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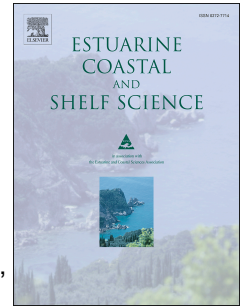
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# Accepted Manuscript

Influence of physico-chemical and biotic factors on the distribution of a penaeid in a temperate estuary

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1 **Influence of physico-chemical and biotic factors on the distribution of a**  
2 **penaeid in a temperate estuary**

3  
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16 **Abstract**

17 The distribution, abundance and size structure of a penaeid with tropical affinities  
18 (*Metapenaeus dalli*) was investigated in a temperate, microtidal estuary in south-western  
19 Australia. Sampling was conducted every lunar month for two years at 20 sites across five  
20 regions (nine subregions) in nearshore waters by hand trawl, and at 16 sites across four  
21 regions (eight subregions) in offshore waters by otter trawl. Densities of *M. dalli* changed  
22 markedly seasonally, with greatest values recorded in nearshore waters from October to  
23 February, and in offshore waters from March to July. These densities also varied spatially,  
24 with the highest recorded in the Lower Canning, Middle Swan, and Upper Melville Water  
25 regions. Spearman's rank correlation showed a positive relationship between the density of  
26 *M. dalli* in nearshore waters and surface water temperature in all nine subregions, whilst  
27 densities of *M. dalli* in offshore waters were negatively correlated with bottom water  
28 temperature in most of the estuary; these correlations reflect the movement of adult prawns  
29 into shallow waters for breeding in summer, as well as the subsequent recruitment and  
30 movement back into deeper waters over the winter months. Mean carapace lengths remained  
31 relatively unchanged over the late autumn and winter months (May to August), before rapidly  
32 increasing with temperature in late spring. The spatial and temporal distribution of *M. dalli*  
33 differed significantly from those of other crustaceans in the estuary, particularly the penaeid  
34 *Penaeus latisulcatus*, which was concentrated mainly in the Lower and Upper Melville Water  
35 regions. The distribution of *M. dalli* was statistically indistinct from that of the apogonid  
36 *Ostorhinchus rueppellii*, which predate heavily on postlarval *M. dalli*, and very similar to  
37 those of two scyphozoans, *Aurelia aurita* and *Phyllorhiza punctata*, that likely predate on  
38 larval *M. dalli*. These findings highlight the partitioning of species within the estuary and the  
39 significance of site selection for maximising the post-release survival of hatchery-reared  
40 *M. dalli* produced by aquaculture-based enhancement programs.

## 41 **1. Introduction**

42 Estuaries are highly productive ecosystems, receiving nutrients from a range of sources  
43 including rivers, run-off, tidal water movement, the atmosphere and waste input (McLusky  
44 and Elliott, 2004; Bianchi, 2006). Their high productivity provides important food sources for  
45 many taxa, enabling their juveniles to grow rapidly. In addition, inhabiting these systems can  
46 lower predation risk due to the reduced presence of large predators (Blaber and Blaber, 1980;  
47 Potter et al., 2016). For these reasons, estuaries are often used as nursery areas by fish and  
48 crustacean species (Beck et al., 2001; Tweedley et al., 2016a). The ecological value of  
49 estuaries for fisheries is reflected in the proportion of fishery species that utilise these  
50 productive, sheltered waters. For example, Lellis-Dibble et al. (2008) estimated that species  
51 that use estuaries contributed 46% by mass and 68% by value to commercial fish and  
52 shellfish landings in the United States between 2000 and 2004. Moreover, Creighton et al.  
53 (2015) estimated that, in Australia, such species comprise > 75% of commercial fish catch  
54 and, in some regions, up to 90% of the recreational angling catch.

55 As estuaries are located at the interface between fresh and marine waters, their  
56 physico-chemical conditions change markedly spatially as well as over a range of temporal  
57 scales, e.g. tidal cycle, monthly, seasonally and inter-annually (e.g. Gallegos et al., 2005;  
58 Sutherland and O'Neill, 2016; Hoeksema et al., 2018; Plenty et al., 2018). Typically, these  
59 conditions are influenced by tidal range and longer-term patterns in weather. For example,  
60 salinity in the Fraser Estuary of British Columbia, Canada, which has a tidal range of 4 m,  
61 varied by almost 30 over a tidal cycle (Geyer and Farmer, 1989). In contrast, the salinity in  
62 permanently-open microtidal estuaries (tidal range < 2 m) changes little over a tidal cycle, but  
63 can change in some locations by > 30 over the course of a year (Tweedley et al., 2016a).

64 Given the dynamic nature of estuaries and their physico-chemical environments, the  
65 composition of their faunal communities also changes spatially and temporally (e.g. Palma et  
66 al., 2013; Becker et al., 2016). In the temperate estuaries of south-western Australia, the  
67 community structure and composition of the fish fauna show major differences associated  
68 with the longitudinal gradient in estuaries with a permanent connection to the ocean, with

69 species 'preferring' a particular physico-chemical environment (e.g. Loneragan et al., 1987;  
70 1989; Valesini et al., 2009; Veale et al., 2014; Potter et al., 2016).

71 Temporal changes in the abundance of benthic macroinvertebrate species have been  
72 related to the timings of spawning and recruitment, and thus are also influenced by physico-  
73 chemical parameters such as water temperature and salinity, which affect growth, survival  
74 and reproductive success (Rainer, 1981; Kalejta and Hockey, 1991; Sardá et al., 1995; Platell  
75 and Potter, 1996). It is therefore expected that the pattern of temporal (i.e. seasonal) variation  
76 in species composition would differ between regions of an estuary, because they often  
77 harbour different suites of species (e.g. Loneragan and Potter, 1990; Young and Potter, 2003).

78 Many penaeid species are associated with coastal and estuarine systems at some stage  
79 of their life cycle, specifically the postlarvae and juveniles of marine-spawning species that  
80 utilise estuarine nursery areas, as well as all life stages of estuarine-spawning species (Dall et  
81 al., 1990; Subramanian, 1990; Rönnbäck et al., 2001; Khorshidian, 2002; Macia, 2004).  
82 Aspects of the spatial distribution of many penaeids in these environments have been  
83 investigated, focusing on the distribution of postlarvae and juveniles from the marine  
84 environment (Vance et al., 1996; 1998; Galindo-Bect et al., 2010) and the habitat (Rönnbäck  
85 et al., 2001; Vance et al., 2002; Taylor et al., 2016; 2017) and substrate preferences (de  
86 Freitas, 1986; Somers, 1987; 1994; Kenyon et al., 2004) of juveniles and/or adults.

87 Physico-chemical variables have been correlated to the distribution of various  
88 penaeids; for example, water temperature, dissolved oxygen concentration and rainfall were  
89 all correlated with the catch of *Metapenaeus macleayi* in the Hawkesbury-Nepean River,  
90 New South Wales (Pinto and Maheshwari, 2012). Water temperature was the major factor  
91 influencing the recruitment of *Penaeus esculentus* in Moreton Bay, Queensland (Kienzle and  
92 Sterling, 2016) and salinity the main driver of the distribution of *Penaeus monodon* and  
93 *Penaeus indicus* in the Saadan Estuary, Tanzania (Mosha and Gallardo, 2013).

94 Understanding the patterns of abundance and distribution of a species are particularly  
95 important for those species that are targeted by fisheries, and complete their life cycle in  
96 estuaries, as there is unlikely to be recruitment from adjacent marine waters to supplement

97 the population if over-exploitation occurs or the population declines for other reasons. The  
98 Western School Prawn *Metapenaeus dalli* is found along the western coast of Australia from  
99 Darwin in the north to Cape Naturaliste in the south, and also in Java, Indonesia (Racek,  
100 1957; Grey et al., 1983). It typically occurs in shallow, inshore marine waters (< 30 m deep),  
101 however, at the southern limit of its distribution (i.e. south of ~31°S), it is found only in  
102 estuaries and completes its life cycle within these systems (Potter et al., 1986; Broadley et al.,  
103 2017; Crisp et al., 2018). *Metapenaeus dalli* is a short-lived species, with a lifespan of up to  
104 two years and exhibits a highly seasonal pattern of growth (Potter et al., 1986; 1989;  
105 Broadley et al., 2017). This species, together with the Western King Prawn, *Penaeus*  
106 (= *Melicertus*) *latisulcatus*, was the focus of a commercial fishery that closed in the mid-  
107 1970s due to sustained low catches, and an iconic recreational fishery that also declined, with  
108 the last significant catches recorded in the late 1990s (Broadley et al., 2017). Because the  
109 population of *M. dalli* has not recovered despite the large reduction in fishing pressure, a  
110 restocking project was initiated between 2012/13 and 2015/16 to evaluate the feasibility of  
111 aquaculture-based enhancement to rebuild the population of this penaeid in this estuary  
112 (Tweedley et al., 2017a). During this time, about 4.5 million *M. dalli* postlarvae were  
113 released into the Swan-Canning Estuary (Crisp et al., 2018).

114 While the general biology of *M. dalli* in temperate south-western Australian estuaries  
115 has been determined (Potter et al., 1986; 1989; Broadley et al., 2017; Crisp et al., 2018), these  
116 studies did not investigate the patterns of *M. dalli* distribution and abundance within the  
117 estuary in detail. This type of fundamental information is needed to guide the aquaculture-  
118 based enhancement of this species in the Swan-Canning Estuary. For example, the  
119 relationships between the distribution and abundance of *M. dalli* and physico-chemical  
120 variables in the estuary will help select suitable times and sites for collecting broodstock and  
121 for the subsequent release of hatchery-reared individuals. The development of optimal release  
122 strategies that maximise the survival of cultured *M. dalli* also requires an understanding of  
123 how the spatial distribution of this penaeid relates to those of potential competitors and  
124 predators.

125 The aims of this study were therefore to: (i) determine the spatial and temporal  
126 patterns of abundance of *M. dalli*, and elucidate whether those patterns are correlated with  
127 any physico-chemical variables; (ii) describe the spatial and temporal patterns of abundance  
128 of different size classes of *M. dalli*; (iii) compare these patterns with those of a potential  
129 penaeid competitor, *P. latisulcatus* and (iv) identify the fish and invertebrate species that  
130 exhibit similar spatial and temporal patterns of distribution to those for *M. dalli*, to evaluate  
131 potential key predators, and how their distribution might affect the *M. dalli* population. This  
132 information is required for adopting a responsible approach to aquaculture-based  
133 enhancement following Lorenzen *et al.* (2010).

134

## 135 **2. Materials and methods**

### 136 **2.1 Study site**

137 The Swan-Canning Estuary is a drowned river valley system located in south-western  
138 Australia, which is ~50 km long, covers an area of ~55 km<sup>2</sup> and remains permanently open to  
139 the Indian Ocean (Brearley, 2005). The estuary comprises a narrow entrance channel that  
140 opens into two basins (Melville and Perth Water) and the tidal portions of the Swan and  
141 Canning rivers, which extend ~29 and 13 km upstream from their entry points into Melville  
142 Water, respectively. Although the majority of the estuary is shallow, i.e. < 2 m in depth, it  
143 reaches a maximum depth of ~20 m in the entrance channel (Valesini *et al.*, 2014). South-  
144 western Australia experiences a Mediterranean climate, with hot, dry summers and cool, wet  
145 winters with ~80% of rainfall occurring between June and September (Hodgkin and Hesp,  
146 1998; Hallett *et al.*, 2017). This, combined with the microtidal tidal regime (< 1 m variation  
147 in tide height), results in marked seasonal variations in physico-chemical conditions in this  
148 salt-wedge estuary. Salinities are typically stable and relatively high throughout much of the  
149 estuary during the austral summer (December to February), but during winter, may vary  
150 markedly along the estuary following substantial freshwater discharge, leading to marked  
151 stratification of the water column (Tweedley *et al.*, 2016a).



152 The Swan-Canning Estuary flows through the capital city of Perth, which supports  
153 ~78% of the 2.6 million people in the state of Western Australia (Australian Bureau of  
154 Statistics, 2015). Despite the estuary being extensively modified by anthropogenic activities,  
155 it is valued highly for its aesthetic, commercial, environmental and cultural importance  
156 (Tweedley et al., 2017b). Recreational fishing is an iconic activity in Western Australia, with  
157 an estimated 711,000 participants in 2014/15 (Ryan et al., 2015), and the Swan-Canning  
158 Estuary is a popular hotspot for recreational fishers, with a 1998/99 survey estimating 30,338  
159 fisher days of effort (Malseed and Sumner, 2001).

160

## 161 **2.2. Sampling procedure**

162 *Metapenaeus dalli* were sampled during the night at two locations within 20 sites in  
163 the shallow, nearshore waters (< 2 m deep; Fig. 1) and 16 sites in the deeper, offshore waters  
164 (2 – 17 m deep) of the Swan-Canning Estuary on the new moon phase of each lunar cycle  
165 between October 2013 and 2015 (i.e. 26 consecutive lunar months). Each site was allocated  
166 to both a region and subregion (Fig. 1). Sampling in nearshore waters was conducted using a  
167 4 m wide hand trawl constructed from 9 mm mesh. Two people operated the hand trawl, each  
168 holding a pole connected to the wings on either end, with the mouth of the net between them.  
169 The width of the hand trawl net during trawling was, on average, ~2.85 m, but varied slightly  
170 amongst trawls depending on the condition of the substratum, presence of submerged  
171 obstacles and localised wind and wave conditions. A hand trawl of 200 m (swept area of  
172 ~570 m<sup>2</sup> each) was carried out at each location in each site on each sampling occasion,  
173 covering a total area of 22,800 m<sup>2</sup> on any single lunar month. Sampling in offshore waters  
174 employed an otter trawl net (4.4 m headline length, 2.6 m wing-end spread), with 25 mm  
175 mesh in the body, and 9 mm mesh in the cod end. The net was towed at a speed of ~1.6 knots  
176 (~3 km h<sup>-1</sup>) for five minutes, covering a distance of ~250 m. An otter trawl of ~650 m<sup>2</sup> was  
177 completed at each location in each site on each sampling occasion covering a total area of  
178 20,800 m<sup>2</sup> over a lunar month.

179 After each hand or otter trawl, the contents of the net were emptied into a container  
180 and each *M. dalli* was counted, sexed, measured and returned alive to the water. The carapace  
181 length (CL), i.e. orbital indent to the posterior edge of the carapace, of each individual was  
182 measured (0.01 mm) using digital vernier callipers. Females were identified by presence of a  
183 thelycum and males by the presence of a petasma. Small individuals, without an obvious  
184 thelycum or petasma, were recorded as juveniles. Female prawns were also inspected to  
185 determine if they were gravid, i.e. had large green ovaries, as described by Crisp et al.  
186 (2017a) and/or possessed a spermatophore. The abundance of each penaeid, stomatopod,  
187 brachyuran, teleost and scyphozoan species collected together with *M. dalli* were also  
188 recorded, except in the case of *Craterocephalus mugiloides*, *Atherinosoma elongata* and  
189 *Leptatherina presbyteroides*, which were grouped together as ‘Atherinidae’. These species  
190 have similar morphologies and are very abundant, and it was not possible to identify them to  
191 species at night while attempting to return them to the water alive. As with the crustaceans,  
192 all teleosts and scyphozoans were returned to the water as quickly as possible, as per the  
193 conditions in Murdoch University Animal Ethics Committee permit #RW2566.

194 Salinity, water temperature and dissolved oxygen concentration at the surface and  
195 bottom of the water column were recorded at each offshore site on each sampling occasion  
196 using a Yellow Springs International Model 556 water quality meter. Offshore surface water  
197 quality measurements were used as a proxy for the nearshore sites, as was shown to be  
198 suitable in Crisp et al. (2018). Data were also obtained from the Department of Water and  
199 Environmental Regulation, Western Australia, which records these variables at sites  
200 throughout the Swan-Canning Estuary every week ([http://wir.water.wa.gov.au/Pages/Water-  
201 Information-Reporting.aspx](http://wir.water.wa.gov.au/Pages/Water-Information-Reporting.aspx)). A salinity stratification index was calculated by subtracting the  
202 salinity at the surface of the water column from that at the bottom (Crisp et al., 2018).  
203 Monthly rainfall and average maximum air temperature data for Perth airport were obtained  
204 from the Bureau of Meteorology (<http://www.bom.gov.au/climate/data/>) between January  
205 2013 and December 2015. The Department of Water and Environmental Regulation provided

206 monthly discharge data from tributaries entering the Swan-Canning Estuary over the same  
207 period.

208

### 209 **2.3. Statistical analyses**

#### 210 *Univariate analyses*

211 The density of *M. dalli* recorded in each sample from sites in the nearshore and  
212 offshore waters in each of the 13 lunar months in each year (2013/14 and 2014/15) were used  
213 to construct separate Euclidean distance matrices, and subjected to two-way Permutational  
214 Multivariate Analysis of Variance (PERMANOVA; Anderson et al., 2008) tests. These  
215 determined whether densities differed significantly among Lunar Month (13 levels and  
216 fixed), Subregion (8 or 9 levels and fixed; Fig. 1) and whether the interactions between these  
217 main effects were significant. Tests were conducted separately for data collected from the  
218 nearshore and offshore waters in each year. Year was not included as a factor due to the  
219 potentially confounding effect of the ongoing restocking program, which released 1,000,  
220 600,000 and 2,000,000 postlarval *M. dalli* into the nearshore waters of the Swan-Canning  
221 Estuary during the 2012/13, 2013/14 and 2014/15 breeding seasons, respectively (Tweedley  
222 et al., 2017a). As the densities of male and female prawns were highly correlated (see  
223 Results), they were combined to investigate the variation in total *M. dalli* density. When a  
224 main effect or interaction term was significant and contributed > 25% to the mean squares, a  
225 pairwise PERMANOVA test was used to identify the pairwise combination of *a priori*  
226 groups responsible for that difference. Prior to analysis, the extent of the linear relationship  
227 between the log-transformed mean and standard deviation for each dataset was examined to  
228 determine whether transformation was required to meet the test assumption of homogenous  
229 dispersions among *a priori* groups (Clarke and Warwick, 2001). These analyses indicated  
230 that no transformations were required.

231 Spearman's rank correlation tests were employed to elucidate whether the density of  
232 *M. dalli* was correlated with any of the environmental variables in the water column, (i)  
233 within a subregion over time, and (ii) within a lunar month and across the subregions. These

234 variables included water temperature, salinity and dissolved oxygen concentration at the  
235 surface of the water column and the density of *M. dalli* in nearshore waters, and water  
236 temperature, salinity and dissolved oxygen concentration at the surface and bottom of the  
237 water column, the stratification index and the density of *M. dalli* in offshore waters. The null  
238 hypothesis of no significant relationship between two variables was rejected when  $p \leq 0.05$ ,  
239 however, due to the limited number of subregions and thus replicates for correlations within a  
240 lunar month,  $p$  values of 0.05 – 0.1 were also classed as being influential.

241 Differences in the mean carapace length (CL) of male and female *M. dalli* recorded in  
242 the nearshore and offshore waters of a region were tested using a non-parametric Kruskal-  
243 Wallis test in SPSS v22. Note that a region was only included in the analysis for a given lunar  
244 month if a minimum of 30 *M. dalli* were caught. To provide a visual indication of the  
245 reason(s) for any pairwise differences in mean CL among regions in a lunar month, the  
246 number of individuals in each 1 mm CL size class in each region/lunar month combination  
247 were calculated. These data were standardised by the percentage contribution each size class  
248 made to the total number of *M. dalli* in each region in each lunar month and used to construct  
249 a shade plot. A white space for a size class indicates that no individuals were collected at that  
250 CL in a region/lunar month combination, and the depth of shading from grey to black is  
251 linearly proportional to the percentage contribution of that size class to the total catch in the  
252 region/lunar month combination (Clarke et al., 2014b).

253

#### 254 *Multivariate analyses*

255 The variation in composition of the fauna was investigated using multivariate analyses  
256 to determine whether the distribution and abundance of *M. dalli* were similar to those of  
257 potential competitors and predators. The densities of all species caught in the nearshore and  
258 offshore waters (i.e. *M. dalli* and other penaeid, stomatopod, brachyuran, teleost and  
259 scyphozoan species) were fourth-root transformed to balance the contributions of common  
260 and rare species, by down-weighting the contributions of taxa with high densities. The  
261 resultant data were used to construct separate Bray-Curtis resemblance matrices for the

262 nearshore and offshore waters, each of which was subjected to a three-way PERMANOVA.  
263 This test determined whether species composition differed among Year (2 levels; fixed),  
264 Lunar Month (26 levels; with 13 nested within each Year) and Subregion (8 or 9 levels;  
265 fixed) and whether any interactions between the main effects were significant. As all main  
266 effects and the interaction terms were significant ( $P = 0.001$ ) in both nearshore and offshore  
267 waters, the fourth-root transformed density of each species in each Subregion/Lunar  
268 Month/Year combination was averaged.

269 These transformed and averaged data were subjected to coherent species analysis  
270 (Somerfield and Clarke, 2013; Tweedley et al., 2015) to determine whether the spatial and  
271 temporal pattern of change in the abundance of *M. dalli* was statistically indistinguishable to  
272 any other species. Species occurring in less than 10 of the 1,040 (< 1%) and 832 (< 1.25%) of  
273 the total number of samples from the nearshore and offshore waters, respectively, were  
274 excluded from this analysis as they add only random noise to the species similarities (Clarke  
275 and Warwick, 2001; Veale et al., 2014). As *M. dalli* were virtually absent from the nearshore  
276 waters between April and September, lunar months falling within this period were removed  
277 from this analysis. The transformed and averaged species density data were used to construct  
278 Bray-Curtis resemblance matrices, which were, in turn, subjected to hierarchical  
279 agglomerative clustering with group-average linking (CLUSTER) and an associated  
280 Similarity Profiles (SIMPROF) test employing the type III SIMPROF permutation procedure  
281 (Somerfield and Clarke, 2013). Separate analyses were carried out for the nearshore and  
282 offshore waters.

283 The 'coherent species groups' were visualised by plotting the transformed densities of  
284 each species in each Subregion/Lunar Month/Year combination on a shade plot (Clarke et al.,  
285 2014b), with species placed in optimum serial order using the Bray-Curtis resemblance  
286 matrix, constrained by the cluster dendrogram (Clarke et al., 2014a). Thus, species (*y*-axis)  
287 are ordered according to their abundance across subregions and lunar months in each year,  
288 and species with statistically indistinguishable patterns of abundance are grouped together.  
289 Subregion/Lunar Month/Year combinations (*x* axis) were ordered from left to right with

290 increasing distance upstream in the estuary, and within each lunar month in chronological  
291 order from October 2013 to October 2015.

292

### 293 **3. Results**

#### 294 *3.1. Climatic and physico-chemical conditions*

295 Mean maximum air temperatures between January 2013 and December 2015 exhibited a  
296 sinusoidal trend, with the lowest values recorded in July of each year (~18 °C), increasing  
297 sequentially to a peak the following February (~34 °C; Fig. 2a). Total annual rainfall ranged  
298 from 704 mm in 2013 to 578 mm in 2015, with the majority of rain (72 – 86%) falling  
299 between May and September (Fig. 2a). In contrast, very little rainfall occurred during the  
300 austral summer, i.e. December, January and February (a total of 1.2 mm in 2013/14, and 29  
301 mm in 2014/15). Annual flows from the Swan and Canning rivers were markedly greater in  
302 2013 and 2014 (218 and 175 GL, respectively) than in 2015 (78 GL; Fig. 2b). The Swan  
303 River was responsible for between 77 and 86% of freshwater discharge into the Swan-  
304 Canning Estuary, with the majority of the flow occurring between July and October (82 –  
305 93%; Fig. 2b). Flows were greatly reduced between December and April, typically < 2 GL  
306 per month (Fig. 2b).

307 As with air temperature, the temperature of the water column in each region  
308 underwent a pronounced seasonal pattern. Surface water temperature typically ranged from  
309 ~15 °C in June/July to ~26 °C in January/February (Fig. 3a). Seasonal differences were  
310 greatest in the Upper Canning Estuary and lowest in Upper and Lower Melville Water and  
311 the Lower Canning Estuary. Temperatures in surface waters were almost always > 20 °C  
312 between October and April and < 20 °C during May-September (Fig. 3a). Temporal patterns  
313 in bottom water temperature mirrored those in the surface waters, but showed less variation,  
314 i.e. temperatures were typically greater in the offshore than nearshore waters in the colder  
315 months between May and September, and the converse applied in the warmer months  
316 between October and March (cf. Fig. 3a,b).

317 Surface salinity ranged from 1 in the Upper Canning Estuary during October 2014 to  
318 38.4 in that same region in March 2014 (Fig. 3c). With the exception of October 2013,  
319 salinities in Lower Melville Water were always  $> 20$ , whereas in all other regions they  
320 declined to  $\leq 10$  at certain times. Ranges in salinity varied markedly among the regions, from  
321 16 in Lower Melville Water to 36 in the Upper Canning Estuary. Within a lunar month,  
322 salinities were most similar across regions during summer (January-April), typically differing  
323 by  $< 5$ , but differed by as much as  $\sim 25$  in May and June 2014. The lowest bottom salinity was  
324 9.7 in the Middle Swan Estuary in October 2013, while the highest was 37.7 in the Lower  
325 Melville Water during March 2014 (Fig. 3d). Salinities in the bottom waters varied far less  
326 than the corresponding surface waters, e.g. bottom salinities in Lower Melville Water  
327 differed by only 7 over the two years. The stratification index exceeded 4 in most regions in  
328 October/November 2013, between May and October in 2014 and in August to October in  
329 2015 (Fig. 3e). The water column was most stratified in the Lower Canning and Lower and  
330 Upper Melville Water, and least stratified in the Middle Swan Estuary.

331 Dissolved oxygen concentrations in the surface waters in each region/lunar month  
332 combination always exceeded  $4 \text{ mg L}^{-1}$  (Fig. 3f). Although values were lower in the bottom  
333 waters, typically they also exceeded  $4 \text{ mg L}^{-1}$ . However, hypoxic conditions (i.e.  $< 2 \text{ mg L}^{-1}$ ;  
334 Tweedley et al., 2016b) were recorded in the Lower Canning Estuary in October/November  
335 2013 and August/September 2014, and in four lunar months between August 2014 and  
336 February 2015 in the Middle Swan Estuary (Fig. 3g).

337

### 338 **3.2 Density of *Metapenaeus dalli***

339 The mean density (prawns  $500 \text{ m}^{-2}$ ) of male and female *M. dalli* in the nearshore  
340 waters of the Swan-Canning Estuary varied markedly among lunar months, being  
341 substantially greater between October and February (1 – 5) than other months ( $< 1$ ), and few  
342 prawns were caught between May and July (Fig. 4a). This marked seasonal pattern was also  
343 present in all four regions of the system. Densities between October and February varied  
344 among regions, being greatest in the Lower Canning Estuary, followed by Upper Melville

345 Water and the Middle Swan Estuary (Fig. 4). Slightly greater densities were recorded during  
346 this time of year in 2014/15 than 2013/14. Substantial densities of *M. dalli* were caught in the  
347 nearshore waters over a longer period in 2014/15 than in the previous year, however,  
348 exhibiting a less pronounced peak in November/December than in 2013/14 (Fig. 4).

349 The seasonal pattern of *M. dalli* density was less pronounced in offshore than  
350 nearshore waters. Generally, densities increased from 0.6 in October 2013 to a peak of 27  
351 *M. dalli* 500 m<sup>-2</sup> in May 2014 before declining until March 2015, reaching a peak in May  
352 2015 (42 *M. dalli* 500 m<sup>-2</sup>) and subsequently declining again until October 2015 (Fig. 4b).  
353 Similar seasonal patterns were present in the Middle Swan Estuary and Lower Canning  
354 Estuary and, to a lesser extent, in Upper Melville Water. The first two regions recorded by far  
355 the greatest densities, with far fewer *M. dalli* recorded in Lower Melville Water (Fig. 4).

356 The mean densities of male and female *M. dalli* were very similar (Fig. 4), and were  
357 highly correlated in both the nearshore and offshore waters ( $r = 0.94$ ,  $n = 20$ ,  $p \leq 0.001$ ; and  $r$   
358  $= 0.92$ ,  $n = 16$ ,  $p \leq 0.001$ , respectively). Thus in all subsequent results, the abundances of  
359 males and females were combined.

360

### 361 **3.3. Spatial and temporal patterns of *Metapenaeus dalli* and relationship to physico-chemical** 362 **conditions**

363 Two-way PERMANOVA of the 2013/14 data detected a significant difference in the  
364 densities of *M. dalli* in nearshore waters of the Swan-Canning Estuary among lunar months  
365 and subregions, and the Lunar Month  $\times$  Subregion interaction was not significant (Table 1a).  
366 The majority of the variation in density was explained by Lunar Month (61%), with densities  
367 being significantly greater in December 2014 ( $\sim 5$  *M. dalli* 500 m<sup>-2</sup>, Fig. 4a), and, to a lesser  
368 extent, October and November of the same year, than between March and August 2015  
369 ( $< 0.25$  *M. dalli* 500 m<sup>-2</sup>; Appendix 1a). Densities in January and February 2015 were also  
370 typically greater than those recorded in May-July (Fig. 4a). Among subregions (which  
371 represented 18% of variation in density), the greatest densities were recorded in North



372 Melville and Perth Water and the Lower and Middle Canning Estuary and least in the  
373 Entrance Channel (Fig. 5b).

374 Densities of *M. dalli* in 2014/15 differed significantly among lunar months,  
375 subregions and the Lunar Month  $\times$  Subregion interaction, with the two main effects  
376 explaining the majority of the variation in the mean squares for density (Table 1b).  
377 Significantly greater densities were recorded between October 2014 and February 2015  
378 (i.e. austral spring and summer) and October 2015 than the lunar months between March and  
379 September 2015 (Appendix 1b; Fig. 5c). In 2014/15, the subregions with the highest mean  
380 densities of prawns were those in the middle of the Swan-Canning Estuary, i.e. Perth Water  
381 and the Lower Canning Estuary and, to a lesser extent, North Melville Water, South Melville  
382 Water, Middle Swan Estuary and the Middle Canning Estuary (Fig. 5d).

383 In the offshore waters, two-way PERMANOVA detected a significant difference in  
384 the densities of *M. dalli* among lunar months, subregions and their interaction in both  
385 2013/14 and 2014/15 (Appendix 2; Table 1c, d). In contrast to the nearshore waters, densities  
386 in 2013/14 were lowest during the austral spring and summer, i.e. September to February  
387 ( $< 10 M. dalli$  500 m<sup>-2</sup>) and significantly greater between March and July, with the highest  
388 values recorded in May, ( $\sim 27 M. dalli$  500 m<sup>-2</sup>, Fig. 5e). This seasonal trend was also present  
389 in 2014/15, albeit less marked, which is reflected by the reduction in the proportion of the  
390 variance explained by Lunar Month (21%) compared with 2013/2014 (53%; Table 1c, d). In  
391 both years, mean densities of *M. dalli* typically increased sequentially in an upstream  
392 direction, with the lowest values recorded in the Entrance Channel and highest in the Lower  
393 Canning Estuary and Middle Swan Estuary (Fig. 5f, h). Differences among subregions were  
394 more pronounced in 2014/15 than 2013/14.

395 Spearman's rank correlations demonstrated that the density of *M. dalli* in seven of the  
396 nine subregions in nearshore waters was positively correlated with surface water temperature  
397 ( $\rho = 0.45 - 0.67$ ; Table 2a). Significant and negative correlations were also detected for  
398 surface dissolved oxygen concentrations in four regions, while single, significant positive and

399 negative correlations were detected in the Middle Swan Estuary and South Melville Water  
400 subregions, respectively (Table 2a). Trends in the correlation between the density of *M. dalli*  
401 and environmental variables were less clear among lunar months. Density was negatively  
402 related to surface water temperature and salinity during February and March 2014, and for  
403 salinity, also in February 2015 (Table 2b). Density was positively correlated to either one or  
404 both of these physico-chemical variables in November and December 2014, January 2015,  
405 and also some lunar months between April and September of both years.

406 Surface and bottom water temperatures were negatively correlated to the density of  
407 *M. dalli* in five and four of the eight offshore subregions ( $\rho = -0.28 - -0.61$  and  $-0.35 - -0.64$ ,  
408 respectively), and positively correlated in Lower Melville Water ( $\rho = 0.50$  and  $0.59$ ,  
409 respectively; Table 2c). Surface salinity was positively correlated to density in Lower  
410 Melville Water, but both surface and bottom salinities exhibited the reverse trend with  
411 density in Perth Water. As with the nearshore waters, the patterns of correlations among lunar  
412 months were less clear than those among subregions. However, surface and bottom salinities,  
413 and to a lesser extent, surface and bottom dissolved oxygen concentrations, were negatively  
414 correlated with *M. dalli* density in most lunar months between October 2014 and October  
415 2015 (Table 2d).

416

### 417 **3.4 Spatio-temporal variation in size of *Metapenaeus dalli***

418 The mean carapace length (CL) of *M. dalli* in both nearshore and offshore waters  
419 combined increased progressively between October 2013 (~13 mm CL) and February 2014  
420 (~20 mm CL), before declining markedly the following lunar month to ~12 mm CL (Fig. 6).  
421 There was little change in mean CL between March and August 2014, after which CL rose  
422 rapidly to ~19 mm in November 2014 before declining to ~11 mm in April 2015 and staying  
423 relatively constant until October. The results of Kruskal-Wallis tests indicated that mean CL  
424 differed significantly among regions in 19 out of the 24 lunar months (Table 3; note this test  
425 was not done in October 2013 and December 2014, due to small sample sizes of *M. dalli*).  
426 Over the two years, a relatively consistent pattern in mean CL was present, with little

427 difference among regions, due to a similar range of individuals occurring in each region  
428 (Figs 6, 7) during the period of rapid growth, i.e. December/January in 2013/14 and  
429 November 2014. Following the decline in mean CL around March, however, mean CL was  
430 typically smaller in the Middle Swan Estuary and Upper Melville Water, due to larger  
431 proportions of *M. dalli* of ~10 mm CL and fewer ~18 mm CL (Figs 6, 7). In 2013/14, the  
432 decline in mean CL in all regions occurred during the same lunar month (March 2014),  
433 whereas in 2014/15, the mean CL decline was sequential among regions, starting in the  
434 Lower Canning Estuary in January, followed by the Middle Swan Estuary and Upper  
435 Melville Water in February, and finally in Lower Melville Water in March/April. Although  
436 mean CL declined first in the Lower Canning Estuary, it remained fairly consistent (~13 mm)  
437 between March and September and was significantly greater than that recorded in both the  
438 Middle Swan Estuary and Upper Melville Water during that period (~11 mm; Fig. 6). During  
439 these lunar months, the Lower Canning Estuary contained a greater proportion of *M. dalli*  
440 > 17 mm CL and a far lower proportion of prawns < 10 mm CL than the other regions (Fig.  
441 7).

442

### 443 3.5 Coherent species groups

444 Coherent species analysis of the fauna present in nearshore waters found that the 24  
445 species (occurring in  $\geq 10$  samples) constituted eight groups and six outliers containing single  
446 species (Fig. 8). A clear serial pattern of progression in species composition was present, with  
447 species segregating themselves along the linear axis of the estuary during the summer  
448 months. *Metapenaeus dalli* had a statistically similar spatial and temporal pattern of  
449 distribution and abundance to the apogonid *Ostorhinchus rueppellii*, with these two species  
450 consistently occurring in moderate densities in most subregions, except the Entrance Channel  
451 and South Melville Water (Fig. 8). The next most similar species to *M. dalli* and *O. rueppellii*  
452 was the atherinid *Atherinomorus vaigiensis*, which covered the same spatial extent of the  
453 estuary, but was caught less consistently. The distributions of two scyphozoans, *Aurelia*  
454 *aurita* and *Phyllorhiza punctata*, also overlapped with that of *M. dalli*, in the subregions  
455 upstream of Melville Water during some lunar months. Other large crustaceans, i.e. the

456 penaeid *P. latisulcatus* and brachyuran *Portunus armatus*, were restricted to the most  
457 downstream subregions, mainly the Entrance Channel (Fig. 8) and showed little overlap with  
458 the distribution of *M. dalli*.

459 In the offshore waters, the 27 species occurring in  $\geq 10$  samples formed eight groups  
460 and four outliers (Fig. 9). As in the nearshore waters, the distribution of species occurred  
461 along a continuum from downstream to upstream, with some species occurring in a limited  
462 suite of subregions, and others such as *M. dalli* occurring throughout the entire area. The  
463 spatial pattern of distribution and abundance of *M. dalli* was statistically indistinguishable  
464 from that of *O. rueppellii* and similar, albeit not significantly, to the scyphozoans *P. punctata*  
465 and *A. aurita*. The lack of a significant match in patterns between these two scyphozoans and  
466 *M. dalli* in deeper waters was likely due to their occurrence in particular lunar months only  
467 (Fig. 9). Although the distribution of *P. latisulcatus* and *P. armatus* extended further  
468 upstream in the offshore than nearshore waters, they had a far more restricted spatial range  
469 than *M. dalli*.

470

#### 471 **4. Discussion**

472 Extensive sampling in nearshore and offshore waters identified major temporal and spatial  
473 patterns of variation in the density and size composition of *Metapenaeus dalli*, a short-lived  
474 penaeid (< 2 years) with tropical affinities, in the temperate Swan-Canning Estuary located  
475 towards the southern limit of its geographic distribution. Monthly densities differed markedly  
476 between nearshore and offshore waters and among areas of the estuary reflecting changes in  
477 physico-chemical variables, particularly water temperature. Furthermore, the spatial and  
478 temporal distribution of *M. dalli* in this estuary closely matched those of the teleost  
479 *Ostorhinchus rueppellii* and two scyphozoans (*Aurelia aurita* and *Phyllorhiza punctata*) that  
480 are either known to, or likely, predate on *M. dalli*, but had minimal overlap with other  
481 abundant crustaceans (*Penaeus latisulcatus* and *Portunus armatus*) that are potential  
482 competitors. These findings highlight the partitioning of species within the estuary and the

483 significance of site selection in maximising the survival of hatchery-reared *M. dalli* produced  
484 by aquaculture-based enhancement programs.

485

#### 486 **4.1. Spatial and temporal patterns of abundance and distribution of *Metapenaeus dalli***

487 Densities of *M. dalli* in the nearshore waters of the Swan-Canning Estuary changed  
488 markedly throughout each year, with the greatest values recorded in the late austral spring  
489 and summer months (October to February) and very few to no individuals recorded between  
490 late autumn and winter (May to July). Spearman's rank correlations showed a positive  
491 relationship between density and surface water temperature in the nearshore waters of all nine  
492 subregions, and were significant in seven of the nine. This reflects the movement of adult  
493 prawns from deeper, offshore waters into the shallow, nearshore waters for breeding during  
494 the summer, when water temperatures exceed ~20 °C (Broadley et al., 2017; Crisp et al.,  
495 2018). Densities in nearshore waters during the October to February period varied between  
496 regions, with highest densities recorded in the Lower Canning Estuary, followed by Upper  
497 Melville Water and Middle Swan Estuary regions, with very few *M. dalli* recorded in the  
498 Entrance Channel. Within these months, inter-regional differences in abundance were rarely  
499 significantly related to either water temperature or salinity, suggesting that the selection of  
500 these nearshore regions of the estuary for spawning may be due to other factors.

501 In microtidal estuaries in Mediterranean climates, the physico-chemical environment  
502 is relatively stable in the summer and autumn, due to a lack of rainfall and fluvial discharge  
503 (Tweedley et al., 2016a), thus providing a conducive environment for the spawning, retention  
504 and survival of eggs/larvae, which is crucial for solely estuarine species e.g. *M. dalli* in south-  
505 western Australia (Potter et al., 2015a; 2015b). Moreover, as *M. dalli* has tropical affinities,  
506 and the Swan-Canning Estuary is located towards the southern limit of its distribution (Grey  
507 et al., 1983), the movement into nearshore waters to breed when temperatures are highest is  
508 likely result in faster growth, facilitating the attainment of sexual maturity and also providing  
509 a suitable environment for larvae (Crisp et al., 2018). It is thus relevant that while penaeids in  
510 tropical environments spawn throughout the year, those in temperate regions spawn during

511 summer (cf. Crocos et al., 2001; Cha et al., 2002). Moreover, Crisp et al. (2017b) determined  
512 that the best conditions for the cultivation of *M. dalli* larvae, were temperatures of 26–30 °C  
513 and a salinity of ~35, i.e. those occurring in the Swan-Canning Estuary during summer  
514 (Fig. 3).

515 In contrast to the nearshore waters, densities of *M. dalli* in the offshore waters were  
516 greatest from autumn to winter (i.e. March to July, peaking in May), and generally lower  
517 throughout the rest of the year. This is due to (i) the recruitment of 0+ individuals that were  
518 spawned in October-March and which have grown to reach a size where they are able to be  
519 caught in the otter trawl (Broadley et al., 2017; Crisp et al., 2018), and (ii) the movement of  
520 1+ individuals from the nearshore waters back into the offshore areas. This conclusion is  
521 supported by the carapace length (CL) distributions for *M. dalli* (Fig. 7; supplementary  
522 figure), which show that over the winter months, the larger individuals (> 18 mm CL), which  
523 are close to or at the size at maturity (~19 mm CL), are recorded in offshore waters and are  
524 virtually absent from the nearshore waters (Fig. 4a, b). This onshore/offshore migratory  
525 pattern in *M. dalli* in the Swan-Canning Estuary was also recorded by Potter et al. (1986), 30  
526 years prior to our study. Moreover, this mirrors the movements of *Metapenaeus endeavouri*  
527 and *Metapenaeus ensis* in Albatross Bay, Gulf of Carpentaria, Australia, with mature females  
528 moving to depths > 40 m in May and July, respectively, and returning to shallower waters  
529 (< 35 m) during their spawning season, i.e. August to October for *M. endeavouri*, and  
530 September to December for *M. ensis* (Crocos et al., 2001).

531 Densities of *M. dalli* in offshore waters were negatively correlated with water  
532 temperature in most regions of the estuary, which is due to these densities being greatest in  
533 the months following recruitment of 0+ individuals (May-August), when water temperatures  
534 are coolest. Among regions, densities of *M. dalli* in the offshore waters were greatest  
535 upstream, in the Middle Swan Estuary and Lower Canning Estuary, that were, in general, less  
536 saline than the other regions. This could be due to spatial partitioning of the system, with the  
537 larger *P. latisulcatus* preferring marine salinities and thus occurring in the regions further  
538 downstream (i.e. the Entrance Channel and Lower Melville Water). This inverse correlation

539 of prawn density with temperature is the opposite of that recorded for another tropical  
540 penaeid at the southern-limit of their distribution, namely *Penaeus esculentus* in Moreton  
541 Bay, Queensland (Kienzle and Sterling, 2016).

542 Although dissolved oxygen concentrations were correlated with the abundance of  
543 *M. dalli*, these are not indicative of a causal relationship, as conditions in the system were  
544 usually normoxic, i.e. dissolved oxygen  $>4 \text{ mg L}^{-1}$ . For example, of the 416 spot  
545 measurements of dissolved oxygen concentrations at the bottom of the water column,  
546 hypoxia (i.e.  $<2 \text{ mg L}^{-1}$ ) and anoxia (i.e.  $<0.5 \text{ mg L}^{-1}$ ) were detected 47 and 21 times,  
547 respectively. Typically, hypoxic conditions occurred in the Middle Swan Estuary and Lower  
548 Canning Estuary regions (Fig. 3g), and during these times, densities of *M. dalli* in the  
549 offshore waters were reduced or zero (Poh, Murdoch University, unpublished data). In  
550 contrast, larger than 'normal' densities of *M. dalli* were recorded in the corresponding  
551 normoxic nearshore waters, where the lowest dissolved oxygen concentration recorded in  
552 measurements was  $4.6 \text{ mg L}^{-1}$  (J. Tweedley, Murdoch University, unpublished data). This  
553 suggests that an onshore movement of *M. dalli* occurs as a mechanism to avoid of areas of  
554 low dissolved oxygen concentrations. Mobile crustaceans are able to detect low oxygen and  
555 avoid areas of hypoxia (Burnett and Stickle, 2001; Wu et al., 2002) and these species are  
556 often not recorded in faunal communities under hypoxic conditions (McAllen et al., 2009;  
557 Tweedley et al., 2016b).

558

#### 559 **4.2. Spatial and temporal patterns in the size of *Metapenaeus dalli***

560 Mean CLs differed throughout the year, reaching a maximum between January and  
561 February in 2013/14, and between November and February in 2014/15, due to the growth of  
562 individuals spawned the previous breeding season once water temperatures increase  
563 (Broadley et al., 2017). The appearance of larger *M. dalli* earlier, and for longer during the  
564 breeding season in 2014/15 than 2013/14, corresponded with much lower freshwater  
565 discharge in 2014/15 than the previous year, and higher than average temperatures in August  
566 and September of 2014 than in 2013 (Fig. 2). This earlier warm weather provides conditions

567 conducive for faster growth (see Fig. 5), and *M. dalli* reached the size-at-maturity (19 mm  
568 CL) sooner in 2014/15 than 2013/14 (Broadley et al., 2017; Crisp et al., 2018). This pattern  
569 of highly seasonal growth of *M. dalli* was reported in this estuary 30 years earlier (Potter et  
570 al., 1986) and also in the Peel-Harvey Estuary, 80 km further south of the Swan-Canning  
571 (Potter et al., 1989).

572 In both 2013/2014 and 2014/2015, mean CLs had declined greatly by April, largely  
573 due to the recruitment of the new cohort that were spawned early in the season (~9 – 13 mm  
574 CL), as well as the loss of the 1+ year males (~17 – 20 mm) and females (~24 – 30 mm)  
575 through natural post-spawning mortality and fishing pressure (Broadley et al., 2017). In  
576 2013/14, the mean CLs rapidly declined from February to March in all regions, whereas in  
577 2014/15, mean CLs declined initially in the Lower Canning, but the overall decline was not  
578 as great in the other regions. This reflects the fact that the earliest recruitment occurs in the  
579 Lower Canning region, so mean CLs remain slightly higher in this region as the early recruits  
580 utilise the remaining warm weather to grow in size. In contrast, the Middle Swan experienced  
581 slower declines in mean CLs, and reached a minimum size much later than in all other  
582 regions. This reflects the delayed breeding occurring in this region, as is shown by the delay  
583 in recruitment compared to the Lower Canning (Fig. 4h, j). Carapace lengths changed little  
584 throughout the winter months, indicating the minimal growth over this period as found by  
585 Broadley et al. (2017). Growth resumed in August/September as water temperatures rises.

586

#### 587 **4.3. Patterns of distribution of *Metapenaeus dalli* and other fauna**

588 The spatial and temporal pattern of *M. dalli* distribution in the nearshore waters of the  
589 Swan-Canning Estuary between October and March was statistically indistinguishable from  
590 that of the apogonid *O. rueppellii* and similar to those of the atherinid *Atherinomorus*  
591 *vaigiensis* and the scyphozoan *A. aurita*. Typically, the individuals of *M. dalli* present in  
592 these waters during this time are sexually mature adults (Potter et al., 1986; Broadley et al.,  
593 2017) and, due to their relatively large size and tail-flip response (Arnott et al., 1998; Guerin  
594 and Neil, 2015), are probably able to avoid predation by small-bodied teleosts and the



595 nematocysts of scyphozoans. However, larval and postlarval *M. dalli* would be extremely  
596 susceptible to predation by these species. In particular, *O. rueppellii* has been identified as the  
597 main teleost predator of *M. dalli* postlarvae (~3 mm total length), accounting for 68% of the  
598 total predation immediately after hatchery-reared larvae were released into the Swan-Canning  
599 Estuary (Poh et al., 2018). This apogonid is a voracious predator, with 300 postlarval *M. dalli*  
600 found in the stomach of one 45 mm *O. rueppellii*. Moreover, in the two hours after the release  
601 of 130,000 postlarvae over a nearshore seagrass meadow in the Swan-Canning Estuary at  
602 night, it was estimated that *O. rueppellii* consumed  $\approx 2,000$  postlarvae  $100 \text{ m}^{-2}$  (Poh et al.,  
603 2018) Additionally, 31% of the predation on the hatchery-reared postlarvae was attributed to  
604 *A. vaigiensis*. Thus, as the distribution of *M. dalli* overlaps with those of these two teleost  
605 species, the postlarvae and small juveniles of *M. dalli* do not have a spatial or temporal refuge  
606 from the two main teleost predators responsible for 99% of their total predation.

607         The similar patterns of abundance and distribution of *M. dalli* and the scyphozoans  
608 *A. aurita* and *P. punctata* in the nearshore waters during the summer are also likely to have a  
609 negative effect on the larval stages of *M. dalli*. Jellyfish can be voracious predators, with  
610 evidence these scyphozoans can influence mesozooplankton communities (Schneider and  
611 Behrends, 1998; Gueroun et al., 2015). Little is known about the feeding habits of these two  
612 jellyfish in the Swan-Canning Estuary, although some information suggests that their ephyral  
613 and small medusa stages predate on rotifers and copepod nauplii, with the rate increasing  
614 with size (Jafri, 1997). Moreover, scyphozoans have been implicated in the decline of  
615 penaeids in both wild fisheries and aquaculture operations (Purcell et al., 2007). The rates of  
616 *P. punctata* predation on rotifers and copepods were 18 and 22 prey predator<sup>-1</sup> hr<sup>-1</sup>,  
617 respectively (Purcell et al., 2007). Stoecker et al. (1987) also found that *A. aurita* selected for  
618 large metazoan micro-zooplankton as a key prey item in their diet. This included copepod  
619 nauplii, which at ~50 – 800  $\mu\text{m}$ , are similar in size to the nauplii of *M. dalli* at ~300  $\mu\text{m}$   
620 (Crisp et al., 2016). Because the nauplius, protozoal and mysis stages of *M. dalli* are pelagic  
621 (Crisp et al., 2016) and relatively poor swimmers, they would be vulnerable to these  
622 scyphozoans (Costello and Collin, 1995; Ruppert and Barnes, 1994).

623 While smaller *M. dalli* are susceptible to predation by small-bodied teleosts and  
624 scyphozoans, those prawns spawned late in the breeding season (e.g. February and March)  
625 would be most at risk of prolonged predation, because they would be smaller for a longer  
626 period of time due to the cooling water temperatures and slowed winter growth of *M. dalli*  
627 (Broadley et al., 2017).

628 The second-most abundant penaeid species in the Swan-Canning Estuary,  
629 *P. latisulcatus*, which spawns in the marine environment, was not recorded in salinities below  
630 26 and appears to be restricted to the lower reaches of the system where salinities remain  
631 close to those of seawater. In contrast, *M. dalli* was found throughout the entire range of the  
632 estuary sampled, including in salinities as low as 0.9 and 3.8 in nearshore and offshore  
633 waters, respectively. This is similar to the nearby Peel-Harvey Estuary where the abundance  
634 of *P. latisulcatus* is positively correlated with salinity and negatively correlated with distance  
635 from the estuary mouth, whereas *M. dalli* occurred further upstream (Potter et al., 1989;  
636 Potter et al., 1991). The trends in both these estuaries indicate that *M. dalli* are much more  
637 euryhaline than *P. latisulcatus*. Our findings of spatial separation between these two species  
638 parallel the distribution patterns of *Metapenaeus macleayi* and *Penaeus plebejus*, two marine  
639 spawning prawns in the lower Hunter River estuary of eastern Australia, where juvenile  
640 *M. macleayi* extend into upstream areas with variable salinities, while *P. plebejus* are  
641 restricted to the lower estuary (Taylor et al., 2016; 2017). It was suggested that this divergent  
642 pattern was related to salinity tolerance, with *M. macleayi* being more euryhaline than  
643 *P. plebejus*, which is relatively stenohaline and halophilic (Ruello, 1973; Taylor et al., 2016).  
644 The minimal overlap in the distributions of *M. dalli* and *P. latisulcatus* is a mechanism that  
645 reduces their potential competition (Ross, 1986).

646

#### 647 **4.4. Implications for aquaculture-based enhancement**

648 This study, which was conducted over a 26-month period, encompassing two annual  
649 breeding periods and multiple cohorts of this short-lived species, has identified the times and  
650 locations where densities of *M. dalli* are greatest in nearshore and offshore waters of the

651 Swan-Canning Estuary. These data can be used to facilitate the collection of broodstock (i.e.  
652 gravid females), which, in turn, can be used to produce hatchery-reared prawns (Jenkins et  
653 al., 2017) for aquaculture-based-enhancement. Moreover, as penaeids spawn in areas most  
654 suitable for the survival of their larvae (Preston, 1985), the identification of these locations  
655 and measurement of their physico-chemical characteristics can be used to develop a sound  
656 release strategy to maximise the survival of the hatchery-reared postlarvae, which are more  
657 sensitive to environmental conditions than larger more-developed individuals. Examination  
658 of the changes in mean CL demonstrated that prawns grew little over the cooler winter  
659 months in either year and thus any release of cultured *M. dalli* should occur early in the  
660 breeding season so the larvae can take advantage of the warmer water and grow more rapidly,  
661 making them less susceptible to predation. Having identified key predator species (see Poh et  
662 al., 2018), coherent species analyses showed that, at a regional level, the spatial and temporal  
663 distribution of *M. dalli* was similar to key teleost (*O. rueppellii* and *A. vaigiensis*) and  
664 scyphozoan predators (*A. aurita* and *P. punctata*). Thus, there is a need to investigate finer-  
665 scale habitat preferences for these species, e.g. sediment and presence of macrophytes, to  
666 determine if releases of *M. dalli* should occur in a particular habitat to maximise the survival  
667 of hatchery-reared individuals. These results demonstrate the value in understanding the  
668 biology and ecology of the target species in the context of the release environment and using  
669 an integrated approach for aquaculture-based enhancement programs (see also Zohar et al.,  
670 2008; Lorenzen, 2010).

671

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680

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## Figure Captions

**Fig. 1.** Map showing (a) the distribution of *Metapenaeus dalli* in inshore marine waters (light grey) and solely in estuaries (dark grey) in Australia and (b) 20 nearshore and 16 offshore sites in Swan-Canning Estuary sampled over 26 consecutive lunar cycles between October 2013 and October 2015. Dotted lines denote the separation among the five broad regions (bold face) of the estuary. Codes for regions and subregions are given in square brackets.

**Fig. 2.** Monthly (a) total rainfall (mm, histogram) and average maximum air temperature (°C, line) for Perth and (b) freshwater discharge volumes (GL) into the Swan-Canning Estuary from the Swan and Canning rivers between January 2013 and December 2015. Climate and flow data obtained from the Bureau of Meteorology (<http://www.bom.gov.au/climate/data/>) and the Department of Water and Environmental Regulation (<http://wir.water.wa.gov.au/Pages/Water-Information-Reporting.aspx>), respectively. Horizontal line denotes the months in which sampling for *Metapenaeus dalli* occurred (i.e. October 2013 to October 2015).

**Fig. 3.** Mean values for (a) surface and (b) bottom water temperatures, (c) surface and (d) bottom salinities, (e) indices of stratification and (f) surface and (g) bottom dissolved oxygen concentrations recorded in each of the five regions of the Swan-Canning Estuary in each lunar month between October 2013 and October 2015. Note two lunar months occurred in the calendar month of January 2014.

**Fig. 4.** Mean densities ( $500\text{ m}^{-2}$ ) of male and female *Metapenaeus dalli* in the (a, c, e, g, i, k) nearshore and (b, d, f, h, j) offshore waters of the Swan-Canning Estuary each lunar month between October 2013 and October 2015 for the system as a whole and for each region separately. (a, b) total estuary, (c, d) Lower and (e, f) Upper Melville Water, (g, h) Middle Swan Estuary and (i, j) Lower and (k) Upper Canning Estuary. Note no offshore data for Upper Canning Estuary for the entire sampling period due to shallow depths and limited data from offshore sites in December 2014 due to a boat malfunction. Note two lunar months occurred in the calendar month of January 2014.

**Fig. 5.** Mean and 95% confidence limits of the densities of *Metapenaeus dalli* among (a, c) lunar months and (b, d) subregions in the nearshore waters of the Swan-Canning Estuary 2013/14 and 2014/15, respectively and in (e, g) lunar months and (f, h) subregions in the offshore waters of the Swan-Canning Estuary 2013/14 and 2014/15, respectively. Subregion codes given in Figure 1. Note two lunar months occurred in the calendar month of January 2014.

**Fig. 6.** Mean carapace lengths of *Metapenaeus dalli* caught in the nearshore and offshore waters of each region of the Swan-Canning Estuary in each lunar month between October 2013 and October 2015. Data for December 2014 not shown due to a boat malfunction. Note two lunar months occurred in the calendar month of January 2014.

**Fig. 7.** Shade plot showing the square-root transformed proportion of *Metapenaeus dalli* in each 1 mm carapace length size class in each region of the Swan-Canning Estuary in January, April, July and October of 2014 and 2015. White areas denote the absence of a size class from a region/lunar month combination and the shading from grey to black the increasing

proportions of that size class. A version of the shade plot showing each of the 26 lunar months is given in the supplementary figure.

**Fig. 8.** Shade plot showing the fourth-root transformed densities ( $500 \text{ m}^{-2}$ ) of each penaeid, brachyuran, teleost and scyphozoan species found in each subregion and each lunar month between October and March of 2013/14 and 2014/15 in the nearshore waters of the Swan-Canning Estuary. Dendrogram on y-axis derived by subjecting a Bray-Curtis resemblance matrix constructed from the fourth-root transformed density of each species to CLUSTER-SIMPROF. Coherent groups of species, i.e. those with statistically indistinguishable patterns of abundance across the Subregion/Lunar Month/Year combinations and are significantly different from those in all other groups, are denoted by the dashed grey lines. Full species names given in supplementary table.

**Fig. 9.** Shade plot showing the fourth-root transformed densities ( $500 \text{ m}^{-2}$ ) of each penaeid, stomatopod, brachyuran, teleost and scyphozoan species found in each subregion and each lunar month between October 2013 and October 2015 in the offshore waters of the Swan-Canning Estuary. Dendrogram on y-axis derived by subjecting a Bray-Curtis resemblance matrix constructed from the fourth-root transformed density of each species to CLUSTER-SIMPROF. Coherent groups of species, i.e. those with statistically indistinguishable patterns of abundance across the Subregion/Lunar Month/Year combinations and are significantly different from those in all other groups, are denoted by the dashed grey lines. Full species names given in supplementary table.

**Table 1.** Mean squares (MS), percentage mean squares (%MS), *pseudo-f* (*pf*) and significance values (*p*) from two-way PERMANOVA tests on the density of *Metapenaeus dalli* per 500 m<sup>2</sup> among lunar months and subregions in the Swan-Canning Estuary between October 2013 and 2015. Significant differences ( $P < 0.05$ ) highlighted in bold. Grey shading denotes factors that were particularly influential (i.e. %MS > 25).

<b>Water depth and Year</b>	<i>df</i>	MS	%MS	<i>pf</i>	<i>p</i>
<b>Nearshore</b>					
<b>(a) 2013/14</b>					
Lunar Month	12	<b>101.21</b>	<b>61.11</b>	<b>6.652</b>	<b>0.001</b>
Subregion	8	<b>29.93</b>	<b>18.07</b>	<b>1.97</b>	<b>0.035</b>
Lunar Month × Subregion	96	19.27	11.63	1.27	0.085
Residual	403	15.22	9.19		
<b>(b) 2014/15</b>					
Lunar Month	12	<b>88.72</b>	<b>36.14</b>	<b>3.79</b>	<b>0.001</b>
Subregion	8	<b>89.22</b>	<b>36.35</b>	<b>3.81</b>	<b>0.001</b>
Lunar Month × Subregion	96	<b>44.12</b>	<b>17.97</b>	<b>1.89</b>	<b>0.002</b>
Residual	403	23.40	9.53		
<b>Offshore</b>					
<b>(c) 2013/14</b>					
Lunar Month	12	<b>33.56</b>	<b>52.80</b>	<b>9.58</b>	<b>0.001</b>
Subregion	7	<b>19.88</b>	<b>31.28</b>	<b>5.68</b>	<b>0.001</b>
Lunar Month × Subregion	84	<b>6.616</b>	<b>10.41</b>	<b>1.89</b>	<b>0.001</b>
Residual	312	3.502	5.51		
<b>(d) 2014/15</b>					
Lunar Month	12	<b>41.92</b>	<b>20.75</b>	<b>13.28</b>	<b>0.001</b>
Subregion	7	<b>145.87</b>	<b>72.21</b>	<b>46.22</b>	<b>0.001</b>
Lunar Month × Subregion	84	<b>11.06</b>	<b>5.47</b>	<b>3.50</b>	<b>0.001</b>
Residual	312	3.16	1.56		

**Table 2.** Rho ( $\rho$ ) values from Spearman ranked correlations between the density of *Metapenaeus dalli* (500 m<sup>-2</sup>) and various water physico-chemical variables among (a, c) regions and (b, d) lunar months in the nearshore and offshore waters of the Swan-Canning Estuary, respectively. Significant differences ( $p \leq 0.05$ ) highlighted in dark grey and those differences where  $p \leq 0.10$  in light grey. Subregion codes given in Figure 1. S, surface; B, bottom; Temp, water temperature; DO, dissolved oxygen concentration; Sal, salinity. Note two lunar months occurred in the calendar month of January 2014.

(a) Nearshore									
	EC	NM	SM	PW	MS	LC	MC	UC	CA
S. Temp.	0.03	0.64	0.18	0.66	0.55	0.53	0.67	0.45	0.56
S. Sal.	-0.13	-0.02	-0.33	0.11	0.40	-0.06	0.12	0.04	0.26
S. DO	-0.08	-0.38	0.03	-0.34	-0.21	-0.30	-0.56	-0.51	-0.11

(b) Nearshore																										
	2013								2014								2015									
	O	N	D	J1	J2	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O
S. Temp.	0.03	-0.23	0.45	-0.13	0.15	-0.56	-0.67	-0.44	No catch	-0.14	No catch	-0.02	-0.56	-0.10	-0.02	0.55	0.75	-0.08	0.20	0.53	-0.28	0.14	0.55	-0.18	0.02	0.56
S. Sal.	-0.14	0.45	-0.35	0.09	-0.11	-0.70	-0.69	0.06	No catch	0.14	No catch	0.53	0.65	0.13	0.53	-0.13	-0.35	-0.54	0.26	-0.01	-0.14	-0.41	0.55	0.13	0.51	-0.09
S. DO	0.66	0.39	0.10	-0.51	-0.33	-0.56	0.37	0.09		0.55		0.64	0.45	0.13	0.64	0.08	0.13	-0.54	-0.15	-0.15	0.14	0.00	0.00	-0.28	0.83	0.03

(c) Offshore								
	EC	LM	MB	UM	PW	MS	LC	MC
S. Temp.	0.23	0.50	-0.39	-0.28	-0.61	-0.59	-0.52	-0.13
S. Sal.	-0.10	0.47	-0.07	0.23	-0.46	0.10	0.08	0.26
S. DO	0.02	-0.35	0.19	-0.08	0.55	0.38	0.07	-0.15
B. Temp.	0.26	0.59	-0.35	-0.25	-0.64	-0.59	-0.47	-0.13
B. Sal.	-0.13	0.27	-0.18	0.27	-0.45	0.31	0.20	0.22
B. DO	0.00	-0.13	0.35	0.20	-0.19	-0.13	0.31	0.03
Strat.	0.10	-0.28	-0.03	-0.27	0.28	0.28	-0.07	-0.38

(d) Offshore																										
	2013								2014								2015									
	O	N	D	J1	J2	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O
S. Temp.	-0.69	-0.05	-0.14	-0.45	-0.21	-0.42	0.12	0.00	-0.64	-0.35	-0.31	0.31	0.02	0.74	0.69	Limited data	0.48	-0.90	0.37	0.38	0.20	-0.35	0.31	0.22	0.30	0.47
S. Sal.	0.34	0.05	0.95	0.65	0.07	0.06	0.14	0.14	-0.81	-0.61	-0.12	0.21	-0.69	-0.93	-0.69	Limited data	-0.60	-0.71	-0.54	-0.86	-0.60	-0.73	-0.88	-0.71	-0.59	-0.26
S. DO	0.07	0.00	-0.18	0.16	0.07	0.47	-0.29	0.36	0.52	-0.35	0.60	-0.05	-0.38	0.07	-0.69	Limited data	-0.14	0.00	-0.06	0.19	-0.72	-0.91	-0.59	-0.64	-0.19	-0.78
B. Temp.	-0.49	0.33	-0.14	-0.60	-0.29	-0.47	0.29	-0.02	-0.55	-0.92	-0.32	0.45	-0.08	0.52	0.71	Limited data	0.76	-0.57	0.24	0.36	0.41	-0.16	0.50	0.60	0.84	0.55
B. Sal.	0.34	-0.10	0.10	0.65	0.24	0.06	0.26	0.19	-0.71	-0.42	-0.12	-0.10	-0.57	-0.76	-0.69	Limited data	-0.62	-0.52	-0.71	-0.81	-0.69	-0.61	-0.91	-0.45	-0.70	-0.22
B. DO	0.36	0.10	0.19	0.93	-0.57	0.20	-0.21	-0.49	-0.45	-0.06	-0.12	0.07	-0.38	-0.95	-0.48	Limited data	-0.19	-0.67	-0.73	-0.69	-0.74	-0.76	-0.74	-0.62	-0.05	-0.78
Strat.	0.13	-0.76	-0.07	-0.48	-0.28	-0.11	-0.26	0.17	-0.91	0.28	0.00	-0.60	-0.52	0.10	-0.86	Limited data	0.19	0.19	-0.41	0.76	0.07	0.71	-0.10	0.02	0.16	0.26

**Table 3.** Overall and pairwise  $p$  values derived from Kruskal-Wallis tests on the carapace length of *Metapenaeus dalli* in four regions of the Swan-Canning Estuary in each lunar month between October 2013 and October 2015. Significant differences are shaded in light grey. NT = no test completed as  $< 30$  individuals caught in a region and Lunar Month/Year combination. LM, Lower Melville Water; UM, Upper Melville Water; MS, Middle Swan Estuary; LC, Lower Canning Estuary; UC, Upper Canning Estuary. Note two lunar months occurred in the calendar month of January 2014.

Lunar month Year	Month	Overall	Pairwise					
			LC-UM	LC-MS	LC-LM	UM-MS	UM-LM	MS-LM
2013	O	NT	NT	NT	NT	NT	NT	NT
	N	0.001	1.000	0.021	0.002	0.172	0.019	1.000
	D	0.270						
	J1	0.406						
	J2	0.095						
	F	0.004	1.000	1.000	1.000	0.854	0.002	1.000
2014	M	0.001	0.124	0.062	1.000	1.000	0.017	0.009
	A	<0.001	<0.001	<0.001	0.008	0.001	1.000	0.001
	M	<0.001	<0.001	<0.001	0.017	1.000	0.064	0.131
	J	0.003	0.504	0.002	0.360	0.130	1.000	1.000
	J	<0.001	<0.001	<0.001	NT	0.028	NT	NT
	A	0.008	NT	NT	NT	0.045	0.011	1.000
	S	0.215						
	O	<0.001	0.297	0.070	0.010	1.000	<0.001	<0.001
	N	0.480	NT	1.000	0.061	NT	NT	0.088
	J	<0.001	<0.001	0.004	NT	0.027	NT	NT
2015	F	<0.001	0.002	0.001	<0.001	1.000	0.002	0.014
	M	<0.001	<0.001	NT	<0.001	NT	<0.001	NT
	A	<0.001	<0.001	<0.001	NT	<0.001	NT	NT
	M	<0.001	0.002	<0.001	NT	0.036	NT	NT
	J	<0.001	<0.001	<0.001	NT	0.032	NT	NT
	J	<0.001	0.018	<0.001	NT	0.117	NT	NT
	A	<0.001	0.006	<0.001	NT	0.001	NT	NT
	S	<0.001	<0.001	<0.001	NT	0.565	NT	NT
	O	<0.001	NT	<0.001	NT	NT	NT	NT

**Highlights**

1. *Metapenaeus dalli* population in a temperate estuary surveyed monthly for two years
2. Densities greatest in shallows in spring and summer as temperatures increase
3. Offshore densities greater in autumn and winter following recruitment
4. *M. dalli* densities greatest in middle estuary, overlapping with key predators
5. Distribution of *M. dalli* differed from two other large marine crustaceans

**Appendix 1.** *t*-values derived from pairwise PERMANOVA tests on the densities of *Metapenaeus dalli* 500 m<sup>-2</sup> in nearshore waters on the Swan-Canning Estuary among lunar months in (a) 2013/14, (b) 2014/15 and (c) subregions in 2014/15. Significant differences highlighted in grey. Subregion codes given in Figure 1. Note two lunar months occurred in the calendar month of January 2014.

(a) Lunar month		2013					2014						
2013/14		O	N	D	J1	J2	F	M	A	M	J	J	A
2013	N	1.55											
	D	4.55	0.62										
	J1	0.17	1.57	4.26									
	J2	0.31	1.63	4.65	0.08								
	F	0.11	1.56	4.33	0.06	0.15							
2014	M	2.10	1.98	5.70	1.19	1.54	1.40						
	A	2.57	2.05	5.89	1.46	1.94	1.70	0.88					
	M	3.12	2.14	6.11	1.78	2.42	2.06	2.31	2.10				
	J	2.92	2.10	6.03	1.65	2.24	1.92	1.75	1.18	2.23			
	J	3.12	2.14	6.11	1.78	2.42	2.06	2.31	2.10	0.00	2.23		
	A	2.10	2.00	5.69	1.25	1.58	1.45	0.22	0.41	1.34	0.97	1.34	
	S	0.58	1.69	4.89	0.25	0.22	0.35	1.52	2.02	2.62	2.39	2.62	1.55

(b) Lunar month		2014					2015						
2014/15		O	N	D	J	F	M	A	M	J	J	A	S
2014	N	0.55											
	D	0.61	0.79										
	J	2.65	1.45	2.46									
	F	1.54	1.13	1.07	1.37								
	M	3.11	1.68	2.98	1.18	2.07							
2015	A	3.95	1.84	4.22	3.31	3.38	0.75						
	M	4.33	1.96	4.75	4.56	4.00	1.40	2.37					
	J	4.29	1.95	4.68	4.38	3.93	1.33	1.96	0.31				
	J	4.37	1.97	4.80	4.71	4.07	1.47	2.76	0.50	0.70			
	A	4.22	1.92	4.59	4.16	3.82	1.21	1.52	0.88	0.50	1.31		
	S	4.18	1.91	4.54	4.06	3.75	1.14	1.29	1.35	0.88	1.90	0.34	
	O	0.38	0.71	0.05	1.36	0.69	1.78	2.18	2.42	2.39	2.44	2.35	2.32

(c) Subregion 2014/15		EC	NM	SM	PW	MS	LC	MC	UC
	NM	4.32							
	SM	2.25	1.81						
	PW	3.92	2.80	3.62					
	MS	3.66	1.38	0.39	2.88				
	LC	1.58	0.90	1.39	0.55	1.03			
	MC	3.32	1.20	0.50	2.80	0.13	1.00		
	UC	1.76	3.44	1.47	3.63	2.40	1.43	3.04	
	CA	1.45	3.88	1.84	3.77	2.28	1.50	2.80	0.74

**Appendix 2.** *t*-values derived from pairwise PERMANOVA tests on the densities of *Metapenaeus dalli* 500 m<sup>-2</sup> in offshore waters of the Swan-Canning Estuary among lunar months in (a) 2013/14 and subregions in (b) 2013/14 and (c) 2014/15. Significant differences highlighted in grey. Subregion codes given in Figure 1. Note two lunar months occurred in the calendar month of January 2014.

(a) Lunar months 2013/14		2013						2014					
		O	N	D	J1	J2	F	M	A	M	J	J	A
2013	N	3.08											
	D	7.48	2.79										
2014	J1	5.52	1.20	1.84									
	J2	6.24	1.65	1.36	0.51								
	F	5.98	1.21	1.96	0.04	0.57							
	M	7.31	2.95	0.28	2.04	1.59	2.17						
	A	7.09	3.72	1.50	2.99	2.61	3.10	1.22					
	M	6.66	4.04	2.15	3.40	3.09	3.49	1.91	0.80				
	J	8.82	4.55	2.17	3.85	3.44	4.02	1.85	0.43	0.47			
	J	6.62	3.10	0.74	2.29	1.89	2.39	0.47	0.71	1.44	1.22		
	A	4.48	0.59	2.43	0.66	1.16	0.66	2.61	3.45	3.80	4.35	2.79	
	S	5.86	1.07	2.15	0.22	0.76	0.19	2.35	3.25	3.62	4.20	2.55	0.49

(b) Subregion 2013/14	EC	LM	MB	UM	PW	MS	LC
LM	2.70						
MB	4.01	0.96					
UM	6.23	2.91	2.06				
PW	3.47	0.75	0.15	2.05			
MS	2.90	0.69	0.08	1.71	0.04		
LC	4.76	2.29	1.55	0.14	1.59	1.38	
MC	1.60	1.23	2.37	4.49	2.01	1.73	3.47

(c) Subregion 2014/15	EC	LM	MB	UM	PW	MS	LC
LM	3.27						
MB	8.15	5.04					
UM	7.11	4.56	0.22				
PW	13.39	10.38	5.34	4.59			
MS	8.97	7.57	4.95	4.63	1.79		
LC	14.36	12.21	8.34	7.61	3.97	1.12	
MC	13.90	11.37	6.96	6.19	2.11	0.34	1.93



