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Title: Do upstream migrating, juvenile amphidromous shrimps, provide a marine subsidy to river ecosystems?

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Summary

1. The upstream migration of juvenile amphidromous shrimps have been proposed as a source of marine or estuarine derived nutrients into freshwater. Although little is known about the size and ecological importance of any such subsidy as there have been few observational or empirical studies on the topic.
2. We investigated the upstream migration of the amphidromous shrimp, *Macrobrachium spinipes* (Schenkel, 1902) in the Daly River, of tropical northern Australia, to determine migration phenology, estimate migration biomass and determine whether migrating shrimps transport marine-derived energy and nutrients upstream.
3. Field observations over two years revealed that juvenile *M. spinipes* migrate upstream en masse during extended periods of declining discharge over a period of 4–6 weeks during the wet season (March–May). In addition, juvenile shrimps from the genus *Caridina* were also observed migrating upstream during the same period.
4. Fine-scale sampling using fyke nets over two years (2013 and 2014) consistently found discharge to be the strongest predictor of *M. spinipes* and *Caridina* spp. biomass, while moon illumination and cloud cover were also important predictors. An estimated 10–20 million shrimps migrated upstream during each wet season, transporting ~100 kg of carbon and ~28 kg of nitrogen per year.
5. Muscle sulphur stable isotopes ($\delta^{34}S$) and exoskeleton strontium isotope ratios ($^{87}Sr/^{86}Sr$) were used to establish if marine carbon was transported upstream by the juvenile *M. spinipes*. Isotope data from migratory *M. spinipes* were compared to the non-migratory freshwater *M. bullatum*. No evidence of a marine signature in body tissue or exoskeleton was found using either technique, suggesting very rapid turnover of body tissues
6. This study provides key insights into the migration phenology of amphidromous shrimps and, importantly, suggests that migrating *M. spinipes* do not transport significant amounts of marine-derived energy and nutrients across the marine/freshwater ecotone.

Introduction

Migratory species in aquatic systems play a vital role in food web ecology and the maintenance of biodiversity. They are widely acknowledged to provide both process and material subsidies to ecosystems (Polis, Anderson & Holt, 1997; Flecker *et al.*, 2010). Process subsidies occur when the behaviour of a migratory species (e.g. grazing, predation, nutrient cycling, physical alteration of stream beds, *inter alia*) influences or substantially controls the dynamics of ecosystem processes in the receiving ecosystem (Crowl *et al.*, 2001; Janetski *et al.*, 2009; Flecker *et al.*, 2010; Tiegs *et al.*, 2011). Material subsidies, in contrast, occur through the transport of nutrients between connected ecosystems (Polis *et al.*, 1997; Flecker *et al.*, 2010). Large-scale material subsides are likely to occur only under a limited range of circumstances such as when the biomass of the migrant is large relative to ecosystem size, the recipient system is oligotrophic, and there is an effective mechanism for releasing the nutrients (Flecker *et al.*, 2010). Salmon migrations are a good example of this, where thousands of kilograms of carbon and nitrogen are estimated to be transported upstream (Gresh, Lichatowich & Schoonmaker, 2000; Jonsson & Jonsson, 2003) and this has resulted in significant bottom-up effects on riverine and riparian communities (e.g. Helfield & Naiman, 2001; Naiman *et al.*, 2002). The contribution of smaller, but often highly abundant, migratory species to material subsidies across ecosystem boundaries is currently unclear (Flecker *et al.* 2010).

Migratory caridean shrimps (Infraorder: Caridea) are a good case study taxa for examining process and material subsidies provided by small and abundant species. Caridean shrimps exhibit a form of diadromy known as “amphidromy”, where larval development occurs in estuarine habitats, after which the post-larvae migrate upstream from the coastal environments into the freshwater reaches of rivers (McDowall, 2007; Bauer, 2013). These migrations have been reported to occur in two general categories; 1), as a short lived large pulse of shrimps, often in rivers with a well-defined annual period of high and low flow (Bauer & Delahoussaye, 2008; Olivier, Handy & Bauer, 2013) or, 2) as a longer term, relatively steady movement of a low number of individuals, often in rivers with a

less seasonally defined hydrological flow regime (Fièvet, 1999b; Benstead, March & Pringle, 2000; Kikkert, Crowl & Covich, 2009). While it has been hypothesized that the biomass of these migrations may be great enough to be an important subsidy this has not been explicitly examined (Bauer & Delahoussaye, 2008). The only evidence is from a recent study using sulphur stable isotopes which indicated that these migrations were transporting marine-derived energy and nutrients upstream (Olivier, 2013). As caridean species migrate upstream as juveniles at a very small size (Post larvae settle at 8 mg wet weight - Lober & Zeng, 2009), the extent to which they constitute a material subsidy is unclear. If the number of individuals involved is high, then, despite their small size, such migrations may potentially supply ecologically significant material subsidies.

Migratory caridean shrimps are also known to have strong ecosystem level effects. They are an important prey species for a range of fishes, influence benthic community composition, play an important role in top-down effects on periphyton production and enhance nutrient recycling (March *et al.*, 2002; Morgan *et al.*, 2004; Cross *et al.*, 2008; Benstead *et al.*, 2010). Consequently considerable ecosystem level effects occur when these consumers are no longer present in the system as a result of anthropogenic disruptions to river connectivity (Freeman *et al.*, 2003; Greathouse *et al.*, 2006). Thus, migratory caridean shrimps may constitute both a material and process subsidy.

Macrobrachium spinipes (Family: Palaemonidae) is a recently described caridean shrimp species (Ng & Wowor, 2011) and occurs throughout tropical Australasia and the Philippines (De Bruyn, Wilson & Mather, 2004; Short, 2004). Recent work has confirmed that this species is amphidromous (Novak *et al.*, 2016) and demonstrated that reproduction occurs during the wet season within freshwater and that there was no evidence of a downstream migration of females to hatch larvae (Novak *et al.*, 2015). Novak *et al.* (2015) also found that recruitment of juveniles was unidirectional, from the estuary to the freshwater, and that this recruitment occurred at the end of the wet season and early dry season. The main aim of this study was to determine the phenology, magnitude and potential

marine subsidy of an amphidromous shrimp migration in a large lowland river system. In particular, we explored the effects of tide, river discharge, and moon phase on the migration and the presence and biomass of co-migrating shrimps. Furthermore, we estimated *M. spinipes* biomass moving upstream, the amount of nitrogen and carbon transported in the migration and if there was marine-derived carbon in the shrimp's body tissue.

Methods

Study site

All observations and samples were collected in the Daly River catchment which is located in the wet/dry tropics of the Northern Territory, Australia (13°S - 16°S and 129°E - 130°30'E) and covers an area of approximately 53,000 km^2 (Figure 1). The catchment area is largely unmodified with 90% of the catchment comprising native open Eucalyptus woodland (Townsend & Padovan, 2005). There are no large dams or impoundments along the length of the river or its tributaries (Schult & Townsend, 2012). The Daly River runs for 355 km in length, rising 50 m in elevation before it splits into the Flora and Katherine Rivers (Faulks, 1998). The Katherine River is the largest tributary in the catchment, it is approximately 328 km long and rises a further 371 m in elevation (Faulks, 1998).

The wet/dry tropical climate is dominated by a long dry season (April to October) with minimal rainfall and high evapotranspiration, followed by a hot, humid wet season (November to March) during which 90% of the region's rain falls. Dry season flows are primarily derived from groundwater and average 20 m^3/s by the end of the dry season at the most downstream gauging station. Wet season flows are highly variable but can exceed 4000 m^3/s during monsoonal events (Faulks, 1998). The period immediately after the wet season is the transition period from high flows and high turbidity to low stable base flow with low turbidity and is a key period in the productivity of tropical rivers (Warfe *et al.*, 2011). The Daly River is extremely oligotrophic during the dry season (Townsend & Padovan, 2005), and consumer biomass is supported by nutrients from outside the local area (Jardine *et al.*, 2012a). The upstream limit of tidal influence (i.e. tidal depth variation) during the dry

season occurs approximately 105 km upstream of the river mouth, although incursion of saline water is restricted to <30 km upstream of the estuary mouth during the dry season.

Observations and sampling of the migration of *Macrobrachium spinipes* was conducted at the Daly River Crossing (13° 46' 00.18"S and 130°42' 39.27"E) (hereafter referred to as the crossing) approximately 105 km upstream from the river mouth (Figure 1). Observations from the crossing suggested a nocturnal upstream movement of juvenile shrimps along the edges of the river, consistent with reports of similar migrations elsewhere for related species (e.g. Raman, 1967; Bauer & Delahoussaye, 2008; Kikkert *et al.*, 2009). At the sampling site shrimps were observed actively swimming just below the surface, similar to observations by Bauer & Delahoussaye (2008). Preliminary investigations by the authors at the Daly Crossing and R178 observed no shrimps migrating (or otherwise) during day light hours. In addition, the crossing is the most downstream location accessible year-round. The site consisted of a large sand bar (approximately 700 m long) on the right bank, a steep sided and vegetated left bank and a road causeway crossing the river (Figure 1). During low flow conditions the causeway creates a constriction in flow and funnelled the shrimps along the bank were they could be observed easily.

Migration phenology

A pilot study consisting of monthly nocturnal observations and sweep netting conducted from 2011 to 2013 identified that the migration of shrimps occurred at the end of the wet season as discharge declined and stabilised. This time period was consequently targeted for fine scale sampling of the migration using fyke nets to: 1) quantify the migration rate over the nocturnal period; 2) determine the composition of the migration in-terms of the number of *M. spinipes* and other migrating shrimps (identified as *Caridina* spp.); 3) determine the influence of environmental variables on the migration, including abundance, mean length and weight of migrating *M. spinipes*; and 4) estimate the biomass of shrimps migrating upstream throughout the sampling period. Fyke nets were selected to sample the migration as they are a proven method for sampling directional movement (see Pattrick &

Strydom, 2014). In this study the migration was observed in the shallow, near bank environment where fyke nets could be effective. It is possible that shrimps may have been migrating in the deeper water across the full width of the river, while we feel that this is unlikely, the estimates provided in this study may represent a lower estimate of biomass migrating upstream.

Sampling was conducted over the 2013 and 2014 wet seasons, and to determine the variation in migration rate throughout the night, across three time periods; 20:00-21:00, 23:00-00:00 and 05:00-06:00. Sampling commenced when the decline in river water level was stabilising and concluded when migrating shrimps were no longer observed and the biomass captured by the fyke nets was insignificant.

In 2013, sampling was completed over three weeks with fyke nets set on 27 occasions including 11 each at 20:00–21:00 and 05:00–06:00 and five at 23:00–00:00. In 2014, sampling continued for six weeks, fyke nets were set on 39 occasions and included 14 each at 20:00–21:00 and 05:00–06:00, and 10 at 23:00–00:00. One additional sample was collected at 03:00–04:00.

Three fyke nets (length = 2 m, two internal funnels, two 2 m wide wings all with a mesh of 2 mm), were set 35 m apart on the banks of a large sandbar approximately 400 m upstream of the Daly River Crossing (Figure 1). The nets were set adjacent to the bank in water 0.5 m deep for 30 minutes on each occasion. Different sampling length periods were trialled and 30 minute sets provided sufficient capture rates without unnecessary mortality to the migrating shrimps. Each sample was sorted to remove inorganic and organic debris, placed in a pre-weighed 0.5 mm mesh bag, hung to drain for 20 seconds and then weighed (to 0.1 g) on a Wedderburn UWHGM4000 balance (Wedderburn, Sydney, Australia).

On each sampling occasion observations of cloud cover, tide, moon position and phase were recorded at the site. The depth gauge closest to the site was damaged early in the 2013/2014 wet season and no longer recorded low flows and so in March 2014, a depth reference point was

constructed by hammering a steel picket into the river bank. Depth measurements were made at the picket at the end of every fyke net set. Water quality measurements including; conductivity, temperature, turbidity, pH, dissolved oxygen (% saturation and mg/L) were collected at the depth reference point on one occasion every night using a Quanta (Hydrolab, Loveland, Colorado).

To determine the species composition in each fyke sample, a 20–30 g subsample (consisting of approximately 400 individuals but sometimes >1000 depending on size of individuals and species composition) was collected. In 2013 subsamples were randomly collected from the fyke samples (n = 29 of 81 fyke samples), in 2014 all fyke samples were subsampled (n = 117). The subsampled prawns were then euthanized using clove oil (Coyle *et al.*, 2005) and stored on ice. The remaining prawns were released alive upstream of the point of capture. Upon return to the laboratory the number of individuals and collective weight of *M. spinipes* or *Caridina* spp. was determined for each subsample and then subsequently scaled to represent the totals collected per 30 minutes sampling. *Macrobrachium spinipes* could be easily distinguished from the *Caridina spp*. during laboratory processing by the much larger eye for a given size, by colouration (*M. spinipes* had a visible dark spot near the base of each pleuron), and, for larger specimens, the visible presence of chela on the second pereiopod.

Further details on *M. spinipes* length, weight and nutrient composition were collected in 2014. Fifteen individuals from each subsample were randomly selected and measured (total length - 1 mm, tip of the rostrum to the end of the telson), weighed (to 0.001 g), dried at 60°C for 24 hours and reweighed (to 0.001 g). Total nitrogen and carbon content of the migrating *M. spinipes* was determined by randomly selecting 30 individuals from the dried specimens described above, 10 from the first week, 10 from the mid three weeks and 10 from the final two weeks. The samples were analysed using the method described for stable isotope analysis below.

Analysis

To determine the influence of environmental variables on the migration biomass (of both *M. spinipes* and *Caridina* spp.) a multiple regression analysis was performed. The potential explanatory variables were selected on the basis of an *a priori* hypothesis that light, discharge, tide and rainfall could each affect the number of migrating shrimps (Table 1).

A correlation matrix was constructed to determine relationships between independent variables. Most independent variables were weakly correlated (r = 0.028–0.31), however, hours since sampling began, water level, and variables describing discharge were highly correlated (r > 0.9). Due to the high correlation between these variables, all variables except 'previous 24 hour's mean discharge' were removed. In the 2013 migration, the model included only five variables; rainfall was removed as no rain was recorded over the sampling period. The dependant variable here was total migrating biomass. In the 2014 migration the regression model included all six predictor variables (rainfall was included) which were used to predict three separate dependant variables: total biomass per set, *M. spinipes* biomass and *Caridina* spp. biomass. Total biomass for each sampling point was calculated by summing the biomass of the three fyke samples. *M. spinipes* and *Caridina* spp. biomass was calculated first for each fyke sample as a proportion of each subsample and was then scaled up to represent the whole sample. The estimates of the three fyke nets were then combined to give a total biomass estimate for *M. spinipes* and *Caridina* spp.

The migration rate data were log10 transformed to satisfy the assumptions of normality and variance homogeneity inherent in linear regression analysis. To determine the best set of predictors for each of the dependant variables we used best subsets multiple regression analysis. To avoid the over parameterisation of the model, Mallows C_p was used to (Mallows, 1973; Quinn & Keough, 2002) to select the best regression models (i.e., high model fit relative to the number of predictor variables). Standardised slope parameter estimates (r*) are given as these equate to the correlation co-efficient for each independent variable. Partial regression slope analysis outputs are given to determine the significant independent variables in each of the best subset models.

To determine if there were significant differences in mean length and weight of migrating *M. spinipes* between sampling weeks in 2014, a nested ANOVA was used. Samples were nested in each week. The raw data provided the best approximation to the assumption of ANOVA and so were used in this analysis. Pairwise comparisons between weeks were completed using Bonferonni post hoc comparisons.

Stable isotopes, strontium analysis and biomass estimate

During 2012, samples of migrating *M. spinipes* were collected from three sites in the Daly River, from 100, 150 and 300 km from the river mouth, to determine how far upstream marine-derived body tissue could be detected. Individuals collected during the 2014 migration were analysed for total nitrogen and carbon content to determine the upstream nutrient content. Muscle tissue for three individuals from each site plus three individuals from the non-migratory freshwater species *Macrobrachium bullatum* were processed for the analysis by drying at 60°C for 24 hours and ground to a fine power before analysis for sulphur (S), carbon (C) and nitrogen (N) stable isotope ratios. The samples collected from the 2014 migration to determine nitrogen and carbon transport upstream were analysed for total carbon and nitrogen content using the same method. Samples were combusted in an EA 3000 elemental analyser (Eurovector, Milan, Italy) and sample gases delivered to an Isoprime mass spectrometer (GV Instruments, Manchester, UK) for isotope analysis of C, N and S. Working standards were liquids calibrated against IAEA CH6, CH7, N1, N2, and NBS-127 and data are presented as parts per thousand deviations from international standards (Peedee Belemnite Carbonate, Atmospheric Nitrogen, Canyon Diablo Triolite).

In addition to using sulphur stable isotopes to detect a marine signature we analysed the strontium isotope ratio ($^{87}Sr/^{86}Sr$), a technique commonly used for detecting marine signatures in fish otoliths (Crook et al. 2015). Decapod exoskeletons are also constructed from a calcium carbonate matrix (Soejoko & Tjia, 2003) and analysis of $^{87}Sr/^{86}Sr$ in exoskeletons of shrimps could also be useful for detecting marine signatures. A limitation, however, is the growth and ecdysis in decapods, whereby

the exoskeleton is shed and replaced, and the calcium carbonate matrix is therefore lost or reworked. In freshwater *Macrobrachium,* calcium is generally resorbed into the body tissues during ecdysis and then used to harden the new exoskeleton post-moult. As a consequence, shrimps retain the majority of its calcium stores during the moulting process (Fieber & Lutz, 1982) and are likely to retain marine $^{87}Sr/^{86}Sr$ in the exoskeleton for a number of moults following transition into fresh water.

Shrimp $^{87}Sr/^{86}Sr$ analysis was conducted using rostrums from the same individuals used in the sulphur isotope analysis. The rostrums were dried at 60°C for 24 hours, mounted to a slide using double sided tape before analysis. The analysis was undertaken using a multi-collector laser ablation inductively coupled plasma mass spectrometer (LA-ICPMS) operated by the University of Melbourne using methods comprehensively detailed in Crook, Wedd and Berra (2015). Each sample was analysed over a 40 second ablation period using laser spot size of 93 nm, a repetition rate of 5 Hz and a laser energy of approximately 90 mJ.

Water $^{87}Sr/^{86}Sr$ data were obtained from samples collected as a part of a separate project (Crook *et al.*, 2016) along an upstream gradient from the river mouth to 405 km upstream. Samples were collected once during the wet season (8 sites, between the 5-13th March 2013) and once during the dry season (12 sites, between the 26th September to the 7th November 2012). Sr isotope analyses were carried out on a Nu Plasma multi-collector ICPMS (Nu Instruments, Wrexham, UK) interfaced with an ARIDUS desolvating system operated by the University of Melbourne (detailed methods outlined in (Crook *et al.*, 2016)).

Analysis

To estimate the biomass of migrating shrimps (*M. spinipes* and *Caridina* spp.), a linear regression model (model 1) was developed using discharge as the predictor. Discharge was chosen for this purpose as it was, in both 2013 and 2014, the strongest predictor of migration rate. Despite the

absence of the other environmental variables in the model, it provided a general estimate of the biomass migrating upstream. In developing the model, biomass for each sampling night was estimated by calculating the mean of the three night samples and using this mean as the biomass for each 30 minute block over the night (from 19:30 to 06:30). When there were only two samples for the night (21:00 and 06:00) the mean of the two midnight samples obtained in each sample block was used. The daily biomass estimate and mean daily discharge (m^3/sec) was then used to determine a regression equation. This equation was used to predict the daily biomass for the days not sampled during the migration period. The model fit reported here was calculated by regression analysis of the estimated daily biomass (calculated from the fyke samples) and the predicted daily biomass.

A second biomass estimate (model 2) was determined by simply calculating the mean migration rate for each sampling time (30 minute blocks) and using this as an estimate of the migration rate throughout the migration period. A nightly migration rate was calculated and extrapolated for the entire migration period. Confidence intervals (95%) were calculated for the mean, and these are presented with the final biomass estimate.

The biomass estimates from both methods were then multiplied by two as the migration was observed on both sides of the river. From the estimated biomass the following outputs were calculated: dry weight, total carbon, total nitrogen, total number of individuals, total number of *M. spinipes* and total number of *Caridina* spp.

Results

Migration phenology

The migration pattern in 2013 was highly variable, especially in the first week of sampling. The general trend showed a decline in migration biomass throughout the sampling period (Figure 2). The trend in migration biomass was best explained by previous 24 hours mean discharge and moon

illumination (R^2=0.632, p<0.001). Of these two variables, mean previous 24 hours discharge was positively correlated (r* = 0.86, p<0.001) with migrating biomass, while moon illumination was negatively correlated (r*=-0.221, p=0.094).

From the 29 subsampled fyke net samples, *M. spinipes* was dominant by biomass but not by the number of individuals with *M. spinipes* constituting 72.9% of the biomass captured. More individual *Caridina* spp. were captured with an estimated 83,942 (63.3%) caught compared to the 48,580 (36.6%) *M. spinipes*.

In contrast to 2013, the migration pattern in 2014 was highly variable both within 24 hours and over the entire 6 week sampling period (Figure 3a). The best model describing total migration biomass included all six predictor variables: previous 24 hours discharge, moon illumination, time of night, cloud cover, tide and rainfall (R^2 = 0.661, p < 0.001). The first four predictors also had significant partial regression slopes (Table 2). Previous 24 hours discharge was the strongest predictor (r* = 0.616, p < 0.001) and was positively correlated to migration biomass. Of the three remaining significant predictors, time of night (r* = 0.247, p = 0.023) and moon illumination (r* = 0.397, p < 0.001) were both positively correlated to migration biomass while cloud cover (r* = -0.243, p = 0.018) was negatively correlated.

Macrobrachium spinipes was the dominant migrant during the 2014 migration period in terms of both biomass and numbers of individuals. From the 39 trapping occasions (117 fyke sets) *M. spinipes* constituted over 83.6% of the biomass captured and more than 67% of the total number (*M. spinipes* and *Caridina* spp.) of migrating individuals.

The pattern of *M. spinipes* migrating biomass was similar to that observed for total biomass; highly variable but declining over the sampling period (Figure 3b). The model best explaining *M. spinipes* biomass had five predictor variables including; discharge, moon illumination, time of night, cloud cover, and rainfall (R^2 = 0.603, p < 0.001). Three of the predictor variables, previous 24 hours

discharge, time of night and moon illumination had significant partial regression slopes. Previous 24 hours discharge was the strongest predictor and was positively correlated to *M. spinipes* biomass ($r^* = 0.597$, $p < 0.001$) (Table 2). Of the remaining two significant predictors both time of night ($r^* = 0.341$, $p = 0.003$) and moon illumination ($r^* = 0.417$, $p < 0.001$) were both positively correlated to *M. spinipes* migration biomass (Table 3).

Migrating *Caridina* spp. biomass increased during the first week of sampling and peaked during week 4, but remained highly variable throughout the sampling period (Figure 3b). The migration appeared to finish by week 5 (April) with the biomass (total biomass from the three fykes) reduced to 1.4 g/30 minutes from a high of 432.5 g/30 minutes during week 4. The best fit model included four predictor variables including; discharge, tide, moon illumination and cloud cover ($R^2 = 0.550$, $p < 0.001$). All four had significant partial regression slopes and the standardised regression coefficients suggested that discharge was the strongest predictor ($r^* = 0.473$, $p = 0.001$) (Table 2). Discharge, tide ($r^* = 0.423$, $p < 0.001$) and moon illumination ($r^* = 0.296$, $p = 0.012$) were all positively correlated with biomass while cloud cover ($r^* = -0.241$, $p = 0.040$) was negatively correlated (Table 2).

Macrobrachium spinipes length and weight

Length and weight of migrating *M. spinipes* varied significantly between sampling weeks ($F_{5,1690} = 132.13$, $p < 0.001$; $F_{5,1690} = 79.90$, $p < 0.001$; and $F_{5,1690} = 17.82$, $p < 0.001$ respectively). Length and weight were significantly higher in the first week than all other weeks ($p < 0.001$; $p < 0.001$; and $p < 0.001$ respectively). Length and weight at week 3 were second highest and significantly different from all other weeks ($p < 0.001$ and $p < 0.021$ respectively). After week 3 mean length and weight both declined and remained low through week 4, 5 and 6 (Figure 4a and b).

Transport of marine carbon

Mean δS^{34} for migrating *M. spinipes* was 12.347 ± 0.48‰ (SE) (Figure 5) and mean carbon δC^{13} was -25.469 ± 0.475‰ (SE). The non-migratory, freshwater *M. bullatum* was sampled for comparison; the mean δS^{34} for these samples was 15.5±0.41‰ (SE) and carbon δC^{13} was -26.16 ±0.53‰ (SE).

Mean $^{87}Sr/^{86}Sr$ in the rostrums of migrating *M. spinipes* was 0.7275 (±0.0006SE); consistently above the marine/estuarine water values recorded in both the wet and dry season (Figure 6). Water $^{87}Sr/^{86}Sr$ at the river mouth was 0.7093 in both the wet and dry season, close to the global marine ratio of 0.7091. $^{87}Sr/^{86}Sr$ in the freshwater reaches of the Daly River was consistently higher in the wet season (0.7318 - 0.7330) than in the dry season (0.7161 – 0.7194) (Figure 6). Mean $^{87}Sr/^{86}Sr$ in the rostrums of *M. spinipes* collected in the wet season from the lower freshwater reaches were slightly depressed compared with the ambient water, but closely reflected water $^{87}Sr/^{86}Sr$ at the most upstream site. These findings likely reflect retention of a small amount of marine derived Sr in the exoskeleton of prawns collected from lower reaches and a gradual loss of the marine Sr as they migrate upstream.

Estimation of migration magnitude

The two biomass estimate methods provided very similar final predictions. In 2013, model 1 estimated 530 kg of *M. spinipes* and *Caridina* spp. biomass moved upstream over the three week sampling period (Figure 7a, Table 3). Model 2 estimated 522 kg migrating biomass with a lower confidence interval (95%) of 344 kg and upper confidence interval (95%) of 700 kg. *Macrobrachium spinipes* biomass was estimated at approximately 381 kg while the *Caridina* spp. biomass approximately 141 kg. It was estimated that the migration had transported 43 kg (lower – 28 kg, upper – 57 kg) of carbon and 12 kg (lower – 8 kg, upper – 16 kg) of nitrogen upstream past the Daly River crossing. *Macrobrachium spinipes* accounts for an estimated 72.9% of the nitrogen and carbon transported upstream. While *M. spinipes* biomass was greater than *Caridina* spp. 1.6 times more individual *Caridina* spp. (8.4 million) migrated upstream compared to *M. spinipes* (5 million).

In 2014, model 1 estimated 958 kg of *M. spinipes* and *Caridina* spp. biomass moved upstream over the six week sampling period (Figure 7b, Table 4). Model 2 predicted 1,254 kg of migrating shrimps with a lower bound of 824 kg and upper bound of 1688 kg. The estimates between models varied, however the estimate provided by model 1 is within the 95% confidence intervals in model 2. *Macrobrachium spinipes* biomass was estimated at 1110 kg (lower – 726 kg, upper – 1,494 kg) while *Caridina* spp. biomass was 110 kg (lower – 94 kg, upper – 194 kg). It was estimated that the migration had transported 102 kg (lower - 67 kg, upper – 138 kg) of carbon and 28 kg (lower – 18kg, upper – 38 kg) of nitrogen upstream past the Daly River crossing. *M. spinipes* accounted for an estimated 88.5% of the nitrogen and carbon transported upstream. Both models estimated a substantial number of shrimps migrated upstream; model 2 estimated 18.6 million shrimps; 13 million *M. spinipes* and 5.6 million *Caridina* spp.

Discussion

The migration of *M. spinipes* was mainly cued by discharge. The migration occurred only on declining water levels and primarily at the end of the wet season; a similar pattern to that observed for *M. ohione* (Bauer & Delahoussaye, 2008). The duration of the migration was short, with the observed migration ceasing after three to six weeks. Specifically, during the migration period the migration rate was strongly associated with discharge and declined as discharge slowed. The influence of tide, cloud cover, moon illumination and time of night on the migration rate differed between sampling years. When in, 2013, the migration occurred later in the season, discharge was the key driver of migration; no other environmental variable had a significant effect on the migration rate. However, in 2014 when the migration occurred one month earlier, still within the wet season period, it was influenced by a range of other environmental variables, in particular; moon illumination, cloud cover and time of night.

The importance of moon illumination and cloud cover on the magnitude of the migration varied greatly in the two years of this study. In 2014 the migration rate of shrimps was higher during

brighter conditions; half-full moon phases and low cloud cover. While in 2013, we found moon illumination had no significant effect. In other migratory shrimps similar variation in the effect of moon illumination and cloud cover has been identified; where moon illumination was negatively correlated with migration rate (Fièvet, 1999a; Kikkert *et al.*, 2009; Bauer, 2011a), and positively correlated to migrating *Macrobrachium* (Kikkert *et al.*, 2009). Work on migratory eels (Anguillidae) has found that while moon phase is an important cue to glass eel migration into the estuaries (greater migration on new moons), the relationship is complex and can be influenced by a range of other factors including tides, time of night, turbidity and temperature (Jellyman & Lambert, 2003; August & Hicks, 2008).

Diel variation in migration rate (total biomass) during the 2014 migration was statistically significant. The biomass of migrating shrimps was greater on the 23:00 sampling than the 05:00 and 21:00 sampling times. The total migration biomass consisted of both *M. spinipes* and *Caridina* spp. and in 2014 the migration was dominated by *M. spinipes* in both number and biomass. Consequently the patterns in *M. spinipes* migration rate had a strong influence on the total migration rate. *Macrobrachium spinipes* migration rate was strongly correlated with time of night whereas *Caridina* spp. migration biomass was not. The evidence in regard to diel variation in migration rates is unclear. For example, Kikkert *et al.* (2009) found no diel variation in *Macrobrachium, Xiphocaris* or *Caridina* migration rates, while Benbow *et al.* (2002); Benbow, Burky and Way (2004) found significant variation in migration rates over the night for *Caridina* spp. with the period after midnight having the highest migration rates.

One possible explanation for the diel change in migration rate in the present study is the effect of tides on the migration rate. The sample collection site in this study is affected by tides. Selective tidal stream transport is a known mechanism for the transport of migratory fish (Levy & Cadenhead, 1995; Hale, Swearer & Downes, 2009). For example, the migration rate in catadromous eels exhibits significant diel variation, largely attributable to the influence of tide (Sugeha *et al.*, 2001; Jellyman &

Lambert, 2003). In the present study, the largest peaks in biomass generally occurred during the spring tide period (2nd, 4th and 6th weeks) at the 23:00 sampling; an effect also noted in glass eels (Sugeha *et al.*, 2001). The effects of the spring tides were observed as an increase in water level and slowing of stream velocity. It is possible that tide may have had an important effect on the migration and more sampling targeting the spring tide periods would help elucidate the effect of tide on the migration of *M. spinipes*.

The largest shrimps (by both weight and length) migrated at the start of the sampling period, and size declined rapidly throughout the first week. Both weight and length remained low throughout the remainder of the study, except week 3. This week coincided with low migrating biomass and a small increase in discharge. Changes in migrant size over the course of a migration has, to our knowledge, not been reported for migratory palaemonids, however, it has been observed in migrating glass eels (Chisnall *et al.*, 2002). Chisnall *et al.* (2002) found that glass eel size was generally larger during the start of the migration and then declined over time. While it was proposed that the differences in size may be related to environmental conditions at sea, they also proposed that it could be a result of age differences in the migrants, especially if spawning occurs over a prolonged time period (Chisnall *et al.*, 2002). The reproductive season of *M. spinipes* extends over the wet season, a period of 4-5 months (Novak *et al.*, 2015), but the migration primarily occurs over a 3-6 week period at the end of the wet season. The larger shrimps at the start of the migration would be expected to have a faster swimming speed, thus when conditions were suitable to migrate they would be captured at the sampling site first.

The presence of the *Caridina* spp. co-migrators was initially unexpected, particularly when, in 2013, abundance was estimated to be greater than *M. spinipes*. While *Caridina* are known to be amphidromous (Cook *et al.*, 2006; Bauer, 2011b; Bauer, 2013), the taxa from the Daly River, in particular, are not well known and are yet to be taxonomically described (Page, von Rintelen & Hughes, 2007). Little has been documented about the ecology of this genus (and Family: Atyidae) in

northern Australia and there is substantial room for more research in this area. In this study migrating *Caridina* biomass was linked to discharge, moon illumination and cloud cover as per *M. spinipes*. Tide was also a significant predictor and positively correlated to biomass, which suggests more migrated during well-lit nights during spring tides.

Biomass estimation and marine-freshwater subsidies

A major aim of this study was to estimate the biomass of prawns migrating upstream at the end of the wet season. This study represents the first attempt to quantify the biomass associated with the migration of an amphidromous shrimp species in a lowland river. We estimated that over 13 million shrimps migrated upstream during the 2013 migration and over 14 million shrimps migrated upstream in 2014. The biomass estimates of approximately 530 and 1250 kg wet weight and 118 and 281 kg dry weight for 2013 and 2014, respectively, and quantity of nutrients transported (2013 - 43 kg C and 12 kg N; 2014 - 102 kg C and 28 kg N), are orders of magnitude less than estimated nutrient transport for diadromous fish species reported in the literature (e.g Atlantic salmon, *Salmo salar* (Jonsson & Jonsson, 2003) and Pacific salmon, *Oncorhynchus spp* (Gresh *et al.*, 2000)). While both migrating juvenile *M. spinipes* and *Caridina* spp. may constitute a possible material subsidy to upstream freshwater, the amounts involved do not suggest that it is a large subsidy. However, frequent and intense predation of the migrating shrimps, particularly by juvenile *Neoarius* catfishes, suggests that there is still an important trophic role of this migration.

In addition, the sulphur and carbon isotope analysis of the muscle tissue show no evidence of marine-derived carbon in the shrimps. The low δS^{34} and high δC^{13} signatures were both inconsistent with a significant marine-derived signature (Fry *et al.*, 2003; Coat *et al.*, 2009). Consistent with the sulphur stable isotope data, the analysis of rostrum $^{87}Sr/^{86}Sr$ showed that the exoskeleton was comprised almost exclusively of freshwater derived Sr. The lack of marine influence detected in this study is likely due to rapid tissue turnover rates. Tissue turnover rates suggest the doubling of biomass would halve a distinct stable isotope signature (Fry & Arnold, 1982; Riera *et al.*, 2000).

Newly settled *M. spinipes* post larvae have been found to have a mean dry weight of up to 0.852 mg (Lober & Zeng, 2009), the smallest juveniles (≤ 15 mm TL, n = 110) captured in this study had a mean dry weight of 3.62 mg, a fourfold increase. The mean weight of all weighed individuals (n = 1729) was 15.4 mg (SE = 0.3 mg), an 18 fold increase. These data suggest that if post larval *M. spinipes* were feeding as they migrated then it would be very unlikely that a marine signature would be detected at our sampling site. Olivier (2013) used sulphur stable isotopes to determine if a marine signature was present in migrating *M. ohione* and found that at the most downstream sites marine sulphur signatures were detected but that it diminished rapidly as the shrimps moved upstream. At around 100 km upstream it was nearly undetectable. If the marine signature and hence marine nutrient transport disappears before the migrating individuals have moved more than 100 km upstream they are unlikely to provide a significant material subsidy to the upstream reaches of the river. It is worth considering then, that the migration of shrimps in the short tropical island streams where these species have been widely studied (e.g. Kikkert *et al.*, 2009; Benstead *et al.*, 2010) could well be providing an important material subsidy.

It is worth considering the usefulness of sulphur isotopes as an indicator of marine-derived nutrients. It has been widely established in North America that marine sulphur isotopes are highly enriched with ^{34}S and that this is assimilated in marine/estuarine phytoplankton, integrated into the food web and reflected by a high $\delta^{34}S$ of approximately 21‰ (Hesslein *et al.*, 1991; MacAvoy, Macko & Garman, 1998; Fry, 2002). Freshwater systems lack the highly enriched heavier isotope and have a $\delta^{34}S$ of considerably less than 21‰ (commonly less than 10‰) (Hesslein *et al.*, 1991; MacAvoy *et al.*, 1998; MacAvoy, Garman & Macko, 2009). However, sulphur isotope signatures of freshwater animals were high in the present study (approximately 15.5‰ for the freshwater *M. bullatum*). Similarly Jardine *et al.* (2012b) reported high ratios for freshwater animals in lowland rivers of Queensland (approximately 20‰). The levels reported here and in Jardine *et al.* (2012b) were higher than typically found for freshwater organisms elsewhere and more consistent with marine levels. The differences in catchment geology may influence the sulphur stable isotope signature in these

catchments and hence reduce the reliability of sulphur as an indicator of marine influence. Carbon isotopes remain an effective indicator of marine-derived nutrients (Jardine *et al.*, 2012b), however in estuaries where salinity is strongly influenced by freshwater flows a marine carbon signature will be rapidly diluted (Fry, 2002). The analysis of shrimp exoskeleton $^{87}Sr/^{86}Sr$ ratio may be an effective alternative. While this technique has been widely applied to fish otoliths (McCulloch *et al.*, 2005; Crook *et al.*, 2015), to our knowledge it has not previously been applied to the analysis of decapod exoskeletons. These findings confirm the suitability of exoskeleton material for $^{87}Sr/^{86}Sr$ analysis and represent a promising new approach for tracing the migrations of decapod crustaceans across marine/freshwater interfaces.

This study has addressed a long speculated hypothesis regarding the upstream transport of marine nutrients by small migratory shrimps in large tropical rivers. We have found that in such systems the direct marine subsidy effect is negligible. However, this finding does not negate the importance of the migration of this species, in both transporting nutrients between reaches and as recruitment of an ecologically important species to the river. In addition, this study has provided valuable insights into the phenology and magnitude of migration of amphidromous shrimps in large tropical rivers. While discharge is the primary cue for the migration other environmental variables such as tide, cloud cover and moon illumination may have an important but temporally variable influence. We propose that the temporally restricted nature of the migration is the reason other environmental variables have a varying influence. When flow conditions are suitable the migration commences very rapidly with a large initial biomass which steadily declines over time. Our data suggested that selective tidal stream transport may play a role, however more work on this aspect is required. This study builds upon the previous findings on the life history of *M. spinipes* (Novak *et al.*, 2015; Novak *et al.*, 2016) and by doing so provides significant insights into the life history and flow ecology of an amphidromous shrimp inhabiting large low land river systems. This is key information for the management of these species should these river systems be impacted by future water resource developments.

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Tables

Table 1. Independent variables selected for multiple regression analysis, their description and data source.

Variable	Description	Data source
Time of night	Decimal time of night when sampling took place. E.g. 00:00=0.00, 12:00=0.5 and 23:59=1.00	Personal observation at the time of sampling
Hour since sampling began	Cumulative hours since the first sample was taken	Personal observation at the time of sampling
Water level	The water level measured from the depth reference point	Personal observation at the time of sampling
Moon illumination	Moon phase, 100=full moon, 0=new moon. When the moon was not above horizon 0 was recorded	Personal observation at the time of sampling and http://www.timeanddate.com
Cloud cover index	0=clear; 0.25=some cloud; 0.5=partly cloudy; 0.75=mostly cloudy; and 1=overcast	Personal observation at the time of sampling
Tide index	Residuals from regression between water level at site and stage height at a stream gauge 10 km upstream (outside of tidal influence)	Water depth recorded at site and stream gauge data from Northern Territory Department of Land and Resource Management
Rainfall	24 hour rainfall in mm from nearest rain gauge	Northern Territory Department of Land and Resource Management
Instantaneous discharge	15 minute discharge recorded from nearest stream gauge	Northern Territory Department of Land and Resource Management
Mean previous 24 hours discharge	Mean discharge of 15 minute measurements for the immediate 24 hours prior to sampling	Northern Territory Department of Land and Resource Management

Table 2. Best subsets model standardised parameter estimates and partial regression slope analysis for each of the dependant variable models from the 2014 migration. If an independent variable is left blank then it was not selected in the best subset model.

Variables	**Total biomass**			***M. spinipes***			***Caridina* spp.**		
	r*	**t(32)**	**p**	**r***	**t(33)**	**p**	**r***	**t(34)**	**p**
Previous 24 hours discharge	0.616	6.295	0.000	0.597	5.702	0.000	0.473	3.836	0.001
Time of night	0.247	2.396	0.023	0.341	3.157	0.003			
Cloud cover index	-0.243	-2.488	0.018	-0.211	-1.993	0.055	-0.241	-2.137	0.040
Moon illumination	0.397	4.087	0.000	0.417	3.961	0.000	0.296	2.669	0.012
Tide index	0.191	1.828	0.077				0.423	4.206	0.000
Rainfall	0.161	1.550	0.131	0.166	1.522	0.137			

Table 3. 2013 migration biomass and nutrient transport predictions. In model 2, upper and lower confidence intervals are given in parenthesis for biomass, dry weight, carbon and nitrogen estimates. R^2 is provided as the model fit for model 1 and the mean migration rate per 30 mins and 95%CI is provided for model 2.

	Model 1. Linear regression with discharge			**Model 2. Mean weight extrapolated**		
	Total	***M. spinipes***	***Caridina* spp.**	**Total**	***M. spinipes***	***Caridina* spp.**
Model R^2/mean (95%CI)	0.929			660.1 g/30min (108.9)		
Single side biomass estimate (kg)	265			261 (172, 350)		
Biomass estimate (kg)	530	386	144	522 (344, 700)	381 (251, 510)	141 (93, 190)
Mean weight per individual (g) (SE)		0.076 (0.003)	0.017 (0.001)		0.076 (0.003)	0.017 (0.001)
Number estimate (million)	13.5	5.1	8.4	13.4 (8.8, 17.9)	5.0 (3.3, 6.8)	8.4 (5.5, 11.2)
Dry weight proportion (SE)	0.224 (0.001)			0.224 (0.001)		
Dry weight estimate (kg)	119	87	32	117 (77, 157)	85	32
Carbon (%) (SE)	36.47 (0.91)			36.47 (0.91)		
Nitrogen (%) (SE)	9.77 (0.24)			9.77 (0.24)		
Carbon (kg)	44	32	12	43 (28, 57)	31	12
Nitrogen (kg)	12	9	3	12 (8, 16)	9	3

Table 4. 2014 migration biomass and nutrient transport predictions. In model 2, upper and lower confidence intervals are given in parenthesis for biomass, dry weight, carbon and nitrogen estimates. R^2 is provided as the model fit for model 1 and the mean migration rate per 30 mins and 95%CI is provided for model 2.

	Model 1. Linear regression with discharge			**Model 2. Mean weight extrapolated**		
	Total	***M. spinipes***	***Caridina* spp.**	**Total**	***M. spinipes***	***Caridina* spp**
Model R^2/mean (95%CI)	0.583			731.2 g/30min (253.2)		
Single side biomass estimate (kg)	479			627 (410, 844)		
Biomass estimate (kg)	958	848	110	1,254 (820, 1,688)	1110 (726, 1,494)	144 (94, 194)
Mean weight per individual (g) (SE)		0.085 (0.005)	0.026 (0.0014)		0.085 (0.005)	0.026 (0.0014)
Number estimate (million)	14.2	10.0	4.2	18.6 (12.2, 25.0)	13.0 (8.6, 17.6)	5.6 (3.6, 7.5)
Dry weight proportion (SE)	0.224 (0.001)			0.224 (0.001)		
Dry weight estimate (kg)	214	190	25	281 (184, 378)	249	32
Carbon (%) (SE)	36.47 (0.91)			36.47 (0.91)		
Nitrogen (%) (SE)	9.77 (0.24)			9.77 (0.24)		
Carbon (kg)	78	69	9	102 (67, 138)	91	12
Nitrogen (kg)	21	19	2	28 (18, 38)	25	3

Figure captions

Figure 1. Map of region and insert showing site of visual observations, sweep net sampling, and fyke net sampling. The causeway and constriction point are shown. Flow direction in image is top to bottom. Photo credit: Mark Christie.

Figure 2. Total migrating biomass, over time, of *M. spinipes* and *Caridina* spp. combined, captured at the Daly River Crossing (DC105) 2013. Discharge (m^3/s) at the Mount Nancar gauging station is shown.

Figure 3. a)Total migrating biomass, over time, of *M. spinipes* and *Caridina* spp. combined, captured at the Daly River Crossing (DC105) 2014, discharge is plotted; b) migrating biomass of *M. spinipes* and *Caridina* spp. during the 2014 migration.

Figure 4. Mean (n = 45) a), length and b), wet weight for migrating *M. spinipes* during the 2014 migration.

Figure 5. Isotope biplot (δ13C and δ34S) of stable isotope data from the 2012 migration for migrating *M. spinipes* at DC105 in April (DC105-April), DC105 in May (DC105-May), R178 in April (R178-April); R298 in April (R298-April) and the non-migratory freshwater *M. bullatum* captured at R178 in April.

Figure 6. Mean (n=3) Strontium isotope ratio ($^{87}Sr/^{86}Sr$) from *M. spinipes* rostrums collected during the 2012 migration from 3 sites along an upstream gradient in the Daly River. Water $^{87}Sr/^{86}Sr$ ratio collected during the dry and wet season along an upstream gradient (water $^{87}Sr/^{86}Sr$ ratio data redrawn from Crook *et al.* (2016)).

Figure 7. Migration biomass model prediction, a) is the biomass prediction from 2013 migration and, b) is the biomass prediction for the 2014 migration. The open circles represent the model predicted biomass and the open squares are the calculated biomass for each day data were available.