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Limnadiid Clam Shrimp Distribution in Australia (Crustacea: Branchiopoda: Spinicaudata)

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Abstract

Clam shrimp (Crustacea: Branchiopoda: Spinicaudata) are ancient freshwater crustaceans inhabiting all continents of our planet. Few detailed distributional studies have been done on clam shrimp in Australia, and the few studies that have been done are quite old. Herein we report data from a series of collections across western, southern and central Australia aimed at delineating the species distributions of clam shrimp in the family Limnadiidae. We found six limnadiid species as well as several unidentified limnadiids distributed throughout Australia. The most successful sampling locations were rock pools located on granite outcrops. Three genera were collected (*Eulimnadia*, *Limnadia,* and *Limnadopsis*), with the former being highly female-biased and the latter two having nearly equal male/female ratios. Males were larger than females in *Limnadia* and *Limnadopsis*, and overall size differed among the three genera, with *Limnadopsis* being the largest and *Eulimnadia* being the smallest. Pool-to-pool variation was significant for both sex ratios and size, even though in many locations the pools were separated by no more than 20m. Overall, clam shrimp were found to be locally abundant, and we encourage taxonomic research to help studies such as these to correctly identify the range of species that inhabit Australia.

Keywords: *Limnadopsis*, *Limnadia*, *Eulimnadia*, sex ratios, adult size variation

Introduction

Branchiopod crustaceans are arguably the most primitive class of the sub-phylum Crustacea (Martin & Davis 2001). Branchiopods are subdivided into three orders: Anostraca, Notostraca, and Diplostraca (Martin & Davis 2001). The latter order is a combination of what was previously recognized as the 'Conchostraca' (common name "clam shrimp") and the Cladocera, both of which are now considered suborders (Martin & Davis 2001). The clam shrimp have had a tumultuous taxonomic history, and are now split into three suborders: Laevicaudata, Spinicaudata, and Cyclestherida both on the basis of their dramatic differences in morphology, (Fryer 1987; Olesen 1998) as well as on DNA comparisons (Spears & Abele 2000; Braband *et al.* 2002).

The largest of the clam shrimp suborders, the Spinicaudata, comprises of three families: Leptestheriidae, Cyzicidae, and Limnadiidae (Martin & Davis 2001). By far the largest family is the Limnadiidae, which comprises six genera: *Imnadia*, *Metalimnadia*, *Eulimnadia*, *Limnadia*, *Limnadopsis*, and *Limnadopsium* (Straskraba 1964). Only the latter four genera have been reported from Australia (Sars 1895; Sayce 1903; Dakin 1914; Webb & Bell 1979), and of these, the last two genera have been collected on no other continent, except as fossils (Tasch 1987).

Most of the reports of Australian clam shrimp have been primarily species descriptions with some location information, and most are quite old (King 1853; Sars 1895, 1896; Spencer & Hall 1896; Sayce 1903; Dakin 1914; Gurney 1927). Herein we present recently collected information about current distributions of six species of Spinicaudata in the family Limnadiidae, including information on sex ratios and size characteristics.

Methods and Materials

We used a combination of field collections and soil hydrations in the laboratory to determine species composition and sex ratios for the 23 locations we sampled (Table 1; Fig. 1). Our field collections included two large collection trips. The first was centred in south-west Western Australia (March 4 to April 27, 2003) while the second was a seven-week trip through central Australia, starting in South Australia, travelling up into the Northern Territory, and finishing in Western Australia (April 5 to May 19, 2004). All collecting trips included a combination of live collections (when shrimp were available) and soil collections for later hydrations in the laboratory. Live shrimp were preserved in 95% ethanol and transported back to the laboratory for species identification, size measurements, and sex ratio calculations.

Soil hydrations consisted of taking a small sample of field-collected soil (50–250 ml soil), placing the soil in the bottom of a glass aquarium (2–35 litres), and adding deionized water. The aquaria had small air stones for continuous aeration. Two laboratory locations were used: one at the University of Western Australia and the other at the University of Akron. For the former, aquaria were placed on a covered balcony, thus affording them natural light and temperature conditions (late summer, 2003). For the latter, aquaria were placed in a temperature controlled wet lab, and kept under continuous artificial light (Durotest Sunlight Simulating fluorescent bulbs) and constant temperatures (26–28°C). Food was a combination of 1:1 ratios of baker's yeast and ground flake food for algae-eating fish, which was suspended in water (1 gm food mix per 100 ml water) and supplied to the aquaria *ad lib* once per day. Such laboratory conditions have demonstrated optimal growth and survival for other Limnadiid shrimp (Weeks *et al.* 1997).

Statistical analyses were performed using JMP (SAS Institute 2003). Differences in sex ratios among pools within locations were assessed using contingency table analyses and differences in size among species, between sexes, and among locations within species were assayed using ANOVA tests.

Results

Limnadiid clam shrimp were collected live or reared from soil from 24 separate sites (Table 1; Fig. 1). Because no comprehensive key for Australian clam shrimp is available, and due to the poor species descriptions from primarily older publications, species identifications were quite difficult. Therefore, from these 24 sites, six Limnadiid species were identified: two *Eulimnadia* (*E. feriensis* Dakin, 1914 and *E. dahli* Sars, 1896), three *Limnadia* (*L. badia* Wolf, 1911, *L. sordida* King, 1855, and *L. stanleyana* King, 1855), and one *Limnadopsis* (*L. tatei* Spencer & Hall, 1896). Of these six species, *E. feriensis* and *E. dahli* were the most widespread, being collected from 7 and 5 separate locations, respectively. *Limnadia badia* was found in three locations, all geographically close to one another (two rock pools and an earthen pool). *Limnadia sordida* was found in two locations (one earthen pool and one rock pool) as was *Limnadopsis tatei* (both earthen pools). *Limnadia stanleyana* was collected from only a single location.

We were unable to determine species from an additional six locations; one sample was classified as *Limnadia* and five were classified as *Limnadopsis* (Table 1). The shrimp in these locations differed in small ways from the other, named species, but were different enough to cause us to question their true identifications. Thus we lumped these unknowns into the "spp." category by genera.

Sex ratios varied dramatically among species and locations, ranging from 69% males to 100% females. However, sex ratios were rather consistent within genera, with the *Eulimnadia* populations being heavily female-biased and the *Limnadia* and *Limnadopsis* populations having a consistent 1:1 sex ratio (Table 1). Among the *Eulimnadia* locations, there were four locations with exceptionally low male proportion (<2%), while the

Figure 1. Sampling locations.

Table 1

Location information and sex ratios for the collected limnadiid clam shrimp.

Species	Location	Latitude	Longitude	Males	Total Females[a]	%Male	(L)ab or (F)ield
Eulimnadia feriensis	Cairns Rock	S31° 51.517'	E118° 50.650'	44	238	15.6%	L
	Outcrop	S31° 51.414'	E117° 36.894'	0	128	0.0%	L
	Tammin Rock	S31° 40.195'	E117° 30.806'	2	182	1.1%	F & L
	Wanara Claypan	S29° 32.750'	E116° 43.866'	3	19	13.6%	F
	Wanara Rock	S29° 31.450'	E116° 47.533'	8	34	19.0%	F & L
	Wave Rock	S32° 26.538'	E118° 53.908'	9	63	12.5%	L
	Yorkrakine Rock	S31° 25.405'	E117° 30.835'	28	167	14.4%	L
			Overall	44	831	10.2%	
Eulimnadia dahli	Pygery Rocks	S32° 59.165'	E135° 28.238'	0	4	0.0%	F
	Bunjil Rocks	S29° 37.833	E116° 23.633'	27	81	25.0%	L
	Green Rock	S29° 31.250'	E116° 38.340'	44	98	31.0%	F
	The Humps	S32° 18.885'	E118° 57.574'	17	52	24.6%	L
	Kadjii-Kadji	S29° 8.233'	E116° 24.833'	0	4	0.0%	L
			Overall	88	239	26.9%	
			Overall *Eulimnadia*	182	1070	14.5%	
Limnadia badia	Wanara Rock	S29° 31.450'	E116° 47.533	14	9	60.9%	F
	Dunn Rock	S33° 20.110'	E119° 29.370'	18	32	36.0%	L
	Dingo Rock	S33° 0.567'	E118° 36.133'	6	6	50.0%	L
			Overall	38	47	44.7%	
Limnadia sordida	Armadale Road	S32° 8.560'	E115° 57.200'	13	12	52.0%	F & L
	Wanara Claypan	S29° 32.750'	E116° 43.867	11	5	68.8%	F
			Overall	24	17	58.5%	
Limnadia stanleyana	Kanangra Walls	S33° 59.933'	E150° 5.133'	140	132	51.5%	F & L
Limnadia spp.	Albany Hwy Rail	S32° 5.280'	E116° 0.370'	5	4	55.6%	L
			Overall *Limnadia*	207	200	50.9%	
Limnadopsis tatei	Kadji-Kadji	S29° 8.233'	E116° 24.833'	63	58	52.1%	L
	Lasseter Hwy.	S25°13.330'	E132° 02.544'	14	14	50.0%	F
				77	72	51.7%	
Limnadopsis spp	Melaleuca Swamp	S33° 53.917'	E118° 31.833'	1	6	14.3%	L
	Pabellup Swamp	S34° 7.050'	E119° 26.833'	14	24	36.8%	L
	Pilbarra, W.A.	S 24° 7.550'	E 119° 41.600'	3	3	50.0%	L
	Tjulun RH, WA	S25° 24.717'	E127° 35.183'	2	4	33.3%	F
	Tardun CBC Dam	S28° 43.033'	E115° 49.067'	9	7	56.3%	L
			Overall *Limnadopsis*	106	116	47.7%	

[a] *Eulimnadia* "females" are most likely hermaphrodites, as in all other *Eulimnadia* species so far examined (Weeks et al., 2006).

remainder had 13–31% males. The average sex ratio among all *Eulimnadia* locations was 14.5% males (Table 1).

The sex ratios were much closer to 1:1 in the remaining two genera. *Limnadia*'s overall sex ratio was 50.9% male (Table 1), with *L. badia* showing a slight female bias (55% females), *L. sordida* a slight male bias (59% males) and *L. stanleyana* much closer to 1:1 (51.5% males). *Limnadopsis*' overall sex ratio was 47.7% male, with *L. tatei* having 51.7% male (Table 1).

Collections were made at more than one pool for five separate locations: three for *E. feriensis,* one for *E. dahli,* and one for *L. stanleyana* (Table 2). In the two *Eulimnadia* species, sex ratios ranged quite dramatically: in the three *E. feriensis* locations (12 pools total), sex ratios ranged from 0.0 to 100% males, with an average of 9.0% males while in the single *E. dahli* location (6 pools total) sex ratios ranged from 0.0 to 50% males, with an average of 31.0% males. In the three *L. stanleyana* pools (Kanangra Walls), sex ratios had lower variation, ranging from 22 – 56% males with an average of 51.5% males. At each *Eulimnadia* location, at least one pool had no males collected or reared from soil. In fact, a series of contingency table analyses revealed significant pool-to-pool variation in sex ratios among pools in all but the Tammin Rock location, even though the pools within locations were separated by no more than 20 meters.

Collections of 328 total shrimp from six species (*Eulimnadia feriensis, Eulimnadia dahli, Limnadia badia, Limnadia stanleyana, Limnadia sordida,* and *Limnadopsis tatei*) were made from nine separate pools to compare sizes within and among species. Of these six species, *E. feriensis, E. dahli,* and *L. sordida* were the smallest followed by *L. badia*, *L. stanleyana,* with *Limnadopsis* the largest of the six (Fig. 2). These differences were significant ($F_{5,316}$ = 1744; P < 0.0001).

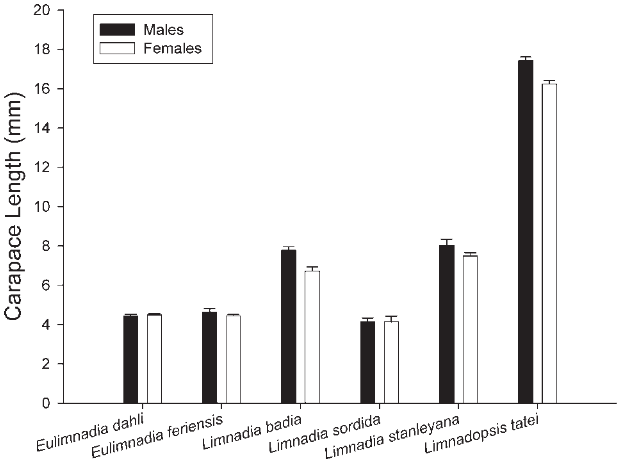

Figure 2. Relative male and hermaphrodite size (measured as carapace length) for *Eulimnadia dahli, Eulimnadia feriensis, Limnadia badia, Limnadia sordida, Limnadia stanleyana*, and *Limnadopsis tatei* (Lasseter Hwy.). Error bars portray one standard error of the mean.

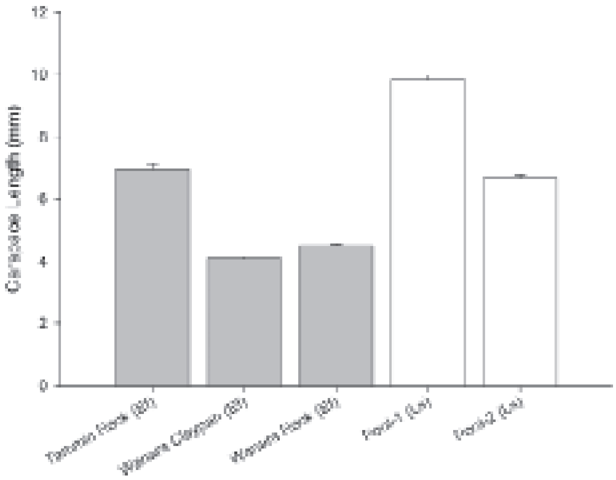

Figure 3. Size (carapace length) variability among pools for *Eulimnadia feriensis* (Ef – gray bars) and *Limnadia stanleyana* (Ls – white bars). Error bars portray one standard error of the mean.

Males were larger than females, on average ($F_{1,316}$ = 22.3; P < 0.0001), but this difference depended on species, with the size difference being more dramatic with the larger species ($F_{5,316}$ = 6.3; P < 0.0001; Fig. 2). Size also significantly varied among locations within species (Fig. 3). Within *E. feriensis*, the Tammin Rock location had the largest shrimp ($F_{2,82}$ = 72.9; P < 0.0001; Fig. 2), while for Kanagra Walls collections, the *L. stanleyana* collected from Pool-1 were significantly larger than those from Pool-2 ($F_{1,32}$ = 504.7; P < 0.0001; Fig. 3).

Discussion

The distribution and ecology of clam shrimp is understudied worldwide, and Australia is no exception. Even though some work has been carried out on Australian clam shrimp in the past 20 years (Timms 1986; Timms & Richter 2002; Richter & Timms 2005), most studies of Australian clam shrimp are over 35 years old (Wolf 1911; Dakin 1914; Glauert 1924; Henry 1924; Bishop 1967, 1968, 1969), and many species have not been reported in the literature for over a century (King 1853; Sars 1895, 1896; Sayce 1903). One might assume that this neglect is due to a difficulty in locating these "elusive" crustaceans, but our collecting trips proved this to be incorrect: clam shrimp are locally abundant in several areas of Australia.

The pools in which we were most successful at collecting limnadiid clam shrimp were rock pools located in Western Australia. We had 100% success in collecting either live clam shrimp or rearing shrimp from soil collected from rocky outcrops that had at least one pool of 10 cm or more in depth. Twelve of the 24 collection locations were on granite outcrops (Bunjil Rocks, Cairns Rock, Green Rock, Outcrop, Tammin Rock, The Humps, Wanara Rock, Wave Rock, Yorkrakine Rock, Pygery Rocks – Eyre Peninsula, Dingo Rock, and Dunn Rock), with most of these sites being populated by *E. feriensis, E. dahli*, or one of the *Limnadia* species (Table 1). *Limnadopsis* was never found in rock pools, but rather preferred swamps or claypans.

Sex ratios among species were consistent with their inferred mode of reproduction. Clam shrimp in the genus *Eulimnadia* have commonly been found to be female biased (Sassaman 1995). In fact, *Eulimnadia* has been described as an "androdioecious" group (Sassaman & Weeks 1993), with males and hermaphrodites (rather than females) and with populations heavily biased towards hermaphrodites (Weeks*, et al.* 2006). Indeed, the average male proportion in populations of *E. texana* is ~23% (Weeks & Zucker 1999). Thus, the observations that the Australian *E. feriensis* populations are ~10% males and that the *E. dahli* averaged ~27% male are consistent with an androdioecious mode of reproduction for these clam shrimp (Weeks*, et al.* 2006). Further work will need to be done to confirm this inference.

The sex ratios of the *Limnadia* and *Limnadopsis* were also completely consistent with their inferred mode of reproduction. Except for one species of *Limnadia* (*L. lenticularis*), all reports of sex ratios for both genera have been either 1:1 or male-biased (Sassaman 1995). These data have been used to infer that species in both genera are obligately outcrossing sexuals (Sassaman 1995), and preliminary results from laboratory-based rearings also confirm this inference: isolated females from these genera do not move eggs to their brood chambers when males are absent, and viable eggs have only been collected from females that have been paired with males (Weeks, pers. obs.). Thus, the Australian species of *Limnadia* and *Limnadopsis* are quite likely obligately outcrossing sexual species.

The significant differences in sex ratios among pools within a location were not expected. Pools separated by no more than 20 m varied from 0 to ~50% males in both *E. feriensis* and *E. dahli*, and three of four *Eulimnadia* locations had significant variation among pools in male:female (hermaphrodite) ratios (Table 2). The differences among pools for *L. stanleyana*, although still significant, were much smaller than for *Eulimnadia*, ranging from 22–56% males. Such high among-pool variation in both species suggests either that these pools have exceptionally divergent selection pressures for male

Table 2

Sex ratios per pool at five clam shrimp locations. Juvs = juvenile shrimp.

Species	Location	Pool	(F)ield or (L)ab	Juvs	Males	Females[a]	%Male	Chi-Square	P-value
Eulimnadia feriensis[a]	Yorkrakine Rock	1	L	0	9	29	23.7%		
		2	L	0	0	36	0.0%		
		5	L	0	4	25	13.8%		
		9[b]	L	0	2	1	66.7%		
		10	L	0	13	76	14.6%	13.4	0.0039
	Tammin Rock	1[b]	F	0	2	0	100.0%		
		2	L	1	0	74	0.0%		
		9	L	0	0	108	0.0%	0.0	1.0000
	Wanara Rock	3	F	6	1	9	10.0%		
		4	F	26	7	7	50.0%		
		7[b]	F	6	0	6	0.0%		
		8	F	0	0	12	0.0%	12.2	0.0022
			Total	39	38	383	9.0%		
Eulimnadia dahli[a]	Green Rock	1	F	52	20	22	47.6%		
		2	F	34	6	6	50.0%		
		3[b]	F	12	0	7	0.0%		
		4	F	31	12	42	22.2%		
		7	F	4	0	11	0.0%		
		8	F	11	6	10	37.5%	17.3	0.0017
			Total	144	44	98	31.0%		
Limnadia stanleyana	Kanangra Walls	1	F	12	3	8	27.3%		
		2	F	16	5	18	21.7%		
		3	L	0	132	106	55.5%	12.8	0.0017
			Total	28	140	132	51.5%		

[a] *Eulimnadia* "females" are most likely hermaphrodites, as in all other *Eulimnadia* species so far examined (Weeks et al., 2006).

[b] Pool not considered for the contingency table analysis due to small sample size.

proportions, or that migration and gene flow among pools is quite limited, thus allowing sex ratios to be highly influenced by colonization events and genetic drift.

Although wind is commonly considered as a major cause of branchiopod dispersal among habitats, Brendonck and Riddoch (1999) found limited evidence for such dispersal of anostracan eggs, collecting wind blown eggs at < 2% of 423 sites studied, and then only at distances no more than 50 cm from their source. These results suggest that wind dispersal is quite limited for branchiopod eggs.

Gene flow has also been estimated to be quite limited. Davies *et al*. (1997) found high among-population genetic differentiation (average $F_{ST} = 0.66$) in the anostracan *Branchinecta sandiegonensis*, indicating low levels of between-pool migration. Brendonck *et al*. (2000) also found high genetic differentiation (average $F_{ST} = 0.29$) among three pools of the anostracan *Branchipodopsis wolfi* in rock pools in Africa. In the clam shrimp *Eulimnadia texana*, Weeks and Duff (2002) reported F_{ST} values of 0.28 and estimated migration rates to be ~0.6 migrants per generation among pools. An analysis of a subset of these pools that were separated by no more than 100 m still revealed significant genetic sub-structure ($F_{ST} = 0.16$) and estimates of migration among pools of 1.3 migrants per generation. All of these studies suggest that migration rates among pools might be quite limited, and this low migration rate could explain the significant variation among pools in male proportion found in the current study.

Size also differed significantly, among species, among pools within species, and between the sexes. The among-pool differences in size are likely due to either density effects and/or to differences in age since hydration for the various pools surveyed. High density is known to cause reduced growth rate per individual in *E. texana* (Weeks & Bernhardt 2004). Because our samples were from the field, we had no control over either factor, and thus such pool-to-pool variation was likely a reflection of one or both of these factors.

The among-species and between-sexes differences are more likely to be at least partially a reflection of genetic differences. Because the between-sexes measures were taken from individuals from the same pools, it is likely that these are reflective of genetic differences between the sexes, with males growing larger than females, at least in *Limnadia* and *Limnadopsis*. Size differences between the sexes were much less evident in *E. feriensis* and *E. dahli*, which is consistent with other studies on *Eulimnadia* wherein the size range of males and females largely overlaps, but the largest males are slightly larger than the largest females (Knoll & Zucker 1995). Larger male size has been shown to confer greater outcrossing probability in clam shrimp (Knoll & Zucker 1995), and thus in species with greater levels of outcrossing (*i.e.*, *Limnadia* and *Limnadopsis*) there may be greater selection for larger males than in species which regularly self-fertilize (Sassaman 1989; Weeks & Zucker 1999).

The significant difference in size among the three limnadiid genera is also likely to be partly genetically determined. Laboratory rearings of all three genera under common garden conditions suggest a greater ultimate size is reached by *Limnadopsis*, followed by *Limnadia* and finally by *Eulimnadia*. Larger size is correlated with a longer age to maturity and a greater lifespan of the former two genera relative to *Eulimnadia* (Weeks, pers. obs.). Thus, although the ages at collection for the three species were not known and density per pool was uncontrolled, the general size differences among genera is likely reflective of a general difference in life history characteristics of these three genera.

To summarise, limnadiid clam shrimp were found to be quite abundant and widespread in temporary pools in Western Australia. Rock pools on granite outcrops were particularly well populated with limnadiids, although no species of *Limnadopsis* were found in such pools. We should note that we only made these collections in two large collecting trips, and that our field collections therefore may under represent the true limnadiid diversity of these areas across the seasons. We hope that these results will encourage others to look for these interesting freshwater crustaceans, and we strongly recommend that the development of an Australian taxonomic key would greatly increase the reporting of these fascinating crustaceans.

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