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Charles Darwin University

## A life-history account of *Macrobrachium spinipes* (Schenkel, 1902) (Cherabin) in a large tropical Australian River

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4 **A life-history account of *Macrobrachium spinipes* (Schenkel, 1902) (Cherabin) in a large**  
5 **tropical Australian River**

6

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20

21 **Abstract:** Rivers in tropical Australia are largely pristine, and ecosystem connectivity is intact,  
22 but water resources in northern Australia are under increasing development pressure. A better  
23 understanding of the role and life histories of key migratory species is urgently needed to  
24 manage the risks posed by development. We investigated the life history of *Macrobrachium*  
25 *spinipes* (Schenkel, 1902) in the Daly River of the Northern Territory, Australia. We carried out  
26 a 13-mo trapping program (2011–2012) at 7 sites along the river between 92 and 405 km from  
27 the estuary. We provide the first detailed account of spatial and temporal changes in relative  
28 abundance and reproduction, and present information on length at first maturity and Fulton’s  
29 body condition factor. Reproduction was strongly seasonal and was restricted to the wet-season  
30 months of November to April, followed by a recruitment pulse 3 to 4 mo later during the early  
31 dry season. Length at first maturity declined as the reproductive season progressed but did not  
32 vary significantly with distance from the estuary. Condition was temporally variable and peaked  
33 for both sexes immediately after the wet season before declining throughout the dry season.  
34 Relative abundance patterns followed a similar pattern. Contrary to results for other  
35 *Macrobrachium* species in rivers of comparable length, we found an increase in the relative  
36 abundance of females throughout the river’s length during the reproductive season and  
37 reproductive effort occurring far upstream, over a restricted time period. This result highlights  
38 the importance of maintaining connectivity for reproductive success of this species and further  
39 recruitment into these upstream reaches.

40 **Key words:** ecosystem connectivity, amphidromy, reproductive phenology, Fulton’s condition  
41 factor, migration, length at first maturity

42

43           Migratory shrimps from the infraorder Caridea, from the families, Atyidae, Xiphocaridae,  
44 and Palaemonidae, are important taxa in tropical river ecosystems (Bauer 2011a, Mancinelli et  
45 al. 2013). These taxa often dominate the biomass of stream macroinvertebrate communities and,  
46 in some small streams, compose most of the faunal community biomass (e.g., Jardine 2014,  
47 Fievet et al. 2001). They also have a strong structuring effect on benthic communities through  
48 trophic interactions (Pringle and Hamazaki 1998, Mancinelli et al. 2013). For example, they can  
49 facilitate growth of benthic algae by removing sand and silt (Pringle et al. 1993), and they  
50 influence the standing crop and structure of benthic algae and small macroinvertebrate  
51 communities through predation and grazing effects (e.g., March et al. 2002, Pringle and  
52 Hamazaki 1998). In addition to their effect on benthic communities, they can be important  
53 dietary component of many fish (e.g., Davis 1985, Covich et al. 2009, Pusey et al. 2010).

54           These migratory shrimp are amphidromous. The larvae require estuarine/brackish water  
55 to develop, and the juveniles migrate upstream to fresh water where they grow and mature  
56 (McDowall 2007, Bauer 2013). The larvae have a limited survival time in fresh water (up to 5 d  
57 for some species), so transport of larvae to the estuary is a critical aspect of the life history of  
58 amphidromous shrimp (Bauer 2013). In short, high-gradient rivers, transport is commonly  
59 achieved through the release of larvae to the river where the high water velocity rapidly  
60 transports the larvae to the estuary (Choudhury 1971, Holmquist et al. 1998, March et al. 1998,  
61 Bertini et al. 2013). In larger, lower-gradient rivers, reproductive females migrate downstream to  
62 the estuary (or nearby) at the start of the wet season (Raman 1967, Rome et al. 2009). Once in or  
63 near the estuary, they spawn, possibly many times (Ling and Merican 1961, Cavalli et al. 2001).  
64 Later, juveniles migrate upstream (Kikkert et al. 2009, Bauer 2013).

65           Their migratory nature makes these shrimps highly vulnerable to modifications of river

66 hydraulic connectivity (Bauer 2013). Dams or even a decrease in velocity caused by water  
67 diversions can cause extirpation or significant reduction in population size of freshwater shrimps  
68 by slowing or stopping the drift of larvae downstream and by impeding the movement of  
69 juveniles back upstream (Holmquist et al. 1998, Benstead et al. 1999, Olivier et al. 2013). The  
70 loss of these species from upstream reaches has wide-ranging ramifications including the loss of  
71 an important process subsidy (Greathouse et al. 2006b, Flecker et al. 2010) and, potentially, the  
72 loss of an important foodweb subsidy from the migration of the juveniles from the estuary to the  
73 fresh water (Bauer and Delahoussaye 2008, MacAvoy et al. 2009). Too often, discovery of such  
74 effects has occurred after development of water-management infrastructure, such as dams or  
75 weirs, has occurred. In areas where river connectivity is still intact, research undertaken to  
76 understand the life-history requirements of migratory shrimp before any development occurs  
77 would be valuable for anticipating (if not preventing) the consequences of development.

78         In northern Australia, most rivers are still unregulated, and hydrologic and ecosystem  
79 connectivity remains intact (Douglas et al. 2005, Warfe et al. 2011, Jardine et al. 2012a, b).  
80 Migratory species are likely to be important in maintaining ecological function and biodiversity,  
81 and ~50% of the freshwater fish species require access to the estuarine/marine ecosystem to  
82 complete their life cycle (Pusey et al. 2011). The migration patterns of some fishes are now well  
83 studied, but other species, such as crustaceans, remain poorly understood. The unmodified flows  
84 of most of these river systems are unlikely to persist given that development of northern  
85 Australia is now viewed as a national imperative (Australian Government 2014), and much of  
86 the proposed development is focussed around the increased use of water resources. Therefore,  
87 we must increase our understanding the life-history requirements of migratory species in this  
88 region before major decisions about water resource development are made.

89           *Macrobrachium spinipes* is a newly described species inhabiting the tropical rivers in the  
90 Australasian region east of the Huxley Line and the Philippines (Wowor et al. 2009, Ng and  
91 Wowor 2011). The species inhabits the range previous thought to be occupied by  
92 *Macrobrachium rosenbergii*. The information currently available in regard to the species'  
93 riverine distribution indicates that *M. spinipes* is highly likely to share the amphidromous life-  
94 history characteristics of *M. rosenbergii* (Ling and Merican 1961, Raman 1967, Short 2004,  
95 Lober and Zeng 2009). The species is an important prey item for a wide range of predators  
96 (Davis 1985, Pusey et al. 2010, Jardine et al. 2012a). Despite its presence in the diet of a wide  
97 range of fishes, *M. spinipes* occupies a moderate-to-high trophic level, similar to that of known  
98 predators, such fork tail catfish (*Neoarius* spp.) (Jardine et al. 2012a, 2013). Thus, *M. spinipes* is  
99 likely to play an important ecological role in the rivers of northern Australia, but an  
100 understanding of the species' basic life history is lacking.

101           Studies on amphidromous *Macrobrachium* life histories have been completed in several  
102 regions, mostly in short (<150 km) rivers (Holmquist et al. 1998, Lara and Wehrtmann 2009,  
103 Hein et al. 2011). Our goal was to explore seasonal patterns in *M. spinipes* life history along a  
104 continuous river gradient of >400 km. We used a trapping approach commonly used in  
105 *Macrobrachium* life-history investigations (Bauer and Delhousaaye 2008, Bertini et al. 2013,  
106 Olivier et al. 2013) to explore spatial and temporal changes in abundance, distribution,  
107 reproductive phenology, including length at first maturity and body condition. Based on studies  
108 of other *Macrobrachium*, we predicted that reproductive females would undertake a pronounced  
109 migration downstream during the reproductive season that would be indicated by a drop in  
110 relative abundance or disappearance at the most upstream sites and an increase in relative  
111 abundance at the most downstream sites. We also predicted that juveniles would undergo an

112 upstream migration that would be indicated by an increase in the relative abundance of juveniles  
113 at the most downstream sites. Ours is the first detailed investigation of the natural life history of  
114 *M. spinipes* and is one of the few studies of the natural life history of an amphidromous shrimp  
115 in a completely undammed and unmodified large river system. We have not attempted to provide  
116 an exhaustive overview of all aspects of its life history. Instead, our goal was to provide the first  
117 step in increasing our understanding of the life history of this important species so that its life  
118 history could be conceptualized and quantified as a basis for its sustainable management.

119

## 120 METHODS

### 121 Site description

122 The Daly river catchment is in the wet-dry tropics of the Northern Territory, Australia  
123 (lat 13–16°S, long 129–130°30'E) and covers an area of ~53,000 km<sup>2</sup> (Fig. 1). The catchment  
124 area is largely pristine, and 90% of the catchment consists of native open *Eucalyptus* woodland  
125 (Townsend and Padovan 2005). Only 5.6% of the native vegetation in the catchment has been  
126 cleared for agricultural, rural, and urban development (Schult and Townsend 2012). The Daly  
127 River is free flowing with no large dams or weirs and is 355 km long. It rises 50 m in elevation  
128 before it splits into the Flora and Katherine Rivers (Townsend and Padovan 2005). Because of  
129 substantial groundwater inputs, the Daly River and its largest tributary, the Katherine River, are  
130 both Class 3 perennial rivers and, thus, differ from most other northern Australian rivers  
131 (Kennard et al. 2010).

132 The wet-dry tropical climate is dominated by a long dry season (April–October) with  
133 minimal rainfall and high evapotranspiration, followed by a hot, humid wet season (November–  
134 March) during which 90% of the region's rain falls. Dry-season flows are derived primarily from

135 ground water and average 20 m<sup>3</sup>/s at the most downstream gauging station. During these  
136 baseflow conditions, the river is considered oligotrophic and is characterized by low turbidity  
137 and high conductivity (~500 µS/cm) (Townsend and Padovan 2005). Wet-season flows are  
138 highly variable but can be >4000 m<sup>3</sup>/s during monsoonal events. During this time, the river is  
139 considered mesotrophic and is characterized by high turbidity, warmer temperatures, low  
140 conductivity (~100–200 µS/cm), and high stream velocities (Townsend and Padovan 2005). The  
141 upstream limit of tidal influence during the dry season occurs 105 km upstream of the river  
142 mouth. This influence is restricted to tidal changes in depth, and the salt-water wedge does not  
143 encroach >30 km upstream during the dry season.

144

#### 145 **Study sites**

146 We selected 7 sites along a distance gradient from the estuary in the Daly River  
147 catchment (Fig. 1). Four sites were on the main stem of the river between 92 to 298 km from the  
148 river mouth at elevations between 1.23 and 40.31 m Australian Height Datum (AHD) (Table 1).  
149 We could not sample closer to the Daly River mouth because of substantial logistical constraints  
150 including: large (5–6 m) tidal variation, inaccessibility requiring long-distance travel by boat,  
151 and increasing risk of encountering large estuarine crocodiles. One site was on the Katherine  
152 River 405 km from the Daly River mouth (86.36 m AHD). We considered this site part of the  
153 main stem of the river. Two other sites were on the Edith and the Fergusson Rivers, small  
154 tributaries of the Daly River both ~380 km from the Daly River mouth at an elevation of ~100 m  
155 AHD. The Edith River is a predominantly perennial stream, and the Fergusson River is an  
156 intermittent river that becomes a series of disconnected in-stream pools during the dry season  
157 (hereafter, we refer to rivers by site code; main stem sites have a prefix of R followed by the



158 distance from the river mouth, and the Edith and Fergusson are T379 and T377 respectively;  
159 Table 1). We also chose sites based on accessibility and proximity to stream gauging stations so  
160 hydrographic records could be obtained. We were unable to sample some sites because of wet  
161 season flooding and road damage (February: R298; March: R92, R178, R113, and T379).

162

### 163 **Field sampling method**

164 We sampled *M. spinipes* populations with baited crustacean traps, a widely used method  
165 for sampling decapods (Short 2004). Traps were 62 cm long, 44 cm wide, and 18 cm high, with a  
166 0.3-mm mesh size and 8-cm-diameter entry holes. Capture efficiency of the traps can vary  
167 spatially and temporally, particularly in response to variation in wetted area caused by seasonal  
168 changes in stream level. In an initial review of the data, we found that relative abundance at all  
169 sites was unrelated to stream discharge ( $R^2 < 0.01$ – $0.22$ ,  $p = 0.162$ – $0.952$ ), which suggested that  
170 changes in water level had a negligible effect on trap efficiency. We trapped monthly at each site  
171 from October 2011 to October 2012. At each site, we set 22 traps along the bank of a 300-m  
172 reach. Banks were typically undercut with fringing vegetation and root masses.

173 We ran a pilot study to test trap 3 trapping periods (1700–2100 h, 0800–1700 h, and  
174 1700–0800 h) and 2 bait types (chicken laying pellets and dried cat food) in paired traps.  
175 Chicken food was the most effective (size range and number) bait, and 1700–0800 was the most  
176 suitable trapping period. Therefore, we baited traps with chicken laying pellets and deployed the  
177 traps from ~1700 to 0800 h, giving an approximate soak time of 15 h (effective for only 12 h  
178 because prawns were not active during daylight hours). We anaesthetised prawns after capture  
179 (clove oil; Coyle et al. 2005), measured them (see below), placed them in a 70-L aerated bucket  
180 until recovery, and then released them near the point of capture.

181 At each site, we made triplicate water-quality measurements (water temperature, pH,  
182 conductivity, dissolved O<sub>2</sub> concentration and % saturation) at the surface (0.15 m) and at the  
183 river bed (if depth was >1 m) at each site using a Hydrolab Quanta multiprobe (Hach Corp.,  
184 Loveland, Colorado). We measured turbidity (NTU) at the surface using a Hach Turbidimeter.  
185 At each trap location, we measured depth (to nearest 0.01 m) and velocity (to nearest 0.1 m/s)  
186 with a FP100 flow probe (Global Water, College Station, USA). We obtained stream-discharge  
187 and stage-height records for the nearest gauging station from the Northern Territory Department  
188 of Land and Resources Management.

189

### 190 **Biological variables**

191 We calculated catch per unit effort (represented as relative abundance) by averaging the  
192 catch at each site and sampling time across the number of traps used to even out the difference in  
193 total catch that may have occurred because of loss or damage of the traps.

194 We measured total length (TL; tip of rostrum to tip of uropod, to 1.0 mm), carapace  
195 length (from orbital margin to dorsolateral invagination of posterior margin), cheliped length (2<sup>nd</sup>  
196 pereiopod; inside edge of the ischium to the tip of the pollex – 1.0 mm), carpus length (inside  
197 edge of the carpus/merus joint to the inside edge of the carpus/prodopus junction), and chela  
198 length (from the inside edge of the prodopus at the carpus junction to the tip of the pollex) in the  
199 field. We measured carapace and chela length with Vernier callipers to 0.1 mm for each  
200 individual. The body mass of each individual was measured to the nearest 1.0 g using a UWE  
201 MII-6000 balance (Universal Weight Enterprise Company Limited, Xindian City, Taiwan).

202 We identified males by the presence of the gonopores on the base of the 5<sup>th</sup> pereiopod  
203 and the appendix masculina on the inside of the 2<sup>nd</sup> pleopod, and we identified females by the

204 lack of an appendix masculina and the presence of the gonopores at the base of the 3<sup>rd</sup> set of  
205 pereiopods (Short 2004). Sex determination was difficult and unreliable for individuals <45 mm  
206 long, these sex-indeterminate individuals were grouped as post-larvae.

207 We classified female reproductive status using 5 stages related to the order of maturation  
208 and egg production: 1) nonreproductive females: animals showing no reproductive condition; 2)  
209 developing ovaries (DO): ripening ovaries visible through the translucent dorsal surface of the  
210 carapace; 3) ovigerous females: presence of a mass of ova held within the pleopods under the  
211 abdomen; 4) recently spent females (RS): sexually mature, nonovigerous females with a widened  
212 pleural space, well developed hairs on the pleopods, and occasionally residual unhatched ova  
213 indicative of previously production and hatching of eggs; and 5) recently spent females, with  
214 developing ovaries (RS/DO). The color of the ova in stage-3 females also was recorded as  
215 orange ova (BO; spawned up to 1–2 wk preceding capture) and brown ova (BB; ova <24 h from  
216 hatching) (Ling and Merican 1961; personal observations of captive specimens).

217

## 218 **Analysis**

219 We used principal components analysis (PCA) to examine spatial and temporal variation  
220 in environmental descriptors (temperature, turbidity, conductivity, pH, dissolved O<sub>2</sub>, minimum  
221 depth, maximum depth, and discharge [average discharge for the period between sampling  
222 occasions]). Turbidity was extremely right skewed, and neither  $\log(x)$  nor  $\sqrt{x}$  transformation  
223 improved the skew, so data were rank transformed. We range-normalized all variables using the  
224 equation  $z = (x - \mu)/\sigma$ , where  $z$  is the standard score,  $x$  is the raw score,  $\mu$  is the mean, and  $\sigma$  is  
225 the standard deviation.

226 We analysed relative abundance with a generalized linear model with a Poisson

227 distribution and log link function to test for differences among sites, months, and sexes (male  
228 and female). Data were over-dispersed (df/Pearson  $\chi^2 = 1.33$ , df/deviance = 1.324) and were  
229 corrected using Pearson's  $\chi^2$  as the dispersion parameter (df/Pearson  $\chi^2 = 1.01$ , df/deviance =  
230 0.988). Because of the problems with access described above, only relative abundance data for  
231 R113, R178, R405, and T377 were included in the analysis (all months excluding March).  
232 Relative abundance of post-larvae was excluded from this analysis because of a "0 pivot  
233 element," which occurred as a result of the high number of 0 counts because no post-larvae were  
234 captured at T377 and R405. Changes in mean TL were analyzed using a 3-way factorial analysis  
235 of variance (ANOVA) to test for differences between site, month, and sex. We used linear  
236 regression to explore the relationship between distance from the river mouth and both mean  
237 length and mean relative abundance.

238 We plotted reproductive status (frequency) and relative abundance of reproductive  
239 females for the 5 mo over which reproductive activity occurred. We used a generalized liner  
240 model with a binomial distribution and logit link function to test whether the distribution of  
241 reproductive females was equal across sites and months. The results indicated quasi-separation  
242 within the data, meaning that 1 factor, in this case month, almost totally predicted the dependent  
243 variable.

244 We calculated length at first maturity with data from the reproductive period only  
245 because *M. spinipes* has a seasonally restricted reproductive period (but large females were  
246 present outside of this period, and maturity cannot visually be determined when females are not  
247 in reproductive condition). Length at maturity (L50) was calculated using the logistic function:

$$248 \quad p = 1/(1 + \exp[-r(TL - TLm)]) \quad (\text{Eq. 1})$$

249 where  $p$  is the proportion of mature individuals,  $r$  is the rate that the proportion of mature

250 individuals increases with each increment of length (slope),  $TL$  is total length, and  $TLm$  is the  
251 total length that corresponds to a proportion of 0.5 in reproductive condition (King 1995). The  
252 function was fitted using the Solver GRG nonlinear algorithm in Microsoft EXCEL (version  
253 2010; Microsoft Corporation, Redmond, Washington; Brown 2001, Kemmer and Keller 2010).  
254 We calculated confidence intervals for the L50 estimate using the methods described by Kemmer  
255 and Keller (2010). We did not adjust raw proportion data because 95 to 100% of a particular size  
256 class was mature (King 1995). We calculated L50 for the entire river to observe changes in L50  
257 on a temporal and spatial scale, for 5 sites throughout the river (R92, R113, R178, R298, and  
258 R405; months combined) and for the 4 mo where sufficient reproductive data were available  
259 (November, December, January, and February; sites combined).

260 Condition indices have been used often to assess relative health of a population and to  
261 describe changes that may be associated with either environmental conditions or reproduction.  
262 We used Fulton's condition factor (Ricker 1975, Nash et al. 2006), a commonly used index for  
263 both fish and crustaceans (Arimoro and Meye 2007, Pinheiro and Fiscarelli 2009). Fulton's  
264 condition factor is calculated as (Ricker 1975)

$$265 \quad K = \frac{M}{TL^3} \quad (\text{Eq. 2})$$

266 where  $K$  = Fulton's condition factor,  $M$  = total mass (g), and  $TL$  = total length (mm). For  
267 convenience, we multiplied  $K$  by 100,000 to obtain a number close to 1.

268 We used a 2-way ANOVA to test whether  $K$  differed among sites, seasons, or the site  $\times$   
269 season interaction. We analyzed male and female condition factor separately and included only  
270 data from R113, R178, R405, and T377 from the months October 2011 to October 2012  
271 (excluding March 2012). We excluded other sites and months from the analysis because of  
272 missing data as a result of accessibility issues. We used linear regression to test for the

273 relationship between distance from the river mouth and mean condition factor.

274 The PCA analysis was carried out using PRIMER software (version 6; PRIMER, Luton,  
275 UK); all other statistical analyses were completed using the statistics package Statistica (version  
276 12; StatSoft, Tulsa, Oklahoma).

277

## 278 RESULTS

### 279 Environmental data

280 The first 2 axes of the PCA explained 40.0 and 25.7% of the variation, respectively  
281 (eigenvalues = 2.8 and 1.92, respectively; Fig. 2). PC1 was correlated most strongly with  
282 discharge, turbidity (rank), and mean depth (eigenvectors = -0.429, 0.457, and -0.451,  
283 respectively). PC2 was strongly correlated with conductivity and pH (eigenvectors = 0.618 and  
284 0.522, respectively). Sites tended to be separated along PC2, with river sites characterized by  
285 higher pH, conductivity, and mean depth, and tributaries characterized by low conductivity and  
286 pH (Table 2). Seasonality was evident along PC1, where the wet season was characterized by  
287 higher discharge, lower turbidity rank (therefore, higher turbidity), and higher temperatures  
288 (Table 2).

289

### 290 Changes in population structure

291 Relative abundance of male and female prawns varied significantly throughout the 13-mo  
292 period and across sites (3-way interaction with site, sex, and month, Wald stat = 53.46, df =  
293 1980,  $p = 0.01$ ). Abundance of both sexes varied significantly with increasing distance from the  
294 estuary (Fig. 3A). Relative abundance of females declined strongly with increasing distance from  
295 the estuary ( $R^2 = 0.91$ ,  $p = 0.001$ ), whereas male relative abundance did not ( $R^2 = 0.02$ ,  $p = 0.74$ ).

296 Female relative abundance peaked in the wet season (December:  $1.79 \pm 0.18$  [SE]/trap), whereas  
297 male relative abundance peaked in the middle of the dry season (June:  $1.3 \pm 0.16$ /trap) (Fig. 4A).  
298 Female relative abundance declined throughout the remainder of the sampling period. In  
299 contrast, male relative abundance remained relatively high throughout the year. Relative  
300 abundance of post-larvae (sex indeterminates <45 mm TL) peaked twice, once in November–  
301 December and again in May–June. Relative abundance of post-larvae declined strongly with  
302 increasing distance from the river mouth ( $R^2 = 0.915$ ,  $p < 0.001$ ). Only 1 post larvae was  
303 captured at R405 and none at T377 and T379.

304 Both male and female *M. spinipes* were larger (mean TL) at sites most distant from the  
305 river mouth ( $R^2 = 0.50$ ,  $p = 0.072$  and  $R^2 = 0.51$ ,  $p = 0.070$ , respectively; Fig. 3B), but average  
306 size changed over time differently for males and females (2-way interaction for sex  $\times$  month:  $F =$   
307  $8.21$ ,  $df = 11$ ,  $p < 0.001$ ; site  $\times$  month:  $F = 3.52$ ,  $df = 33$ ,  $p < 0.001$ ). Male and females were  
308 largest at the end of the dry season in October 2011 ( $146 \pm 4.1$  mm and  $111 \pm 3$  mm,  
309 respectively) before declining during the wet season (Fig. 4B). Male TL was smallest in January,  
310 whereas female TL was lowest in February. Male TL increased quickly over the remainder of the  
311 wet season and then remained consistent over the dry season. Female TL remained low  
312 throughout the remaining period.

313

#### 314 **Changes in reproductive patterns**

315 Reproduction for *M. spinipes* was strongly seasonal. The reproductive season extended  
316 from November to April (Fig. 4C). The largest proportion of reproductive females occurred in  
317 December and January (Fig. 4C) when female relative abundance was greatest (Fig. 5). Relative  
318 abundance of reproductive females increased at all sites throughout the wet season and peaked in

319 January. Females in reproductive condition were absent from the river during the dry-season  
320 months of May, June, July, and August (Fig. 4C). Reproductive maturation stages shifted  
321 gradually throughout the reproductive period from the initial high number of DO females to  
322 dominance of DO/RS females, and eventually only RS females (Fig. 5). Early in the reproductive  
323 period (November and December) females in DO condition predominated (up to 80%) at all  
324 sites. During peak relative abundance of reproductive females in January, ovigerous females in  
325 both early and late stages (BO and BB) of development were present at all sites. Females in  
326 DO/RS reproductive stage were most prevalent at this time. Relative abundance was much lower  
327 in February, but BO and BB ovigerous females dominated at all sites. Reproduction had finished  
328 by April when only the only reproductive females were in RS stage.

329         Length at first maturity for *M. spinipes* in the Daly river with data combined for all sites  
330 and months was 80.0 mm ( $\pm 2.3$  mm 95% confidence interval [CI]). L50 increased gradually  
331 along an upstream gradient (Fig. 3C), but based on the size of the 95% CIs the increase is  
332 unlikely to be biologically significant. Temporally, L50 dropped 25 percentage points between  
333 November and January (Fig. 4D), and this decline was not related to the observed decline in TL  
334 ( $R^2 = 0.13$ ,  $p = 0.63$ ).

335

### 336 **Condition factor**

337         The body condition of both males and females increased significantly during the wet  
338 season (Fig. 4E). Female condition was highest in February ( $1.3 \pm 0.06$ ; from a low in October of  
339  $0.94 \pm 0.03$ ) and in the sites closest to and furthest from the river mouth (2-way interaction:  $F =$   
340  $4.24$ ,  $df = 30$ ,  $p < 0.001$ ; Fig. 3D). Female body condition was not significantly related to  
341 distance from the estuary ( $R^2 = 0.18$ ,  $p = 0.83$ ). Male body condition was highest 3 mo earlier, in



342 November ( $1.25 \pm 0.03$ ; 2-way interaction:  $F = 5.25$ ,  $df = 30$ ,  $p < 0.001$ ), and was highest at the  
343 sites farthest from the mouth, but this relationship was not significant ( $R^2 = 0.23$ ,  $p = 0.26$ ).  
344 Female and male body condition reached the low point in August ( $0.73 \pm 0.03$  and  $0.99 \pm 0.19$ ,  
345 respectively).

346

## 347 **DISCUSSION**

### 348 **Reproduction**

349         Reproduction in *M. spinipes* was strongly seasonal, occurring primarily in the early to  
350 middle wet season (November, December, and January), and no females in reproductive  
351 condition were observed during the dry season (May–August). Key aspects of the life history of  
352 amphidromous *Macrobrachium* (e.g., *Macrobrachium ohione* and *Macrobrachium*  
353 *völlenhovenii*) include a strongly seasonal reproductive phenology timed to coincide with high  
354 current velocities and a pronounced migration of females downstream toward the estuary in large  
355 rivers (Raman 1967, Etim and Sankare 1998, Bauer and Delahoussaye 2008, Rome et al. 2009,  
356 Bauer 2011b). Larvae of amphidromous *Macrobrachium* require salt water for development and  
357 must reach the estuary within as little as 4 to 5 d after hatching (Rome et al. 2009, Lal et al.  
358 2012). These tactics (movement of females toward the estuary and reproduction coincident with  
359 high flows) presumably increase the chances of larvae reaching the estuary in the required time  
360 (Etim and Sankare 1998, March et al. 1998, Bauer and Delahoussaye 2008) to ensure survival  
361 and to allow access to the rich productivity of lowland rivers and estuaries during the wet season  
362 (Junk et al. 1989).

363         We predicted that female *M. spinipes* would undergo downstream migration during the  
364 reproductive season to hatch larvae in or close to the estuary. We also expected that this

365 migration would be detected as an observed decrease in the relative abundance of females in the  
366 upstream reaches and an increase in the downstream reaches (Bauer and Delhousaaye 2008,  
367 Raman 1967, Olivier and Bauer 2011). However, we did not observe a reduction in the relative  
368 abundance of reproductive females in upstream river reaches during the breeding season. Instead,  
369 the relative abundance of females increased at all sites during the reproductive season. We  
370 cannot conclusively say, without mark–recapture studies, that the females are not migrating  
371 downstream to hatch larvae, but our results suggest that female *M. spinipes* are reproducing  
372 along the length of the river. This type of reproductive behavior is more common in short, high-  
373 gradient rivers of up to 150 km in length, where larvae are likely to be transported downstream to  
374 the estuary in a matter of days (March et al. 1998, Bauer 2011b, Bertini et al. 2013). However, in  
375 a river as long as the Daly, the high relative abundance of reproductive females at the most  
376 upstream site sampled (405 km from the estuary) was unexpected. Furthermore, the Daly River  
377 is low gradient (~0.015%), and a flood wave can take 5 d to travel just 200 km through the  
378 middle reaches (Paiva 2000). Thus, if larval survival times of *M. spinipes* are similar to those of  
379 other species, then it is unlikely that larvae released far upstream will reach the estuary within  
380 the critical period observed in other river systems (Rome et al. 2009, Lal et al. 2012). Oviparous  
381 females at the Daly River upstream sites might potentially move downstream rapidly to hatch  
382 their ova near the estuary, but the presence at upstream sites of females for which hatching was  
383 imminent or had occurred very recently suggests this scenario of rapid downstream movement is  
384 unlikely and that larvae had hatched and were released to the water at these sites. Olivier and  
385 Bauer (2011) observed breeding *M. ohione* females up to 400 km upstream in the Mississippi  
386 River, and in contrast, observed a significant migration of females downstream to breed in the  
387 adjacent Atchafalaya River. They also found yearly variation in the strength of the downstream

388 migration, which may suggest that the mechanics of the migration vary temporally and spatially  
389 over time and could be specific to individual rivers. Thus, the lack of migration we observed in  
390 the Daly River might possibly be related to yearly changes in environmental conditions. Another  
391 possibility is that *M. spinipes* larvae have a longer survival time in freshwater than do other  
392 shrimps, and thus, can survive the long drift time. Perhaps the larvae released at the upstream  
393 sites do not make it to the estuary and develop any further. A final possibility is that amphidromy  
394 for *M. spinipes* may be facultative rather than obligate. Further investigations to evaluate the  
395 amphidromous nature of *M. spinipes* are required and could include laboratory studies of  
396 freshwater tolerance by larvae (e.g., Rome et al. 2009). We are currently undertaking such  
397 research for this species as part of a larger study.

398 L50 was consistent throughout the length of the river system but decreased over the wet  
399 season. The decline in L50 over the reproductive season is consistent with findings by Bertini et  
400 al. (2013) who found that L50 of *Macrobrachium acanthurus* declined during periods of intense  
401 reproduction and increased when reproduction slowed. In our study, L50 declined from a peak of  
402 103.6 mm in November to 78.8 mm in January. This drop coincided with an initial increase in  
403 the number of reproductive females from November to December before abundance declined by  
404 >70% between January and February. Bertini et al. (2013) proposed that the reduction in L50 as  
405 reproduction peaked was an adaption by the prawns to maximize reproductive potential during a  
406 limited breeding season. The larger L50 at the start of the breeding season may reflect the  
407 presence of large females in the river, probably those >1 y old, whereas the decline may reflect  
408 rapid maturation of smaller females during optimum reproductive conditions and the loss,  
409 possibility from mortality, of the large females from the river.

410

411 **Spatial and temporal dynamics in abundance, length, and condition**

412 We identified 2 peaks in relative abundance throughout the 13-mo sampling period. The  
413 first occurred during the wet season at a time of elevated discharge, turbidity, and temperature  
414 and was primarily associated with an increase in female relative abundance. An increase in the  
415 relative abundance of post-larvae also occurred early in the wet season (November–December).  
416 The body condition of females increased during the wet season and peaked in February. In  
417 contrast to results of other studies of *Macrobrachium* species (Rao 1967, Arimoro and Meye  
418 2007), the peak in body condition did not coincide with the peak in reproductive activity and  
419 relative abundance. High body condition can be associated with rapid growth and ecdysis (Rao  
420 1967). We observed an increase in the relative abundance of post-larvae in November and  
421 December followed by a decrease in average length of females in December and January, and it  
422 is likely that the post-larvae grew rapidly into adults during this time. The peak in male body  
423 condition was associated with the onset of the wet season and reproductive activity. Similar  
424 changes in male body condition were observed for *M. rosenbergii* and *Macrobrachium dux* (Rao  
425 1967, Arimoro and Meye 2007). In addition, the increase in body condition observed for *M.*  
426 *spinipes* may have been caused by the allometric growth of the large chelipeds in dominant  
427 males (Kuris et al. 1987, Short 2004). The largest males were caught during this period, and the  
428 large chelipeds developed by dominant males resulted in heavier prawns for a given length.

429 The 2<sup>nd</sup> peak in relative abundance of males, females, and post-larvae occurred in May  
430 and June, 2 mo after the reproductive season concluded. The abundance of post-larvae dropped  
431 rapidly with increasing distance from the estuary, and this observation combined with an  
432 increasing average length of males and females with increasing distance from the estuary  
433 suggests directional movement of recruitment. In support of this notion, we observed a mass

434 migration similar to that reported by Bauer and Delahoussaye (2008) (*M. ohione*) and Lee and  
435 Fielder (1979) (*Macrobrachium australiense*) of *M. spinipes* juveniles in April and May (PN,  
436 personal observation). A strong seasonal pulse of recruitment, often associated with mass  
437 migration, has been observed for a number of other amphidromous *Macrobrachium* species  
438 (Raman 1967, Etim and Sankare 1998, Bauer and Delahoussaye 2008, Kikkert et al. 2009). We  
439 propose 2 probable causes for the strong seasonality of recruitment. First, strong seasonality of  
440 reproduction creates a cohort of post-larvae in the estuary ready to migrate. Second, recruitment  
441 occurs during periods of high flow, so the migration upstream is strongly tied to the declining  
442 limb of the hydrograph because lower flows at this period make the upstream journey easier  
443 (Bauer and Delahoussaye 2008, Kikkert et al. 2009, Bauer 2011b). Multiple peaks in upstream  
444 migration were observed for species that reproduce year round, but each peak followed a flow  
445 event (Benstead et al. 2000).

446         The ecological consequences of these migrations are substantial and include both process  
447 and material subsidies (Flecker et al. 2010). Process subsidies have been documented through the  
448 subsequent ecosystem impacts following loss of these species caused by dam development  
449 (Benstead et al. 1999, Greathouse et al. 2006a, b). Material subsidies by migratory shrimp have  
450 not been evaluated in any detail. Instead, investigators have proposed that the large mass  
451 migrations observed for species, such as *M. ohione*, may transport marine nutrients into fresh  
452 water (Bauer and Delahoussaye 2008). Thus, juveniles of *M. spinipes* may be involved in  
453 substantial longitudinal movement of nutrients and energy between different parts of the Daly  
454 River catchment. An investigation to quantify the duration of the migration and the biomass  
455 moving upstream and to determine whether marine/estuarine nutrients are transported upstream  
456 during this migration would be invaluable in assessing the contribution of *M. spinipes* to

457 ecosystem connectivity in Northern Australia.

458       Following the peak in relative abundance associated with recruitment in May and June,  
459 relative abundance declined for the remainder of the year to reach its lowest point in October.  
460 The decline in relative abundance co-occurred with a decline in body condition. Moreover, the  
461 average length of the prawns did not vary greatly throughout the dry season, suggesting that  
462 growth was limited. The decline in relative abundance, body condition, and flat growth (no TL  
463 increase) in both males and females during the dry season is interesting. Loss to predation may  
464 increase during the dry season as water levels recede, the number of refugia decreases, and the  
465 density of prawns and their predators increase. Predation may account for a large part of the  
466 decline in relative abundance. The decline in body condition and limited growth may have been  
467 caused by a postulated decline in resource availability throughout this period (Junk et al. 1989,  
468 Warfe et al. 2011). However, productivity of benthic algae and submerged macrophytes in the  
469 Daly River increases during the dry season (Webster et al. 2005), and benthic algae contribute to  
470 the diet of other *Macrobrachium* species (March and Pringle 2003). However, C sources  
471 assimilated for growth and reproduction of fish and large crustaceans in tropical Australian rivers  
472 appear to vary by flow regime and season. Biofilms and benthic algae are strongly coupled to  
473 consumers in river systems that exhibit seasonal drying with short floodplain inundation times  
474 (Jardine et al. 2012b). In rivers with stable base flows and longer floodplain inundation periods,  
475 C from external sources, such the inundated flood plain and estuary, is vital (Hunt et al. 2012,  
476 Jardine et al. 2012b). Furthermore, Jardine et al. (2012a) found that during the dry season  
477 *Macrobrachium* in the Daly River were not assimilating C from local biofilms and that C was  
478 coming from allocthonous sources. Thus, *M. spinipes* probably gain most of their biomass during  
479 the wet season or in the few months immediately after, and the dry season is a period of predator

480 avoidance and survival.

481

## 482 **Conclusion**

483       Very few investigators of *Macrobrachium* life history have studied changes in population  
484 dynamics along a long (>400 km) river gradient (e.g., Olivier and Bauer 2011). Most have  
485 included estuary sites or sites  $\leq 150$  km of the river mouth because many of these studies were  
486 done in short rivers in small catchments (Raman 1967, Rao 1967, March and Pringle 2003,  
487 Bauer and Delahoussaye 2008, Rome et al. 2009, Bertini et al. 2013). We have investigated the  
488 life history of an amphidromous prawn species, *M. spinipes*, along a continuous gradient in a  
489 large river and this investigation has provided unique insights into their ecology. It also  
490 highlighted possible vulnerabilities of the species to river regulation. The entire length of our  
491 study reach could be important for the reproduction of this species, and reproduction is  
492 seasonally restricted to the wet-season months. Our data support the hypothesis that this species  
493 is migratory by showing that recruitment is directional (abundance of post-larvae at the most  
494 downstream sites and the increase in size with increasing distance from the estuary), and that  
495 recruitment occurs at the end of the wet season concurrent with recruitment of other  
496 amphidromous *Macrobrachium* species. However, uncertainties remain regarding the nature of  
497 the amphidromy for *M. spinipes*, and more work is needed to fully understand the ecological role  
498 of this species. Further research to assess whether *M. spinipes* is facultatively or obligately  
499 amphidromous and the dynamics of the upstream migration, including whether marine C is  
500 transported upstream, is essential in understanding the contribution of this species to maintaining  
501 the ecological connectivity of tropical rivers.

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510



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701

702 **FIGURE CAPTIONS**

703 Fig. 1. Daly River catchment and sites showing major townships and national park boundaries.

704 Fig. 2. Principal components analysis of environmental data collected from all sites separated  
705 into 4 seasons: wet (November–January), early dry (April, May), mid-dry (June–August),  
706 and late dry (September, October). The variation explained by each axis is in parentheses  
707 after the axis name and the variable names and eigenvectors (in parentheses), for the most  
708 correlated variable for each axis have been included. Cond = specific conductivity, Temp  
709 – water temperature, DO = dissolved O<sub>2</sub>.

710 Fig. 3. Mean ( $\pm 1$  SE) relative abundance (RA)/trap (A), total length (TL) (B), length at first  
711 maturity (C), and Fulton's condition factor (D) for *Macrobrachium spinipes* combined  
712 for all months as a function of distance from the mouth of the Daly River mouth. PL =  
713 post-larvae.

714 Fig. 4. Mean ( $\pm 1$  SE) relative abundance (RA)/trap (A), total length (TL) (B), % reproductive  
715 females (C), length at first maturity (D), and Fulton's condition factor (E) for  
716 *Macrobrachium spinipes* combined for all sites for each sampling month. PL = post-  
717 larvae, dates are formatted Month-last 2 digits of year.

718 Fig. 5. Percentage of females in each reproductive stage and relative abundance (RA) of females  
719 in November (A), December (B), January (C), February (D), and April (E). DO =  
720 developing ovaries, BO = ovigerous, ova to hatch within 2 wk, BB = ovigerous, ova to  
721 hatch within 24 h, RS = ova recently hatched, DO/RS = ova had recently hatched and  
722 developing further ova.

723

724 Table 1. Sites position and distance from the Daly River mouth. Elevation data are the 0 gauge  
 725 level of the gauging station closest to the site. AHD = Australian height datum.

Site name	Site code	Latitude	Longitude	Elevation* (m AHD)	Distance from mouth (km)
Wooliana	R92	13°46'09.99"S	130°42'51.13"E	1.23	92
Mt Nancar	R113	13°49'34.30"S	130°43'49.15"E	1.46	113
Beeboom	R178	13°51'43.89"S	131°04'29.20"E	13.32	178
Claravale	R298	14°21'47.50"S	131°33'24.12"E	40.31	298
Katherine R	R405	14°32'52.64"S	132°07'47.47"E	86.36	405
Fergusson R	T377	14°04'16.92"S	131°58'25.31"E	(N/A)	377
Edith R	T379	14°13'49.83"S	131°55'37.39"E	101.80	379

726

727

728 Table 2. Mean and SE of environmental variables for the study period. Wet = all data from  
 729 November to April, dry = all months from May to October. Temp = temperature, DO = dissolved  
 730 O<sub>2</sub>.

Site	Conductivity				pH				Temp (°C)				DO (mg/L)		Turbidity (NTU)		Depth (m)		Discharge (m <sup>3</sup> /s)	
	(mS/cm)																			
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet		
R92	0.53	0.28	8.16	7.89	26.4	30.3	6.94	5.96	8.72	33.8 <sup>a</sup>	1.48	1.75	59.4	317.8						
SE	0.01	0.03	0.04	0.12	0.69	0.51	0.22	0.11	0.55	4.7	0.05	0.37	9.30	142.6						
R113	0.53	0.31	8.16	7.94	26.2	30.3	7.00	6.26	7.42	140.7	1.37	2.30	59.4	317.8						
SE	0.01	0.03	0.04	0.10	0.66	0.45	0.22	0.10	0.53	46.9	0.08	0.90	9.30	142.6						
R178	0.54	0.35	8.06	7.84	27.0	30.7	7.03	6.26	4.57	77.4	1.38	1.54	50.4	142.0						
SE	0.03	0.03	0.02	0.09	0.71	0.30	0.20	0.12	0.19	26.2	0.05	0.05	7.28	36.4						
R298	0.51	0.24	8.03	7.61	25.7	30.8	7.52	6.24	5.46	66.3	1.40	1.30	22.5	76.1						
SE	0.02	0.04	0.05	0.11	0.69	0.32	0.12	0.11	0.46	12.6	0.09	0.21	5.06	13.7						
R405	0.39	0.10	7.82	7.27	26.6	30.3	6.98	6.41	3.07	45.4	1.10	0.88	7.10	55.5						
SE	0.03	0.01	0.02	0.07	0.65	0.25	0.23	0.07	0.16	10.2	0.06	0.09	1.63	15.1						
T377	0.04	0.03	7.31	7.17	26.2	29.3	7.16	6.73	4.15	35.8	0.68	0.68	0.38	4.14						
SE	0.00	0.00	0.06	0.08	0.76	0.24	0.15	0.11	0.41	3.91	0.03	0.11	0.21	1.57						
T379	0.02	0.02	6.94	7.03	24.0	28.5	6.91	6.55	2.26	12.4	0.63	0.49	1.23	8.74						
SE	0.00	0.00	0.09	0.09	0.72	0.32	0.20	0.14	0.09	3.11	0.03	0.16	0.44	3.35						

731 <sup>a</sup>Measured for only 2 mo because of equipment failure