males, so decreasing
420 the period in which rigidity is lost. The longer intermoult period may also allow a greater period in
421 which to build up cuticle rigidity, although measurements of the comparative rigidity of males and
422 female cuticles are presently lacking in any euphausiid species.

423 Eye diameter

424 Relative eye diameter was around 50% larger in *E. crystallorophias* compared to the other two
425 species. In a comparative physiological study carried out by Hiller-Adams and Case (1988), it was
426 shown that visual resolution increased with increasing eye size within and between euphausiid
427 species. Furthermore, they found eyes grew more slowly with respect to body size at deeper water
428 depths. With respect to habitat, *E. crystallorophias* is the only one of the three species that almost
429 exclusively focusses on under-ice habitats, where light will be considerably attenuated by the
430 prevailing ice-cover. To some degree, this greater light attenuation may simulate light levels found at
431 deeper depths, where euphausiids have smaller eyes. The fact that the opposite is found in *E.*
432 *crystallorophias* suggests that the selective pressures determining eye size are not solely to do with
433 prevailing light levels. *E. crystallorophias* is omnivorous (Hopkins 1987; O'Brien 1987; Kattner and
434 Hagen 1998) and is capable of capturing potentially fast moving, surface-dwelling micro- and
435 mesozooplankton, for which high levels of visual resolution are required. Conversely, deeper
436 euphausiids are likely to exhibit a greater dependence on detritivory (Mauchline and Fisher 1969)
437 where tactile foraging, using flagellae, may be more effective. The comparatively large eyes in *E.*
438 *crystallorophias* allow it to maintain sufficient visual resolution despite the high levels of light
439 attenuation in its under-ice habitat. Although *E. triacantha* may also have to contend with low light
440 levels during the deep phase of its vertical migration, its main feeding habitat is in the surface layers
441 where it feeds at dusk and dawn as well as during the night, which may be relatively well illuminated
442 during the polar summer (Liszka 2018). *E. superba* remains limited to the top 50 m during both day
443 and night (Tarling et al. 2009) and so feeds within well-lit surface layers throughout the diel cycle.
444 Significant intraspecific differences in eye diameter was only found in *E. superba*, with adult males
445 having significantly larger eyes than adult and sub-adult females, juveniles and sub-adult males.
446 Comparatively larger eyes in male *E. superba* has been previously noted by Bargmann (1937) and
447 Färber-Lorda (1990). Eye-diameter has sometimes been used as a preferred indicator of age given

448 the capacity of euphausiids to shrink in body length during periods of starvation while eye size is
449 preserved (Sun et al. 1995). One hypothesis therefore is that males in the present study population
450 were older than equivalently sized females due to male shrinkage. Taking into account that male
451 shrinkage appears to be rare in nature (see above), there is other evidence from the present study to
452 refute such an explanation. Fig. 10 showed that eye diameter of the males was already larger than
453 females at comparatively small sizes and that this difference became progressively larger with
454 increasing body size. A further explanation could be that males may occupy a deeper habitat than
455 females where a larger eye-size is required to compensate for the attenuation of light. The
456 occupation of different depth strata by males and females has been observed in northern krill
457 (*Meganyctiphanes norvegica*, Tarling 2003) but there is no evidence of different eye sizes between
458 sexes in that species. Furthermore, there is little present evidence of any depth partitioning of sexes
459 in *E. superba*.

460 To explore potential drivers of eye size further, it is well known that an increase in eye-size will
461 increase visual resolution, which could enhance (i) predator avoidance, (ii) prey capture and (iii)
462 mate location. In relation to (i), females are more common in the diets of certain krill predators (Hill
463 et al. 1996), although it is difficult to disentangle whether this is a result of predator preference for
464 the higher nutritional content of females or better prey avoidance by males. In terms of (ii), studies
465 of the diet of krill have found little to separate male and female krill, both in terms of stomach
466 contents and stable isotopes (Schmidt and Atkinson 2016). For (iii), there has historically been a
467 dearth of information regarding the process of mating in euphausiids. However, Ross et al. (1987)
468 noted in the laboratory that there was a period of chase prior to mating. In situ, Kawaguchi et al.
469 (2011a) similarly noted a chase period before an embrace, firstly through the krill connecting
470 ventrally to each other and then by the male forming a C shape around the cephalothorax of the
471 female. At some point during this sequence, the spermatophore is transferred. How males identify
472 females that are ready to be mated is less known, although there is a distinct difference in the
473 colouration of the thelycum of a female that is ready to be mated (bright red) compared to that of a

474 mated female (dark red to brown, Makarov and Denys 1980). Enhanced visual resolution is likely to
475 provide an advantage in identifying females that are ready to be mated. Nevertheless, this selective
476 pressure will be prevalent across all euphausiid species, while evidence of differences in eye size or
477 shape between sexes is limited to *E. superba*, *Thysanoessa* species (Nemoto 1966) and *Stylocheiron*
478 species (Mathew 1980). This suggests that other drivers of sexual dimorphism must also be
479 operating.

480 Can swarming drive sexual dimorphism?

481 In his review of mate searching in zooplankton, Kjørboe (2008) identified one major driver to be a
482 limitation to the period over which females are receptive to mating. This would result in inter-male
483 competition, with a race between males to find females that are ready to be mated. Mate encounter
484 rate then becomes a priority since a potential mate may already be fertilised if the male is too slow
485 to locate it. Time limitation occurs in euphausiids because females become receptive to receiving
486 new spermatophores only in the period just subsequent to moulting (Cuzin-Roudy and Buchholz
487 1999), which occurs at intervals of around 2 to 3 weeks during the productive period (Tarling et al.
488 2006).

489 Although swarming is not exclusive to *E. superba*, the obligate level to which this species performs
490 this behaviour may provide the unique combination of factors that lead to sexual dimorphism. In
491 being part of a swarm, there is greater potential to mate with a number of receptive females during
492 a time-limited window. In aggregations that are more diffuse, distances between individuals are
493 larger, which gives more of an advantage to nearest neighbours over prolific swimmers. Altering
494 morphology to become a specialised searcher and swimmer is unlikely to enhance reproductive
495 fitness in a dispersed aggregations since there is little chance of beating a slower male that
496 immediately neighbours a receptive female (Kjørboe 2008). The sexual dimorphism observed in *E.*
497 *superba* suggests that, in being part of a swarm, those odds of beating slower neighbouring males to
498 receptive females are improved. Specialisms in swimming (e.g. larger abdomen and longer pleopods)

499 and searching (e.g. larger eyes) will have fitness benefits since there is a realistic chance of increasing
500 the number of times an individual can mate successfully. This hypothesis is supported by the recent
501 findings of Färber-Lorda and Ceccaldi (2020) where carotenoids, which are an indirect indicator of
502 higher levels of activity and stress, are more highly concentrated in mature males, while lipid
503 reserves are comparatively lower. Both findings are consistent with a life-style of time-limited mate
504 searching.

505 Concluding remarks

506 This study of the comparative morphology of three *Euphausia* species that dominate the biomass of
507 the Southern Ocean euphausiid community has been instructive in examining their ecology.
508 Morphological differences between species are consistent with what is presently known about the
509 habitat and behaviour of the respective species. Although the origin of our samples was limited to
510 the Atlantic sector of the Southern Ocean, including the Antarctic Peninsula region, we consider our
511 findings to be indicative of these species traits throughout the Southern Ocean since this region
512 typifies the environmental and biotic drivers found more widely in this ocean. In making interspecific
513 comparisons, we have revealed the unique degree to which *E. superba* exhibits sexual dimorphism.
514 Our identification of these sexual dimorphic features has, in turn, provided insights into the major
515 selective pressures that have acted on these organisms over evolutionary time. It also emphasises
516 the intimate relationship between the many distinctive aspects of the Southern Ocean environment
517 and the morphology and behaviour of the *Euphausia* species that have exploited it so successfully.

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525 **References**

- 526 Amakasu K, Ono A, Moteki M, Ishimaru TJPS (2011) Sexual dimorphism in body shape of Antarctic
527 krill (*Euphausia superba*) and its influence on target strength. Polar Sci 5: 179-186.
528 <https://doi.org/10.1016/j.polar.2011.04.005>
- 529 Baker AdC (1959) Distribution and life history of *Euphausia triacantha*. Discovery Rep XXIX: 309-340
- 530 Baker AdC, Boden BP, Brinton E (1990) A practical guide to the euphausiids of the world. British
531 Museum (Natural History), London
- 532 Bargmann HE (1937) The reproductive system of *Euphausia superba*. Discovery Rep 14: 327-349
- 533 Belcher A, Tarling G, Manno C, Atkinson A, Ward P, Skaret G, Fielding S, Henson S, Sanders R (2017)
534 The potential role of Antarctic krill faecal pellets in efficient carbon export at the marginal
535 ice zone of the South Orkney Islands in spring. Polar Biol 40: 1-13.
536 <https://doi.org/10.1007/s00300-017-2118-z>
- 537 Boden BP, Johnson MW, Brinton E (1955) Euphausiacea (Crustacea) of the North Pacific. Bull Scripps
538 Inst Oceanogr 6: 287–400
- 539 Croxall J, Reid K, Prince P (1999) Diet, provisioning and productivity responses of marine predators to
540 differences in availability of Antarctic krill. Mar Ecol Prog Ser 177: 115-131.
541 <https://doi.org/10.3354/meps177115>
- 542 Cuzin-Roudy J, Amsler MO (1991) Ovarian development and sexual maturity staging in Antarctic Krill,
543 *Euphausia superba* Dana (Euphausiacea). J Crust Biol 11: 236-249.
544 <https://doi.org/10.1163/193724091X00059>
- 545 Cuzin-Roudy J, Buchholz F (1999) Ovarian development and spawning in relation to the moult cycle
546 in Northern krill *Meganyctiphanes norvegica* (Crustacea: Euphausiacea), along a climatic
547 gradient. Mar Biol 133: 267-281. <https://doi.org/10.1007/s002270050466>
- 548 Cuzin-Roudy J, Irisson J, Penot F, Kawaguchi S, Vallet C (2014) Southern Ocean Euphausiids. In: De
549 Broyer C, Koubbi P (eds) Biogeographic Atlas of the Southern Ocean. Scientific Committee on
550 Antarctic Research, Cambridge, UK, pp 309-320

551 Dalpadado P, Hop H, Rønning J, Pavlov V, Sperfeld E, Buchholz F, Rey A, Wold A (2016) Distribution
552 and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and
553 Rijpfjorden (Svalbard) and changes in their relative importance as key prey in a warming
554 marine ecosystem. *Polar Biol* 39: 1765-1784. <https://doi.org/10.1007/s00300-015-1874-x>

555 Einarsson H (1942) Notes on Euphausiacea I-III: On the systematic value of the spermatheca, on
556 sexual dimorphism in *Nematoscelis*, on the male in *Bentheuphausia*. *Vidensk Medd fra*
557 *Dansk naturh Foren* 106: 263-286

558 Endo Y (1989) Allometric differences observed on the same sized immature and mature males of the
559 Antarctic krill (*Euphausia superba* Dana). *Bull Plankt Soc Japan*

560 Everson I (1987) Some aspects of the small scale distribution of *Euphausia crystallorophias*. *Polar Biol*
561 8: 9-15. <https://doi.org/10.1007/Bf00297158>

562 Färber-Lorda J (1990) Somatic length relationships and ontogenic morphometric differentiation of
563 *Euphausia superba* and *Thysanoessa macrura* of the Southwest Indian-Ocean During
564 Summer (February 1981). *Deep Sea Res Part A* 37: 1135-1143.
565 [https://doi.org/10.1016/0198-0149\(90\)90055-Z](https://doi.org/10.1016/0198-0149(90)90055-Z)

566 Färber-Lorda J (1991) Multivariate approach to the morphological and biochemical differentiation of
567 Antarctic krill (*Euphausia superba* and *Thysanoessa macrura*). *Deep Sea Research Part A*
568 *Oceanographic Research Papers* 38: 771-779

569 Färber-Lorda J, Beier E, Mayzaud P (2009) Morphological and biochemical differentiation in Antarctic
570 krill. *J Marine Syst* 78: 525-535. <https://doi.org/10.1016/j.jmarsys.2008.12.022>

571 Färber-Lorda J, Ceccaldi HJ (2020) Relationship of morphometrics, total carotenoids, and total lipids
572 with activity and sexual and spatial features in *Euphausia superba*. *Scientific reports* 10: 1-
573 15. <https://doi.org/10.1038/s41598-020-69780-8>

574 Hamner WM (1984) Aspects of schooling of *Euphausia superba*. *J Crust Biol* 4 (Special Issue): 67-74.
575 <https://doi.org/10.1163/1937240x84x00507>

576 Hamner WM, Hamner PP (2000) Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging,
577 and antipredatory behavior. Can J Fish AquatSci 57: 192-202. [https://doi.org/10.1139/cjfas-](https://doi.org/10.1139/cjfas-57-S3-192)
578 57-S3-192

579 Hill HJ, Trathan PN, Croxall JP, Watkins JL (1996) A comparison of Antarctic krill *Euphausia superba*
580 caught by nets and taken by macaroni penguins *Eudyptes chrysolophus*: Evidence for
581 selection? Mar Ecol Prog Ser 140: 1-11. <https://doi.org/10.3354/meps140001>

582 Hiller-Adams P, Case J (1988) Eye size of pelagic crustaceans as a function of habitat depth and
583 possession of photophores. Vision Res 28: 667-680. [https://doi.org/10.1016/0042-](https://doi.org/10.1016/0042-6989(88)90047-8)
584 6989(88)90047-8

585 Hopkins T (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Mar Biol 96: 93-106.
586 <https://doi.org/10.1007/Bf00394842>

587 James P (1973) Distribution of dimorphic males of three species of *Nematoscelis* (Euphausiacea).
588 Mar Biol 19: 341-347. <https://doi.org/10.1007/BF00348905>

589 Johnson ML, Tarling GA (2008) Influence of individual state on swimming capacity and behaviour of
590 Antarctic krill *Euphausia superba*. Mar Ecol Prog Ser 366: 99-110.
591 <https://doi.org/10.3354/meps07533>

592 Kattner G, Hagen W (1998) Lipid metabolism of the Antarctic euphausiid *Euphausia crystallorophias*
593 and its ecological implications. Mar Ecol Prog Ser 170: 203-213.
594 <https://doi.org/10.3354/meps170203>

595 Kawaguchi S, Kilpatrick R, Roberts L, King RA, Nicol S (2011a) Ocean-bottom krill sex. J Plankt Res 33:
596 1134-1138. <https://doi.org/10.1093/plankt/fbr006>

597 Kawaguchi S, Kilpatrick R, Roberts L, King RA, Nicol S (2011b) Ocean-bottom krill sex. Journal of
598 Plankton Research 33: 1134-1138. <https://doi.org/10.1093/plankt/fbr006>

599 Kils U (1979) Swimming speed and escape capacity of Antarctic krill, *Euphausia superba*.
600 Meeresforsch 27: 264-266

601 Kiørboe T (2008) Optimal swimming strategies in mate-searching pelagic copepods. *Oecologia* 155:
602 179-192. <https://doi.org/10.1007/s00442-007-0893-x>

603 Liszka C (2018) Zooplankton-mediated carbon flux in the Southern Ocean: influence of community
604 structure, metabolism and behaviour. PhD Thesis. Dept Environmental Sciences, Norwich,
605 UK

606 Makarov RR, Denys CJ (1980) Stages of sexual maturity of *Euphausia superba* (BIOMASS Handbook).
607 Scientific Committee for Antarctic Research, Cambridge

608 Mathew K (1980) Sexual dimorphism in *Stylocheiron indicum* Silas and Mathew (Crustacea:
609 Euphausiacea). *J Mar Biol Assoc India* 22: 39-44

610 Mauchline J (1988) Egg and brood sizes of oceanic pelagic crustaceans. *Mar Ecol Prog Ser* 43: 251-
611 258. <https://doi.org/10.3354/meps043251>

612 Mauchline J, Fisher LR (1969) The biology of euphausiids. *Adv Mar Biol* 7: 1-454

613 McLaughlin PA (1965) A redescription of the euphausiid crustacean, *Nematoscelis difficilis* Hansen,
614 1911. *Crustaceana*: 41-44

615 Miller D (1983) Variation in body length measurement of *Euphausia superba* Dana. *Polar Biol* 2: 17-
616 20. <https://doi.org/10.1007/Bf00258280>

617 Murphy DW, Webster DR, Kawaguchi S, King R, Yen J (2009) Locomotory biomechanics of Antarctic
618 krill. *Integr Comp Biol* 49: E121-E121

619 Nemoto T (1966) *Thysanoessa* euphausiids, comparative morphology, allomorphy and ecology. *J*
620 *Sci Rep Whales Res Inst* 20: 109-155

621 O'Brien DP (1987) Direct Observations of the Behavior of *Euphausia superba* and *Euphausia*
622 *crystallorophias* (Crustacea, Euphausiacea) under Pack Ice During the Antarctic Spring of
623 1985. *J Crust Biol* 7: 437-448. <https://doi.org/10.2307/1548293>

624 Ross R, Quetin L, Amsler M, Elias M (1987) Larval and adult Antarctic krill, *Euphausia superba*,
625 winter-over at Palmer Station. *Ant J, US* 22: 205-206

626 Ross RM, Quetin LB (2000) Reproduction in Euphausiacea. In: Everson I (ed) Krill: Biology, Ecology
627 and Fisheries. Blackwell Science Ltd, Oxford, pp 150-181

628 Santora JA, Reiss CS, Loeb VJ, Veit RR (2010) Spatial association between hotspots of baleen whales
629 and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent
630 predation. Mar Ecol Prog Ser 405: 255-269. <https://doi.org/10.3354/meps08513>

631 Schmidt K, Atkinson A (2016) Feeding and food processing in Antarctic krill (*Euphausia superba*
632 Dana). In: Siegel V (ed) Biology and Ecology of Antarctic Krill. Springer, pp 175-224

633 Siegel V (1982) Relationship of various length measurements of *Euphausia superba* Dana.
634 Meeresforsch 29: 114-117

635 Sogawa S, Sugisaki H, Tadokoro K, Ono T, Sato E, Shimode S, Kikuchi T (2017) Feeding habits of six
636 species of euphausiids (Decapoda: Euphausiacea) in the northwestern Pacific Ocean
637 determined by carbon and nitrogen stable isotope ratios. J Crust Biol 37: 29-36.
638 <https://doi.org/10.1093/jcabi/ruw014>

639 Suh H-L, Choi S-D (1998) Comparative morphology of the feeding basket of five species of Euphausia
640 (Crustacea, Euphausiacea) in the western North Pacific, with some ecological considerations.
641 Hydrobiol 385: 107-112. <https://doi.org/10.1023/A:1003435622123>

642 Sun S, Delamare W, Nicol S (1995) The compound eye as an indicator of age and shrinkage in
643 Antarctic krill. Ant Sci 7: 387-392. <https://doi.org/10.1017/S0954102095000538>

644 Tarling G, Hill S, Peat H, Fielding S, Reiss C, Atkinson A (2016) Growth and shrinkage in Antarctic krill
645 *Euphausia superba* is sex-dependent. Mar Ecol Prog Ser 547: 61-78.
646 <https://doi.org/10.3354/meps11634>

647 Tarling GA (2003) Sex-dependent diel vertical migration in northern krill *Meganyctiphanes norvegica*
648 and its consequences for population dynamics. Mar Ecol Prog Ser 260: 173-188.
649 <https://doi.org/10.3354/meps260173>

650 Tarling GA, Cuzin-Roudy J, Thorpe SE, Shreeve RS, Ward P, Murphy EJ (2007) Recruitment of
651 Antarctic krill *Euphausia superba* in the South Georgia region: adult fecundity and the fate of
652 larvae. Mar Ecol Prog Ser 331: 161-179. <https://doi.org/10.3354/meps331161>

653 Tarling GA, Johnson ML (2006) Satiation gives krill that sinking feeling. Curr Biol 16: 83-84.
654 <https://doi.org/10.1016/j.cub.2006.01.044>

655 Tarling GA, Klevjer T, Fielding S, Watkins J, Atkinson A, Murphy E, Korb R, Whitehouse M, Leaper R
656 (2009) Variability and predictability of Antarctic krill swarm structure. Deep Sea Res Part I 56:
657 1994-2012. <https://doi.org/10.1016/j.dsr.2009.07.004>

658 Tarling GA, Shreeve RS, Hirst AG, Atkinson A, Pond DW, Murphy EJ, Watkins JL (2006) Natural growth
659 rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting
660 intermolt period. Limnol Oceanogr 51: 959-972. <https://doi.org/10.4319/lo.2006.51.2.0959>

661 Tarling GA, Thorpe SE (2014) Instantaneous movement of krill swarms in the Antarctic Circumpolar
662 Current. Limnol Oceanogr 59: 872-886. <https://doi.org/10.4319/lo.2014.59.3.0872>

663 Tarling GA, Thorpe SE, Fielding S, Klevjer T, Ryabov A, Somerfield PJ (2018) Varying depth and swarm
664 dimensions of open-ocean Antarctic krill *Euphausia superba* Dana, 1850 (Euphausiacea) over
665 diel cycles. J Crust Biol 38: 716-727. <https://doi.org/10.1093/jcbiol/ruy040>

666 Thomas P, Ikeda T (1987) Sexual regression, shrinkage, rematuration and growth in spent females
667 *Euphausia superba* in the laboratory. Mar Biol 95: 357-363.
668 <https://doi.org/10.1007/BF00409565>

669 Watkins JL, Morris DJ, Ricketts C, Murray AWA (1990) Sampling biological characteristics of krill:
670 effect of heterogenous nature of swarms. Mar Biol 107: 409-415.
671 <https://doi.org/10.1007/BF01313422>

672

673 **Figure Legends:**

674 **Fig. 1:** Body plan of a typical *Euphausia* specimen showing the dimensions of the morphological
675 measurements made in the present study. RL – Reference length, S3 – standard length 3, S6 –
676 carapace length, TS – length of the telson, AS6 – length of the 6th abdominal segment, d0 – eye
677 diameter. Note pleopod measurements were also made (see [Fig. 2](#))

678 **Fig. 2:** Measured dimensions of the 1st and 4th pleopods. P4U - Upper segment of the 4th pleopod,
679 P4L – lower segment of the 4th pleopod, P1U – upper segment of the 1st pleopod, P1L – lower
680 segment of the 1st pleopod

681 **Fig. 3:** *Euphausia* spp.: Frequency plots of the reference lengths (mm) of *E. triacantha*, *E. superba*
682 and *E. crystallorophias* specimens used in the present analysis

683 **Fig. 4:** *Euphausia* spp.: Relationship between reference length (*rl*, mm) and carapace length (*s6*, mm)
684 in sex-stage categories of the 3 species, showing fitted linear regression ($s6 = 0.361rl - 2.4802$, $t_{slope,319}$
685 $= 59.85$, $p < 0.0001$, $r^2 = 0.9187$) and 95% confidence band. *E.crys* – *Euphausia crystallorophias*;
686 *E.sup*- *E. superba*; *E.tri* – *E. triacantha*

687 **Fig. 5:** *Euphausia* spp.: Principal Component Analysis of the morphological characters of *E.*
688 *crystallorophias*, *E. superba* and *E. triacantha* showing the first two principal components. Vectors of
689 the morphometric variables are superimposed. Morphological measurements were standardised
690 prior to analysis through dividing by standard length (*s3*). Codes for the morphological characters are
691 provided in [Table 2](#)

692 **Fig. 6:** *Euphausia* spp.: Box plots of the standardised measurements of 7 morphological characters
693 for *E. crystallorophias* (*E. cry*), *E. superba* (*E. sup*) and *E. triacantha* (*E. tri*). The box extends from the
694 first to the third quartile. The line in the box is the median and the whiskers are the minimum and
695 maximum values, while the dots are outliers. Morphological measurements were standardised

696 through dividing by standard length (s_3). *E.crys* – *Euphausia crystallorophias*; *E.sup*- *E. superba*; *E.tri*
697 – *E. triacantha*

698 **Fig. 7:** *Euphausia* spp.: Box plot of the Differentiation index for different sex-stage categories of *E.*
699 *crystallorophias*, *E. superba* and *E. triacantha*. The box extends from the first to the third quartile.
700 The line in the box is the median and the whiskers are the minimum and maximum values, while the
701 dots are outliers. *Ec* – *E. crystallorophias*, *Es* – *E. superba*, *Et* – *E. triacantha*, *F* – female, *J* – juvenile,
702 *M* – male, *FA* – adult female, *FS* – sub-adult female, *MA* – adult male, *MS* – sub-adult male

703 **Fig. 8:** *Euphausia* spp.: Principal Component Analysis of the morphological characters of sex-stage
704 categories of *E. crystallorophias* (upper), *E. superba* (middle) and *E. triacantha* (lower) showing the
705 first two principal components. Vectors of the morphometric variables are superimposed.
706 Morphological measurements were standardised prior to analysis through dividing by standard
707 length (s_3). Codes for the morphological characters are provided in [Table 2](#).

708 **Fig. 9:** *Euphausia* spp.: Box plots of the standardised measurements of 7 morphological characters
709 for *E. crystallorophias*, *E. superba* and *E. triacantha*. Each of the measurements was normalised
710 according to average values per species of the respective morphological character. The box extends
711 from the first to the third quartile. The line in the box is the median and the whiskers are the
712 minimum and maximum values, while the dots are outliers. Codes for the morphological characters
713 are provided in [Table 2](#). *Ec* – *E. crystallorophias*, *Es* – *E. superba*, *Et* – *E. triacantha*, *F* – female, *J* –
714 juvenile, *M* – male, *FA* – adult female, *FS* – sub-adult female, *MA* – adult male, *MS* – sub-adult male

715 **Fig. 10:** *Euphausia superba*: Relationship between standard length (s_3) and the lower segment of
716 pleopod 4 ($p4l$, left) and eye diameter ($d0$, right) for sub-adult and adult females (red) and sub-adult
717 and adult males (cyan) of *E. superba* only. Lines indicate best fit regressions (bold) bounded by 95%
718 confidence bands. All measurements are in mm.

Species	Sample Location	Cruise Number	Date of Collection
<i>Euphausia superba</i>	South Georgia, Antarctica	JR245	24/12/2010
<i>Euphausia triacantha</i>	South Georgia, Antarctica	JR177	02/02/2008
<i>Euphausia crystallorophias</i>	Deception Island, Antarctica	JB05	10/03/1985

Table 1. Sample populations examined during the present study. Samples from collections at the British Antarctic Survey

Measurements	Description
Reference Length (<i>rl</i>)	Horizontal distance from the base of eyestalk at the anterior edge of the carapace, to posterior tip of telson. <i>Measurement provides baseline reference length for each animal. Used here for considering population structure.</i>
Standard length (<i>s3</i>)	Horizontal distance from the base of eyestalk at the anterior edge of the carapace, to the posterior ventral edge of the sixth abdominal segment. <i>Measurement mitigates impact of damage to telson on reliability of data. Used here to standardize measurements of other morphological characters.</i>
Carapace (<i>s6</i>)	Horizontal distance from the base of eyestalk at the anterior edge of the carapace, to the posterior edge of carapace. <i>Measurement provides baseline reference length of cephalothorax.</i>
Abdominal Segment 6 (<i>as6</i>)	Horizontal distance from the anterior edge to the posterior edge of abdominal segment 6.
Telson (<i>ts</i>)	Horizontal distance from the anterior junction of the telson with the sixth abdominal segment, to the posterior tip of the telson (excluding setae and uropods).
Upper segment of Pleopod 1 (<i>p1u</i>)	Vertical distance from the articulation where the upper segment of Pleopod 1 adjoins the abdomen, to the articulation between the upper and lower segments of Pleopod 1.
Lower segment of Pleopod 1 (<i>p1l</i>)	Vertical distance from the articulation between upper and lower segments of Pleopod 1, to the tip of paddle (excluding setae). <i>Note that there is differentiation in the male reproductive organ located on the inner paddle of the lower segment of pleopod 1 in euphausiid species.</i>
Upper segment of Pleopod 4 (<i>p4u</i>)	Vertical distance from the articulation where the upper segment of Pleopod 4 adjoins the abdomen, to the articulation between the upper and lower segments of Pleopod 4.
Lower segment of Pleopod 4 (<i>p4l</i>)	Vertical distance from the articulation between upper and lower segments of Pleopod 4, to the tip of paddle (excluding setae).
Diameter of Eye (<i>d0</i>)	Vertical distance between dorsal and ventral lateral edges of left eye.

Table 2. Morphological measurements made on each individual specimen of the three study species. See [Fig. 1](#) and [Fig. 2](#) for further indication of the location of these measurements.

	EcF	EcJ	EcM	EsFA	EsFS	EsJ	EsMA	EsMS	EtFA	EtFS	EtJ	EtMA
EcJ	1.4											
EcM	17.6	45.5										
EsFA	0.1	0.1	0.1									
EsFS	0.1	0.1	0.1	0.1								
EsJ	0.1	0.1	0.1	1	21.7							
EsMA	0.1	0.1	0.1	0.1	0.9	3.1						
EsMS	0.1	0.1	0.1	0.3	8.1	76.2	1.8					
EtFA	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1				
EtFS	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	75.6			
EtJ	0.3	1.4	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1		
EtMA	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	40.9	12.2	0.1	
EtMS	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	13.4	21.4	0.3	41.5

Table 3. *Euphausia spp.*: Dissimilarity matrix of all measured morphological characters in each sex-stage category for each species as derived by an ANOSIM analysis (see text). A value of 0.1 (grey shading) indicates a significant level of dissimilarity in morphology between the respective pair, with values >0.1 (bold) indicating the level of similarity. Ec – *E. crystallorophias*, Es – *E. superba*, Et – *E. triacantha*, F – female, J – juvenile, M – male, FA – adult female, FS – sub-adult female, MA – adult male, MS – sub-adult male.

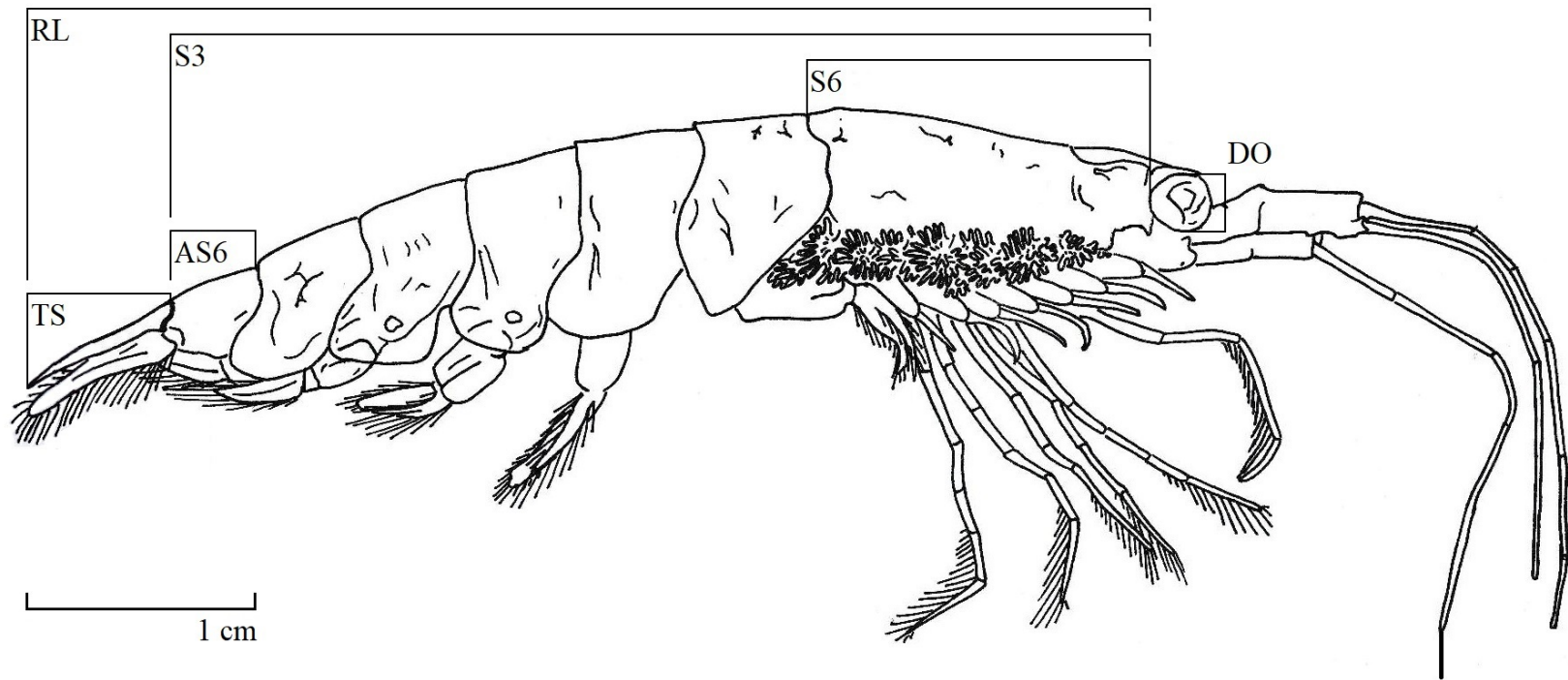


Fig. 1

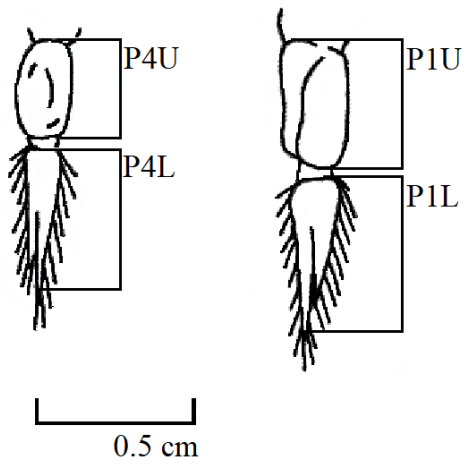


Fig. 2

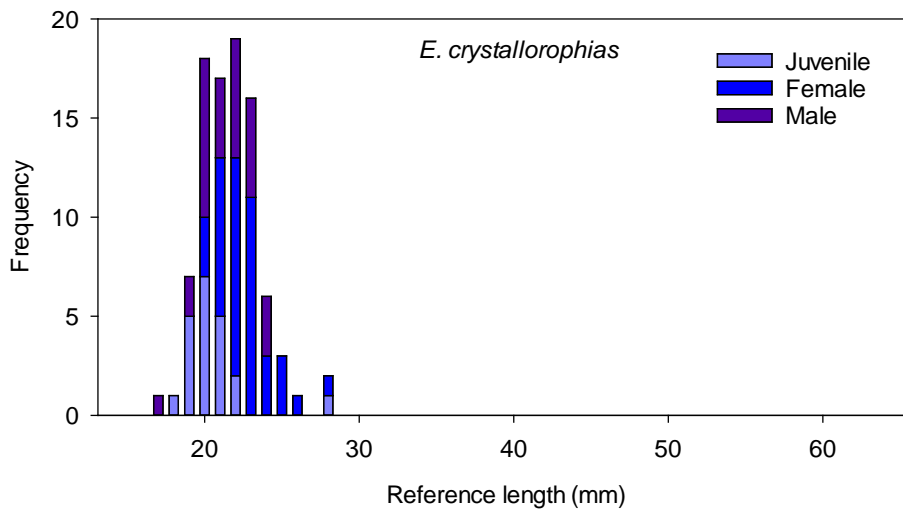
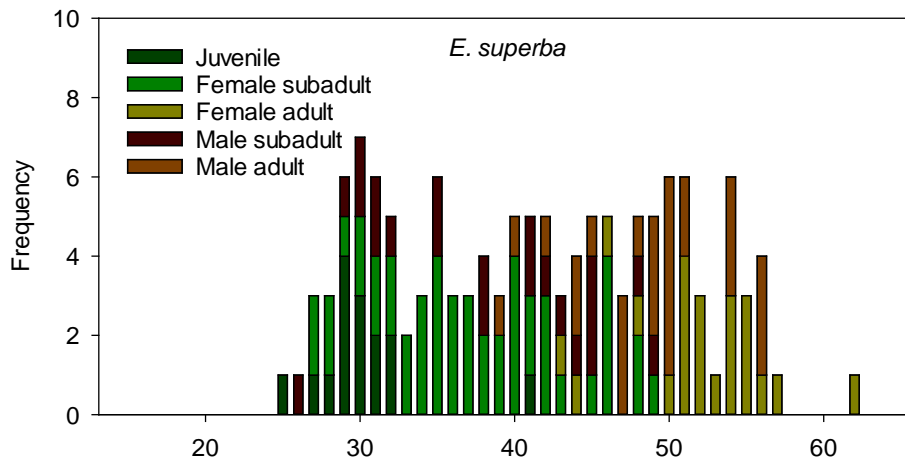
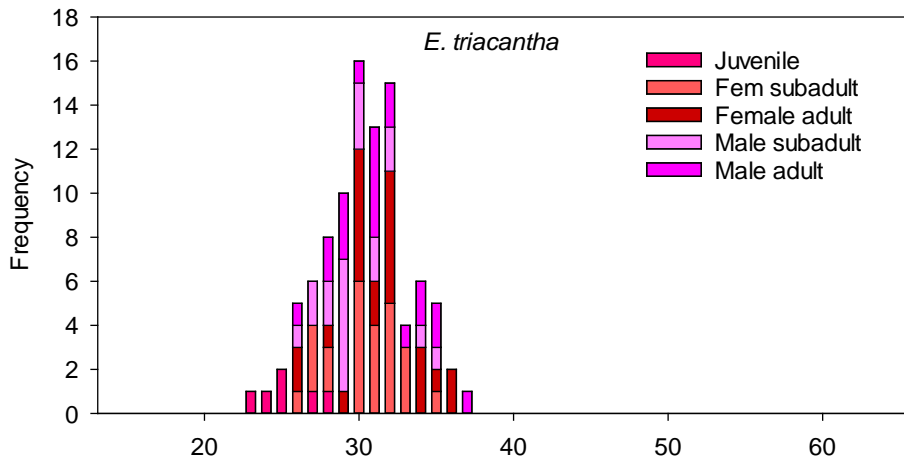


Fig. 3

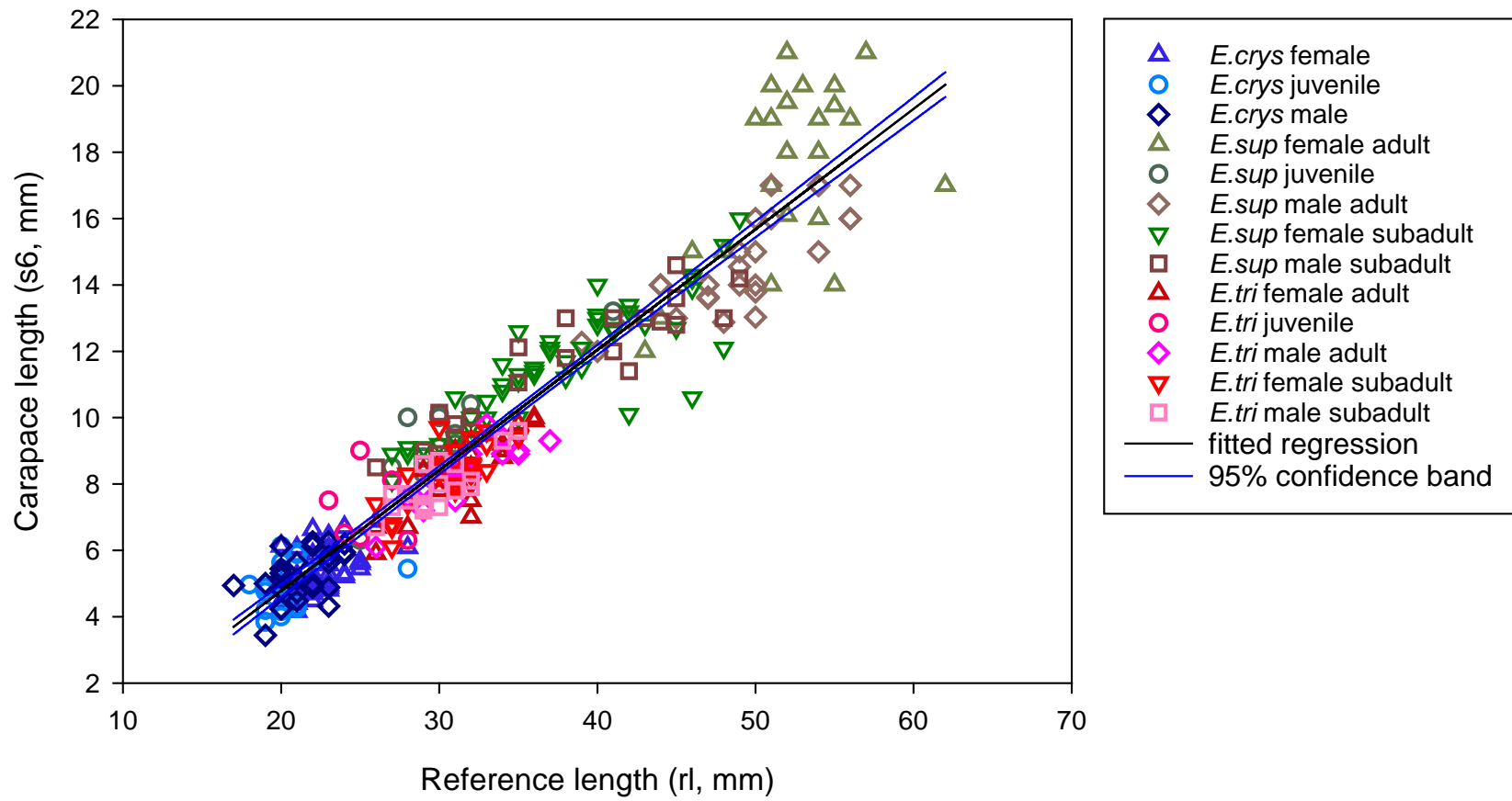


Fig. 4

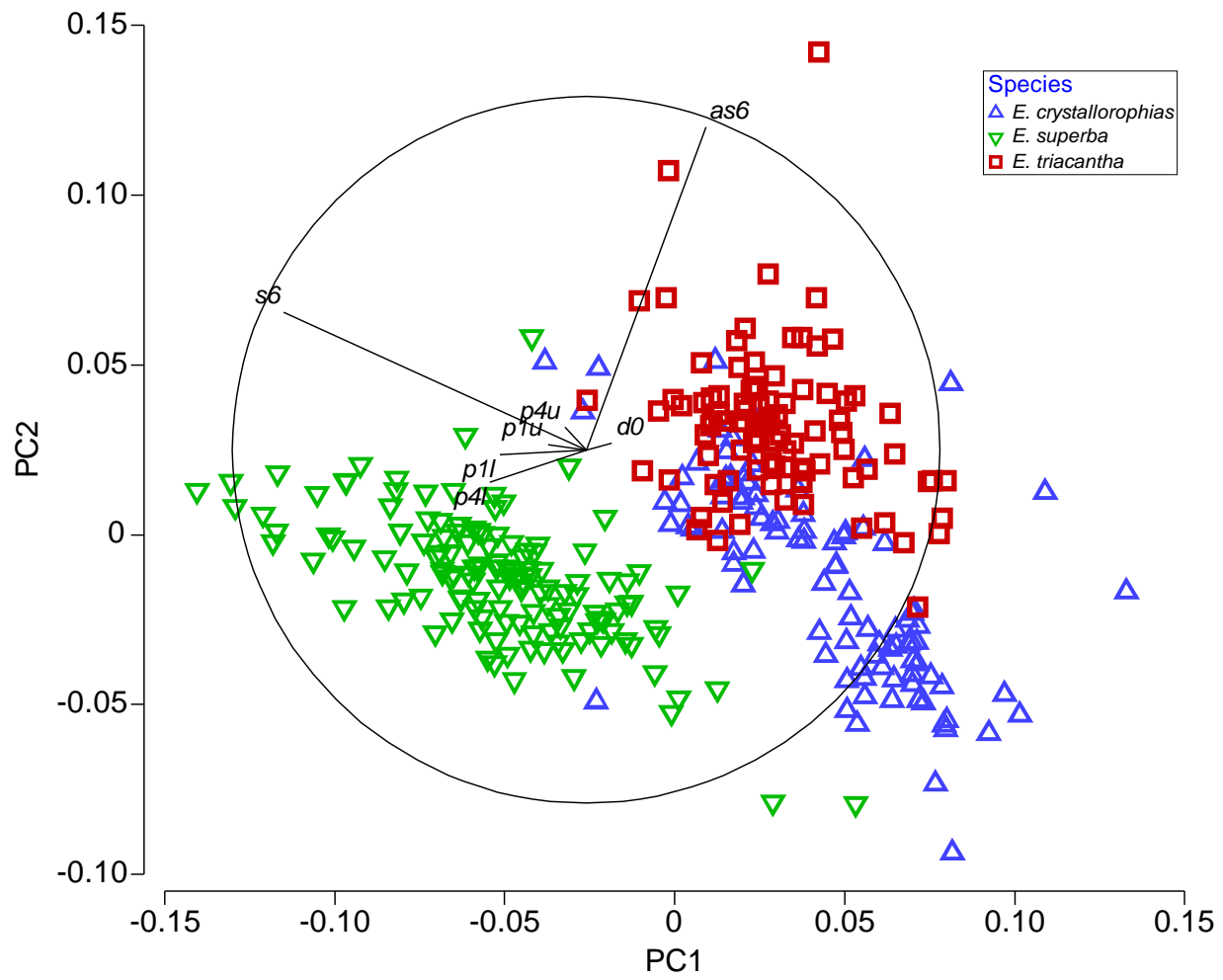


Fig. 5

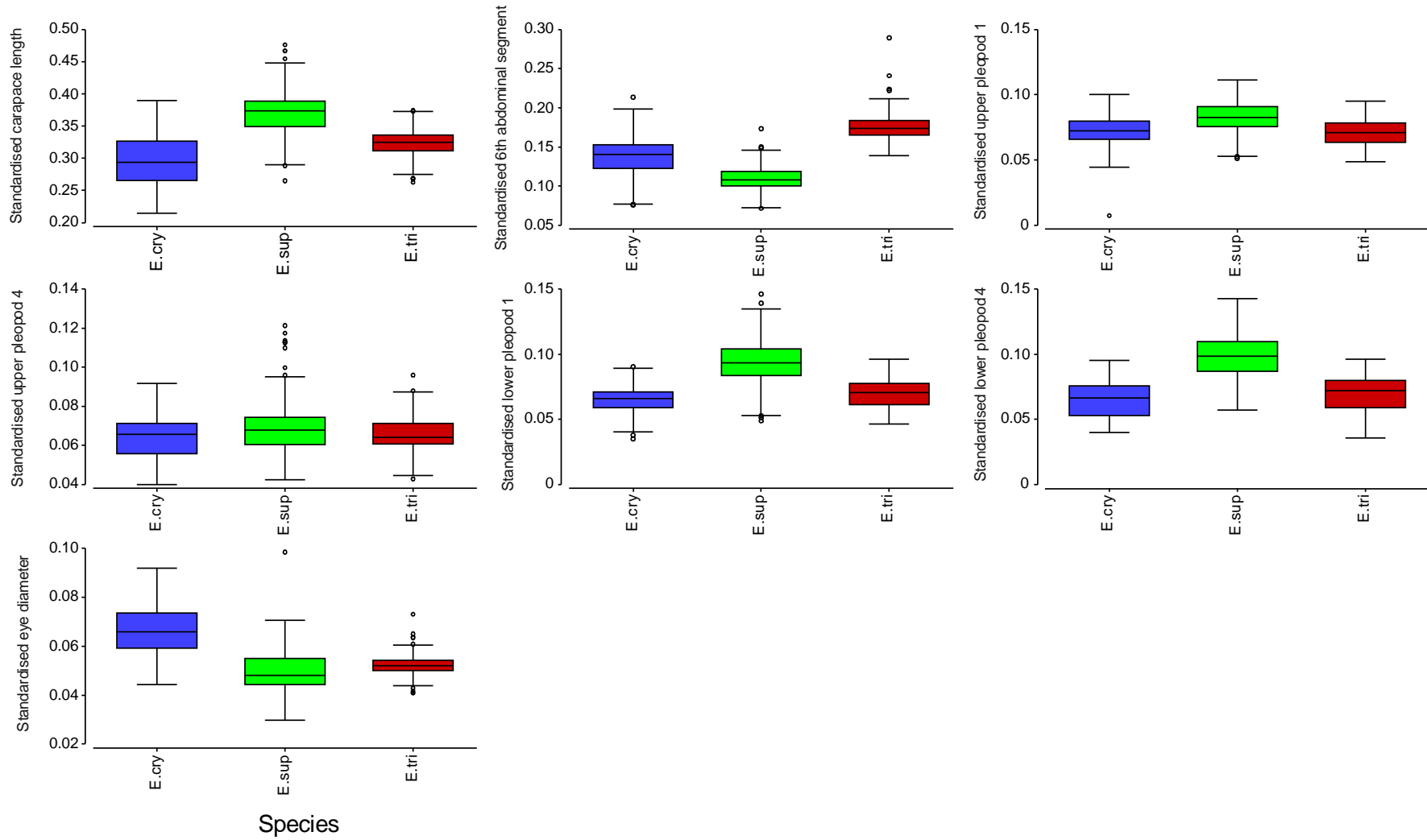


Fig. 6

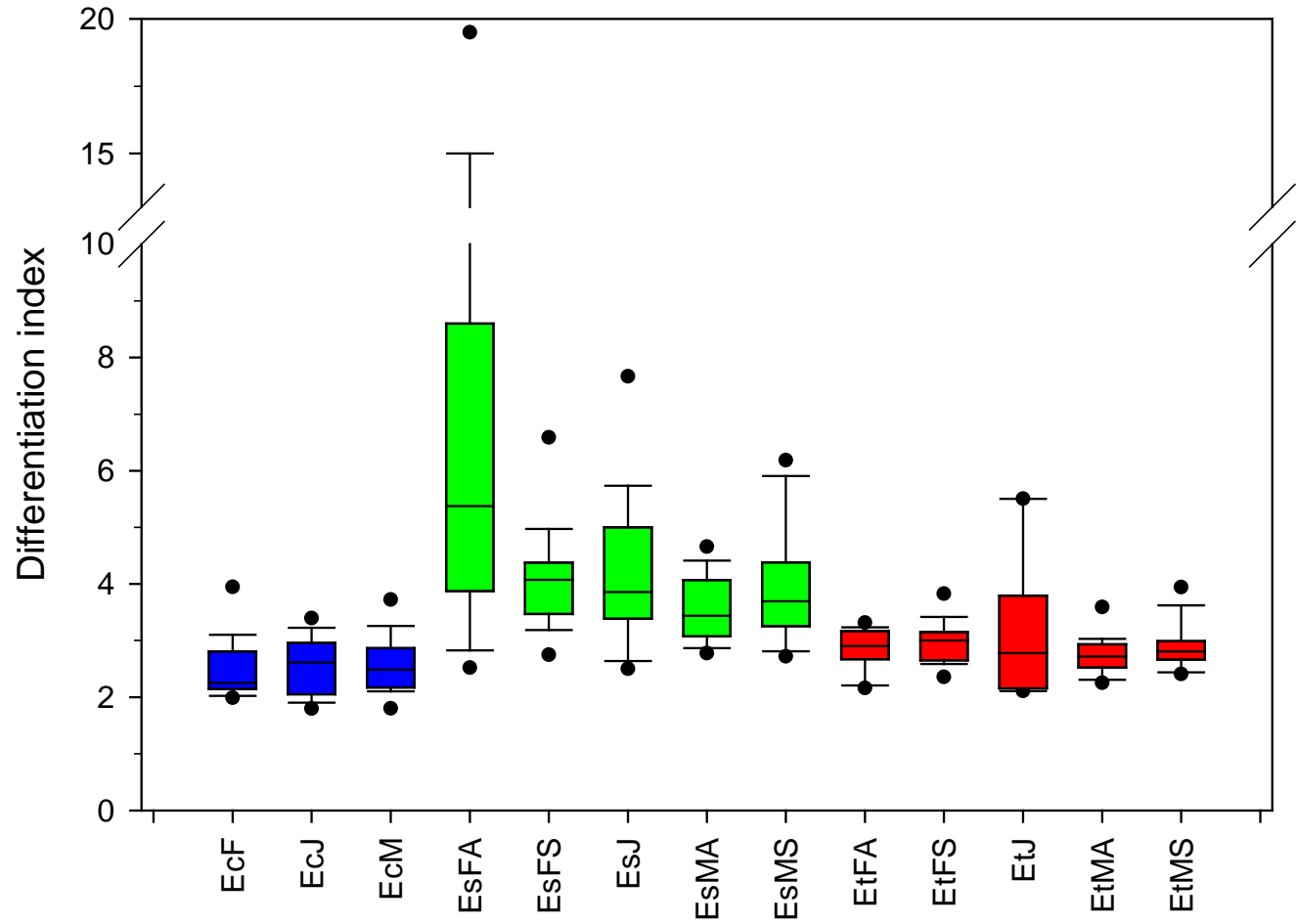


Fig. 7

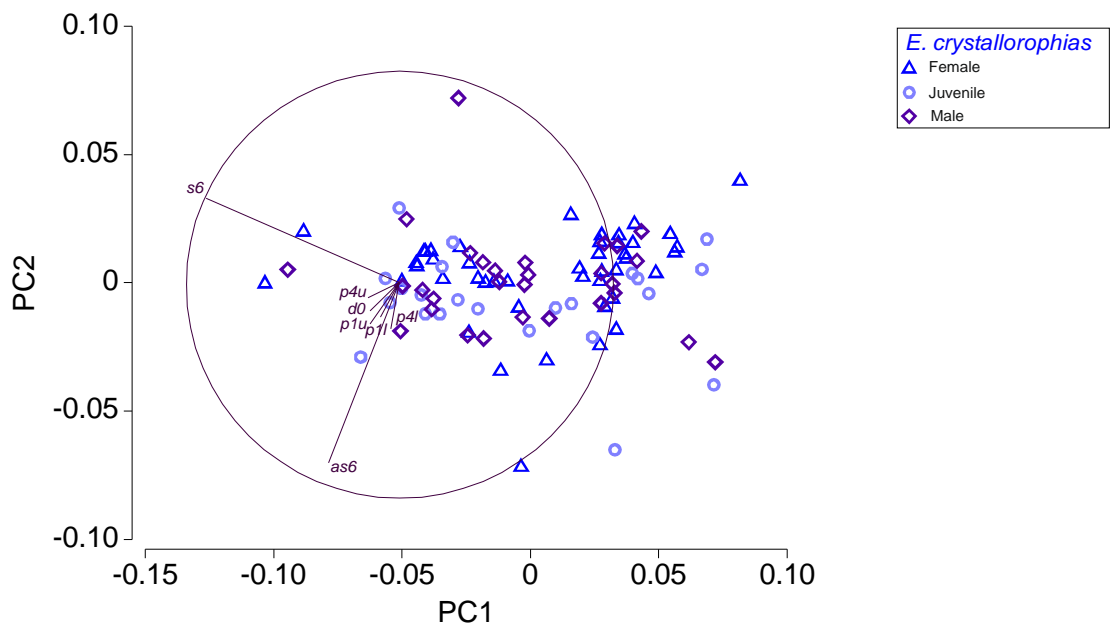
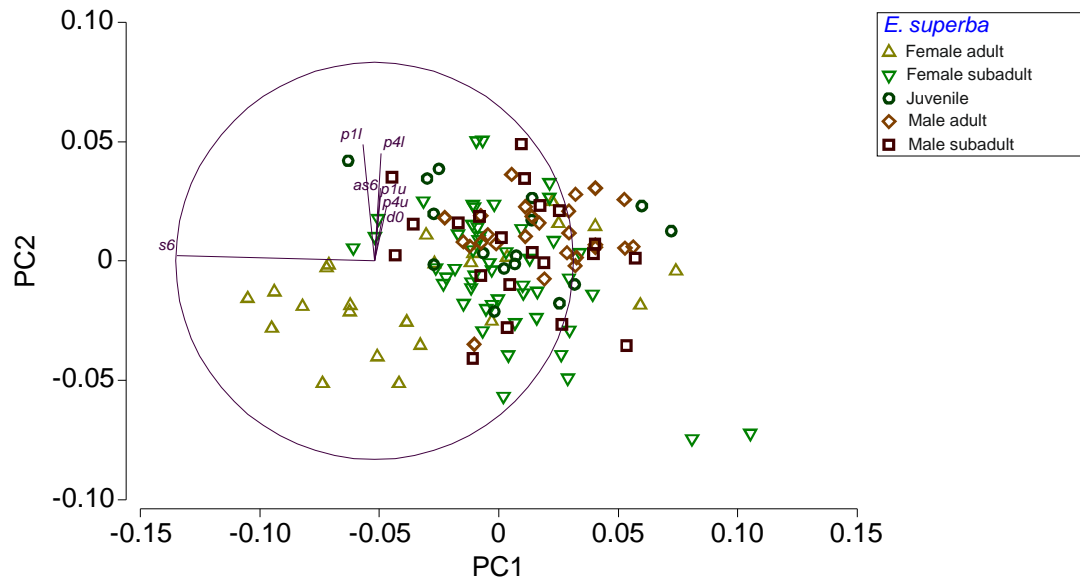
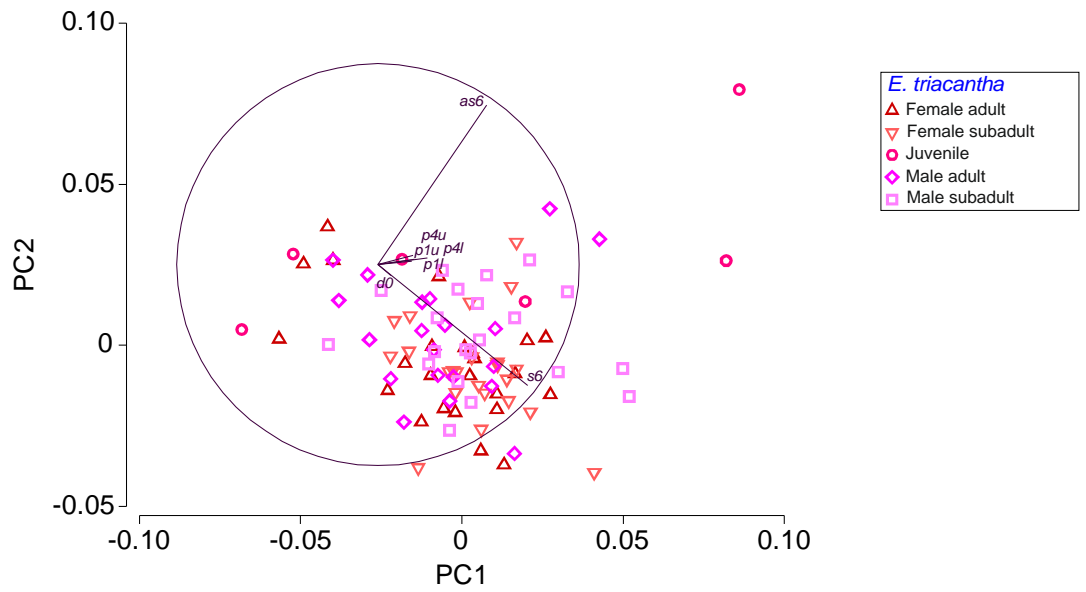


Fig. 8

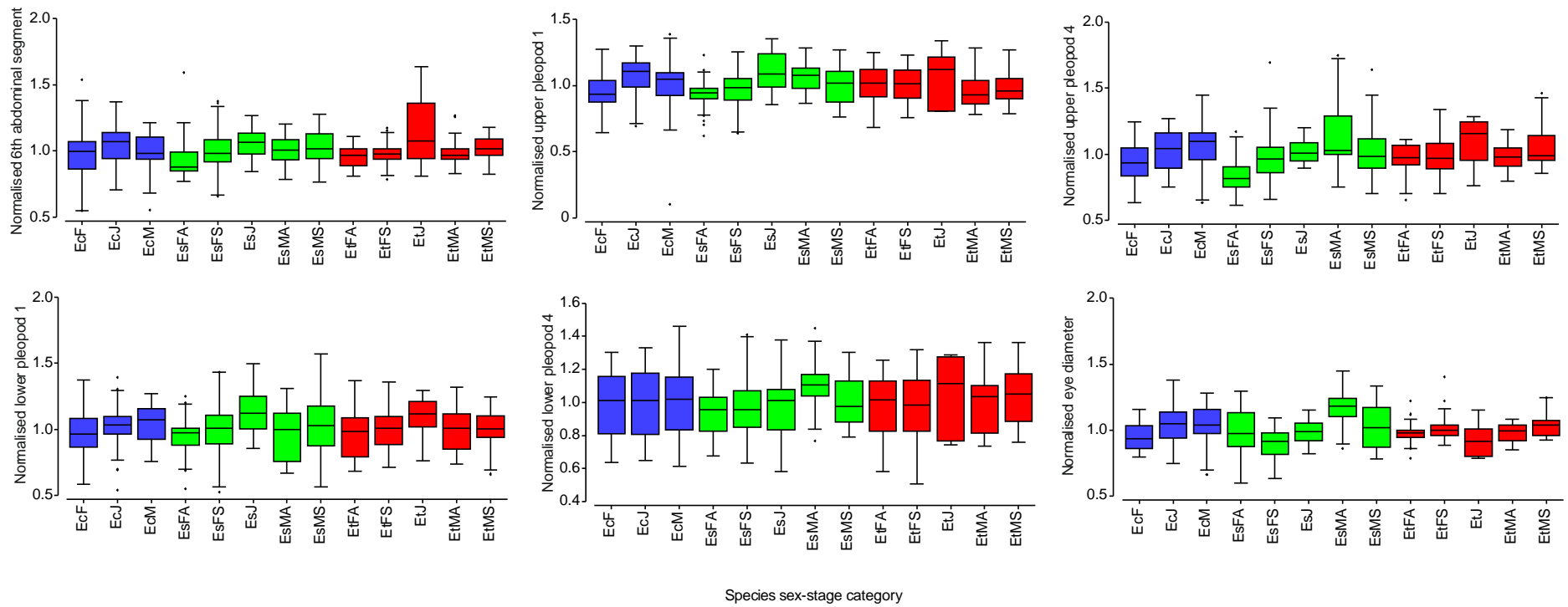


Fig. 9

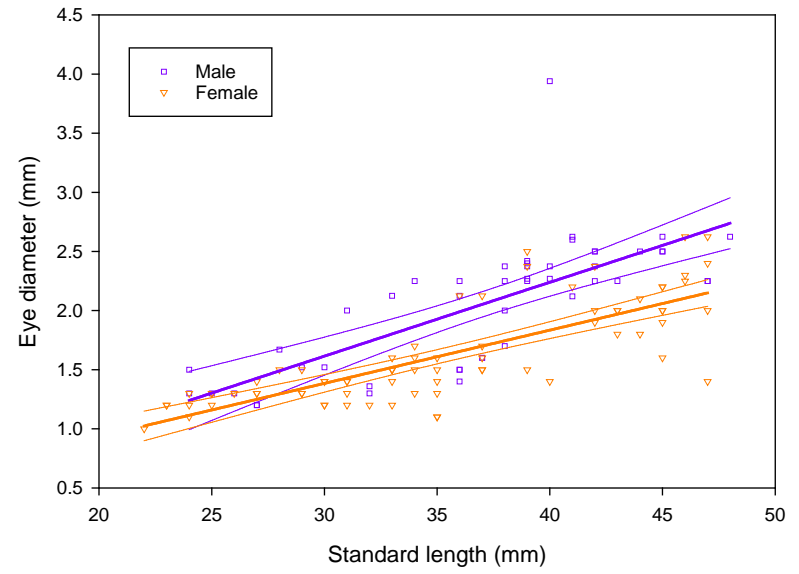
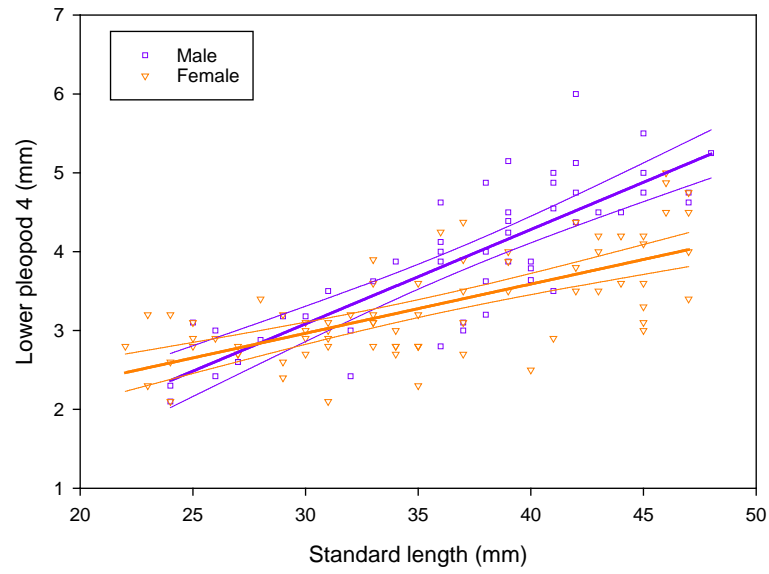


Fig. 10