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

Novak, Peter; Douglas, Michael; Garcia, Erica; Bayliss, Peter; Pusey, Bradley J

Published in:
Freshwater Science

DOI:
10.1086/681526

Published: 01/06/2015

Document Version
Peer reviewed version

Citation for published version (APA):

General rights
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.
A life-history account of *Macrobrachium spinipes* (Schenkel, 1902) (Cherabin) in a large tropical Australian River

Peter A Novak¹,4, Michael M Douglas¹,5, Erica A Garcia¹,6, Peter Bayliss²,7, Brad J Pusey³,8

¹Research Institute for Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory, 0810, Australia

²Commonwealth Scientific and Industrial Research Organisation, Brisbane, Queensland, 4067, Australia

³Centre of Excellence in Natural Resource Management, University of Western Australia, Albany, Western Australia, 6330, Australia

E-mail addresses: ⁴peter.novak@cdu.edu.au; ⁵michael.douglas@cdu.edu.au;
⁶peter.bayliss@csiro.au; ⁷bpusey@westnet.com.au

Received 17 May 2014; Accepted 24 February 2015; Published online XX Month 2015.
Abstract: Rivers in tropical Australia are largely pristine, and ecosystem connectivity is intact, but water resources in northern Australia are under increasing development pressure. A better understanding of the role and life histories of key migratory species is urgently needed to manage the risks posed by development. We investigated the life history of *Macrobrachium spinipes* (Schenkel, 1902) in the Daly River of the Northern Territory, Australia. We carried out a 13-mo trapping program (2011–2012) at 7 sites along the river between 92 and 405 km from the estuary. We provide the first detailed account of spatial and temporal changes in relative abundance and reproduction, and present information on length at first maturity and Fulton’s body condition factor. Reproduction was strongly seasonal and was restricted to the wet-season months of November to April, followed by a recruitment pulse 3 to 4 mo later during the early dry season. Length at first maturity declined as the reproductive season progressed but did not vary significantly with distance from the estuary. Condition was temporally variable and peaked for both sexes immediately after the wet season before declining throughout the dry season. Relative abundance patterns followed a similar pattern. Contrary to results for other *Macrobrachium* species in rivers of comparable length, we found an increase in the relative abundance of females throughout the river’s length during the reproductive season and reproductive effort occurring far upstream, over a restricted time period. This result highlights the importance of maintaining connectivity for reproductive success of this species and further recruitment into these upstream reaches.

Key words: ecosystem connectivity, amphidromy, reproductive phenology, Fulton’s condition factor, migration, length at first maturity
Migratory shrimps from the infraorder Caridea, from the families, Atyidae, Xiphocaridae, and Palaemonidae, are important taxa in tropical river ecosystems (Bauer 2011a, Mancinelli et al. 2013). These taxa often dominate the biomass of stream macroinvertebrate communities and, in some small streams, compose most of the faunal community biomass (e.g., Jardine 2014, Fievet et al. 2001). They also have a strong structuring effect on benthic communities through trophic interactions (Pringle and Hamazaki 1998, Mancinelli et al. 2013). For example, they can facilitate growth of benthic algae by removing sand and silt (Pringle et al. 1993), and they influence the standing crop and structure of benthic algae and small macroinvertebrate communities through predation and grazing effects (e.g., March et al. 2002, Pringle and Hamazaki 1998). In addition to their effect on benthic communities, they can be important dietary component of many fish (e.g., Davis 1985, Covich et al. 2009, Pusey et al. 2010).

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

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

In northern Australia, most rivers are still unregulated, and hydrologic and ecosystem connectivity remains intact (Douglas et al. 2005, Warfe et al. 2011, Jardine et al. 2012a, b). Migratory species are likely to be important in maintaining ecological function and biodiversity, and ~50% of the freshwater fish species require access to the estuarine/marine ecosystem to complete their life cycle (Pusey et al. 2011). The migration patterns of some fishes are now well studied, but other species, such as crustaceans, remain poorly understood. The unmodified flows of most of these river systems are unlikely to persist given that development of northern Australia is now viewed as a national imperative (Australian Government 2014), and much of the proposed development is focussed around the increased use of water resources. Therefore, we must increase our understanding the life-history requirements of migratory species in this region before major decisions about water resource development are made.
Macrobrachium spinipes is a newly described species inhabiting the tropical rivers in the Australasian region east of the Huxley Line and the Philippines (Wowor et al. 2009, Ng and Wowor 2011). The species inhabits the range previous thought to be occupied by Macrobrachium rosenbergii. The information currently available in regard to the species’ riverine distribution indicates that *M. spinipes* is highly likely to share the amphidromous life-history characteristics of *M. rosenbergii* (Ling and Merican 1961, Raman 1967, Short 2004, Lober and Zeng 2009). The species is an important prey item for a wide range of predators (Davis 1985, Pusey et al. 2010, Jardine et al. 2012a). Despite its presence in the diet of a wide range of fishes, *M. spinipes* occupies a moderate-to-high trophic level, similar to that of known predators, such fork tail catfish (*Neoarius* spp.) (Jardine et al. 2012a, 2013). Thus, *M. spinipes* is likely to play an important ecological role in the rivers of northern Australia, but an understanding of the species’ basic life history is lacking.

Studies on amphidromous *Macrobrachium* life histories have been completed in several regions, mostly in short (<150 km) rivers (Holmquist et al. 1998, Lara and Wehrtmann 2009, Hein et al. 2011). Our goal was to explore seasonal patterns in *M. spinipes* life history along a continuous river gradient of >400 km. We used a trapping approach commonly used in *Macrobrachium* life-history investigations (Bauer and Delhousaaye 2008, Bertini et al. 2013, Olivier et al. 2013) to explore spatial and temporal changes in abundance, distribution, reproductive phenology, including length at first maturity and body condition. Based on studies of other *Macrobrachium*, we predicted that reproductive females would undertake a pronounced migration downstream during the reproductive season that would be indicated by a drop in relative abundance or disappearance at the most upstream sites and an increase in relative abundance at the most downstream sites. We also predicted that juveniles would undergo an
upstream migration that would be indicated by an increase in the relative abundance of juveniles at the most downstream sites. Ours is the first detailed investigation of the natural life history of *M. spinipes* and is one of the few studies of the natural life history of an amphidromous shrimp in a completely undammed and unmodified large river system. We have not attempted to provide an exhaustive overview of all aspects of its life history. Instead, our goal was to provide the first step in increasing our understanding of the life history of this important species so that its life history could be conceptualized and quantified as a basis for its sustainable management.

**METHODS**

**Site description**

The Daly river catchment is in the wet-dry tropics of the Northern Territory, Australia (lat 13–16°S, long 129–130°30′E) and covers an area of ~53,000 km² (Fig. 1). The catchment area is largely pristine, and 90% of the catchment consists of native open *Eucalyptus* woodland (Townsend and Padovan 2005). Only 5.6% of the native vegetation in the catchment has been cleared for agricultural, rural, and urban development (Schult and Townsend 2012). The Daly River is free flowing with no large dams or weirs and is 355 km long. It rises 50 m in elevation before it splits into the Flora and Katherine Rivers (Townsend and Padovan 2005). Because of substantial groundwater inputs, the Daly River and its largest tributary, the Katherine River, are both Class 3 perennial rivers and, thus, differ from most other northern Australian rivers (Kennard et al. 2010).

The wet-dry tropical climate is dominated by a long dry season (April–October) with minimal rainfall and high evapotranspiration, followed by a hot, humid wet season (November–March) during which 90% of the region’s rain falls. Dry-season flows are derived primarily from
ground water and average 20 m³/s at the most downstream gauging station. During these baseflow conditions, the river is considered oligotrophic and is characterized by low turbidity and high conductivity (~500 µS/cm) (Townsend and Padovan 2005). Wet-season flows are highly variable but can be >4000 m³/s during monsoonal events. During this time, the river is considered mesotrophic and is characterized by high turbidity, warmer temperatures, low conductivity (~100–200 µS/cm), and high stream velocities (Townsend and Padovan 2005). The upstream limit of tidal influence during the dry season occurs 105 km upstream of the river mouth. This influence is restricted to tidal changes in depth, and the salt-water wedge does not encroach >30 km upstream during the dry season.

Study sites

We selected 7 sites along a distance gradient from the estuary in the Daly River catchment (Fig. 1). Four sites were on the main stem of the river between 92 to 298 km from the river mouth at elevations between 1.23 and 40.31 m Australian Height Datum (AHD) (Table 1). We could not sample closer to the Daly River mouth because of substantial logistical constraints including: large (5–6 m) tidal variation, inaccessibility requiring long-distance travel by boat, and increasing risk of encountering large estuarine crocodiles. One site was on the Katherine River 405 km from the Daly River mouth (86.36 m AHD). We considered this site part of the main stem of the river. Two other sites were on the Edith and the Fergusson Rivers, small tributaries of the Daly River both ~380 km from the Daly River mouth at an elevation of ~100 m AHD. The Edith River is a predominantly perennial stream, and the Fergusson River is an intermittent river that becomes a series of disconnected in-stream pools during the dry season (hereafter, we refer to rivers by site code; main stem sites have a prefix of R followed by the
distance from the river mouth, and the Edith and Fergusson are T379 and T377 respectively; Table 1). We also chose sites based on accessibility and proximity to stream gauging stations so hydrographic records could be obtained. We were unable to sample some sites because of wet season flooding and road damage (February: R298; March: R92, R178, R113, and T379).

Field sampling method

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

We ran a pilot study to test trap 3 trapping periods (1700–2100 h, 0800–1700 h, and 1700–0800 h) and 2 bait types (chicken laying pellets and dried cat food) in paired traps. Chicken food was the most effective (size range and number) bait, and 1700–0800 was the most suitable trapping period. Therefore, we baited traps with chicken laying pellets and deployed the traps from ~1700 to 0800 h, giving an approximate soak time of 15 h (effective for only 12 h because prawns were not active during daylight hours). We anaesthetised prawns after capture (clove oil; Coyle et al. 2005), measured them (see below), placed them in a 70-L aerated bucket until recovery, and then released them near the point of capture.
At each site, we made triplicate water-quality measurements (water temperature, pH, conductivity, dissolved O₂ concentration and % saturation) at the surface (0.15 m) and at the river bed (if depth was >1 m) at each site using a Hydrolab Quanta multiprobe (Hach Corp., Loveland, Colorado). We measured turbidity (NTU) at the surface using a Hach Turbidimeter. At each trap location, we measured depth (to nearest 0.01 m) and velocity (to nearest 0.1 m/s) with a FP100 flow probe (Global Water, College Station, USA). We obtained stream-discharge and stage-height records for the nearest gauging station from the Northern Territory Department of Land and Resources Management.

**Biological variables**

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

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

We identified males by the presence of the gonopores on the base of the 5ᵗʰ pereiopod and the appendix masculina on the inside of the 2ⁿᵈ pleopod, and we identified females by the
lack of an appendix masculina and the presence of the gonopores at the base of the 3rd set of pereiopods (Short 2004). Sex determination was difficult and unreliable for individuals <45 mm long, these sex-indeterminate individuals were grouped as post-larvae.

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

Analysis

We used principal components analysis (PCA) to examine spatial and temporal variation in environmental descriptors (temperature, turbidity, conductivity, pH, dissolved O2, minimum depth, maximum depth, and discharge [average discharge for the period between sampling occasions]). Turbidity was extremely right skewed, and neither log(x) nor √(x) transformation improved the skew, so data were rank transformed. We range-normalized all variables using the equation \( z = (x - \mu)/\sigma \), where \( z \) is the standard score, \( x \) is the raw score, \( \mu \) is the mean, and \( \sigma \) is the standard deviation.

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

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

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

$$p = 1/(1 + \exp[-r(TL - Tlm)])$$

(Eq. 1)

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

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

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

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

We used a 2-way ANOVA to test whether K differed among sites, seasons, or the site × season interaction. We analyzed male and female condition factor separately and included only data from R113, R178, R405, and T377 from the months October 2011 to October 2012 (excluding March 2012). We excluded other sites and months from the analysis because of missing data as a result of accessibility issues. We used linear regression to test for the
relationship between distance from the river mouth and mean condition factor.

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

RESULTS

Environmental data

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

Changes in population structure

Relative abundance of male and female prawns varied significantly throughout the 13-mo period and across sites (3-way interaction with site, sex, and month, Wald stat = 53.46, df = 1980, p = 0.01). Abundance of both sexes varied significantly with increasing distance from the estuary (Fig. 3A). Relative abundance of females declined strongly with increasing distance from the estuary ($R^2 = 0.91, p = 0.001$), whereas male relative abundance did not ($R^2 = 0.02, p = 0.74$).
Female relative abundance peaked in the wet season (December: 1.79 ± 0.18 [SE]/trap), whereas male relative abundance peaked in the middle of the dry season (June: 1.3 ± 0.16/trap) (Fig. 4A). Female relative abundance declined throughout the remainder of the sampling period. In contrast, male relative abundance remained relatively high throughout the year. Relative abundance of post-larvae (sex indeterminates <45 mm TL) peaked twice, once in November–December and again in May–June. Relative abundance of post-larvae declined strongly with increasing distance from the river mouth ($R^2 = 0.915, p < 0.001$). Only 1 post larva was captured at R405 and none at T377 and T379.

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

### Changes in reproductive patterns

Reproduction for *M. spinipes* was strongly seasonal. The reproductive season extended from November to April (Fig. 4C). The largest proportion of reproductive females occurred in December and January (Fig. 4C) when female relative abundance was greatest (Fig. 5). Relative abundance of reproductive females increased at all sites throughout the wet season and peaked in
January. Females in reproductive condition were absent from the river during the dry-season months of May, June, July, and August (Fig. 4C). Reproductive maturation stages shifted gradually throughout the reproductive period from the initial high number of DO females to dominance of DO/RS females, and eventually only RS females (Fig. 5). Early in the reproductive period (November and December) females in DO condition predominated (up to 80%) at all sites. During peak relative abundance of reproductive females in January, ovigerous females in both early and late stages (BO and BB) of development were present at all sites. Females in DO/RS reproductive stage were most prevalent at this time. Relative abundance was much lower in February, but BO and BB ovigerous females dominated at all sites. Reproduction had finished by April when only the only reproductive females were in RS stage.

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

**Condition factor**

The body condition of both males and females increased significantly during the wet season (Fig. 4E). Female condition was highest in February (1.3 ± 0.06; from a low in October of 0.94 ± 0.03) and in the sites closest to and furthest from the river mouth (2-way interaction: $F = 4.24, df = 30, p < 0.001$; Fig. 3D). Female body condition was not significantly related to distance from the estuary ($R^2 = 0.18, p = 0.83$). Male body condition was highest 3 mo earlier, in
November (1.25 ± 0.03; 2-way interaction: $F = 5.25$, df = 30, $p < 0.001$), and was highest at the sites farthest from the mouth, but this relationship was not significant ($R^2 = 0.23$, $p = 0.26$).

Female and male body condition reached the low point in August (0.73 ± 0.03 and 0.99 ± 0.19, respectively).

**DISCUSSION**

**Reproduction**

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

We predicted that female *M. spinipes* would undergo downstream migration during the reproductive season to hatch larvae in or close to the estuary. We also expected that this...
migration would be detected as an observed decrease in the relative abundance of females in the upstream reaches and an increase in the downstream reaches (Bauer and Delhousaaye 2008, Raman 1967, Olivier and Bauer 2011). However, we did not observe a reduction in the relative abundance of reproductive females in upstream river reaches during the breeding season. Instead, the relative abundance of females increased at all sites during the reproductive season. We cannot conclusively say, without mark–recapture studies, that the females are not migrating downstream to hatch larvae, but our results suggest that female *M. spinipes* are reproducing along the length of the river. This type of reproductive behavior is more common in short, high-gradient rivers of up to 150 km in length, where larvae are likely to be transported downstream to the estuary in a matter of days (March et al. 1998, Bauer 2011b, Bertini et al. 2013). However, in a river as long as the Daly, the high relative abundance of reproductive females at the most upstream site sampled (405 km from the estuary) was unexpected. Furthermore, the Daly River is low gradient (~0.015%), and a flood wave can take 5 d to travel just 200 km through the middle reaches (Paiva 2000). Thus, if larval survival times of *M. spinipes* are similar to those of other species, then it is unlikely that larvae released far upstream will reach the estuary within the critical period observed in other river systems (Rome et al. 2009, Lal et al. 2012). Ovigerous females at the Daly River upstream sites might potentially move downstream rapidly to hatch their ova near the estuary, but the presence at upstream sites of females for which hatching was imminent or had occurred very recently suggests this scenario of rapid downstream movement is unlikely and that larvae had hatched and were released to the water at these sites. Olivier and Bauer (2011) observed breeding *M. ohione* females up to 400 km upstream in the Mississippi River, and in contrast, observed a significant migration of females downstream to breed in the adjacent Atchafalaya River. They also found yearly variation in the strength of the downstream
migration, which may suggest that the mechanics of the migration vary temporally and spatially over time and could be specific to individual rivers. Thus, the lack of migration we observed in the Daly River might possibly be related to yearly changes in environmental conditions. Another possibility is that *M. spinipes* larvae have a longer survival time in freshwater than do other shrimps, and thus, can survive the long drift time. Perhaps the larvae released at the upstream sites do not make it to the estuary and develop any further. A final possibility is that amphidromy for *M. spinipes* may be facultative rather than obligate. Further investigations to evaluate the amphidromous nature of *M. spinipes* are required and could include laboratory studies of freshwater tolerance by larvae (e.g., Rome et al. 2009). We are currently undertaking such research for this species as part of a larger study.

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

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

The 2nd peak in relative abundance of males, females, and post-larvae occurred in May and June, 2 mo after the reproductive season concluded. The abundance of post-larvae dropped rapidly with increasing distance from the estuary, and this observation combined with an increasing average length of males and females with increasing distance from the estuary suggests directional movement of recruitment. In support of this notion, we observed a mass
migration similar to that reported by Bauer and Delahoussaye (2008) (*M. ohione*) and Lee and Fielder (1979) (*Macrobrachium australiense*) of *M. spinipes* juveniles in April and May (PN, personal observation). A strong seasonal pulse of recruitment, often associated with mass migration, has been observed for a number of other amphidromous *Macrobrachium* species (Raman 1967, Etim and Sankare 1998, Bauer and Delahoussaye 2008, Kikkert et al. 2009). We propose 2 probable causes for the strong seasonality of recruitment. First, strong seasonality of reproduction creates a cohort of post-larvae in the estuary ready to migrate. Second, recruitment occurs during periods of high flow, so the migration upstream is strongly tied to the declining limb of the hydrograph because lower flows at this period make the upstream journey easier (Bauer and Delahoussaye 2008, Kikkert et al. 2009, Bauer 2011b). Multiple peaks in upstream migration were observed for species that reproduce year round, but each peak followed a flow event (Benstead et al. 2000).

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

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

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

We thank the following people for assistance in the field: Joanne O’Connor, Guillaume Puig, Celenie Christophe, Frank Nicol, Nina Trikojus, Liam Golding, Ben Croser, Mark Grubert, Emma Ligtermoet, and Nathalie Mauraud. We also thank Emma Ligtermoet for proof reading the manuscript and Damien McMaster for creating the site map. Funding was provided for this project by the National Environmental Research Program – Northern Australia Hub and the Northern Territory Government Research and Innovation Scholarship.
LITERATURE CITED


Mancinelli, G., F. Sangiorgio, and A. Scalzo. 2013. The effects of decapod crustacean
macroconsumers on leaf detritus processing and colonization by invertebrates in stream


March, J. G., and C. M. Pringle. 2003. Food web structure and basal resource utilization along a

shrimp assemblages on benthic communities along an altitudinal gradient of a tropical

McDowall, R. M. 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. Fish
and Fisheries 8:1–13.

setting the record straight. Fisheries 31:236–238.

Ng, P. K. L., and D. Wowor. 2011. On the nomenclature of the palaemonid names *Palaemon
spinipes* Desmarest, 1817, *Palaemon spinipes* Schenkel, 1902, and *Macrobrachium

Olivier, T. J., and R. T. Bauer. 2011. Female downstream-hatching migration of the River
Shrimp *Macrobrachium ohione* in the Lower Mississippi River and the Atchafalaya

Olivier, T. J., K. Q. Handy, and R. T. Bauer. 2013. Effects of river control structures on the
juvenile migration of *Macrobrachium ohione*. Freshwater Biology 58:1603–1613.


FIGURE CAPTIONS

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

Fig. 2. Principal components analysis of environmental data collected from all sites separated into 4 seasons: wet (November–January), early dry (April, May), mid-dry (June–August), and late dry (September, October). The variation explained by each axis is in parentheses after the axis name and the variable names and eigenvectors (in parentheses), for the most correlated variable for each axis have been included. Cond = specific conductivity, Temp – water temperature, DO = dissolved O₂.

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

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

Fig. 5. Percentage of females in each reproductive stage and relative abundance (RA) of females in November (A), December (B), January (C), February (D), and April (E). DO = developing ovaries, BO = ovigerous, ova to hatch within 2 wk, BB = ovigerous, ova to hatch within 24 h, RS = ova recently hatched, DO/RS = ova had recently hatched and developing further ova.
Table 1. Sites position and distance from the Daly River mouth. Elevation data are the 0 gauge level of the gauging station closest to the site. AHD = Australian height datum.

<table>
<thead>
<tr>
<th>Site name</th>
<th>Site code</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation* (m AHD)</th>
<th>Distance from mouth (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wooliana</td>
<td>R92</td>
<td>13°46'09.99&quot;S</td>
<td>130°42'51.13&quot;E</td>
<td>1.23</td>
<td>92</td>
</tr>
<tr>
<td>Mt Nancar</td>
<td>R113</td>
<td>13°49'34.30&quot;S</td>
<td>130°43'49.15&quot;E</td>
<td>1.46</td>
<td>113</td>
</tr>
<tr>
<td>Beeboom</td>
<td>R178</td>
<td>13°51'43.89&quot;S</td>
<td>131°04'29.20&quot;E</td>
<td>13.32</td>
<td>178</td>
</tr>
<tr>
<td>Claravale</td>
<td>R298</td>
<td>14°21'47.50&quot;S</td>
<td>131°33'24.12&quot;E</td>
<td>40.31</td>
<td>298</td>
</tr>
<tr>
<td>Katherine R</td>
<td>R405</td>
<td>14°32'52.64&quot;S</td>
<td>132°07'47.47&quot;E</td>
<td>86.36</td>
<td>405</td>
</tr>
<tr>
<td>Fergusson R</td>
<td>T377</td>
<td>14°04'16.92&quot;S</td>
<td>131°58'25.31&quot;E</td>
<td>(N/A)</td>
<td>377</td>
</tr>
<tr>
<td>Edith R</td>
<td>T379</td>
<td>14°13'49.83&quot;S</td>
<td>131°55'37.39&quot;E</td>
<td>101.80</td>
<td>379</td>
</tr>
</tbody>
</table>
Table 2. Mean and SE of environmental variables for the study period. Wet = all data from November to April, dry = all months from May to October. Temp = temperature, DO = dissolved O2.

<table>
<thead>
<tr>
<th>Site</th>
<th>Conductivity (mS/cm)</th>
<th>pH</th>
<th>Temp (°C)</th>
<th>DO (mg/L)</th>
<th>Turbidity (NTU)</th>
<th>Depth (m)</th>
<th>Discharge (m³/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dry</td>
<td>Wet</td>
<td>Dry</td>
<td>Wet</td>
<td>Dry</td>
<td>Wet</td>
<td>Dry</td>
</tr>
<tr>
<td>R92</td>
<td>0.53</td>
<td>0.28</td>
<td>8.16</td>
<td>7.89</td>
<td>26.4</td>
<td>30.3</td>
<td>6.94</td>
</tr>
<tr>
<td>SE</td>
<td>0.01</td>
<td>0.03</td>
<td>0.04</td>
<td>0.12</td>
<td>0.69</td>
<td>0.51</td>
<td>0.22</td>
</tr>
<tr>
<td>R113</td>
<td>0.53</td>
<td>0.31</td>
<td>8.16</td>
<td>7.94</td>
<td>26.2</td>
<td>30.3</td>
<td>7.00</td>
</tr>
<tr>
<td>SE</td>
<td>0.01</td>
<td>0.03</td>
<td>0.04</td>
<td>0.10</td>
<td>0.66</td>
<td>0.45</td>
<td>0.22</td>
</tr>
<tr>
<td>R178</td>
<td>0.54</td>
<td>0.35</td>
<td>8.06</td>
<td>7.84</td>
<td>27.0</td>
<td>30.7</td>
<td>7.03</td>
</tr>
<tr>
<td>SE</td>
<td>0.03</td>
<td>0.03</td>
<td>0.02</td>
<td>0.09</td>
<td>0.71</td>
<td>0.30</td>
<td>0.20</td>
</tr>
<tr>
<td>R298</td>
<td>0.51</td>
<td>0.24</td>
<td>8.03</td>
<td>7.61</td>
<td>25.7</td>
<td>30.8</td>
<td>7.52</td>
</tr>
<tr>
<td>SE</td>
<td>0.02</td>
<td>0.04</td>
<td>0.05</td>
<td>0.11</td>
<td>0.69</td>
<td>0.32</td>
<td>0.12</td>
</tr>
<tr>
<td>R405</td>
<td>0.39</td>
<td>0.10</td>
<td>7.82</td>
<td>7.27</td>
<td>26.6</td>
<td>30.3</td>
<td>6.98</td>
</tr>
<tr>
<td>SE</td>
<td>0.03</td>
<td>0.01</td>
<td>0.02</td>
<td>0.07</td>
<td>0.65</td>
<td>0.25</td>
<td>0.23</td>
</tr>
<tr>
<td>T377</td>
<td>0.04</td>
<td>0.03</td>
<td>7.31</td>
<td>7.17</td>
<td>26.2</td>
<td>29.3</td>
<td>7.16</td>
</tr>
<tr>
<td>SE</td>
<td>0.00</td>
<td>0.00</td>
<td>0.06</td>
<td>0.08</td>
<td>0.76</td>
<td>0.24</td>
<td>0.15</td>
</tr>
<tr>
<td>T379</td>
<td>0.02</td>
<td>0.02</td>
<td>6.94</td>
<td>7.03</td>
<td>24.0</td>
<td>28.5</td>
<td>6.91</td>
</tr>
<tr>
<td>SE</td>
<td>0.00</td>
<td>0.00</td>
<td>0.09</td>
<td>0.09</td>
<td>0.72</td>
<td>0.32</td>
<td>0.20</td>
</tr>
</tbody>
</table>

*Measured for only 2 mo because of equipment failure