THE ECOLOGY OF *Australatya striolata* (McCulloch and McNeill) (DECAPODA: ATYIDAE)

Thesis submitted by

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in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology of James Cook University of North Queensland.

Abstract

The ecology of the protandrous freshwater shrimp, *Australatya striolata* (McCulloch and McNeill), was studied in two stream systems in north Queensland, in the context of its distribution in eastern Australia.

The size frequency distributions of the populations studied were found to be bimodal, with the left mode consisting primarily of males, and the right mode of females. The modal size classes did not vary through time, although recruitment was found to be seasonal.

The most likely mechanism for the maintenance of this bimodal distribution was a two-stage growth curve of an initial phase of relatively rapid growth of juveniles followed by very slow growth of mature males, then a relatively rapid transition from male to female size followed by very slow growth of mature females. This explanation was well supported by a sigmoidal growth curve for individuals between the modal size classes, low levels of recruitment and negligible growth of tagged and caged males and females. Analysis of length frequency distributions through time also indicated very slow growth for mature males and females (1 mm in 870 days) , and rapid growth of juveniles (2-3 mm in 61 days). This growth pattern is possibly unique in the recorded literature.

Breeding was seasonal and coincided with the summer wet season. Eggs were brooded and larvae released by the females in freshwater. The first larval stage was a zoea which was lecithotrophic and required salinities in excess of 20‰ for further development. In lower salinities they could survive for up to 30 days on their yolk supplies. This was shown to be more than would be required for drift to the estuary (about 17 days in Yuccabine Creek and 8 days in Douglas Creek). The subsequent upstream migration of juveniles required 12 to 18 months in the stream systems studied.

A. striolata was shown to be primarily a filter feeder, but sweeping the substratum with the cheliped fan was used in periods of low stream flow. The predominant food was particulate organic matter, the abundance of which was not limiting for naturally occurring densities of shrimp.

Predation and disease were shown to be minimal sources of mortality in the populations of adults studied, and the maintenance of near 1:1 sex ratios, despite the greater age of females, indicated high survival.

The species was shown to be distributed in coastal streams from the Claudie River, Cape York Peninsular (12°45' S, 143°12' E), to the Genoa River, Victoria (37°29' S, 149°35' E). The lowest observed altitude for adult populations tended to decrease with increasing latitude. The northern limit to the distribution was shown to be restricted by habitat availability. It is suggested that the observed differences in the size frequency distributions over the geographic range were due to different rates of recruitment.

The adaptive significance of the life history of the species is discussed, with particular reference to the preference of adults for low order streams, and the advantages of the marine larval stage.

Declaration

I declare that this thesis is my own work and has not been submitted in any other form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

11-4-87

Ross E.W Smith

October 1987

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Ross B.W. Smith October, 1987

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Chapter 1 Introduction

The filter feeding, or *Atya*-like shrimp species of the family Atyidae are conspicuous inhabitants of the tropical streams and rivers of the world. They are often used for human consumption in the more populous countries in the tropics (see Hobbs and Hart, 1982 and Chace, 1983) and have been suggested as suitable candidates for aquaculture (Hunte, 1977). However, although the functional morphology of their unique feeding mechanisms have been subjected to detailed study by Fryer (1977) and Felgenhauer and Abele (1983), very little is known about the ecology and life history of the species of the group.

Hobbs and Hart (1982) extensively reviewed the literature concerning the members of the genus *Atya (sensu stricto)*, while Chace (1983) dealt similarly with the *Atya*-like shrimp of the Indo-Pacific region. However, neither works considered the available knowledge of the biology of the groups to be in any way adequate. Table 1.1 summarises the extent of the literature dealing with the ecology or life history of the groups considered by the two works. Chace (1983) cited an average of only 2.2 papers per species dealing with the ecology of each species, and an average of 1.7 papers dealing with the life history of the species. Except for *Atya scabra* (Leach, 1815) which was disproportionately represented by papers describing the type of habitat it was collected in (see Table 1.1), Hobbs and Hart (1982) cited an average of 2.5 papers dealing with the ecology of the species of *Atya* and 1.4 papers dealing with their life history. Of the papers that

Table 1.1 The number of papers and authors or combinations of authors which dealt with (a) the ecology and (b) the life history of species of *Atya*-like shrimp that were cited by Chace (1983) and Hobbs and Hart (1982).

	Chace 1983	Hobbs and Hart 1982 including *Atya scabra*	Hobbs and Hart 1982 excluding *A. scabra*
a) Ecology			
Papers	12	21	45
Author combinations	11	18	31
b) Life history			
Papers	10	13	17
Author combinations	8	13	17

were cited by the two works, the great majority of ecological notes were records of habitat types, and most life history notes recorded only the presence of ovigerous females. The only *Atya*-like shrimp for which the larval stages have been described are *Atyoida serrata* (Bate, 1888) (Bordage, 1908, 1909), *Atyoida bisulcata* Randall, 1840 (Edmondson, 1929), *Micratya poeyi* (Guérin-Méneville, 1855) (Hunte, 1977, 1979a) and *Atya innocous* (Herbst, 1792) (Hunte, 1977, 1979b).

Thus, despite their importance to some human societies, and the important roles they must play as large, numerically abundant filter feeders in the communities in which they occur, there exists only minimal knowledge of the biology of the *Atya*-like shrimp. This is the first detailed study of the life history and biology of a filter feeding atyid.

The species studied here, *Australatya striolata* (McCulloch and McNeill, 1923), is the only *Atya*-like shrimp in Australia. It was first recorded as *Atya striolata* by McCulloch and McNeill (1923) from Norton's Basin, on the Nepean River, New South Wales. They noted that: "These shrimps appear to occur only in running water and in rock localities ... where there are stones for them to hide under. They apparently dislike any but clear water..."; the shrimp "readily left a shallow dish of water by crawling over its sides"; and that "[they] also run freely over the surface of a flat table, and if thrown on their sides, will speedily regain their normal position".

Roux (1926) added a few more details and measurements from some specimens supplied by A.R. McCulloch. In a footnote to Roux's article, the editor, Anderson (1926), recorded that the species had also been collected from the Upper reaches of the Woronora River near Sydney. McNeill (1929) added a third locality in the Myall River, north of Newcastle. Riek (1953) gave the first Queensland record from Cave Creek, near the Queensland-New South Wales border. He noted that specimens could only be found at the overflow of one pool, and that they differed slightly from the topotypes examined. Later, Riek (1959) described the species as an atyid "relict element". Bishop (1967) also described *A. striolata* as a relict species and recorded specimens as "facultative troglobes" from Gloucester Caves, New South Wales. Bishop (1967) considered that the Atyidae invaded Australia via Indonesia and New Guinea, a view that was supported by Williams (1977) with regard to the genus *Paratya*.

Smith and Williams (1982) reinstated the genus *Atyoida* and ascribed *A. striolata* to it. They also fully redescribed the species, including the male form. They demonstrated that it was a protandrous species on the basis of histological evidence and length frequency distributions from their collections from the Shoalhaven River, New South Wales, and Currumbin Creek, Queensland. On the basis of the species' occurrence in short, fast flowing coastal streams, they suggested that the life cycle may involve the downstream migration of ovigerous females to release large numbers of larvae in estuaries or other marine situations, and a subsequent upstream migration of juveniles. They extended the known limits of the geographical range of the species north to 25 km north

of Cooktown, far north Queensland, and south to the Shoalhaven River, southern New South Wales. However, they considered the species to be remarkably uniform in its morphology over this range with no detectable clinal variation, although they they stated that far north Queensland specimens tended to have a relatively shorter rostrum and more deeply excavated carpi on peraeopods 1 and 2.

Chace (1983) erected the genus *Australatya* for this species on the basis of the broadly rounded pterygostomian margin of the carapace, the reduced epipods on the third and fourth peraeopods, the absence of mastigobranchs and the elongate appendix masculina spinose on less than the distal third of its length.

The northern limit to the distribution of *A. striolata*, a member of a circum-tropical group, would be expected to extend further north than Cooktown, provided there was suitable habitat available, if the Atyidae invaded Australia via New Guinea as proposed by Bishop (1967). The known southern limit to the distribution was extended by Richardson (1985) who recorded *A. striolata* from Mumbulla Creek, a coastal stream in southern New South Wales. It is possible that *A. striolata* occurs in Victoria as Bouvier (1905) discussed two specimens of *Atya scabra* held by the Muséum d'Histoire Naturelle in Paris, which were purported to have been collected by Baron Von Mueller in Victoria. Hobbs and Hart (1982) recorded one specimen of *Atya margaritacea* (A. Milne-Edwards, 1864) held by the Muséum d'Histoire Naturelle which was also attributed to Von Mueller. Since Von Mueller was never in a position to have collected either *A. scabra* or *A. margaritacea* (Kynaston, 1981),

if he did send specimens of *Atya*-like shrimp to the Muséum d'Histoire Naturelle they were almost certainly *Australatya striolata*.

This study examines some aspects of the ecology of *A. striolata* in two catchments in north Queensland, in the context of the distribution and habitat preferences of the species in eastern Australia. The aims of the study were:

(i) to examine the structure and dynamics of the populations in the two systems, and if possible to produce life tables for the populations;

(ii) to examine the reproductive strategy of the species, with particular reference to the larval stages;

(iii) to examine the feeding of *A. striolata* and predation on it by other species;

(iv) to re-examine the geographical distribution of the species and the extent of morphological variation over that range.

These points are addressed sequentially in the following chapters.

CHAPTER 2. The Study Sites

2.1 Adult Sites

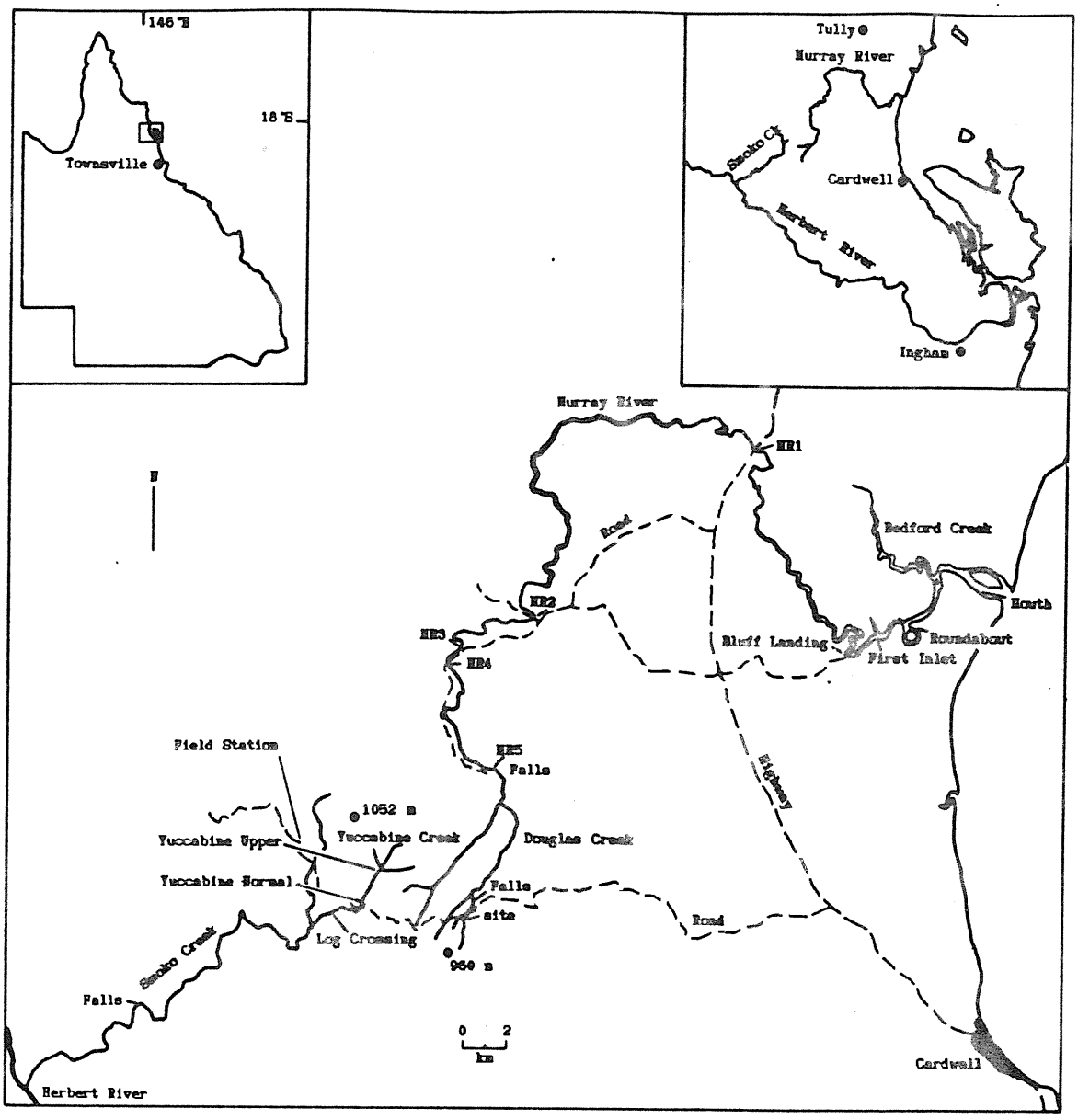
2.1.1 Description

Fig. 2.1 shows the locations of the two streams chosen for this study, Douglas Creek and Yuccabine Creek, both in the Kirrama range north of Cardwell, north Queensland.

Yuccabine Creek is a third order stream and is the subject of an on-going ecological study (see Pearson *et al.*, 1986). It was known to support a sizeable population of *A. striolata*. Figure 2.2(a) shows that Yuccabine Creek rises at about 800-900 m and descends rapidly for the first few kilometres. The gradient then lessens and the stream broadens and joins Smoko Creek, which, after a series of falls, joins the Herbert River.

The riparian vegetation of Yuccabine Creek is mixed rainforest (mainly mesophyll vine forest *sensu* Webb, 1959) and sclerophyll (largely eucalypt) forest. Physico-chemical characteristics of Yuccabine Creek had been recorded monthly at Pearson's site since 1981. I chose a site approximately 100 m downstream in order to make use of this background information and to minimise interference between the two studies. In addition I chose sites approximately 2 km upstream and downstream of this main site (Figure 2.1). A detailed description of the three sites follows.

Figure 2.1 Map of the study sites with insets showing the relative sizes of the two systems studied, and location in Queensland.



Chapter 2 The Study Sites

The most downstream site (Figure 2.1; Plate 1(a)), called Log Crossing because of a log causeway in the stream bed on the access track, was the most downstream section of rocky substratum (ø -5 to -6) in the stream. Between this site and Smoko Falls the substratum is mainly sand. *A. striolata* show a strong preference for rocky riffles (McCulloch and McNeill, 1923), and adults were not observed downstream of this site. The riparian vegetation was rainforest on the eastern bank. The western bank of this site was an island in the stream bed and was inundated during spates. The fringing vegetation on the west bank proper was again rainforest. The riffle section was 20m long.

The middle site, called Yuccabine Normal (Figure 2.1; Plate 1(b)), was a 35m rocky (ø -6 to -8) riffle section delimited by pools. The riparian vegetation was rainforest. Some collections of *A. striolata* had been made at this site by R.G. Pearson (unpublished) prior to the commencement of this study.

The third site, Yuccabine Upper (Figure 2.1; Plate 1(c)), contained sections of two rocky riffles with an intervening, deep, narrow pool. It was delimited downstream by the end of the access track, and upstream by a tributary. The substratum was mostly large boulders (ø -8) and the stream had a higher current velocity and greater water depth than at the other two sites. The total length of stream sampled was 50m.

Since it was likely that the life cycle of *A. striolata* included an estuarine larval stage (Smith and Williams, 1982), sampling in the lowland section of at least one system was necessary. The Herbert

Plate 1 Study sites in Yuccabine Creek.

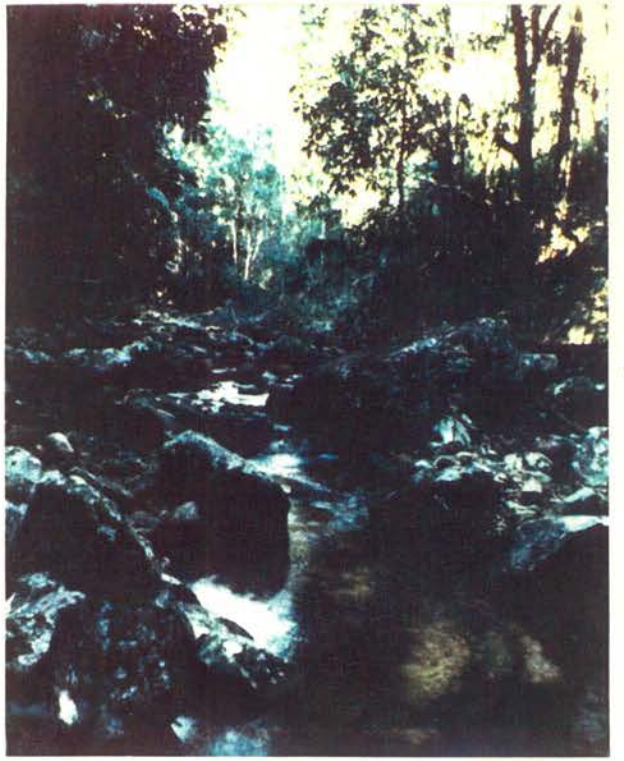
(a) Log Crossing

(b) Yuccabine Normal

(c) Yuccabine Upper

(a)

(b)



(c)

River has limited access which, along with its size, precluded an adequate sampling programme for this study. The Murray River system, including Douglas Creek, was selected to meet this requirement.

Douglas Creek (Figure 2.1; Plate 2(a)), is a second order stream approximately 4.5 km east of Yuccabine Creek. It rises at 800 m and descends rapidly to its junction with the Murray River (Figure 2.2(b)). Access to the stream was limited to the main Kirrama road crossing, but access to the Murray River was good. Douglas Creek was fringed with dense rainforest which formed a complete canopy over the entire stream. The substratum was mostly large boulders (ϕ -8) many of which were covered by moss and ferns, and large, partly submerged logs were a common feature. The current and water depth were similar to that of Yuccabine Upper, and preliminary investigations showed that a large population of *A. striolata* existed at this site. Downstream of the sampling site are two 30 m waterfalls (Figure 2.1; Plate 2(b) & (c)) and numerous smaller falls. A 40m section of stream was sampled.

2.1.2 Physico-chemical Characteristics

Methods

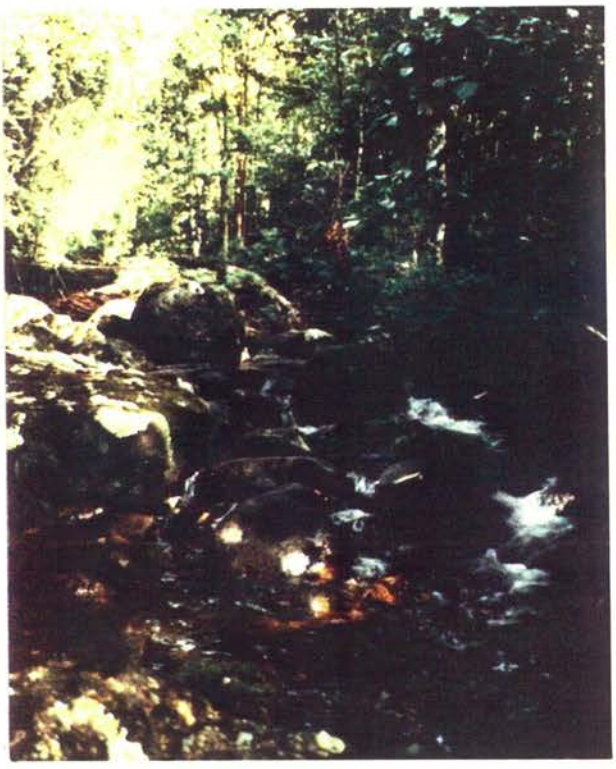
Rainfall was measured at the James Cook University Field Station approximately 3 km north-east of Yuccabine Creek (Figure 2.1). A standard Meteorological Bureau gauge was used until April 1985 after which a smaller (275 mm capacity) model was used.

Plate 2 Study site in Douglas Creek and major waterfalls downstream of the study site.

(a) Douglas Creek study site

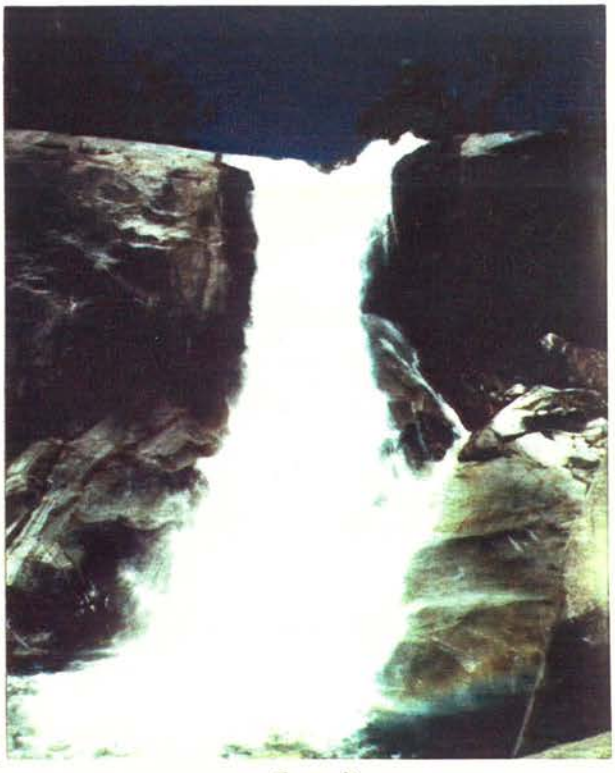
(b) Douglas Creek falls

(c) Murray falls



(a)

(b)



(c)

Figure 2.2a Profile diagram of Yuccabine Creek and Smoko Creek showing the positions of the study sites and major falls. The lowest point on the diagram represents the junction with the Herbert River.

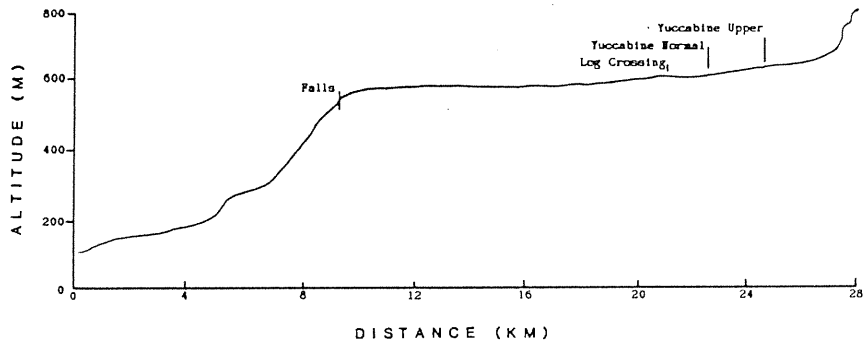
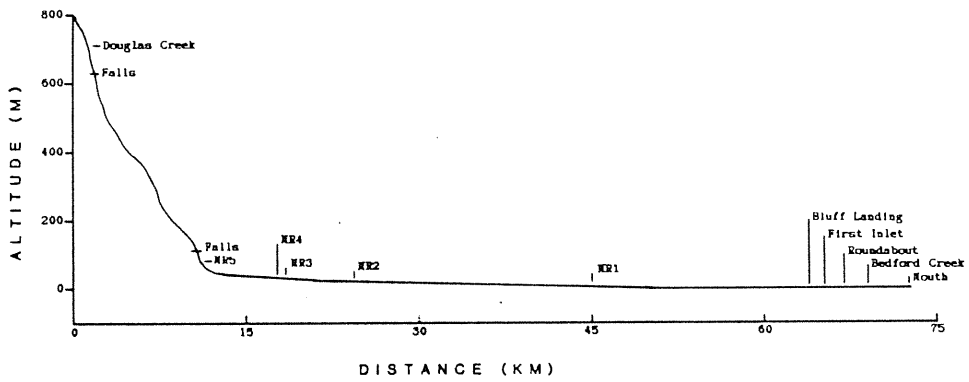


Figure 2.2b Profile diagram of Douglas Creek and the Murray River showing the positions of the study sites and known major falls.



Discharge was estimated from cross-sectional area and current velocity data. In Yuccabine Creek a concrete pipe in the main causeway was used, but at very low stream discharge, seepage under the causeway resulted in no flow through the pipe. In Douglas Creek a V-shaped cleft in the bedrock streambed downstream of the study site was used. Prior to October 1984, current velocity was determined using a Marsh-McBirney current meter. When this instrument failed, current speed was determined by timing small objects dropped into the stream. However turbulence often caused an underestimation of mean current velocity using this method. From June 1985, small quantities of milk were released into the water and timed over a fixed distance, overcoming the turbulence problems.

Monthly water temperatures were recorded using maximum/minimum thermometers secured in the stream bed. These were regularly lost in spates in Douglas Creek. Oxygen concentrations were measured monthly using a YSI meter, and conductivity was measured with a Hach Mini-conductivity meter.

Results and Discussion

Rainfall patterns at Kirrama are distinctly seasonal, with a wet season between October and May (Australian Meteorological Bureau data). However, Figure 2.3 shows that in both 1985 and 1986 January was the driest month. The bulk of the rainfall in February 1986 was due to Cyclone Winifred which passed near the Kirrama ranges on 1 - 2 February and which caused the rain gauge to overflow. It is most

Figure 2.3 (a) Discharge in the two study streams during the study period. (b) Rainfall at the James Cook University field station during the study period. (c) Rainfall at the James Cook University field station from September 1982 until September 1986.

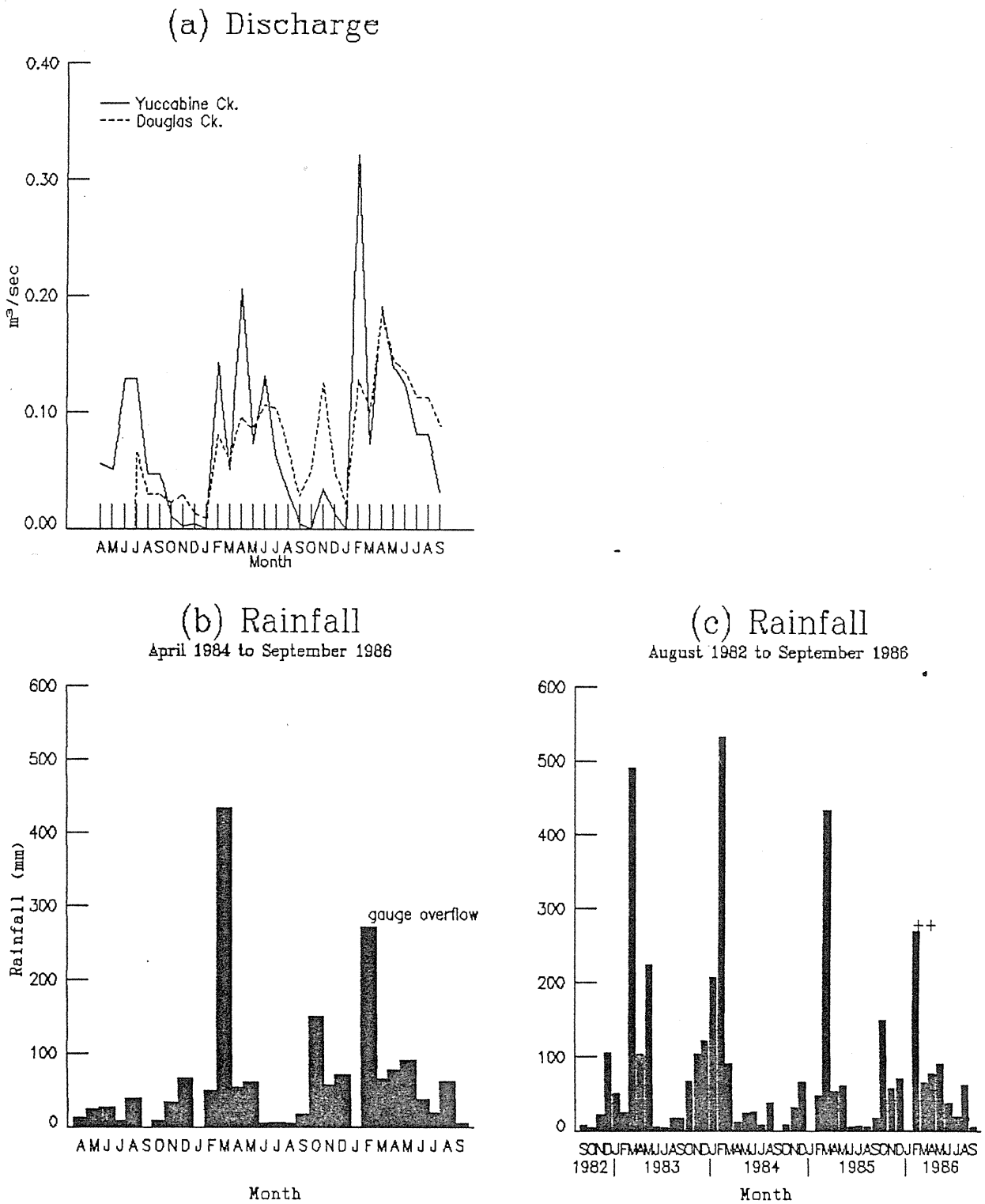


Table 2.1 Wet season (November to May) rainfall (mm) from November 1982 to May 1986, and the average rainfall at the James Cook University field station (Australian Meteorological Bureau data).

Time period	Rainfall
November 1982 to May 1983	1026
November 1983 to May 1984	1097
November 1984 to May 1985	696
November 1985 to May 1986	634*
Average November to May	1257

* Gauge overflowed during Cyclone Winifred.

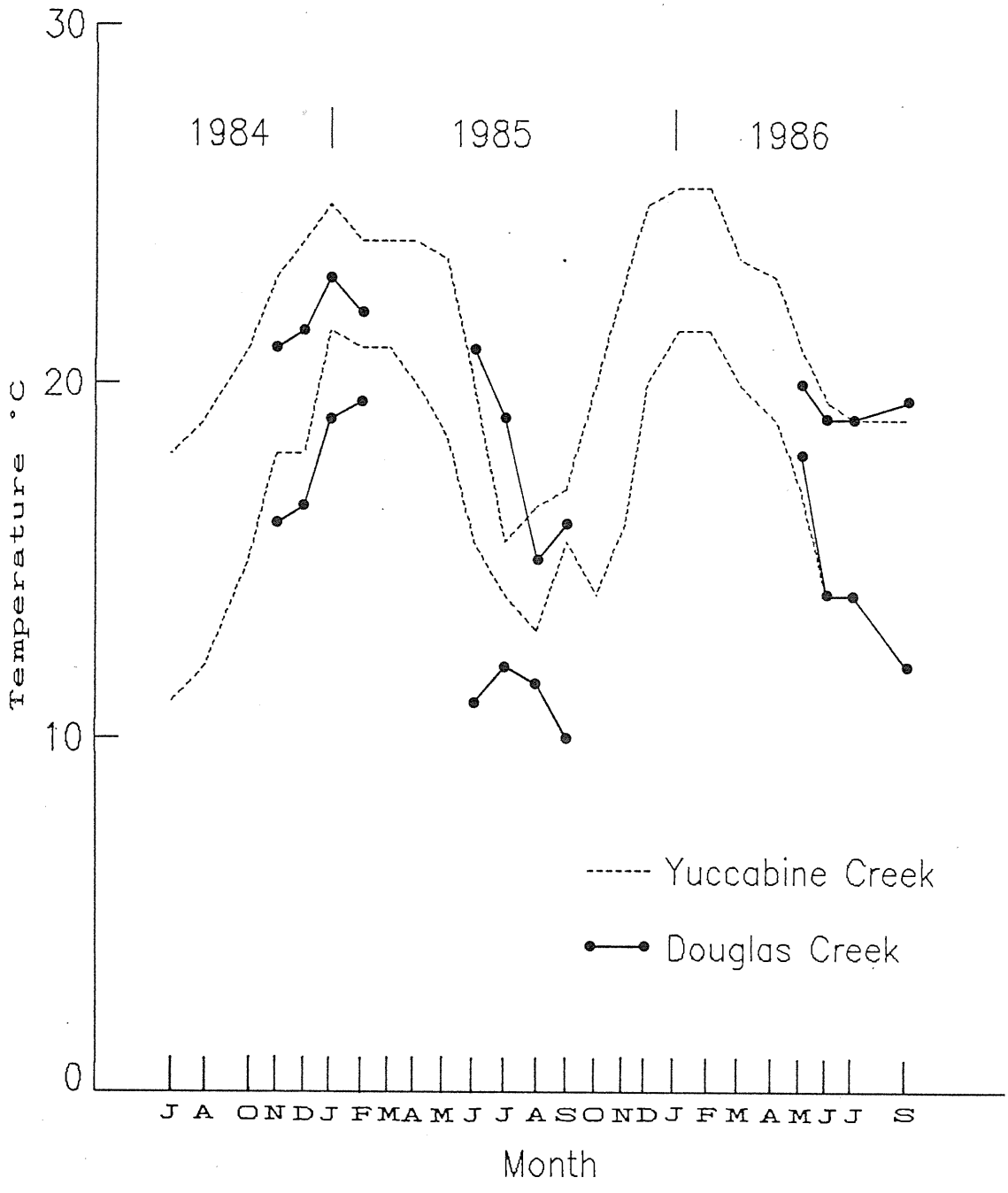
likely that this was the wettest month of the study period. Following Cyclone Winifred, 1986 had higher rainfall than the previous two years. Due to its position on the north-east slopes of the Kirrama range, Douglas Creek receives more of the prevailing rainfall than does Yuccabine Creek or the field station. It was not possible to position a rain gauge close to Douglas Creek because of the density of the vegetation.

Table 2.1 shows a comparison of wet season (November to May) rainfall from November 1982 to May 1986, and the average wet season rainfall for the field station. The monthly rainfall from September 1982 to September 1986 is shown in Figure 2.3. The rainfall during the period of this study was, apart from the influence of Cyclone Winifred, lower than for the previous two years, and was considerably lower than the long-term average.

Figure 2.3 shows that stream discharge closely followed rainfall. Because of its position, Douglas Creek maintained a higher base flow than did Yuccabine Creek despite its smaller size, although Yuccabine Creek could spate to a much higher level as in February 1986. Yuccabine Creek had a very seasonal discharge, reaching zero flow by January each year at the causeway, although some flow persisted at the sampling sites. Douglas Creek continued to flow throughout the study period.

Figure 2.4 shows the water temperature maxima and minima recorded in both streams. The streams have highly seasonal temperature ranges

Figure 2.4 Monthly maximum and minimum water temperatures recorded in the two study streams. Breaks in data for Douglas Creek are due to losses of instruments in spates.



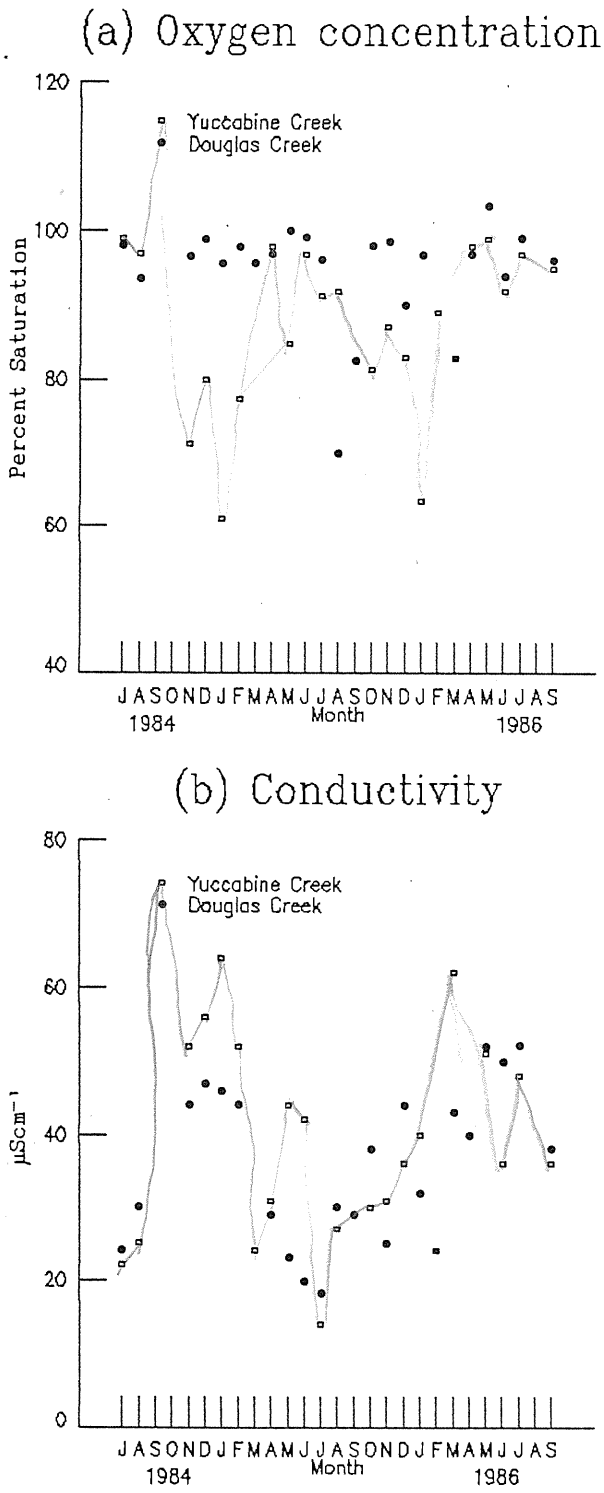
with a recorded range during this study of 11 to 25.5°C for Yuccabine Creek, and of 10 to 23°C for Douglas Creek. In general, Douglas Creek had lower monthly minima than Yuccabine Creek, although its maxima were higher at times. Spot temperatures on the same day (not presented here) were usually one or two degrees cooler in Douglas Creek even though it was visited after Yuccabine Creek, in mid-afternoon. Clearly this temperature difference was due to the greater shading of Douglas Creek.

Oxygen concentration and conductivity data are presented in Figure 2.5. Although only limited conclusions can be drawn from spot oxygen concentrations taken at variable times of day, it would appear that Douglas Creek in general had a higher concentration of dissolved oxygen than Yuccabine Creek. The latter had oxygen minima in January of 1985 and 1986, when discharge was close to zero. Low concentrations may have been due to the crowding of the organisms in the stream, depressing oxygen tensions. This phenomenon is well documented for temporary waters (e.g. Barclay, 1966; Moore, 1970; Khalaf and MacDonald, 1975; Tramer, 1977; and Morton and Bayly, 1978) and was recorded for pools in an intermittent stream in north Queensland by Smith and Pearson (1987). Figure 2.5 shows that Yuccabine Creek had a greater range of conductivity, but the levels of conductivity in both streams were low.

Pearson *et al* (1986) have pointed out that Yuccabine Creek is probably representative of many streams in the geographically widespread seasonal, wet tropics, despite common conceptions that tropical streams

Figure 2.5 (a) Oxygen concentrations recorded in the two study streams.

(b) Conductivity recorded in the two study streams.



are aseasonal. Douglas Creek was more shaded than Yuccabine Creek and had less variable discharge, but had a wider temperature range than would be commonly expected for a tropical stream.

2.2 Immature Stage Sites

2.2.1 Estuarine Sites

Figure 2.1 shows the locations of the sites used for sampling for *A. striolata* larvae in the estuary of the Murray River. Bluff Landing was the most downstream road access to the Murray River. It was tidal, but saltwater mangroves only extend approximately 2 km further upstream. "First inlet" was a site in the Murray River opposite the junction of the river with a small unnamed tributary. "Roundabout" was so named because of the round island to one side of a lagoon on a bend of the river. Current patterns within the lagoon were very complex due to the island and a sand bank at the downstream end of the lagoon. The Bedford Creek site was in a deep, and relatively narrow channel of the river opposite the mouth of the largest estuarine tributary. Apart from the channel, the river was shallow in this region. The "Mouth" site was approximately 500 m inside the river mouth in the main channel. No sampling was done outside the river.

2.2.2 Lowland Freshwater Sites

Five sites were selected in the lowland, freshwater section of the Murray River for collection of migrating *A. striolata*. The sites were

Plate 3 Study sites in the lowland, freshwater reaches of the Murray River.

(a) MR1

(b) MR2

(c) MR3

(d) MR4

(a)

(b)

(c)

(d)

chosen on the basis of road access and suitability for electrofishing. A description of these sites follows.

MR1 (Figure 2.1, Plate 3a) was a section of the river 100 m downstream of the main arterial highway. The substratum was mostly sand with scattered snags. Extensive *Valisneria* sp. beds fringed both banks. This site was not sampled in the periods February to March 1985, and February to June 1986, during which the water level was too high.

MR2 (Figure 2.1, Plate 3b) extended from beneath a small road bridge to 30 m downstream. Numerous snags had collected beneath the bridge, and a few rocks protruded from the sand substratum downstream from the bridge. Most of the snags and rocks were removed during Cyclone Winifred.

MR3 (Figure 2.1, Plate 3c) was a causeway across the river providing access to a banana plantation. Sampling was largely confined to the rocky riffles on the downstream side of the causeway. In February 1986 the causeway was covered with sand by the spate caused by Cyclone Winifred. This sand was subsequently scoured away by March 1986.

MR4 (Figure 2.1, Plate 3d) was a 50 m section of the river upstream of the access road to the Murray Upper community. The substratum was sand and two large logs. A paragrass, *Brachiaria mutica* (Forssk.), stand fringed the eastern bank. Following the cyclone, the logs were buried in sand, but a 5 m sand and rock riffle was exposed at the upstream limit of the site.

MR5 (Figure 2.1) was within the Murray River Falls Environmental Park. Because of the sensitive nature of electrofishing in a public environmental park, this was sampled only once, on 4 December 1984.

Chapter 3 Population Biology

3.1 Introduction

It is not possible to fully explain the processes of communities or ecosystems without having some understanding of the dynamics of the populations of the species in that system. Knowledge of the life cycles and feeding roles of dominant or abundant species is particularly important. *Australatya striolata* is a conspicuous species of the stream communities of the tropical upland rainforests of eastern Australia. It is numerically abundant, but perhaps more importantly, is one of the larger invertebrates and, as a filter-feeder, presumably must play a significant role in the energy processing of the stream.

To date, apart from a few anecdotal accounts (e.g. McCulloch and McNeill, 1923; Riek, 1953 and Bishop, 1967) and the brief consideration of its probable life history by Smith and Williams (1982), there have been no studies of the life history of *A. striolata* . The extent of the knowledge of the ecology of the species was that it was an inhabitant of fast-flowing streams on the east coast of Australia and that it probably had an estuarine larva.

In view of this lack of knowledge for *A. striolata*, and the fact that *A. striolata* inhabits streams some distance from the sea (e.g. 145 km for Yuccabine Creek and 65 km for Douglas Creek), major effort was put into a study of the life history of the species.

3.2 Methods

3.2.1 Population Sampling

The rocky nature of the study sites, offering many refuges for *A. striolata* , and the variability of stream discharge, made the selection of a reliable collecting technique difficult. In the past, Atyidae have been collected with box samplers (e.g. Hart, 1981; Bright, 1982), by sweeping with dip nets (e.g. Carpenter, 1982, 1983; De Silva, 1982; Dudgeon, 1985), or even by hand (Darnell, 1956). These methods were not appropriate for an agile shrimp in the rocky riffles of this study. It had been found prior to the commencement of this study that *A. striolata* responded well to electrofishing, and this method was adopted. Electrofishing causes a shrimp to repeatedly flex its tail in the typical escape response of Natantia. This lifts the shrimp into the water column where it can be collected with the anode net of the electrofisher. By progressing in an upstream direction, advantage can be taken of the stream current sweeping stunned shrimp from under rocks. Clearly, the efficiency of this technique will be related to the depth of water and the current speed.

A comparative test of dip-netting and electrofishing carried out as a student exercise on 4/5 September 1985 in 4 equal subdivisions of Yuccabine Upper gave a mean catch per five minutes for dip-netting of 0.63 (n=24) and for electrofishing of 27.75 (n=4).

The instrument used was a Smith-Root Inc. type XI electrofisher, producing 600-900 volts DC at a frequency of 60-120 Hz. Twenty 10-second periods of electrofishing effort were applied to each site where stream area permitted. The number of shrimp caught per interval was recorded. Douglas Creek and Yuccabine Upper were covered once per sample, while Yuccabine Normal was usually worked twice. Because of the restricted rocky-riffle habitat at Log Crossing, and the low density of shrimp at that site, from 10 to 16 intervals were electrofished there each month until October 1985. Thereafter, that site was sampled intensively with only the total time of electrofishing recorded.

Each site was sampled approximately monthly from April 1984 for Yuccabine Normal and Douglas Creek, and October 1984 for Yuccabine Upper and Log Crossing. In January 1985 and February 1986 it was not possible to reach Yuccabine Upper due to tree fall on the access track, so no samples were taken at those times for that site.

The shrimp were measured and sexed on site, and returned alive to the site of capture. Carapace length (from the tip of the rostrum to the posterior margin of the carapace) was found to be the most accurate and consistent length parameter for field measurement. Males were determined by the presence of appendix masculina on the second pleopods (Smith and Williams, 1982), and juveniles by their small size and lack of a brood chamber. Small, primary females (*i.e.* females which had not undergone protandry) may have been confused with juveniles, but their relative rarity (see Smith and Williams, 1982, and

Figure 3.2, below) and the visibility of developed ovaries through the body wall of females during the breeding season, greatly reduced this problem. The presence of recently moulted individuals, as indicated by a soft exoskeleton, was recorded for each sample. Usually, 50 to 60 randomly selected individuals were measured on each occasion. Until January 1986, sub-samples from Yuccabine Upper and Log Crossing were preserved in 70% alcohol and returned to the laboratory for analysis.

3.2.2 Tagging

From August 1985 for Yuccabine Normal and Douglas Creek, and January 1986 for Yuccabine Upper and Log Crossing, until September 1986, the measured individuals were marked with a numbered streamer tag approximately 25mm long and 2mm wide, specially developed with Hallprint Pty. Ltd. for use on small shrimp. Despite their small size, the tags allowed up to 9999 individual marks to be used. Initially, the streamer tags were green in colour, but as this proved to be very noticeable, clear tags were used from January 1986 onwards. A triple catch was performed at Yuccabine Normal on 6, 7, 8 August 1985. Estimation of population size parameters was performed using the method of Fisher and Ford (1947) and the Jolly-Seber method (Jolly, 1965 and Seber, 1965).

Twenty-four individuals were tagged on 18 July 1985 and kept in an aquarium in the laboratory until 18 December 1986. They were fed with powdered commercial goldfish food and wheatgerm in a 50:50 mix, and any mortalities were noted.

3.2.3 Caging

In order to investigate growth in untagged individuals, four cages were constructed from plastic boxes 600×400×250 mm with two 190×170 mm holes cut in the larger sides and a 300×200 mm hole in the lid. The holes in the sides were covered with 5×4 mm mesh and those in the lid with 2×1.5 mm mesh. Rocks from the stream were placed in the boxes and the boxes were positioned in the stream near Yuccabine Upper so that the current flowed through the mesh sides. *A. striolata* of seven size classes between 8.5 and 14.5 mm carapace length were placed in the cages, as indicated in Table 3.1, on 11 March 1986. The shrimp were subsequently measured on 18 April, 13 May and 9 June.

3.2.4 Additional Collecting

Supplementary searching for recaptures near Yuccabine Normal was carried out monthly in the riffles from approximately 100 m downstream to 200 m upstream from Yuccabine Normal until 14 March 1986. Any tagged shrimp thus collected were measured and returned where found. Further collections were made in the next riffle upstream from Yuccabine Normal on 9 July 1986, 28 and 30 August 1986, 1, 3 and 4 September 1986 and 4 and 5 April 1987. This riffle is approximately 100 m long and includes Pearson's site (Pearson *et al*, 1986). Yuccabine Upper was sampled for recaptures on 22 June 1987.

Table 3.1 Initial stocks in cages in Yuccabine Creek. Measurements are carapace length (mm) for each individual added to each cage.

Cage	A		B		C		D
	13.5	9.5	14.4	10.4	11.5	8.6	12.6
	13.6	9.4	14.4	10.5	11.5		12.6
	13.6	9.6	14.5	10.4	11.5		12.4
	13.6	9.6	14.5	10.4			12.6
	13.5	9.6	14.6	10.5			12.6
	13.4	9.6	14.4	10.5			
	13.5	9.6	14.4	10.4			
	13.5	9.4	14.4	10.4			
	13.6	9.6	14.5	10.4			
	13.4	9.4		10.4			
	13.6	9.6		10.4			
	13.5	9.6		10.5			
	13.6	9.4		10.4			
	13.6	9.6		10.4			
	13.5	9.6		10.6			
	13.4	9.4					
	13.5	9.6					
	13.6						
	13.5						
	13.6						
	13.5						
	13.5						
X	13.53	9.54	14.45	10.44	11.5	8.6	12.56
n	22	17	9	15	3	1	5

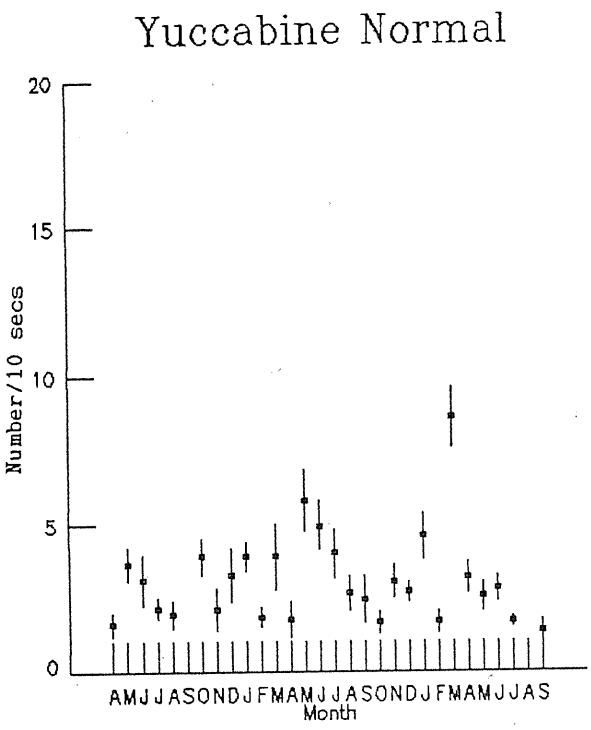
3.3 Results

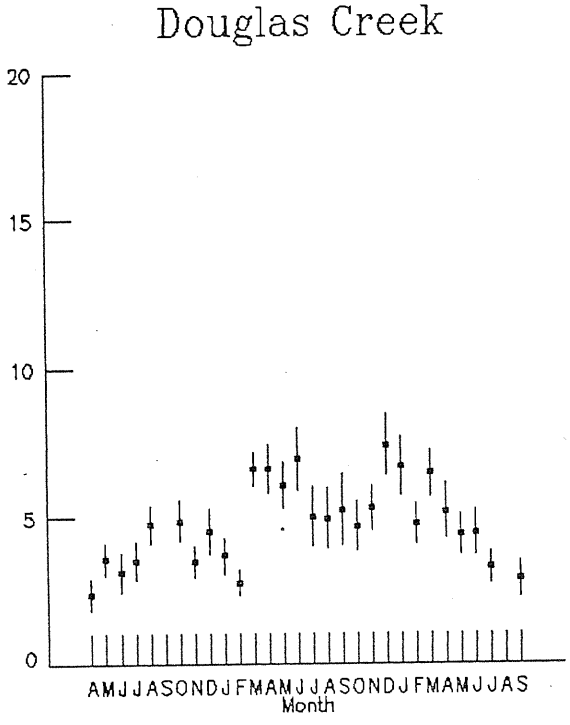
3.3.1 Catch Per Unit Effort

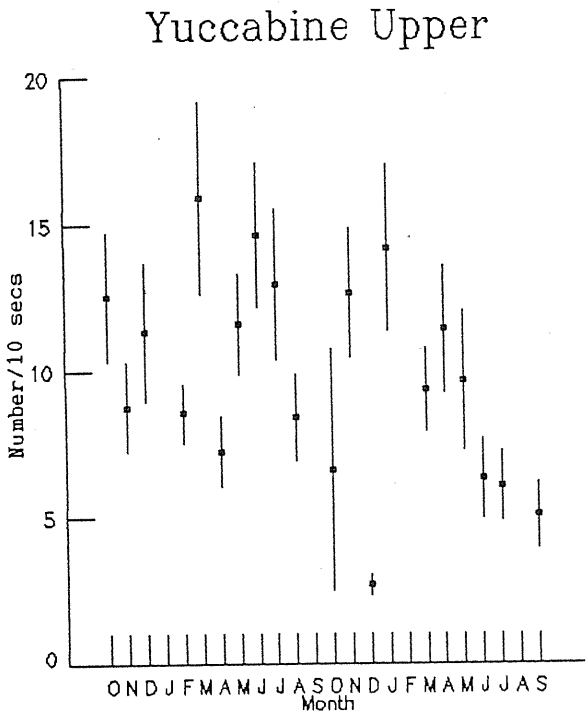
The mean monthly catch per 10 seconds (CPUE) for each of the four sites is shown in Figure 3.1. There was considerable variation between months at each site. It is possible that at least part of this variation was due to changes in water levels and current; however, there was no significant correlation between CPUE and discharge despite the fact that collection was extremely difficult when the discharge was low. There were significant differences in the mean CPUE between sites (anova $0.05>p>0.02$) and in general the arrangement of the sites in descending order of CPUE was: 1) Yuccabine Upper, 2) Douglas Creek, 3) Yuccabine Normal and 4) Log Crossing.

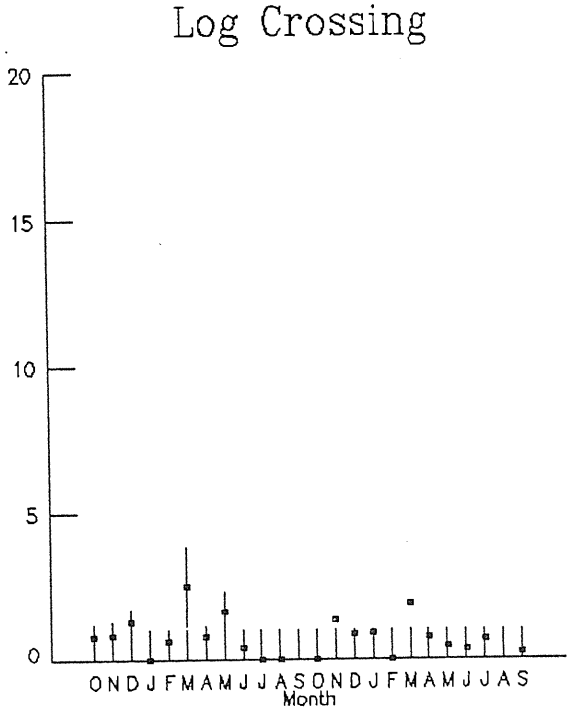
A two-way analysis of variance of 10 second period number and date was performed for each site except Log Crossing. There was a significant date effect ($p<0.01$) for each site and a significant period number effect for Douglas Creek and Yuccabine Upper ($p<0.01$) but not for Yuccabine Normal ($p>0.05$). There was no discernible pattern to the variation in CPUE through time for Yuccabine Upper or Douglas Creek, but at Yuccabine Normal there was a peak in March declining to a low in September/October in 1985 and 1986. The CPUE between October 1985 and March 1986 was highly variable at that site.

Figure 3.1 Monthly mean catch per 10 seconds ± one standard error at each of the study sites.









3.3.2 Size Frequency Distributions

The length frequency distributions for the four sites are presented in Figure 3.2. Except for Log Crossing, which had very small sample sizes, the distribution was bimodal in all cases. The left hand mode was largely composed of males while the right hand mode was composed of females. Whilst this pattern may not be unexpected for a seasonally breeding protandrous hermaphrodite, it was surprising that the modes did not move in time other than to oscillate between the 9.5 and 10.5 mm size classes for the males and from 12.5 to 14.5 mm for the females. Further, there were never more than a few individuals between the two modes. The proportion that were juveniles was also very low, always being much less than the proportion of males present. Therefore it is not possible to follow a cohort through time using these length frequency distributions.

Carpenter's (1983) method of plotting modal size classes through time was employed using 0.5 mm length intervals. The distributions were restructured to compensate for zero and low frequency values near peaks via the Elefan system of programmes (see Brey and Pauly (1986) for a complete description). This technique was only applied to the three most populated sites i.e. Yuccabine Normal, Yuccabine Upper and Douglas Creek. It was found that combining the Yuccabine samples to increase sample sizes was inappropriate due to the differences between the length-frequency distributions at those sites. Figure 3.3 shows that this technique highlights a number of modes between the main two modes

Figure 3.2 Length frequency distributions for each sample at each study site. Date of sampling and total number measured are indicated in each case. Samples with no individuals are not included.

striped bars	juveniles
solid bars	males
open bars	non-ovigerous females
stippled bars	ovigerous females

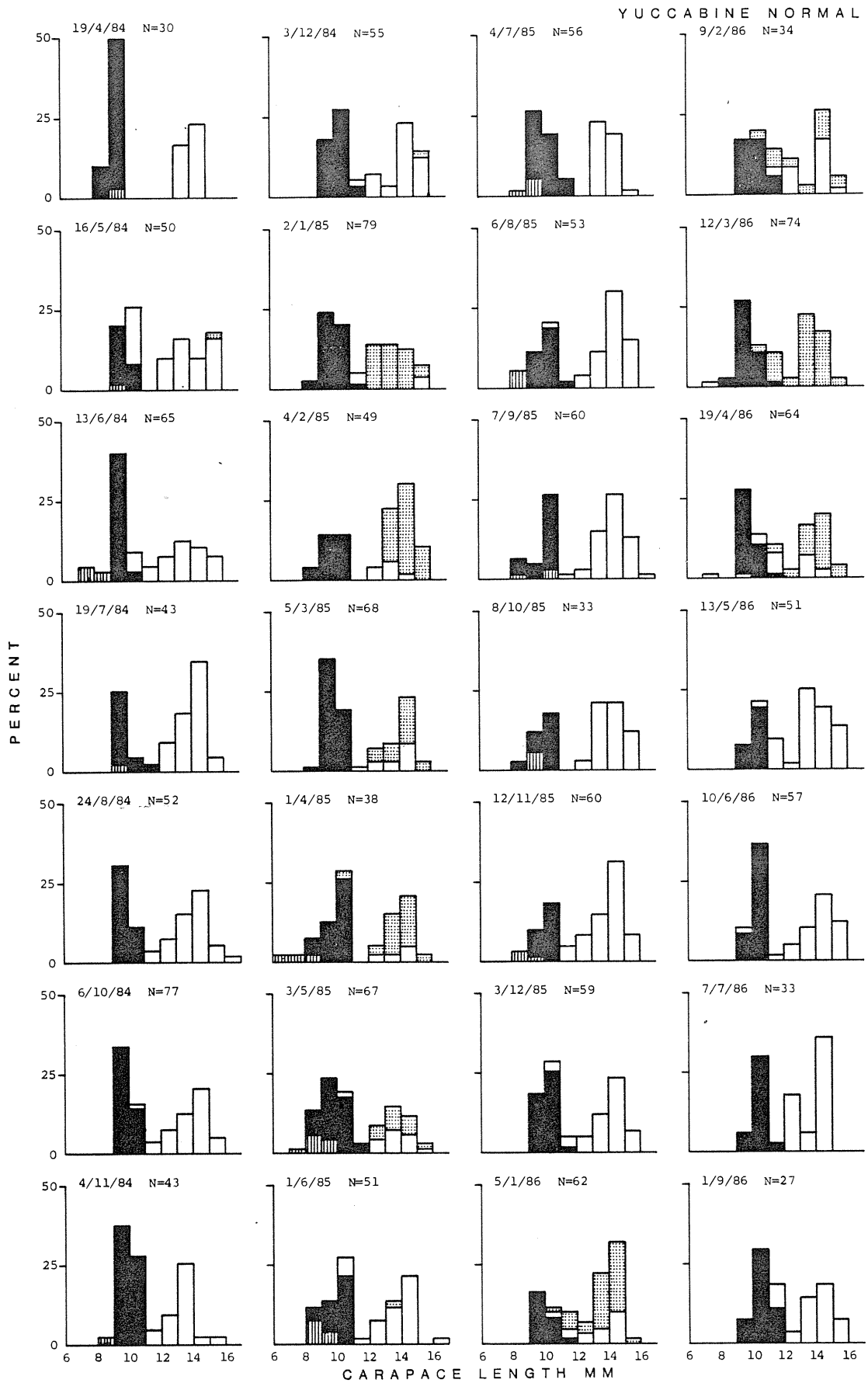

YUCCABINE NORMAL
19/4/84 N=30
3/12/84 N=55
4/7/85 N=56
9/2/86 N=34
16/5/84 N=50
2/1/85 N=79
6/8/85 N=53
12/3/86 N=74
13/6/84 N=65
4/2/85 N=49
7/9/85 N=60
19/4/86 N=64
19/7/84 N=43
5/3/85 N=68
8/10/85 N=33
13/5/86 N=51
24/8/84 N=52
1/4/85 N=38
12/11/85 N=60
10/6/86 N=57
6/10/84 N=77
3/5/85 N=67
3/12/85 N=59
7/7/86 N=33
4/11/84 N=43
1/6/85 N=51
5/1/86 N=62
1/9/86 N=27
PERCENT
0
25
50
6 8 10 12 14 16
CARAPACE LENGTH MM

Figure 3.2 continued

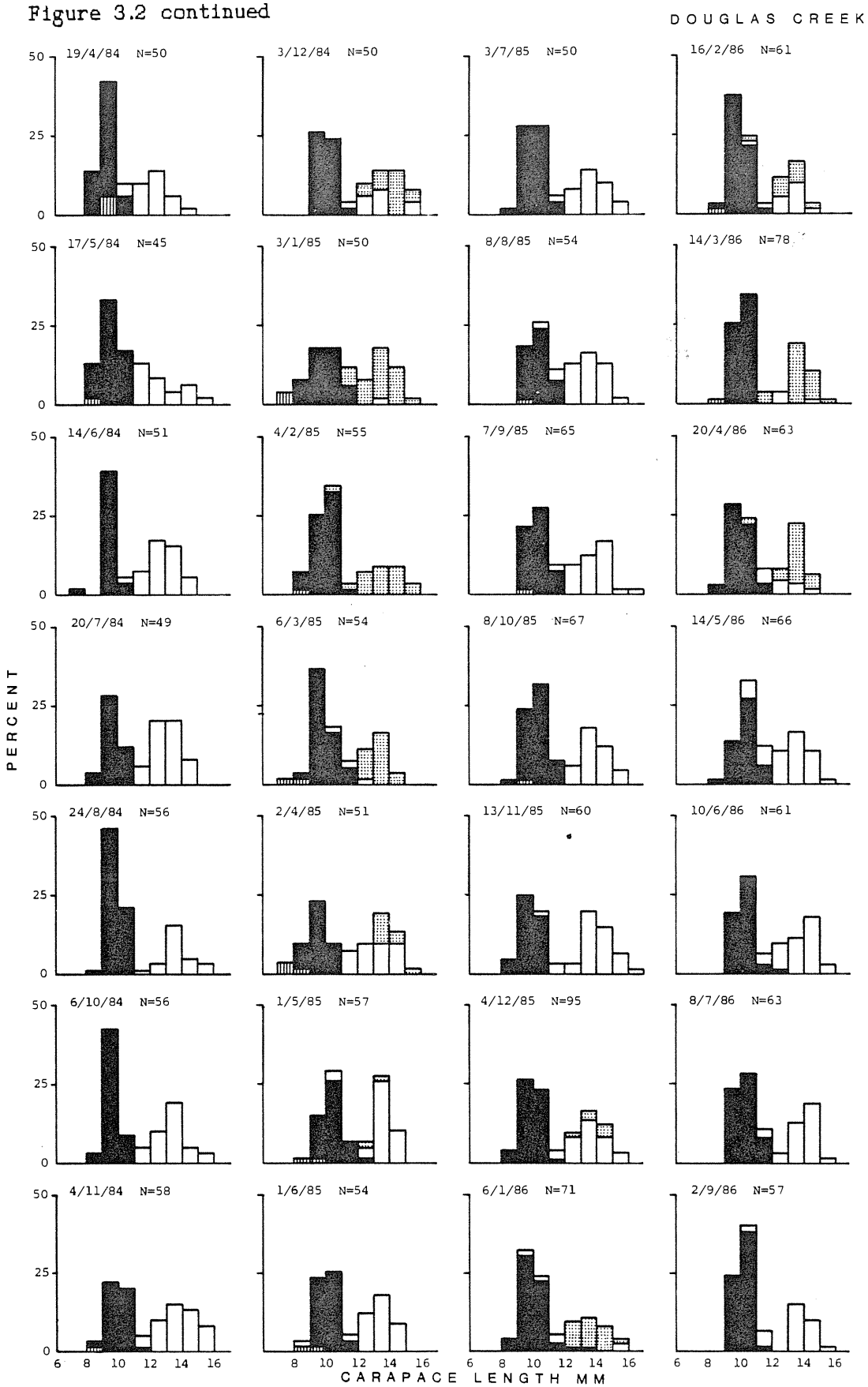


Figure 3.2 continued

YUCCABINE UPPER

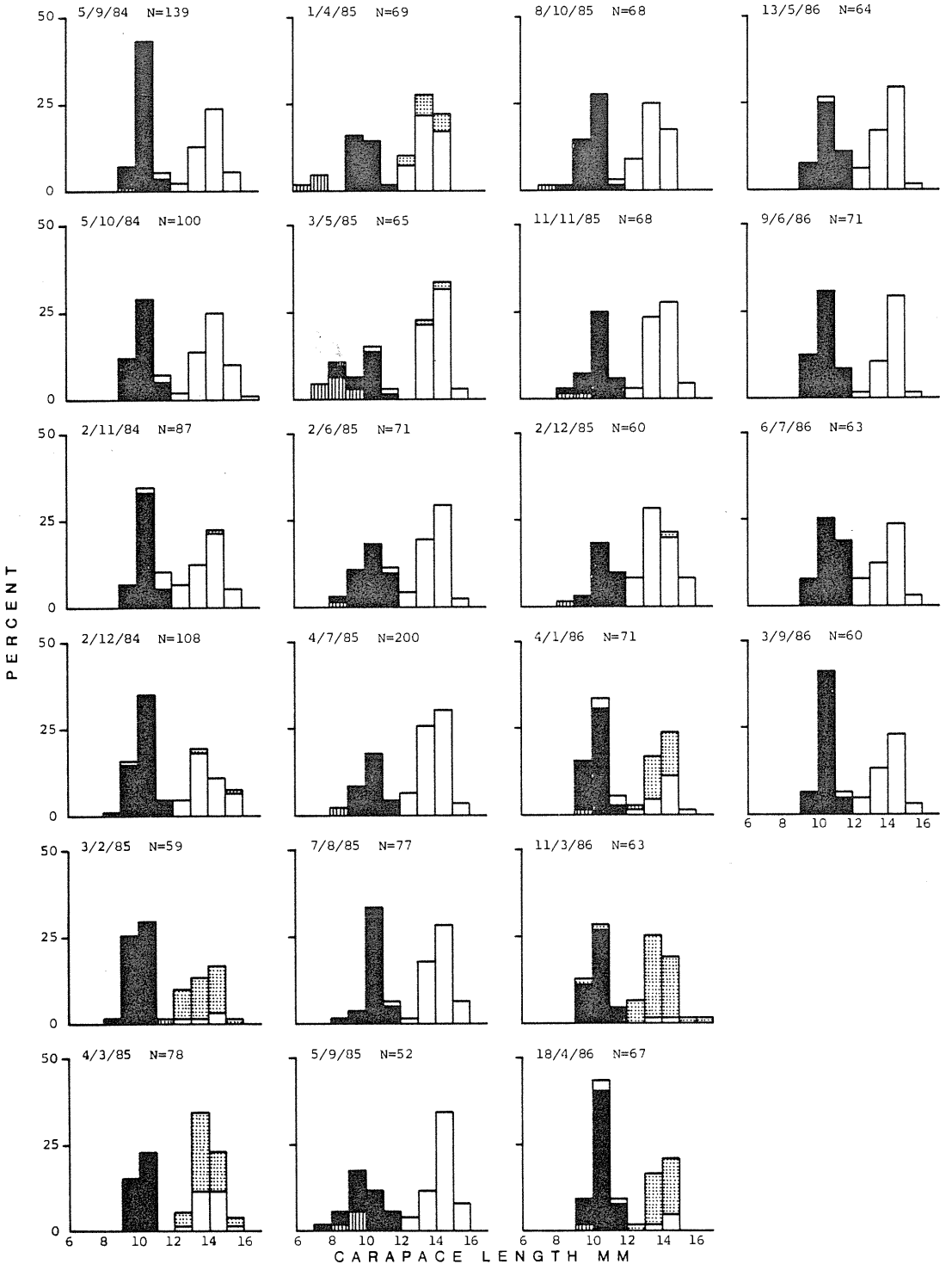


Figure 3.2 continued

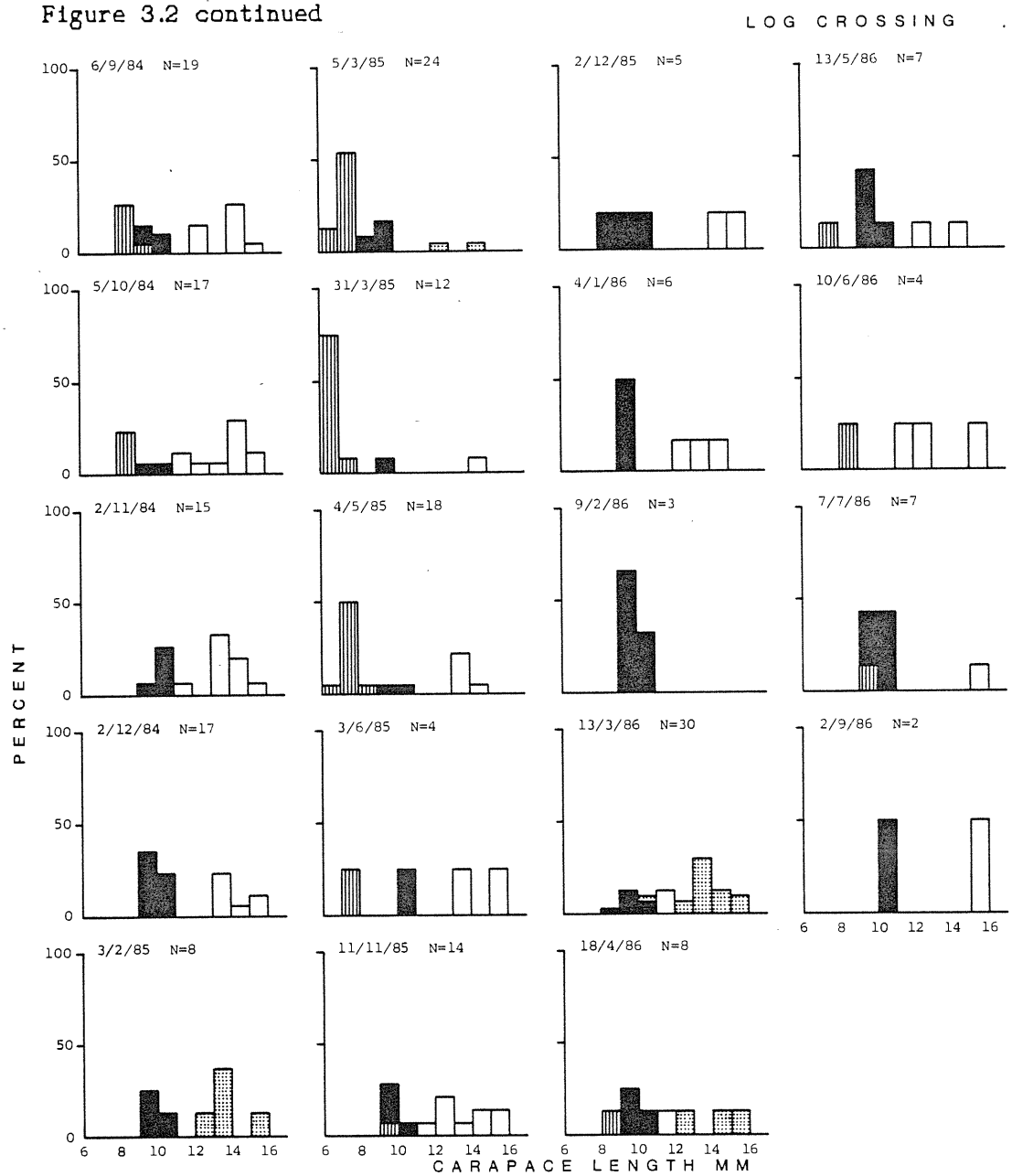
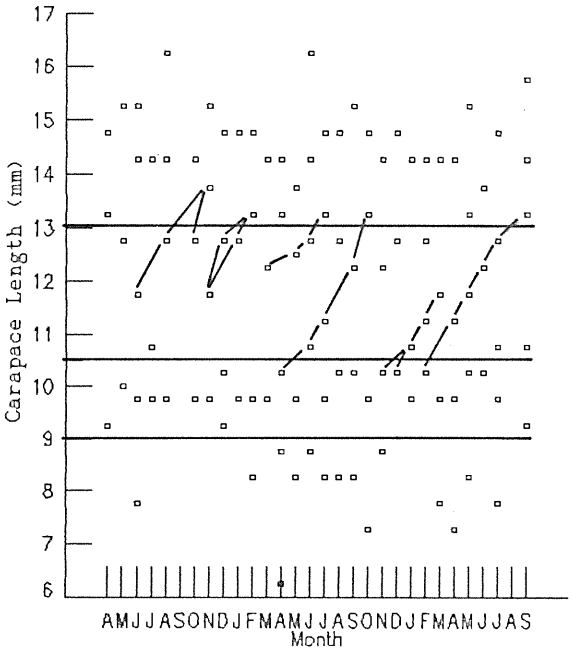
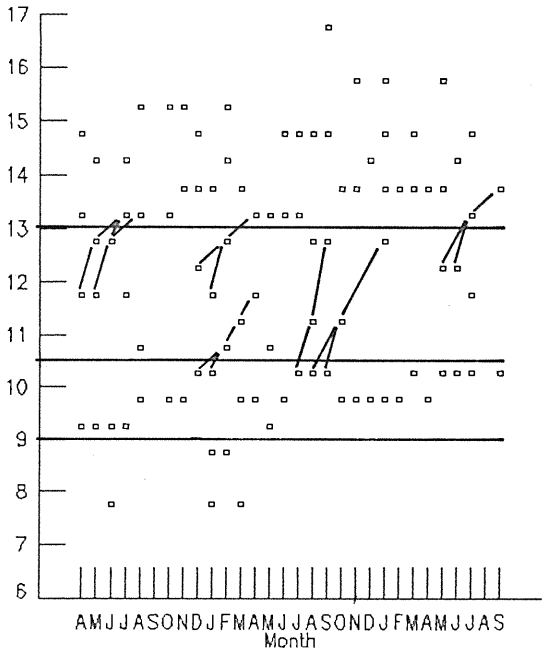


Figure 3.3 Modes in the length frequency distribution for each sample at each of the three main sites. Overlay indicates the series of modes used in the analysis (see text) and delineates mature males (between lower two horizontal lines) and mature females (above upper line)

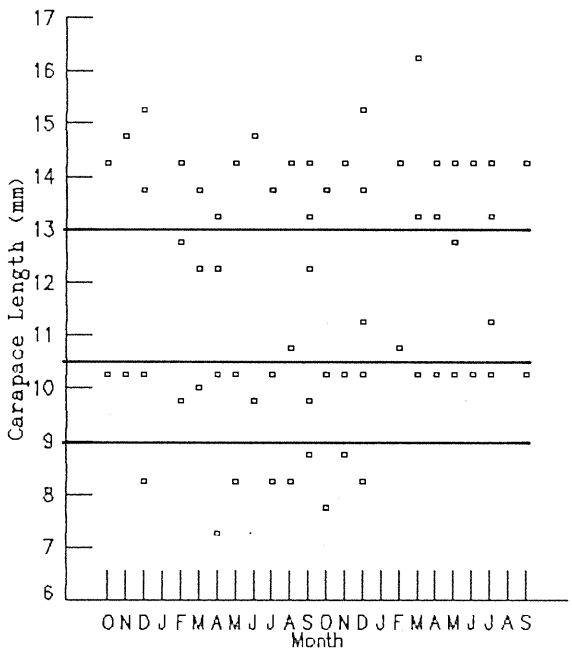
Yuccabine Normal



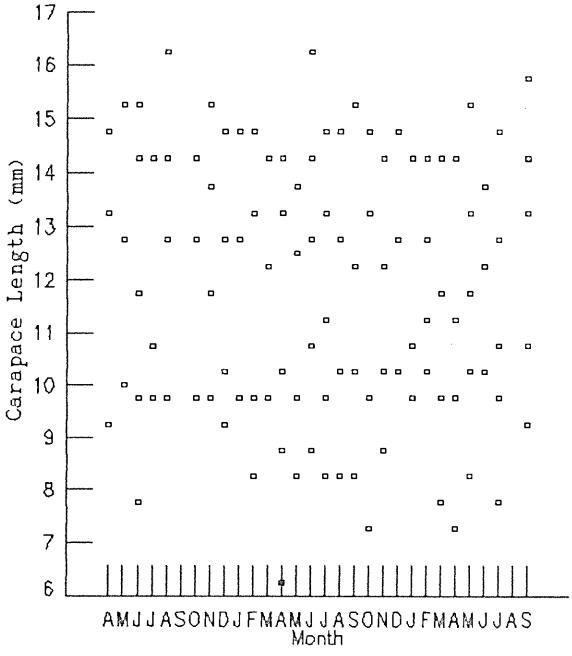
Douglas Creek



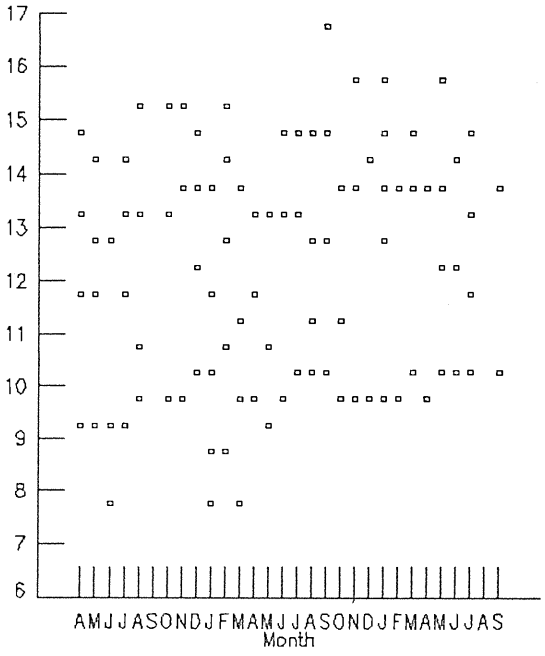
Yuccabine Upper



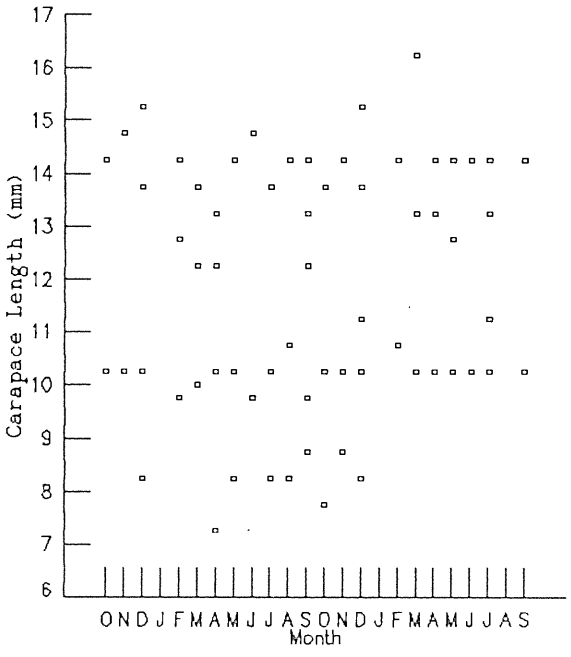
Yuccabine Normal



Douglas Creek



Yuccabine Upper



(the latter were usually between 9.25 and 10.75, and 13.25 and 14.75 mm carapace length respectively), although there are fewer intermediate modes in the case of Yuccabine Upper. Further there appears to be a positive progression of these modes through time at least in some cases.

If these progressions are real representations of growth of groups of individuals between the male and female modes, then an investigation of the rate of increase in the position of these modes could give an indication of the growth rate of individuals in this size range. To this end, groups of three or more modes were selected which met the following criteria:

i) primary selection was for modes between 10.75 and 13.0 mm but a series was taken from a minimum of 10.25 mm or continued to a maximum of 13.75 mm provided the following two criteria were met;

ii) the increase in size between two successive modes was not more than 1.5 mm;

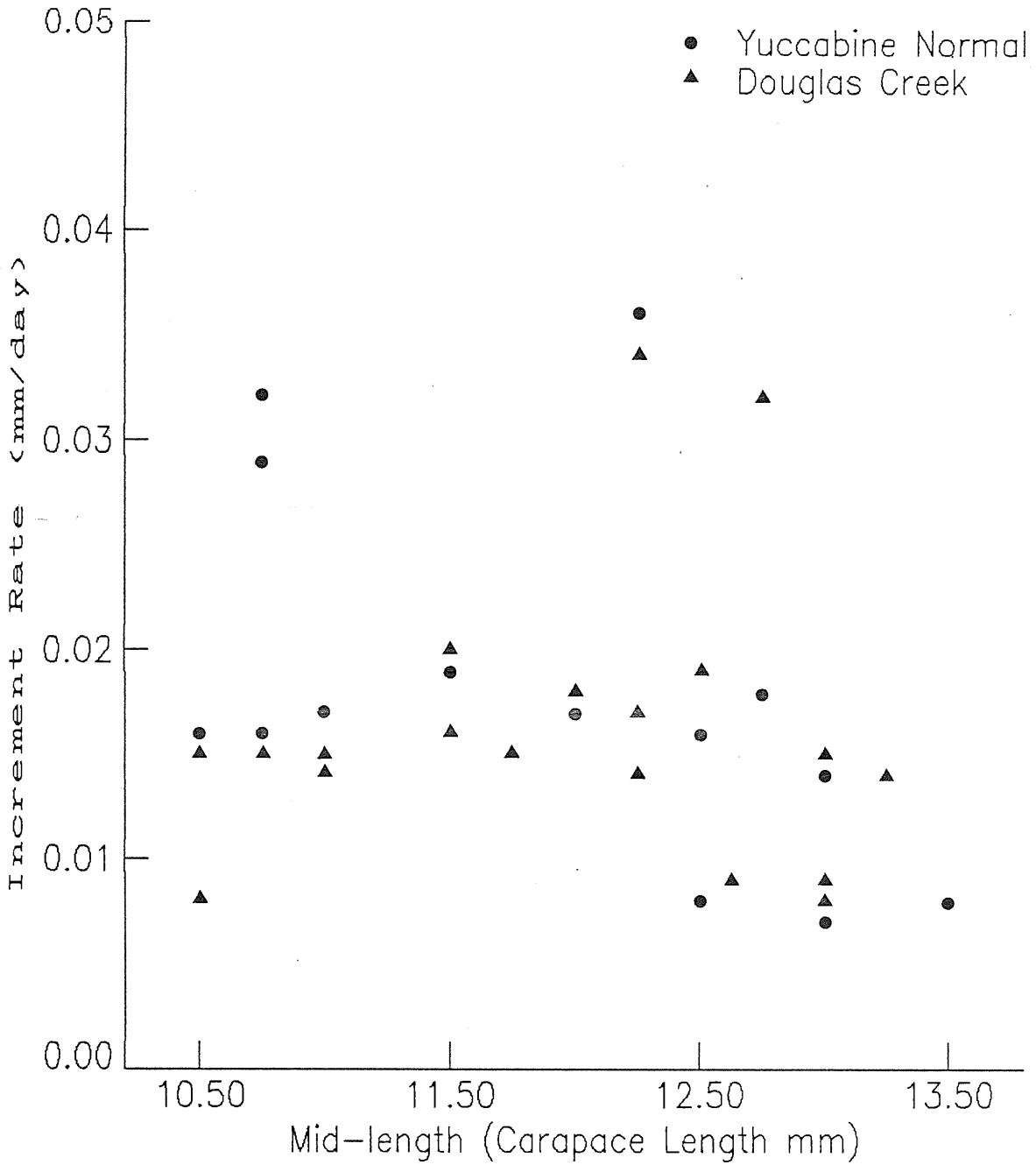
iii) it was assumed that growth was positive and would include a time element of 1 to 3 months between observed successive modes.

This restricted the analysis to series of modes between the two size groups which were reasonably close to one another and would therefore be most likely to represent growth of a cohort, rather than a number of random points.

The series thus selected are demonstrated by the overlay for Figure 3.3. There were no series which met all criteria for Yuccabine Upper. For each pair of successive modes in the selected series, the mean length and apparent growth increment in millimetres per day were calculated. These are plotted for both sites in Figure 3.4. There are three groups of points on this graph, *viz.* those with a growth rate of less than 0.01 mm per day, those from 0.01 to 0.02 mm per day (inclusive) and those greater than 0.028 mm per day. These three groups represent three separate possible growth hypotheses which for convenience can be termed slow, medium and fast growth. The second group is by far the best represented for all sizes except for those with a mid-length of 10.5 mm, and those with a mid-length of 13.0 mm or more. As shown in Figure 3.2, the latter two mid-lengths are outside the general range of overlap of males and females, and would therefore represent individuals that were functional males or females respectively. Therefore the growth rate of individuals within the sex overlap would most likely be represented by the points in the second group.

The type of growth curve indicated by the data in group 2 does not fit the usual Von Bertalanffy pattern and is not well explained by a simple linear regression ($r=0.05$, $p>0.10$). It is well explained by a fifth degree polynomial ($r=0.53$, $p<0.02$), which would indicate that growth could follow a sigmoidal curve for this size range. Interestingly, if the data from the "slow " group are included in the analysis, higher correlation coefficients are obtained for all degree polynomials.

Figure 3.4 Increment rate between pairs of modes in the series indicated in Figure 3.3.



This analysis gave equivalent r values for polynomials of degrees 5 to 8 (r = 0.61, $p<0.001$). The degree 5 equation is

$$\text{Growth rate (mm/day)} = 2{,}39\times10^{-6}\,X^5 - 5{,}04\times10^{-5}\,X^4 + 2{,}16\times10^{-4}\,X^3 - 8{,}37\times10^{-3}\,X^2 + 0{,}2055\,X - 1{,}1635$$

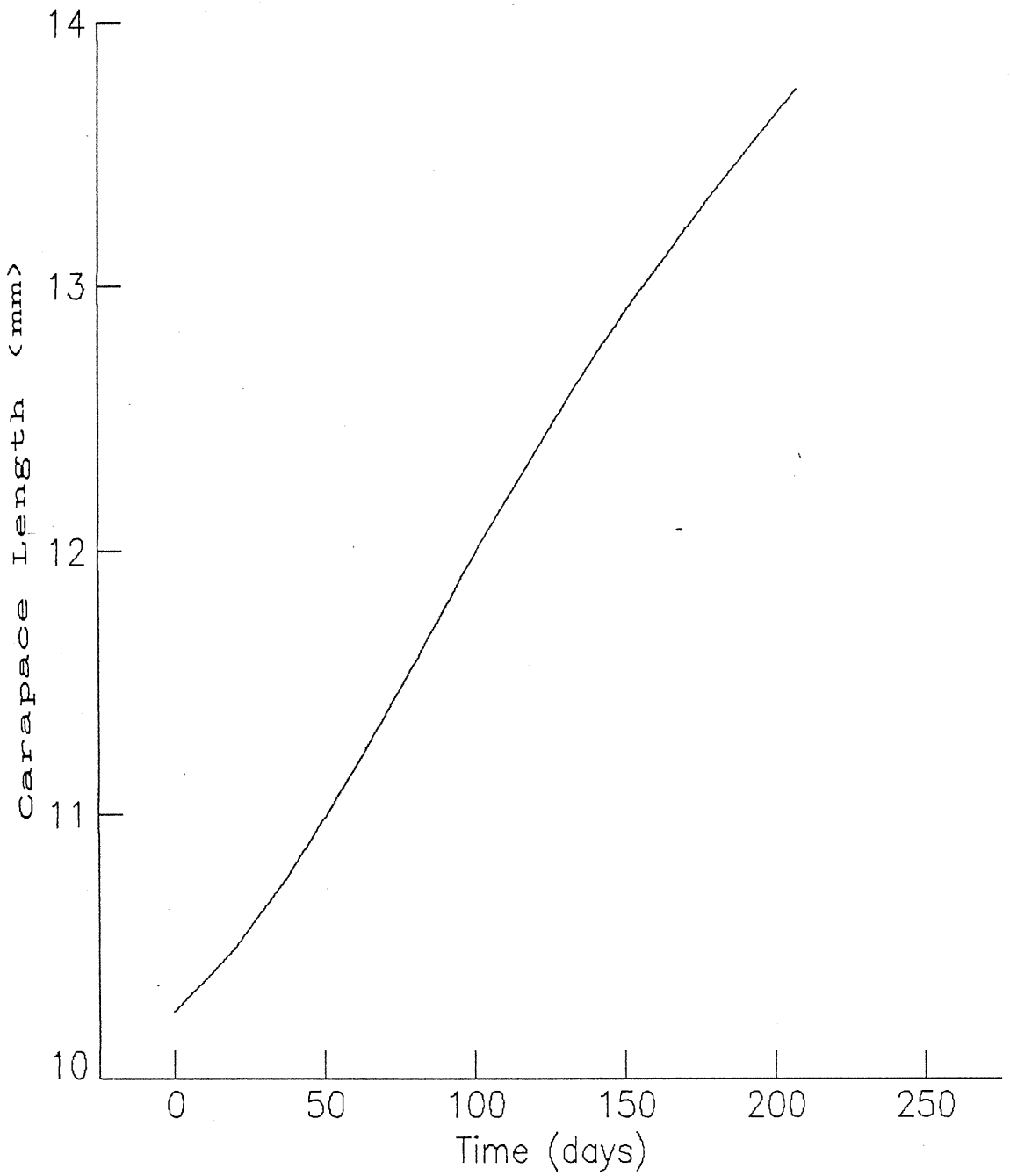
where X is carapace length in millimetres.

From the above equation for the growth rate, a numerical integral was obtained using Simpson's Rule to give a growth curve for the intermediate size classes. This growth curve is presented in Figure 3.5. Assuming that this is a true representation of growth for these size classes, then it would seem that the time required for individuals to grow from male size to female size (i.e. 10.25 mm carapace length to 13.75 mm carapace length) is about 200 days.

There were no equivalent series of modes for the juvenile size classes, and there were too many horizontal series of modes within the male and female size groups for similar analyses for those sizes.

Figure 3.2 clearly shows the seasonality of breeding, with ovigerous females present from December to May. Although juveniles were present in low numbers in most samples, they were most common in the Yuccabine Creek sites between April and June 1984 and March and June 1985. Only small numbers were present in Yuccabine Creek in 1986. In Douglas Creek, juveniles were most abundant between April and June 1984, January and April 1985 and November 1985 and May 1986. Thus

Figure 3.5 Growth curve for the intermediate size classes derived from the mode series analysis.



recruitment, in terms of juveniles arriving at the adult habitats, occurred following the breeding season in Yuccabine Creek, and overlapped with the breeding season in Douglas Creek. These juveniles probably represented offspring from previous breeding seasons (see Chapter 4).

3.3.3 Sex Ratio

Figure 3.6 shows the proportion of males in the sample for each month for the three main sites. The overall proportion of males for each site (±SE) was as follows:

Douglas Creek - 0.57 ±0.012

Yuccabine Normal - 0.44 ±0.018

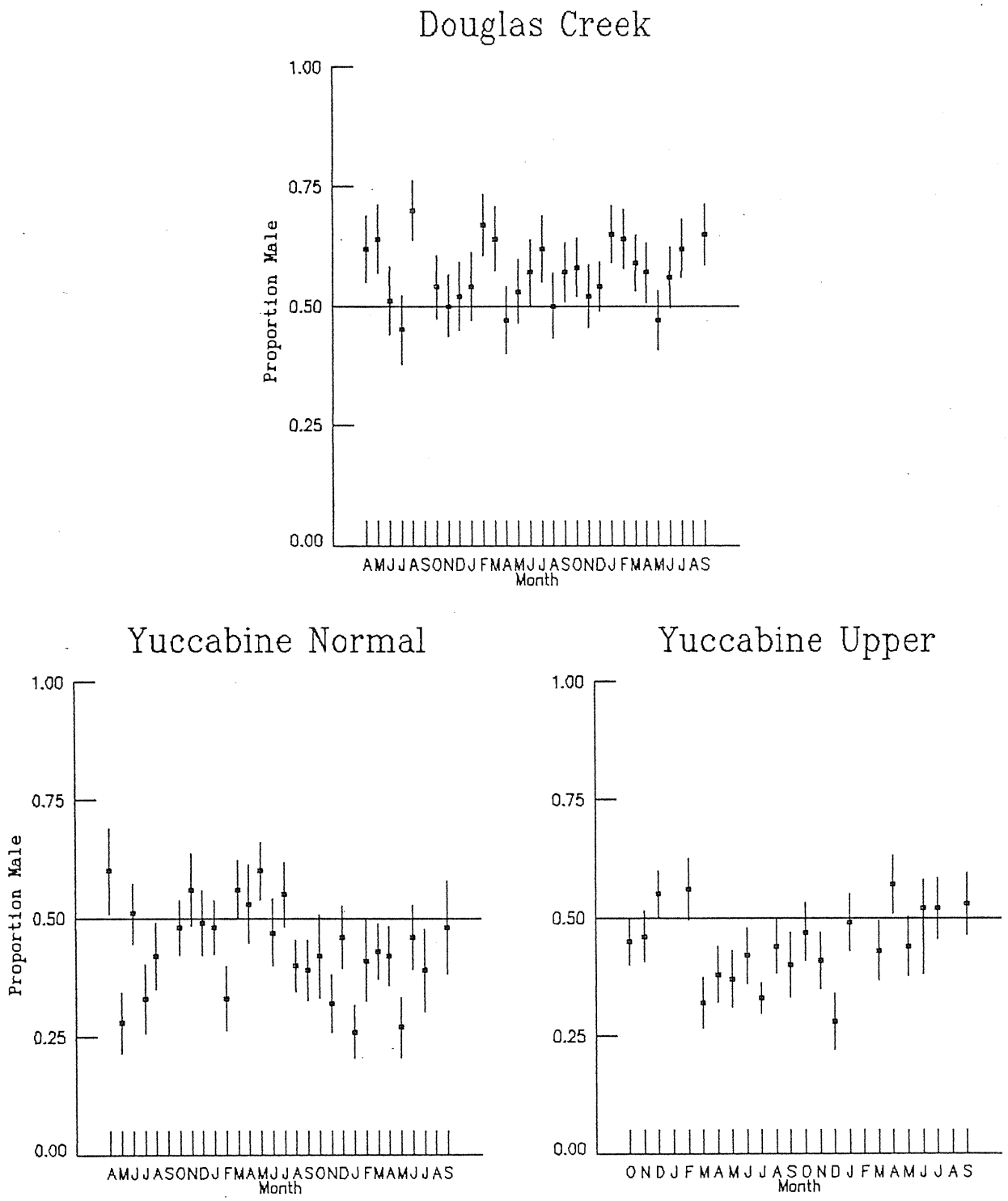
Yuccabine Upper - 0.44 ±0.020

All were significantly different from 0.5 (means test; $p<0.001$, $p<0.005$ and $p<0.01$, respectively). Thus, while there was considerable variation from month to month, males tended to predominate in Douglas Creek while females predominated in Yuccabine Creek. The patterns of change in the sex ratio do not show any relationship with the timing of the breeding season, or with the times of greatest recruitment.

3.3.4 Moulting Rates

Since *A. striolata* females must moult to reproduce, as is usual among the Natantia (Hartnoll, 1985), females are excluded from the following analyses of moulting rates for samples taken during the breeding

Figure 3.6 Proportion of each sample that were males for each of the main sites.



season. Therefore, the following analyses relate to moulting for growth rather than reproduction. Figure 3.7 shows the percentage of individuals that were recently moulted each month for all sites combined. There were insufficient numbers of recent moults to allow comparisons between sites. There were peaks in moulting in October/December, February/March and June each year which correspond to just before, during and just after the breeding season. Figure 3.7 also shows the proportion of recently moulted shrimp for three size classes: less than 9.0 mm; 9.0 to 10.9 mm; and 11.0 to 12.9 mm carapace length. These classes correspond largely to juveniles, males and intermediates (between the male and female modes, see Figure 3.2). The peaks in these groups concurred with the peaks in the combined graph, although some of the peaks of the latter were absent in each case. Hence, moulting was most common during three periods of the year.

3.3.5 Tagging Results

Laboratory Survival

Figure 3.8 shows the survival rate of marked individuals in the laboratory. Although survival was high after the first 40 days (ϕ=0.987), the condition of the shrimp as indicated by the rigidity of their tests declined markedly with time, and their size diminished by an average of 7.3% in the first 7 months of the experiment. Obviously the conditions in the aquarium were not adequate in some way, probably due to insufficient or inadequate food or water quality. Nevertheless,

Figure 3.7 Percent of individuals in samples from all sites that had recently moulted for all sizes, individuals <9.0 mm carapace length (juveniles), individuals from 9.0 to 10.9 mm carapace length (males) and individuals from 11.0 to 12.9 mm carapace length (intermediate). N indicates the total number of recently moulted individuals in each category.

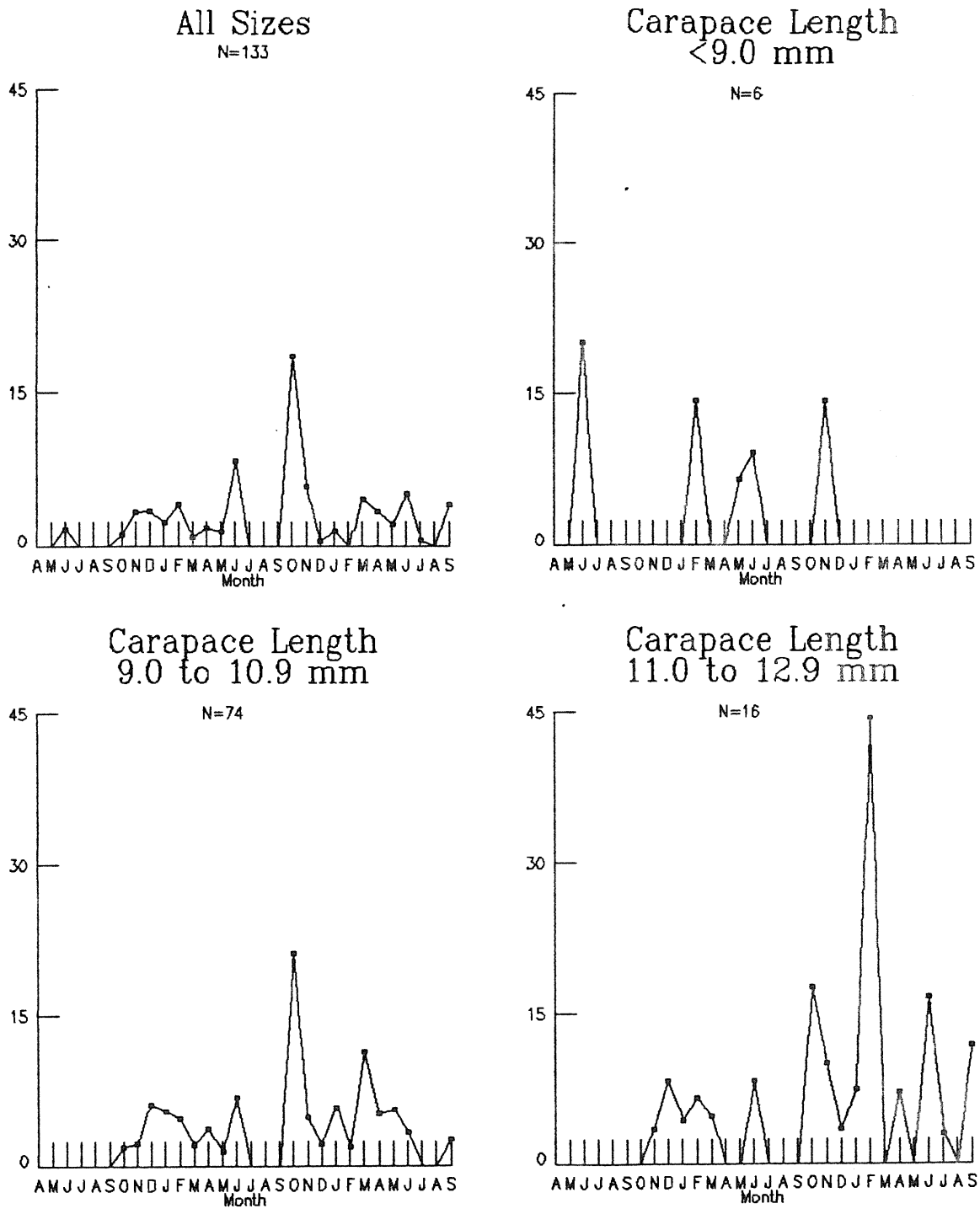


Figure 3.8 Survival of tagged individuals in the laboratory.

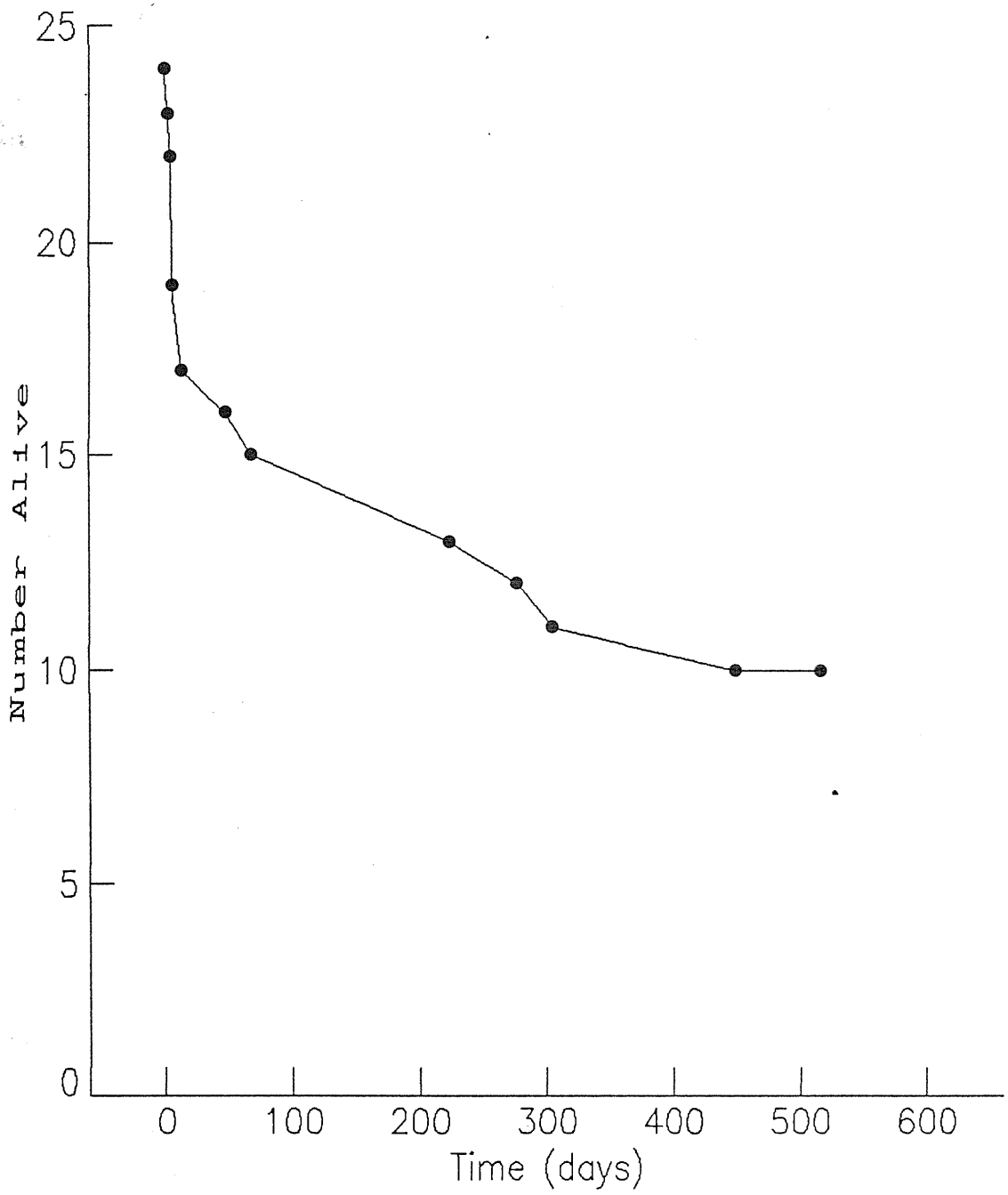
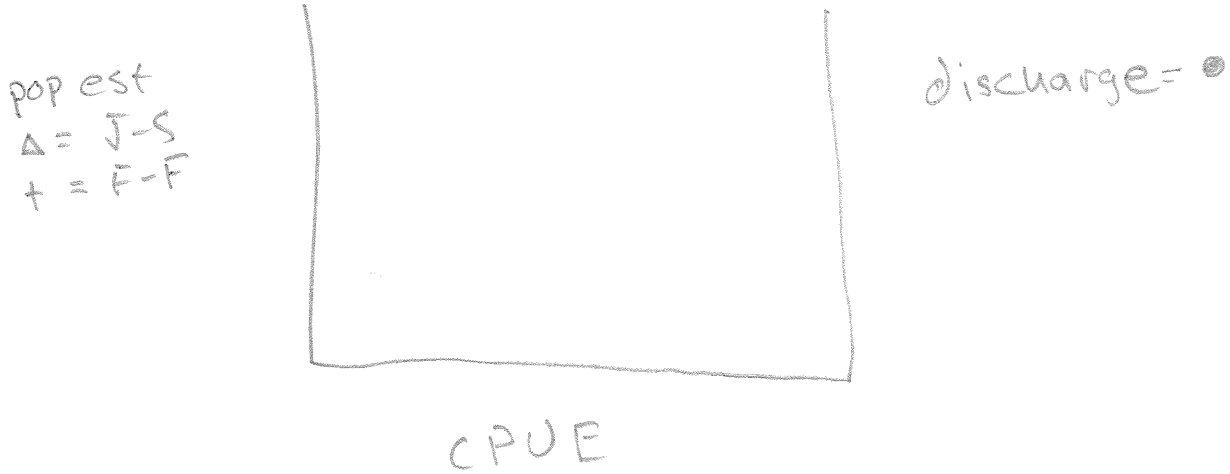


Figure for CPUE vs FF, JS pop ests and discharge.



the results indicate that tagging should not greatly increase mortality of marked individuals after the first 40 days.

Mark-recapture Model Estimates

The data used to estimate the population parameters for the three mark-recapture models are given in Table 3.2(a) along with the resulting estimates (Table 3.2(b)). The data for Log Crossing are very limited, and consequently the estimates derived from them are not reliable. The table also shows that the population size (N) and survival rate (ø) estimates produced by the Fisher-Ford model were usually within two standard errors of the Jolly-Seber estimates, but that the estimates of N from the former had less between-month variability than from the latter (although the Fisher-Ford model does not produce an estimate for the standard error of the estimate). However, χ^2 tests for constancy of the survival rate with time (Begon, 1979) were not significant (H_o rejected at $P<0.001$ level) for Yuccabine Normal, Yuccabine Upper and Douglas Creek. Therefore the main assumption of the Fisher-Ford model was not met.

Interestingly, when the regression analyses of catch per unit effort (CPUE) with the two estimates of N and discharge were performed the only significant regressions involved the Fisher-Ford estimate of N (Table 3.3). Therefore, assuming that CPUE is correlated with population size, which seems very likely because of the nature of electrofishing (see section 3.2.1), then the Fisher-Ford estimate is probably closer to the real value than the Jolly-Seber estimate for

Table 3.2(a) Data parameters for mark-recapture models. Parameters are as follows:

	Jolly-Seber	Fisher-Ford	Triple catch
r_i	total released	new releases	total released
m_i	total recaptures		recaptures released on day i
m_{ij}		recaptures on day j released on day i	
y_i	total subsequent recoveries		
z_i	previous releases not caught on day i but caught later		
n_i	total catch		
d_i		time in days	

Site	Date	Jolly-Seber					Fisher-Ford														Triple catch				
		r_i	m_i	y_i	z_i	n_i	n_i	r_i	d_i	m_{ij} 1	2	3	4	5	6	7	8	9	10	11	12	date	n	r	m_1	m_2
Yuccabine Normal	7/8/85	68	0	17	0	80	80	68	0													6/8/85		42		
	7/9/85	49	11	17	9	49	49	48	31	11												7/8/85	32	31	10	
	8/10/85	29	18	5	9	32	32	11	62	9	9											8/8/85	16		3	8
	12/11/85	52	4	7	7	61	61	48	97	1	2	1														
	3/12/85	25	5	4	10	54	59	20	118	0	2	0	3													
	5/1/86	46	11	1	2	69	69	35	151	0	3	1	5	2												
	9/2/86	25	1	5	1	34	34	24	186	0	1	0	0	0	0											
	12/3/86	44	3	5	3	163	163	41	217	0	0	0	0	0	0	3										
	19/4/86	33	6	5	4	64	64	27	254	0	0	0	0	0	0	2	5									
	13/5/86	37	0	2	5	51	51	37	279	0	0	0	0	0	0	0	1	0								
	10/6/86	48	5	3	2	56	56	43	307	0	0	0	0	1	0	1	1	1	1							
	7/7/86	27	3	0	2	34	34	24	334	0	0	0	0	0	0	0	0	1	0	2						
	1/9/86	2	2	0	0	27	27	0	391	0	0	0	0	0	0	0	0	0	1	1	0					
Yuccabine Upper	4/1/86	69	0	3	0	213	213	69	151																	
	11/3/86	58	2	9	1	187	187	56	217	2																
	18/4/86	29	4	8	8	228	228	25	254	1	3															
	13/5/86	43	3	7	12	160	160	40	279	0	2	1														
	9/6/86	68	8	7	13	126	126	60	307	0	3	3	2													
	7/7/86	63	12	2	6	121	121	51	334	0	4	3	2	3												
	3/9/86	8	8	0	0	101	101	0	391	0	0	2	2	2	2											
Log Crossing	13/3/86	29	0	4	4	30	30	29	217																	
	18/4/86	8	2	1	3	8	8	6	254	2																
	13/5/86	7	1	0	2	7	7	6	279	1	0															
	10/6/86	4	2	1	1	4	4	2	307	2	0	0														
	7/7/86	7	1	0	0	7	7	6	334	1	0	0	0													
	2/9/86	0	0	0	0	2	2	0	391	0	0	0	0	0												
Douglas Creek	8/8/85	54	0	10	0	100	100	54	0																	
	7/9/86	66	2	11	9	94	94	64	30	2																
	8/10/85	75	8	9	13	84	84	67	61	2	5															
	13/11/85	61	5	5	19	106	106	56	97	1	2	2														
	4/12/85	52	8	7	15	126	126	44	118	3	2	2	1													
	6/1/86	59	9	3	12	105	105	50	151	3	1	3	0	2												
	16/2/86	59	3	7	11	95	95	56	192	1	0	1	0	0	1											
	14/3/86	54	8	5	12	132	132	46	218	2	0	1	0	2	0	2										
	20/4/86	33	6	3	12	104	104	27	255	0	1	0	1	0	0	2	2									
	14/5/86	46	4	2	10	88	88	42	279	1	0	0	0	0	0	1	2	0								
	10/6/86	59	7	3	5	89	89	52	306	1	1	0	0	0	1	1	3	0	0							
	8/7/86	63	3	0	4	65	65	60	334	0	1	0	0	1	0	0	0	0	1	0						
	2/9/86	4	4	0	0	57	57	0	394	0	0	0	0	0	0	1	0	1	0	2	0					

Table 3.2(b) Population parameter estimates from mark-recapture models

Site	Date	Jolly-Seber N	SE	ϕ	SE	gains	Fisher-Ford N	ϕ	gains	losses	Triple catch N
Yuccabine Normal	7/8/85	0	0	,621	,160	0	0	,545	154	0	62
	7/9/85	154	35,5	,778	,308	-23	154		-4	70	
	8/10/85	122	45,8	,690	,390	612	80		343	37	
	12/11/85	694	317,8	,649	,364	174	387		221	176	
	3/12/85	619	308,4	1,177	1,353	-93	431		-34	196	
	5/1/86	601	647,2	,043	,050	80	201		552	91	
	9/2/86	105	77,2	,980	,626	1111	661		1019	301	
	12/3/86	1205	730,3	,460	,260	-199	1380		-421	628	
	19/4/86	300	148,9	1,557	1,337	4390	330		778	150	
	13/5/86	4810	-	,286	,274	-1019	958		-140	436	
	10/6/86	351	264,9	,000	,000	0	382		188	174	
	7/7/86	0	0	,000	,000	0	397		136	181	
	1/9/86	0	0	,000	,000	0	352			160	
Yuccabine Upper	4/1/86	0	0	,121	,090	0	0	,628	2718	0	
	11/3/86	529	360,2	,512	,198	1307	2718		1152	1010	
	18/4/86	1511	555,5	1,323	,621	1352	2860		415	1060	
	13/5/86	3088	1282,6	1,151	,575	-1523	2212		-348	822	
	9/6/86	1895	788,3	1,035	,837	-14	842		177	313	
	7/7/86	1886	1421,7	,000	,000	0	706		455	,262	
	3/9/86	0	0	,000	,000	0	899			334	
Log Crossing	13/3/86	0	0	,897	,894	0	0	40	3480	0	
	18/4/86	78	76,7	,000	,000	0	3480		47360	$-1,36\times10^{5}$	
	13/5/86	0	0	,000	,000	0	186560		-4352667	$-7,28\times10^{6}$	
	10/6/86	10	7,8	,000	,000	0	3109733		$1,74\times10^{8}$	$-1,21\times10^{8}$	
	7/7/86	0	0	,000	,000	0	$-2,99\times10^{8}$		$-2,99\times10^{9}$	$-1,16\times10^{10}$	
	2/9/86	0	0	,000	,000	0	$-8,96\times10^{9}$			$-3,49\times10^{11}$	
Douglas Creek	8/8/85	0	0	1,037	,410	0	0	,883	1509	0	
	7/9/85	1773	695,3	,969	,409	-593	1509		-285	177	
	8/10/85	1099	414,5	1,292	,683	2815	1047		1682	123	
	13/11/85	4223	1986,7	,408	,225	-19	2606		217	306	
	4/12/85	1685	666,7	1,499	1,007	181	2517		-141	295	
	6/1/86	2597	1570,2	,324	,217	1470	2081		3381	244	
	16/2/86	2297	1004,8	,907	,501	-17	5217		-593	612	
	14/3/86	2033	967,6	,752	,518	600	4012		263	471	
	20/4/86	2070	1214,3	1,418	1,266	1330	3804		1051	446	
	14/5/86	4165	3095,1	,382	,350	-389	4408		-1015	517	
	10/6/86	1185	783,4	,000	,000	0	2876		1942	338	
	8/7/86	0	0	,000	,000	0	4480		-560	526	
	2/9/86	0	0	,000	,000	0	3395			398	

Table 3.3 Significance of regressions of CPUE with Fisher-Ford and Jolly-Seber estimates of N and stream discharge for three sites

Independent Variables	Yuccabine Normal	Yuccabine Upper	Douglas Creek
Fisher-Ford	***	**	ns
Jolly-Seber	ns	ns	ns
Fisher-Ford & Jolly-Seber	*	ns	ns
Fisher-Ford & Jolly-Seber & discharge	*	ns	ns

ns not significant, * significant at 0.05 level, ** significant at 0.01 level, *** significant at 0.001 level

Yuccabine Normal and Yuccabine Upper, despite the invalidity of the assumption of constant survival. A less likely possibility is that both CPUE and the Fisher-Ford estimate may be related to some aspect of behaviour unrelated to the population size.

The standard errors of the Jolly-Seber estimates of ø are so large that no real conclusions can be drawn from them. Therefore the estimates of losses and gains are unlikely to be accurate - a conclusion which is supported by the occurrence of negative estimates for gains for both models at all sites.

Growth

An advantage of using individually marked animals is that the history of individuals within the population can be followed, especially with regard to such problems as growth and longevity. Figure 3.9 is a Gulland-Holt plot (Gulland and Holt, 1959) for all recaptured shrimp which shows that while growth in tagged shrimp was variable, many recaptured shrimp had decreased in length. The mean percent increase between captures, ±SE, was -0.94 ± 0.175% and the mean increment per day, ±SE, was -0.0022 ± 0.0005 mm. Since the majority of recaptures were made in the first one to three months after release and mortality was high for the first 40 days in the laboratory, it is possible that the tags interfered with the viability of marked individuals and thus caused this apparent shrinking. However, this seems unlikely because, firstly, many tagged females became ovigerous while tagged, suggesting that they were not unduly disturbed by the tags; and, secondly, in

Figure 3.9 Gulland-Holt (1959) plot for all recaptured individuals.

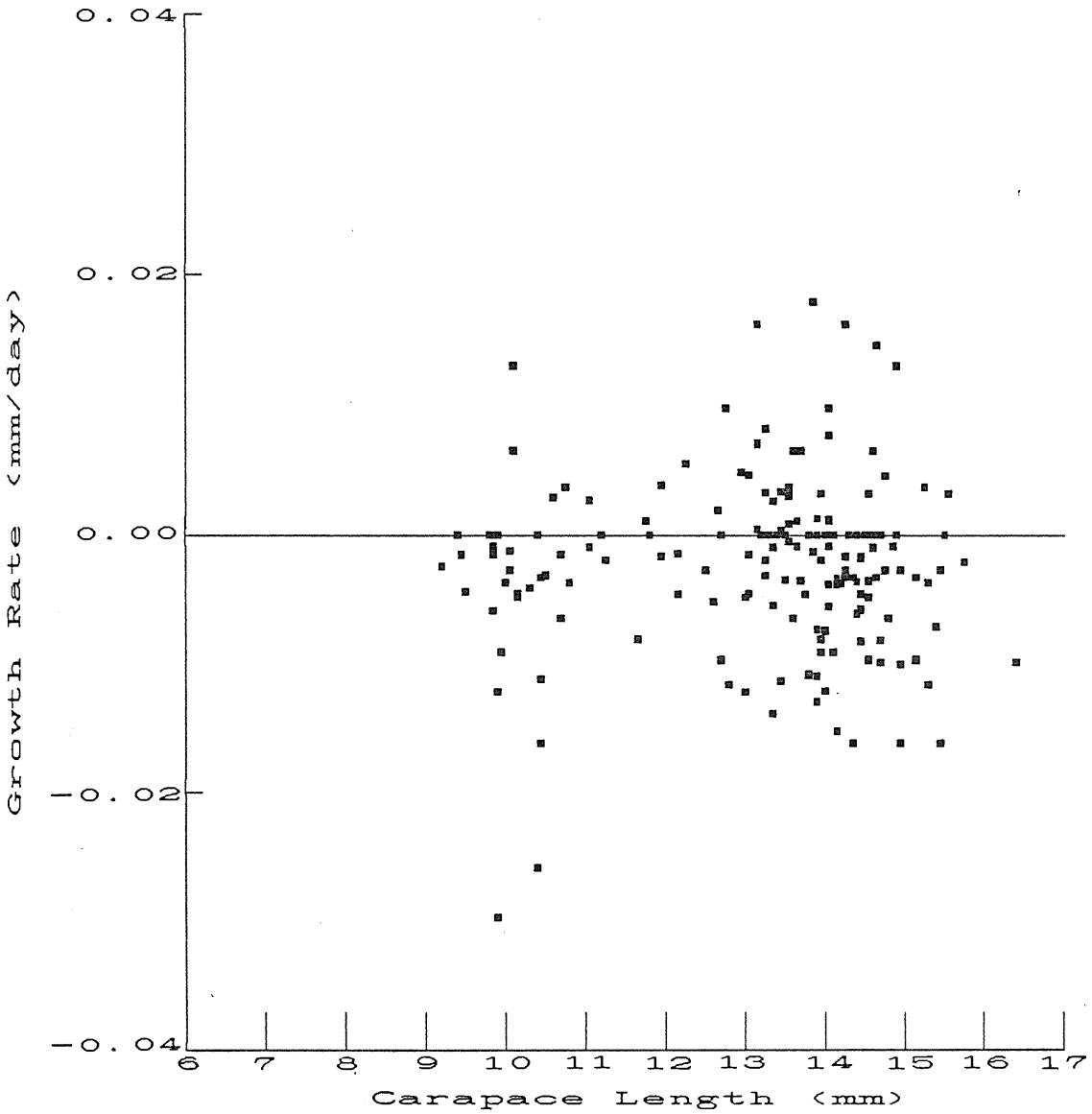


Table 3.4 Size change in tagged individuals recaptured after more than 6 months.

Site	Size when released	Size when recaptured	Time (days)	% Increase	Increment per day (mm)
Yuccabine Normal	14,1	14,0	188	-0,71	-0,0005
	13,9	13,9	394	0,00	0,0000
	14,6	14,2	298	-2,74	-0,0013
Yuccabine Upper	14,0	13,4	299	-4,29	-0,0020
	12,0	11,9	271	-0,83	-0,0004
	14,5	14,1	455	-2,76	-0,0009
Douglas Creek	14,7	14,5	218	-1,36	-0,0009
	12,6	12,5	306	-0,79	-0,0003
	14,6	14,3	192	-2,05	-0,0016
	13,7	14,1	279	2,92	0,0014
	13,4	13,6	304	1,49	0,0007
	12,3	12,0	225	-2,44	-0,0013
	13,1	13,2	216	0,76	0,0005
	13,6	13,5	202	-0,74	-0,0005
	14,7	14,6	299	-0,68	-0,0003
	14,9	14,5	269	-2,68	-0,0015
Mean				-1,06	-0,0006
SE				0,45	0,0002

individuals recaptured after more than 6 months, mean growth was still statistically significantly less than 0 (Table 3.4), but the value was so low at -1.06% that it was less than the accuracy of measurement. Thus, the growth of tagged individuals during the course of this study was negligible.

A single tagged male was subsequently recaptured as a female. The individual was released at Yuccabine Upper on 11 March 1986 with a carapace length of 10.6 mm and was recaptured at that site on 13 May 1986 as a 10.4 mm carapace length female.

A single female, released on 4 January 1986 was recaptured at Yuccabine Upper on 22 June 1987. When released it was 10.9 mm carapace length, and when recaptured it was 12.3 mm carapace length. Although this growth rate was lower than would be predicted by the numerical integral derived above, it is possible that the presence of the tag may have decreased its growth rate.

Emigration from Yuccabine Normal

Of the total of 426 shrimp that were tagged and released into Yuccabine Normal, 7 (= 1.6%) were recaptured outside of that site, compared with a total of 56 (= 13.1%) recaptured within that site. Since the region sampled for migrants was approximately 10 times the length of the site itself, and sampling for migrants was far less intense than sampling for residents, this would indicate that emigration from the site was high.

3.3.6 Growth in Cages

Table 3.5 shows the mean carapace length for each caged size class for the four months of the caging experiment. It is obvious that the cages did not adequately contain small individuals, with only one individual of the less than 11 mm groups remaining after one month. The only size class that was at all adequately retained was the 13 mm size class in cage A, and there was considerable attrition in this group after the second month. Further, there was a degree of immigration into cages A and C in the fourth month, although immigration does not appear to have occurred before this time (the seals on the cages were noted to have deteriorated in June). However, for those individuals that remained in the cages, growth was negligible for the first three months of the experiment in all represented size classes, and some individuals became smaller while in the cages. Thus, untagged individuals can shrink, indicating that the shrinking of tagged individuals was not necessarily due to the tag. It is not likely that the cages themselves caused shrinkage as they were sufficiently favourable sites for voluntary colonisation. Shrinking would therefore appear to be a common occurrence for *A. striolata*.

3.4 DISCUSSION

In any study of the population biology or ecology of a species, it is highly desirable to obtain some estimate of the population size, or the population density. This has proved to be extremely difficult to do

Table 3.5 Monthly mean size ±SE for caged individuals. Figure in parentheses is n in each case.

Date	Cage A		B		C		D
11/3/86	13,53±0,015 (22)	9,54±0,023 (17)	14,46±0,024 (9)	10,44±0,016 (15)	11,5 (3)	8,6 (1)	12,56±0, (5)
18/4/86	13,37±0,056 (22)	-	14,5 (1)	10,5 (1)	11,30±0,100 (3)	-	12,7 (1)
13/5/86	13,5±0,200 (2)	-	-	-	-	-	-
9/6/86	13,67±0,167 (3)	-	-	-	14,7±0,300 (2)	10,3 (1)	- -

for *Australatya striolata*. Whilst it would appear on *a priori* grounds that CPUE by electrofishing would be correlated with the population density, it has not been possible to test this hypothesis. The population estimates from the three mark-recapture models, were either invalid (Fisher-Ford estimates), or lacking precision (Jolly-Seber estimates), or were only done on one occasion (Triple catch estimate). The multiple mark-recapture estimates were probably affected by the observed high emigration rate from the sites. The frequency of capture models for population estimates discussed by Caughley (1977) have fewer basic assumptions than the more traditional methods such as the Jolly-Seber or Fisher-ford models, but the high migration rate at the study sites, and the evidence of mortality of tagged individuals in the laboratory would invalidate even these methods. However, some future development along these lines may facilitate population size estimates from the data obtained during this study.

Since area-related sampling procedures such as dip-netting and box-sampling are very inefficient in catching individuals of *A. striolata*, and as it was not possible to exhaustively sample areas by electrofishing, the number of individuals in a sample area could not be used to estimate population density.

This study clearly demonstrates that *A. striolata* has a highly unusual life history strategy which cannot be unravelled using standard techniques. The length frequency distributions were remarkably stable (Figure 3.2) and even the use of the the mode plotting technique of Carpenter (1983) on restructured distributions only gave evidence for

growth for a section of the size range. The possibility that this difficulty was due to inadequacies of the sampling technique is very unlikely due to the very consistency of the pattern, which holds even for samples taken from other populations over the geographic range of the species (see Chapter 6) and is independent of the sample size, except for very small samples such as those from Log Crossing.

An attempt to shed light on the life history using individual tags served only to show that growth of individuals in the two major size classes was negligible over the period of the tagging programme. Caging untagged individuals produced a similar result over a three month period. Both techniques demonstrated that some individuals actually decreased in length. In an organism which must moult in order to maintain its fitness (especially in order to maintain its feeding filter), if no energy is devoted to growth, continued moulting must result in a slow decrease in size.

Since the shape of a length frequency distribution is a function of recruitment to each size class and the time spent by individuals within that size class, the only sensible interpretation of these results is that the life history of this species involves two periods of very slow or suspended growth, when an individual is either a functional male or female, with a relatively rapid growth spurt between. The apparent sigmoid shape of the growth curve for the intermediate size classes lends support to this hypothesis. The lack of discernible progressing modes for the juvenile size classes would indicate that growth was similarly rapid for recruits and/or recruitment was very low. Thus the

growth curve should be of the shape indicated in Figure 3.10. Whether or not all members of a cohort have a similar growth pattern or whether the slow or suspended growth period varies in length between individuals cannot be determined at this stage.

It is reasonable to assume that when a group of individuals grow from one size class to another, the percentage of the catch in the smaller size class should decrease relative to that of the larger size class. Therefore, by plotting the percentage of the catch in each size class through time it may be possible to follow the growth of cohorts. Such "time - length frequency" plots are presented in Figure 3.11 for the Yuccabine Creek samples combined and for Douglas Creek. While these plots certainly serve to highlight the seasonality of the numbers of recruits (<9.0 mm carapace length) in the two streams, there were no obvious progressions of cohorts through time except for the progression of a peak in the 6.5 mm size class on 1 April 1985 to a peak in the 8.5 mm size class on 3 May 1985 for Yuccabine Creek. The 8.5mm size class returned to pre-May levels by 1 June 1985, possibly indicating that new recruits reach male (>9.0 mm) size within 61 days of arriving at the adult habitat.

The results of regression analyses of the percent in each size class are presented in Table 3.6. The regression for the 8.5 mm size class at Douglas Creek appears to result from decreasing recruitment over the period of the study (see Figure 3.11). The regressions for the 9.5 and 10.5 mm size classes at Yuccabine Creek indicate that the 10.5 mm size class increased in size to the deficit of the 9.5 mm size class over

Figure 3.10 Proposed growth curve for *Australatya striolata*.

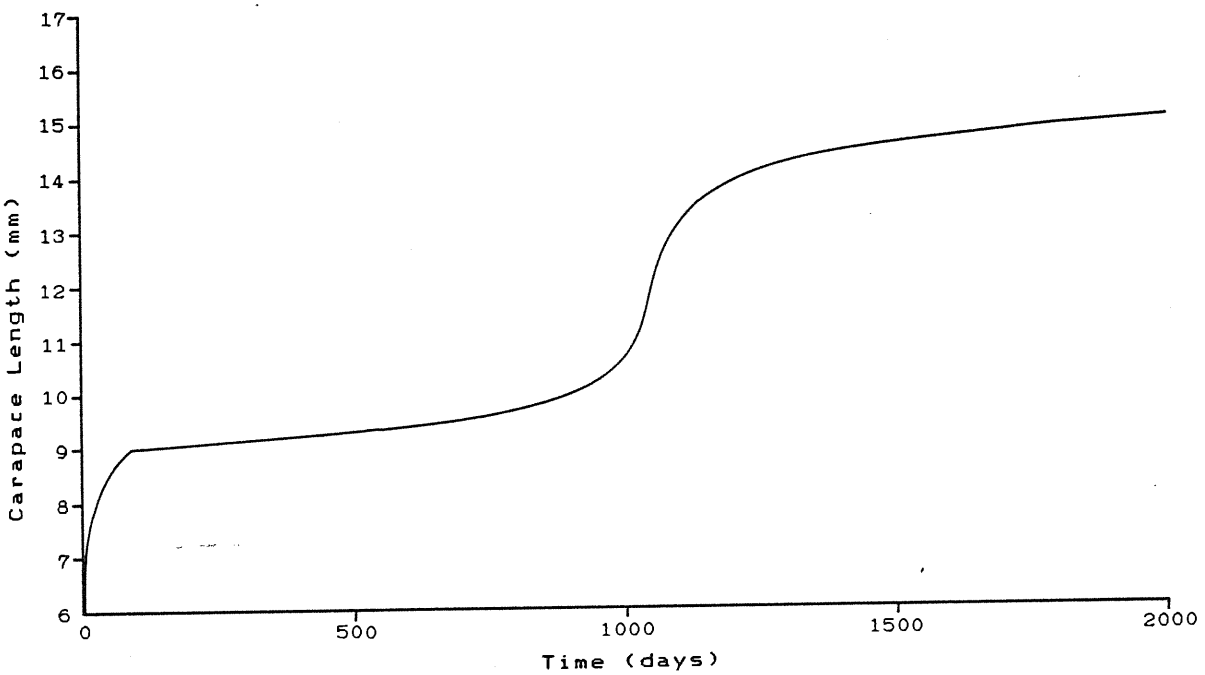


Figure 3.11 Percent of total sample in each size class during the study period for Yuccabine Creek (all sites combined) and Douglas Creek.

Yuccabine Creek

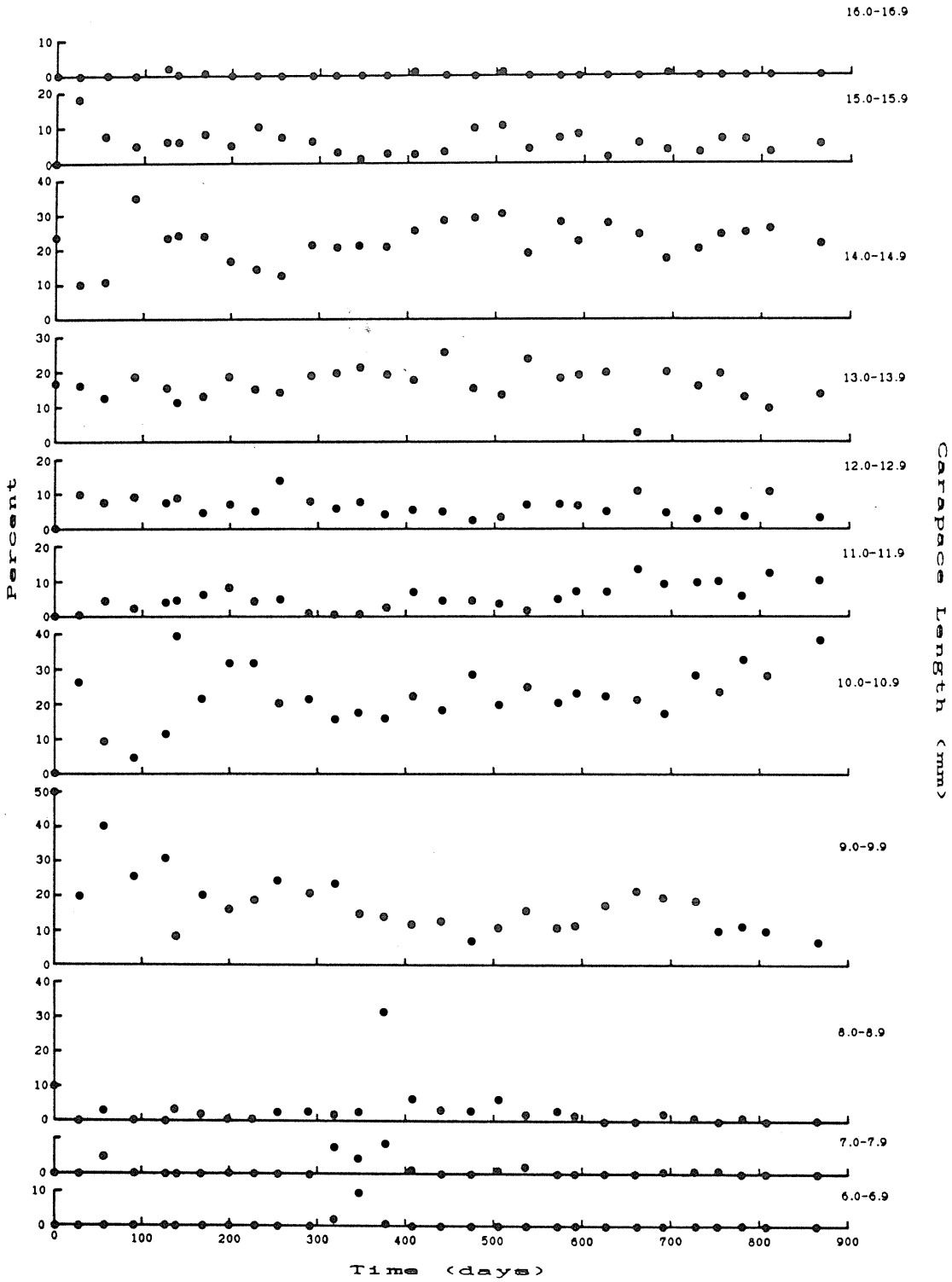
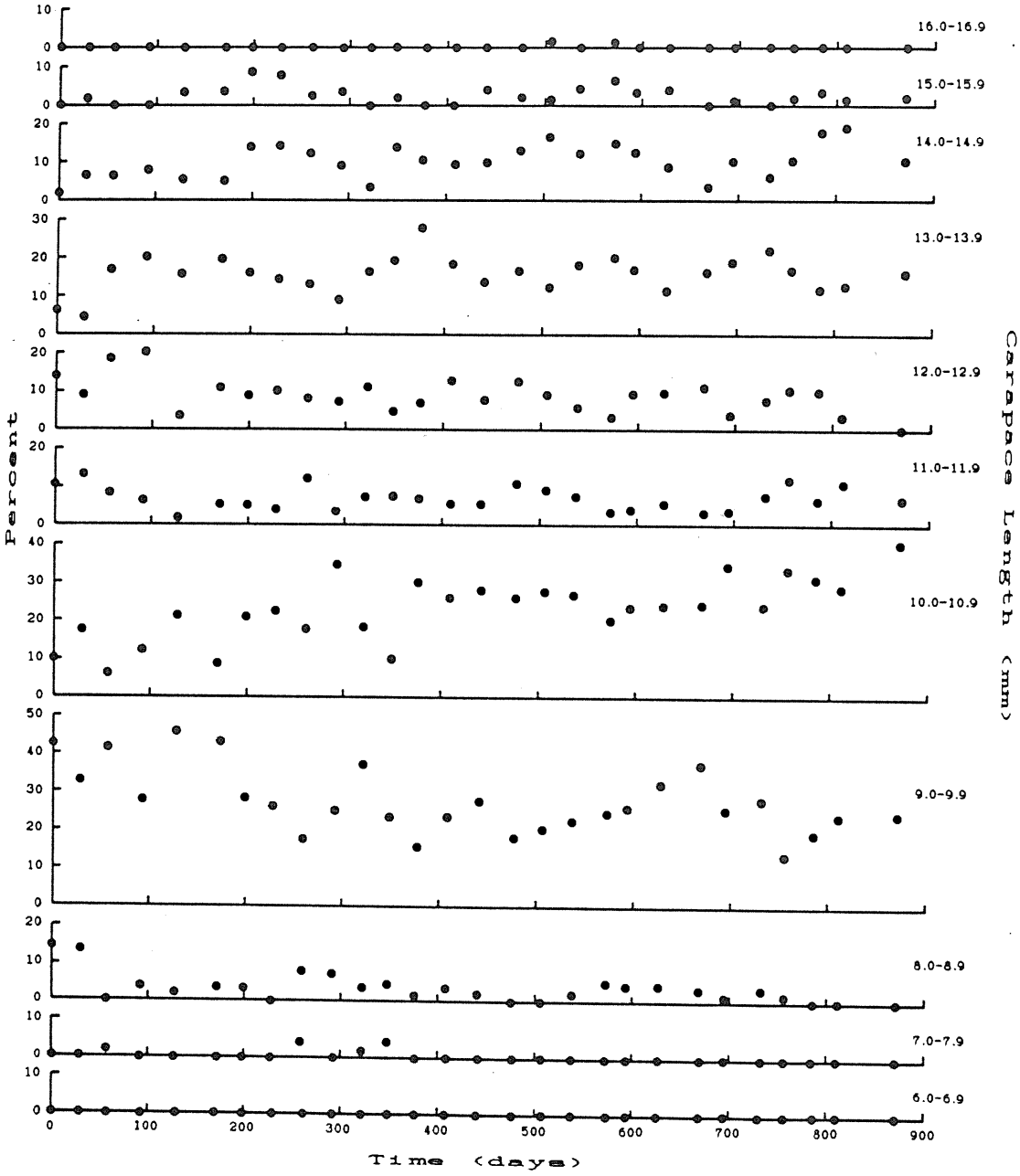


Figure 3.11 continued

Douglas Creek



the course of this study. Similarly, the 10.5 and 14.5 mm size classes at Douglas Creek increased while the 12.5 mm size class decreased. If these changes in the relative abundance of these size classes represent growth of groups of individuals from one size class to another, then they would indicate that individuals may remain as males or females for periods longer than the 870 days of this study. It would also indicate that recruitment was greater at some time prior to the commencement of this study than it was during this study. Since the period of this study was unusually dry apart from the influence of Cyclone Winifred (see Chapter 2), this is a distinct possibility.

The use of 1mm size classes and the summation of the samples from Yuccabine Creek in the above analyses would have tended to obscure the small peaks examined previously by the mode plotting technique, and the observed trends in the 11.5 mm size class in Yuccabine Creek and the 12.5 mm size class in Douglas Creek are most probably due to trends associated with the extremes of the normal distributions of non-transitional individuals (i.e. individuals that are remaining as males or females) about the 10.5 mm and 14.5 mm size classes respectively. That is, as the mean size of males in Yuccabine Creek increased, there would tend to be a greater spill over of non-transitional individuals into the 11.5 mm size class and, conversely, as the mean size of females in Douglas Creek increased, there would have been a correspondingly smaller spill over into the 12.5 mm size class. This effect was deliberately avoided in the mode plotting analysis by the selection of only observable series of modes.

Table 3.6 Significant regressions of percent in each size class with time. Size classes are indicated by mid-length (mm carapace length).

Site	Size class	Equation	r	Significance b≠0
Yuccabine Creek	9,5	Y=27,5-0,023 X	-0,62 (p<0,01)	p<0,001
	10,5	Y=15,6+0,015 X	0,45 (p<0,05)	0,02>p>0,01
	11,5	Y=1,4+0,010 X	0,69 (p<0,01)	p<0,001
Douglas Creek	8,5	Y=6,8-,008 X	-0,51 (p<0,01)	0,01>p>0,005
	9,5	Y=34,8-0,016 X	-0,49 (p<0,01)	,01>p>0,005
	10,5	Y=13,0+0,024 X	0,73 (p<0,01)	p<0,001
	12,5	Y=12,9-0,009 X	-0,51 (p<0,01)	0,01>p>0,005
	14,5	Y=7,0+0,007 X	0,30 (p<0,05)	0,02>p>0,01

Since the number of juveniles and small males decreased during the course of the study in Douglas Creek and the 9.5 mm size class decreased in relative abundance in Yuccabine Creek, the observed increase in the proportion of the 10.5 mm size class in the two streams is not likely to be due to increased recruitment over the period of the study.

Thus, the analysis of size-class frequencies through time supports the hypothesis of a very slow growth rate when individuals are functionally male or female, perhaps of less than 1 mm carapace length in 870 days. This time scale is used in the model presented in Figure 3.10

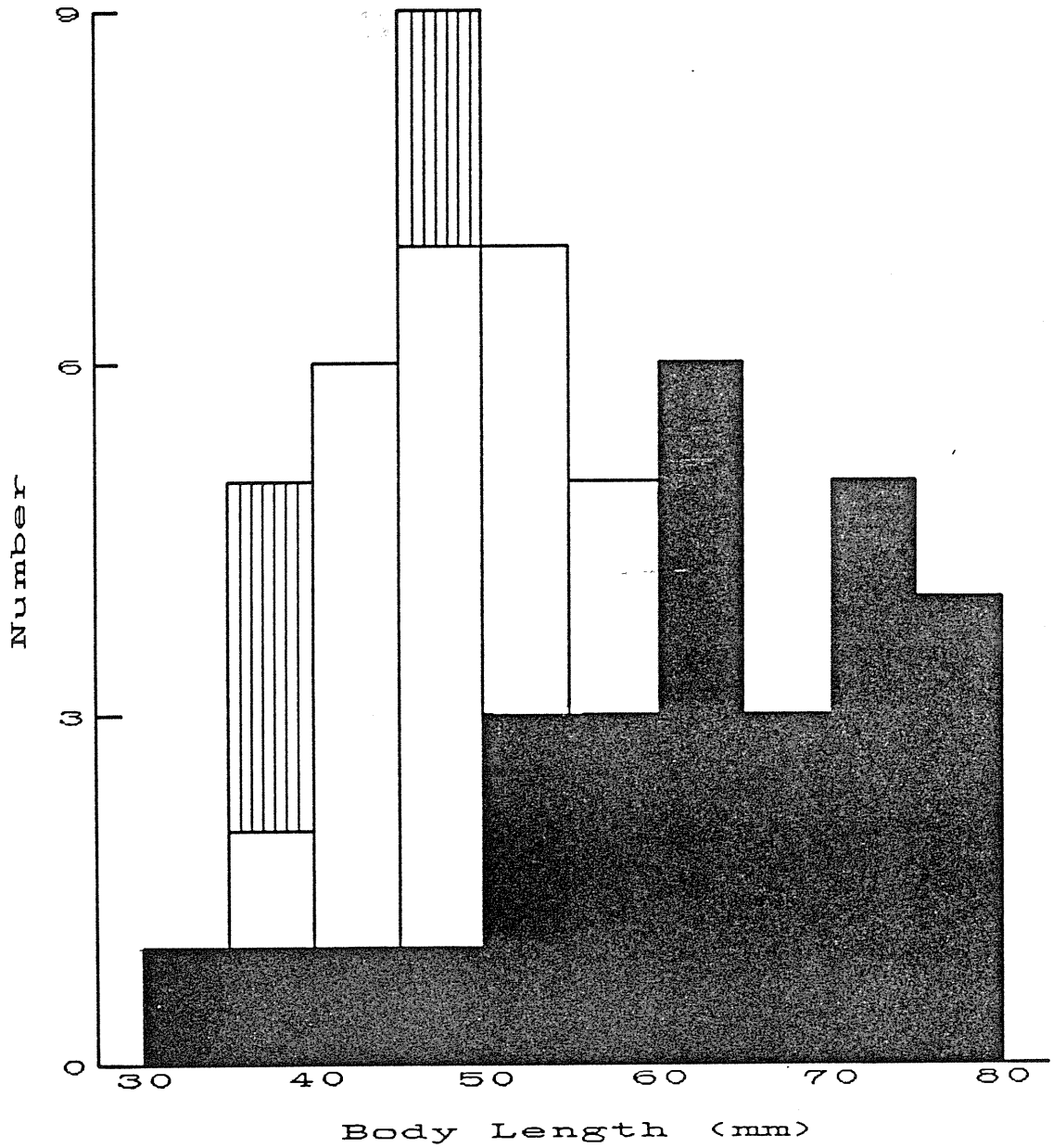
The maintenance of near 1:1 sex ratios in the two streams, despite the fact that females must be older than males, and therefore subject to greater mortality, indicates that individuals remain as females for longer than they remain as males. The smaller gradient for the regression of the 14.5 mm size class in Douglas Creek compared with that of the 10.5 mm size class lends support to this hypothesis. The maintenance of 1:1 sex ratios for a protandrous hermaphrodite was also found by Hoagland (1978) for artificial populations of the mesogastropod *Crepidula fornicata* (Linn.) regardless of the initial ratio, although in dense populations the percentage of males was slightly higher. The higher proportion of males at Douglas Creek was most likely due to that site being only half the distance from the estuary (the source of recruitment, see Chapter 4) of the Yuccabine Creek sites.

At no time was there an absence of females from any sample site, and tagged females were observed to release eggs at the sample sites (see Chapter 4), so the migration of ovigerous females to the estuary postulated by Smith and Williams (1982) does not occur.

To completely resolve the question of the life history of *A. striolata* would necessitate a longer-term study than the present one allowed, preferably with a much extended and more intense tagging programme; nevertheless, support for a growth curve similar in shape to that shown in Figure 3.10 is strong. The interpretations presented here are based on an unusually difficult set of data. The difficulties were not the result of any inadequacies in the sampling programme, but were due to the unique life history strategy of *A. striolata*.

It would be of value to examine the population biology of related species, but so far there have only been two relevant studies of *Atya*-like species, both of which were very limited. Darnell (1956) made a single collection of 46 individuals of *Atya scabra* from a riffle in the Rio Sabinas, Mexico, and obtained a further 5 specimens from a nearby backwater. The length frequency distribution of that collection is reproduced in Figure 3.12. This distribution is quite different from that of *Australatya striolata*, but as several authors have noted habitat differences between males and females for *Atya scabra* (see Hobbs and Hart, 1982, pp 127-130), it probably represents the habitat selection of the species. There is no evidence for protandry (or protogyny) for species of the genus *Atya*, but males do tend to become larger than females (Hobbs and Hart, 1982).

Figure 3.12 Length frequency distribution of *Atya scabra* collected by Darnell (1956) from a riffle. Open bars represent females, solid bars, males and striped bars, additional females collected from a backwater.



Bright (1982) studied the secondary benthic production of a stream in Palau, Caroline Islands, in a sampling programme that employed a box sampler. On the basis of seasonal variations in age structure, density and standing crop of *Atyoida pilipes* (Newport, 1847) (the age structure was not presented in the paper) he concluded that the species had a univoltine life cycle. While this is probably true, the efficiency of a Surber sampler in catching shrimp is questionable (see section 3.2.1).

Since the species of the genus *Atyoida* are the only other *Atya*-like shrimp which are suspected of being protandrous (Carpenter, 1978; Chace, 1983), investigations of their population biology would be most interesting in view of the results of the present study. It is unfortunate that Bright (1982) did not include the length frequency distributions of his collections of *Atyoida pilipes*.

The only other protandrous species of the Atyidae that has been studied in any detail is *Paratya curvirostris* (Carpenter, 1978, 1982, 1983). It also has negligible growth of functional males and females but the maximum length of post-larval life is probably about 2 years. *P. curvirostris* is a smaller shrimp than *A. striolata* , with a maximum post-orbital carapace length of 10 mm, and with males becoming sexually functional above 3.0 mm carapace length. It inhabits the transition zone in streams between fresh and brackish water. Its length-frequency distributions bear little resemblance to those of *A. striolata* as it has a male to female sex ratio of 7:1, causing a suppression of the female mode. Also there is an obvious progression

of the male mode through time, as would be expected for such a short life cycle.

Whilst Hoagland (1978) mentioned that size could not be used as an estimator of age for the protandrous gastropod genus *Crepidula*, she did not elaborate the life history further in terms of growth and longevity, being primarily concerned with the lability of sex determination for the group.

I have been unable to find any examples of animal species, protandrous or otherwise, which have a life history similar to that of *A. striolata*. Perhaps the closest parallels are those of the larger mammals which, as stated by Goodman (1981), are characterised by long life spans, high adult survival rates, low effective fecundity and late reproductive maturity (in the analysis of life tables usually only females are considered). He also demonstrated that one of the consequences of these characteristics was that the population exhibits high stability under moderate fluctuations in the effective fecundity. Some large mammals, including man, have a two stage growth curve with a pubescent growth spurt (e.g. Perrin *et al*, 1976 and Perrin *et al*, 1977). If *A. striolata* does indeed have a life history similar to that postulated here, then it does have a relatively long life-span and late female reproductive maturity. Its effective fecundity and potential adult survival rate will be the subject of subsequent chapters of this thesis.

The advantages of this pattern to a species with an estuarine planktonic larva, and an upland stream-inhabiting adult are obvious. The survival of larvae and juveniles must be extremely low and highly dependent on environmental factors, so the ability to cope with low and variable recruitment is of the utmost importance. The larvae must be robust enough to withstand the journey downstream, and since food for planktonic larvae in stream water is likely very limited due to the paucity of plankton, would need adequate food supplies to last the journey. This must place a lower limit on the size of the larvae, and therefore the eggs. Ghiselin's (1969) size advantage hypothesis for sequential hermaphroditism must favour protandry in this case. The irregularity of rainfall in Australia, which results in periodic cessation of stream flow even in the seasonal wet tropics (see Pearson *et. al.*, 1986), would favour long life spans, enabling individuals to breed for several seasons. This strategy would maximise the likelihood of successfully producing adult offspring, and therefore increasing the ability of the population to withstand low and variable recruitment. A vital link in understanding the population biology of this species is resolving its reproduction and larval life-history, which is the topic of the following chapter. It is clear however, that the life history strategy of *A. striolata* is unparalleled among studies of invertebrates.

Chapter 4 Reproduction and Development

4.1 Introduction

Apart from the work of Edmondson (1929), the studies of Hunte (1977, 1979a, 1979b), and the serendipity of Bordage (1908, 1909), the modes of reproduction of the *Atya*-like shrimp are unknown.

Bordage (1908, 1909) demonstrated complete development of *Atyoida serrata* despite heavy rain causing severe siltation in the masonry basins used to hold the shrimp. Larval development took 12 days in fresh water.

Edmondson (1929) demonstrated that a "swift current" was required for successful larval development of *Atyoida bisulcata*. In the presence of strong current, larvae hatched as a mysis stage approximately 6 mm long, which was negatively phototactic, rheotropic, and demersal. In the absence of current, zoeae could hatch but did not develop further. Development occurred entirely in fresh water.

Hunte (1977, 1979a, 1979b) successfully reared both *Atya innocous* and *Micratya poeyi*. The optimum salinity for development was 30 and 32‰ respectively, and the time required was 55 days and 80 days respectively. Hunte (1978) suggested that crustacean larvae could select suitable streams in Jamaica on the basis of their salinity preferences. In Jamaica, high gradient streams tend to have small estuaries while low gradient streams tend to have large estuaries.

Species which inhabit high gradient streams, such as *A. innocous* and *M. poeyi*, have a requirement for high salinities for larval salinity.

In their considerations of the species of *Atya*, Hobbs and Hart (1982) suggested that *A. africana, A, gabonensis, A.innocous, A. margaritacea* and *A. scabra* were likely to have planktonic larvae with high salinity requirements. These conclusions were based variously on reports of juveniles in estuarine environments, larval requirement of saltwater to moult, the studies of Hunte (*op cit.*), and egg size and number. They considered this to be the basic pattern for the genus. Chace (1983) suggested that *Atyopsis moluccensis* (De Haan, 1849) probably had marine larvae on the basis of remarks to that effect by Joins (1958, 1965), but found no supporting evidence.

The population biology of the *Atya*-like shrimp is little known, and there have been only scattered reports of ovigerous females. However, in their review, Hobbs and Hart (1982) listed the presence of ovigerous females in most months of the year in which collections have been made, for 7 out of 11 species.

Carpenter (1978) demonstrated protandry in *Paratya curvirostris*, and suggested that *Atyoida bisulcata* and *A. serrata* were also protandrous on the basis of the unbalanced sex ratios of ortmannioid (with non-filter feeding chelae) and atyoid (with typical *Atya*-like chelae) forms, and the histological studies of Radir (1930). Chace (1983) was non-committal on the possibility except to note that in the collections available to him, male *A. bisulcata* ranged in size from 8.2 to 9.8 mm

carapace length while females ranged from 7.2 to 12.5 mm carapace length. He did present evidence for at least partial protandry in *Atyoida pilipes* in the form of size frequency distributions and sex ratios relative to size for 647 specimens.

Smith and Williams (1982) presented histological evidence for protandry in *Australatya striolata* and suggested that the life cycle involved the migration of ovigerous females to the estuary to release larvae, and a subsequent upstream migration of juveniles.

In this study, the reproduction and development of *A. striolata* was examined in three ways: the timing of breeding and fecundity of females was examined concurrently with the study of the adult populations; larval development was examined in laboratory studies and field collections; and migration and development of juveniles were examined by sampling in the adult habitats and in the lowland sections of the Murray River. The methods and results of each are described separately below; the results are discussed together in section 4.5.

4.2 Breeding

4.2.1 Methods

During the regular population sampling at each site (see Chapter 3), all females were examined for the presence of eggs attached to the pleopods. From October 1984 until July 1986, a sub-sample of shrimp

was taken from the Yuccabine Normal sample and preserved in alcoholic Bouin's fluid for examination of gonad conditions. Shrimp were selected to represent each size class present in the sample (unless numbers in a particular size class were very low), and to represent each sexual state (i.e. juvenile, male, female and ovigerous female) present in individuals of that size class. The preserved shrimp were dissected in the laboratory to determine gonad condition according to the scheme presented in Table 4.1, after they had been sexed on external features (see Chapter 3).

Twenty-two ovigerous females were selected from the Yuccabine Upper samples between December 1984 and May 1985 for determination of the number of eggs carried by reproductive females. A further eight ovigerous females of less than 12.5 mm carapace length were selected from samples from all sites. The egg mass was removed from each female and a sample of approximately 500 eggs were counted and after the removal of excess moisture on filter paper, were weighed. The weight of the remaining eggs was then similarly determined, and the number of eggs carried by each female estimated.

The length and width of ten eggs from each of the less than 12.5 mm carapace length females and a further six larger females were determined using an optical micrometer. Egg volume was estimated from the formula:

$$\text{Egg volume} = 4/3\pi \text{ length} \times \text{width}^2$$

Table 4.1 Gonad condition indices.

Gonad type	Gonad stage	Description
Ovary	O0	ovary small and white in colour, oocytes not discernible under a dissecting microscope.
	O1	ovary small and white in colour with discernible oocytes scattered within tissue.
	O2	ovary small and yellow in colour, oocytes small but densely packed.
	O3	ovary yellow with large oocytes.
	O4	ovary yellow with large oocytes, organ extending to anterior of third abdominal segment.
	O5	similar to O4 but ovary extending to posterior of third abdominal segment or further and full width of dorsal musculature.
	JO	as for O0 but in juvenile individual.
Testis	T1	testis small and undeveloped.
	T2	testis well developed, epididymis not swollen or extended.
	T3a	testis well developed, last loop of epididymis swollen but not extended.
	T3b	testis well developed, last loop of epididymis extended anteriorly but not swollen.
	T4	testis well developed, last loop of epididymis swollen and extended anteriorly.
	T5	as for T4 but loop of epididymis extending further anteriorly than the heart.
	JT	as for T1 but in a juvenile.
Ovo-testis	OT	gonad with both oviduct and vas deferens

which assumes that the eggs were ellipsoidal. The developmental stage of the embryos of the measured eggs were noted for each brood.

4.2.2 Results

The proportions of females that were ovigerous are shown for each month and site in Figure 4.1. There was a distinct breeding season between November and June each year, coinciding with the summer wet season (see Figure 2.3). The percentage of females that were ovigerous was generally high during the breeding season, being 50% or more for 28 of the 46 site × months where ovigerous females were recorded.

A number of females became ovigerous while tagged, or were tagged while ovigerous. Table 4.2 summarises the observed duration of brooding in those individuals. Whilst no tagged individuals were observed to go from being non-ovigerous to ovigerous to non-ovigerous, and the sampling interval of one month restricts precision, the available data do provide some indication of the duration of brooding. The longest observed retention of eggs was 103 days, but this record was for an individual which was only recaptured once, three months after release, and may have shed its eggs and spawned again in that time. Two other retention records span two months and were not recaptured on the intervening sampling period. The remainder were observed to retain their eggs for at least one month. Of the tagged females observed to shed their eggs, six shed within one sampling interval, nine within two sampling intervals, five within three intervals and two within five sampling intervals. Those observed to shed within three or five

sampling intervals were not collected on the intervening periods. Of those individuals for which both upper and lower limits could be determined, two shed between one and three sampling intervals, and two shed between one and two sampling intervals.

Of the 17 females recaptured on the next sampling occasion after they were found to be ovigerous, 64.7% remained ovigerous, while of the 11 females recaptured two sampling periods later, 81.8% were not ovigerous. Therefore, it is most probable that the average duration of brooding is between one and two months. Thus in a breeding season which can extend for seven months (Figure 4.1), each female has the potential to spawn two or three times.

The pattern of gonad condition during the study is shown in Figure 4.2 for males, females and juveniles. Stage 4 and stage 5 testes were found between November and April while stage 4 and stage 5 ovaries were found between November and March. Stage 2 and stage 3 testes were present for most of the study period as were stage 0 and stage 1 ovaries, while stage 2 and stage 3 ovaries were scattered over the study period. Thus, mature gonads were only developed during the reproductive period and there is no evidence of a gradual allocation of resources into reproductive tissue during the year. The coincidence of both mature and developing or resting stage ovaries during the breeding season and the presence of mature testes with stores of gametes through most of the breeding season indicates that females reproduced more than once each year. This was further indicated by the presence of ovigerous females with stage 4 or stage 5 ovaries.

Figure 4.1 Percent of females that were ovigerous in each sample at each site.

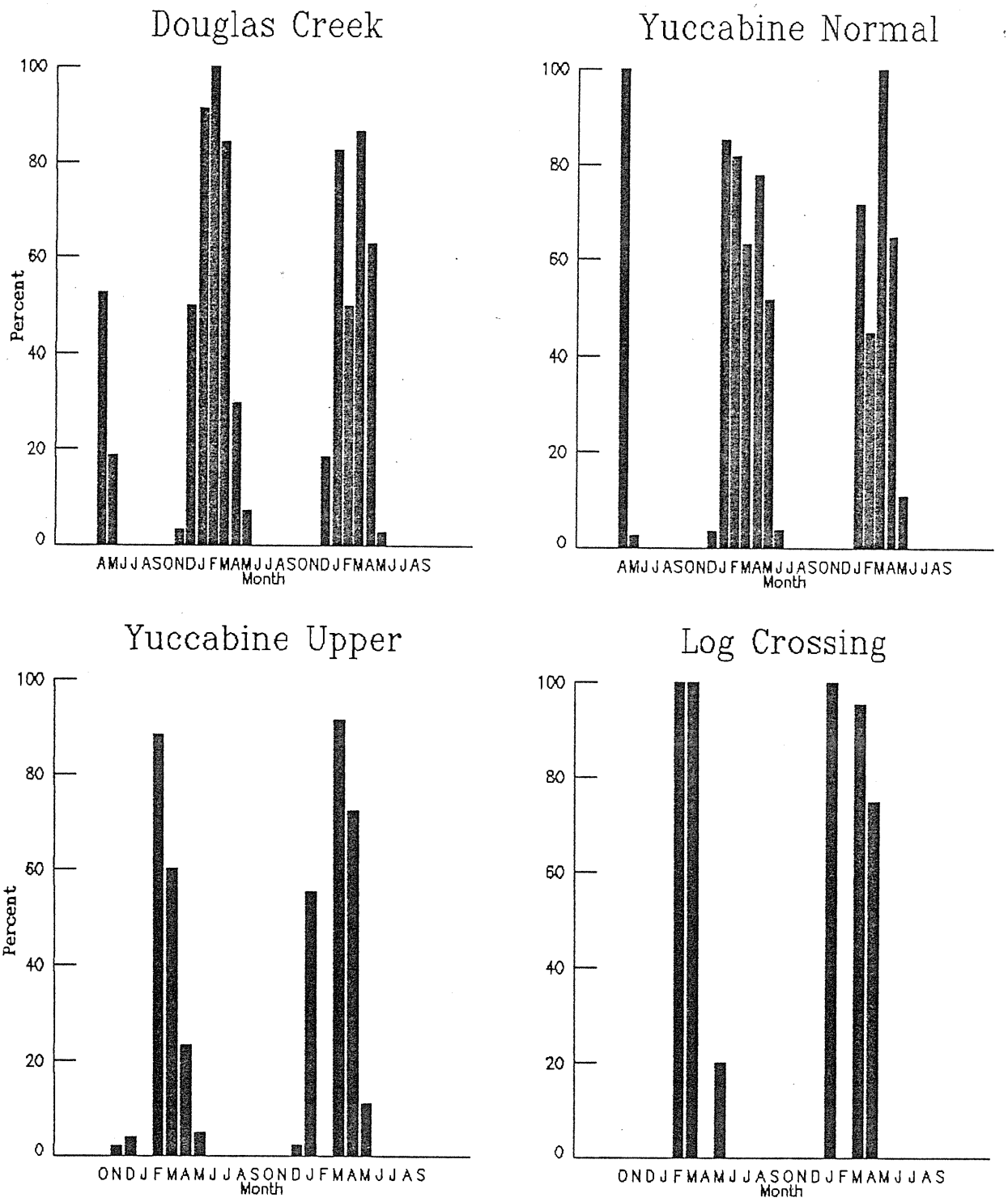
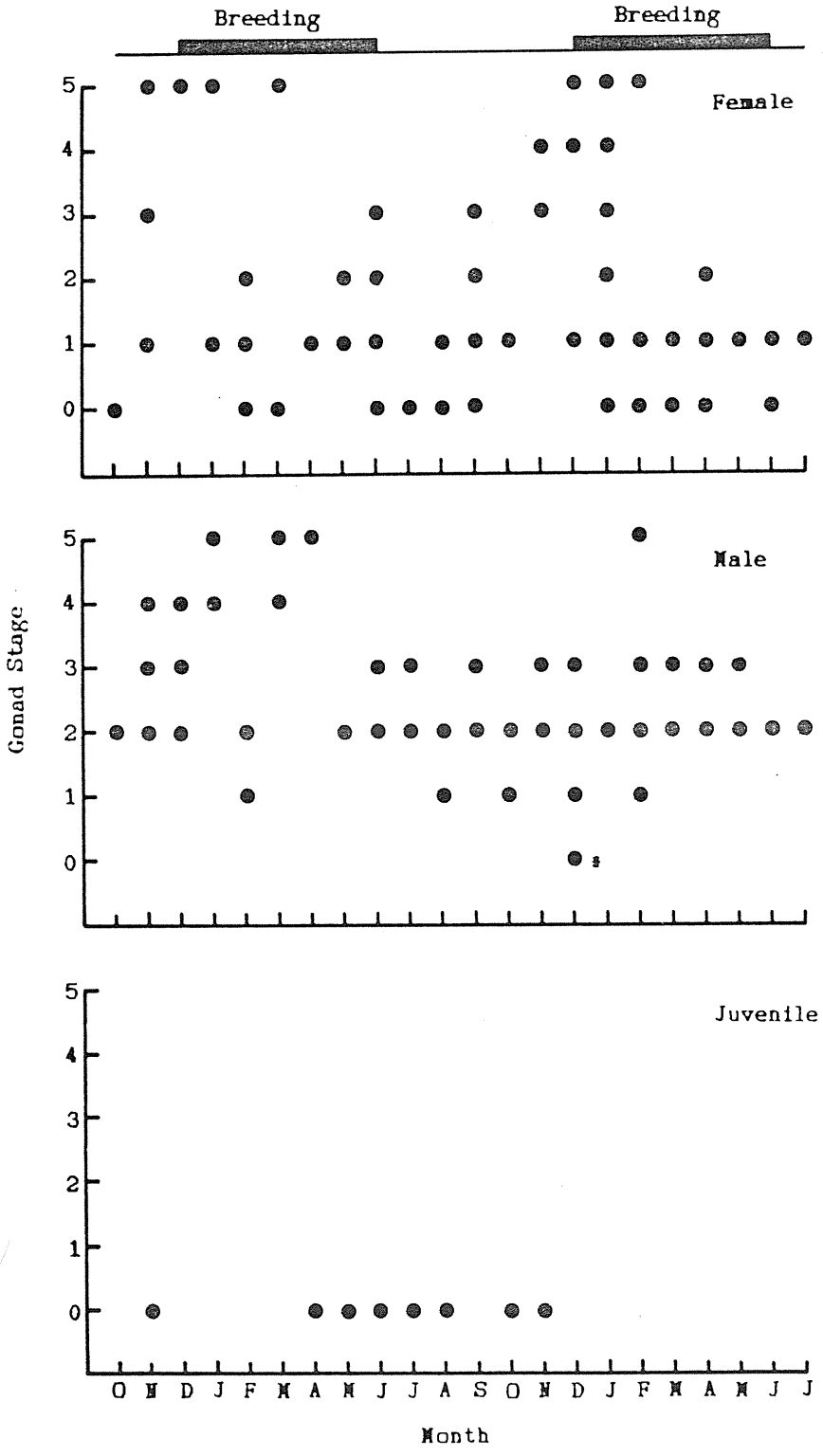


Table 4.2 Observed duration of brooding in females in days. Figures listed under > represent females still ovigerous at time of recapture; figures listed under < represent females recaptured without eggs. Size is carapace length in mm.

Size	Observed duration of brooding	
	>	<
10.7	-	68
11.1	-	37
11.5	-	37
11.8	31	-
12.8	-	156
12.9	66	-
13.0	-	68
13.1	-	62
13.2	-	62
13.3	37	-
13.3	-	53
13.4	-	90
13.4	-	37
13.5	-	35
13.6	66	-
13.9	37	-
13.9	37	90
14.0	-	156
14.1	37	62
14.1	-	90
14.1	103	-
14.1	-	62
14.3	31	-
14.3	-	62
14.4	-	25
14.5	37	62*
14.7	37	-
14.7	-	25
14.9	37	-
14.9	37	90
15.2	37	90

* remained non-ovigerous for one further month

Figure 4.2 Occurrence of the six gonad stages for each sex during the study period. Solid blocks represent the breeding season as defined by the presence of ovigerous females. * ovotestis.



Two individuals, one 10.9 mm carapace length and the other 11.6 mm carapace length, both with appendix masculina, were found to have ovo-testes. Morphologically, the gonads resembled undeveloped ovaries, but with some indication of a coiled tubular structure posteriorly. Of the 10 juveniles examined, seven had juvenile testes (size range 6.9 to 8.6 mm carapace length) and three had juvenile ovaries (8.7 to 9.8 mm carapace length).

Figure 4.3 shows the number of eggs per female for the predominant size range for females (see Figure 3.2). The number per female was very variable and there was no significant regression for this size range (r=0.19, $p>0.1$). However, when the unusually small ovigerous females were added to the analysis (Figure 4.4) a significant regression equation was obtained:

$$\text{Egg number} = 392.5 \times CL - 2537.5 \quad (0.01>p>0.001)$$

where CL is carapace length in mm.

The relationship between egg volume and female size is shown in Figure 4.5 for the three observed embryo stages. Embryos with pale eyes had encompassed the yolk in the eggs but had no developed appendages and the eyes were in an early stage of development, while dark eyed embryos were close to hatching. In general, egg volume increased with developmental stage. Table 4.3 presents the results of regressions of egg volume with female size for polynomial models of degree 1 to 4, and the equation of best fit is shown in Figure 4.5 for each developmental

Figure 4.3 Number of eggs carried by females greater than 12.5 mm carapace length

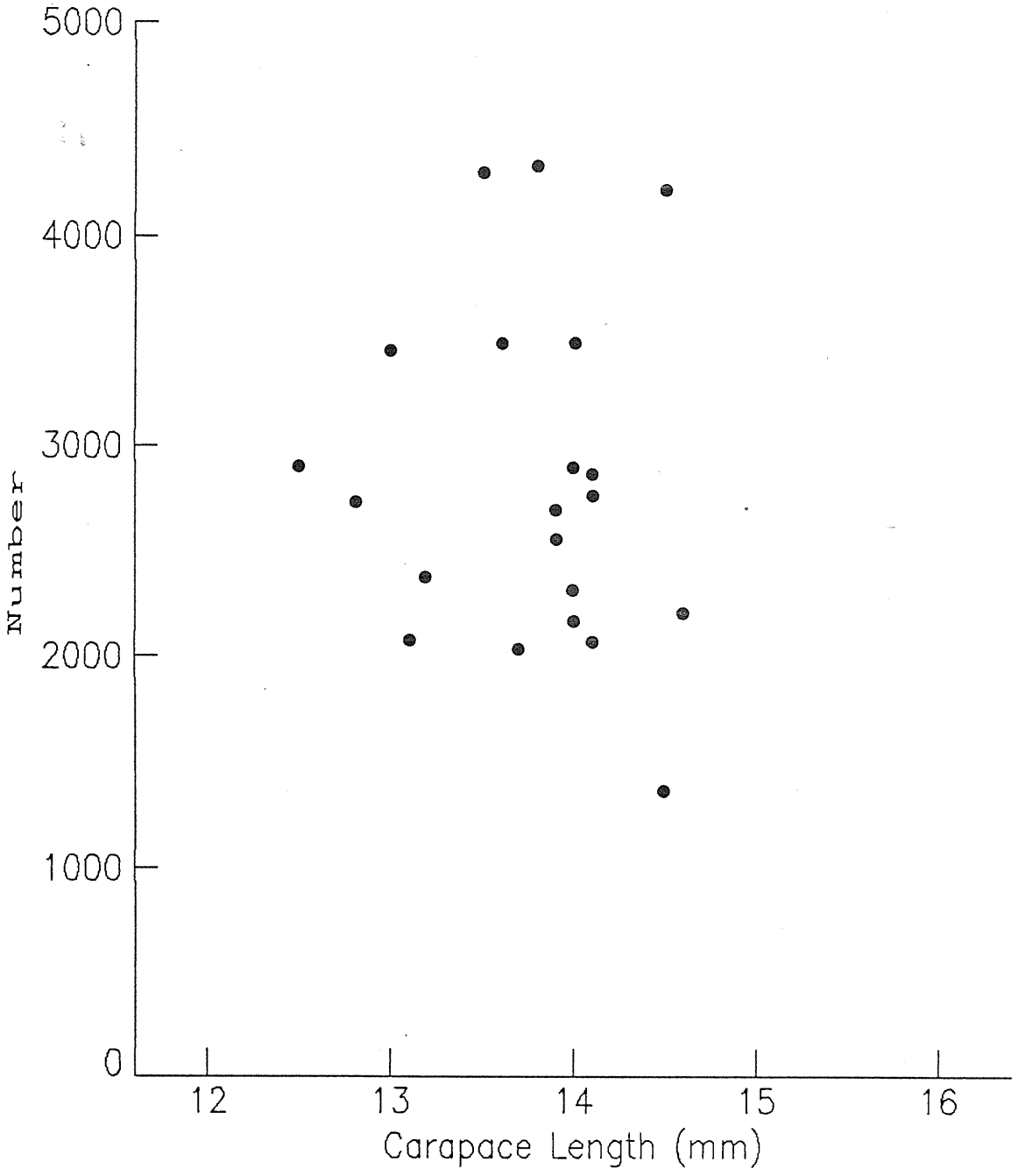


Figure 4.4 Number of eggs carried by females greater than 10.0 mm carapace length.

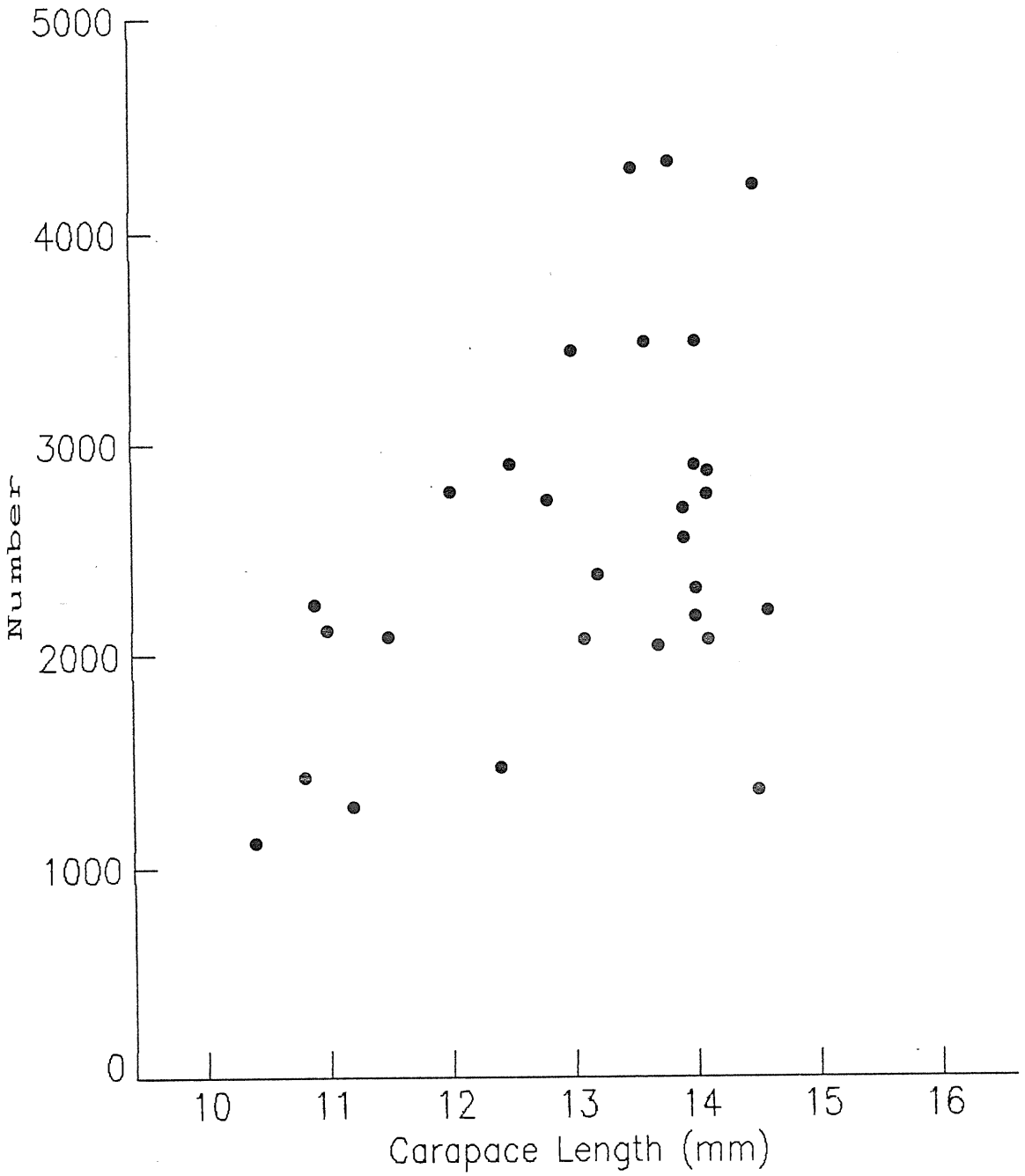


Figure 4.5 Relationship between female size and egg volume for each of three embryo stages. Regression line equations are given in each case. (a) egg mostly yolk; (b) embryo with pale eyes; (c) embryo with dark eyes; (see text for further description of stages).

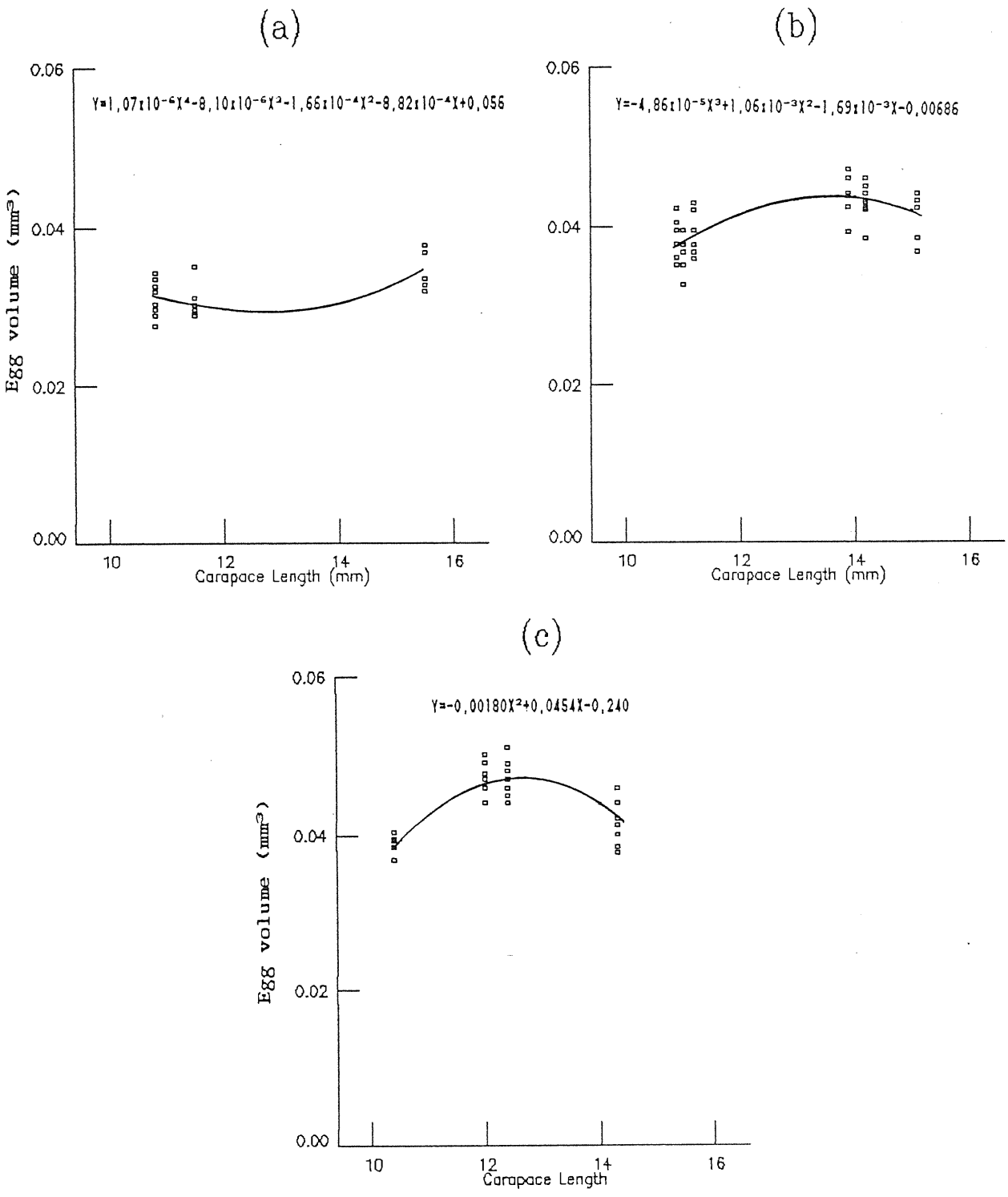


Table 4.3 Significance of polynomial regression models for volume of eggs with three embryo stages with female size. n.s. indicates not significant. * indicates best fit in each case.

Embryo	Polynomial degree			
Stage	1	2	3	4
Yolk	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$*
Pale eye	$p<0.001$	$p<0.001$	$p<0.001$*	$p<0.001$
Dark eye	n.s.	$p<0.001$*	$p<0.001$	$p<0.001$

stage. For all three embryo stages, the best fit was for a polynomial of degree greater than 1. For pale eyed embryos, the model of best fit had a maximum egg volume for females of 13.7 mm carapace length, while the model of best fit for dark eyed embryos had a maximum for females of 12.7 mm carapace length.

4.3 Larval Life History

4.3.1 Methods

The larval life history of *A. striolata* was examined both in the field and in the laboratory. Rearing experiments were conducted to determine the salinity requirements for development and the likely duration of the larval stages, and in order to be able to distinguish larvae of *A. striolata* from other crustacean larvae. Nine rearing experiments were performed in the laboratory using zoeae hatched from ovigerous females brought from the study sites. Although ovigerous females usually carry between 2000 and 5000 eggs (see above), it was difficult to obtain sufficient larvae to compensate for high mortality rates, even with a restricted number of treatments. It was not possible to obtain sufficient larvae to successfully test both temperature and salinity tolerances. Additional larvae were added to the experiments where possible to increase the likelihood of complete larval development. The problem of low hatching rates may have been due to adverse effects of electrofishing, transportation, or both, on the developing embryos. Although three females held in an aquarium which had been maintained

at 29°C from July 1984 became ovigerous on 24 November 1984, they shed their eggs without releasing any larvae, and aquarium specimens could not be induced to spawn again during this study.

Much of my experimental design was therefore based on the successes of Hunte (1977, 1979a, 1979b) with *Atya innocous* and *Micratya poeyi*. The best food for both species was a preparation of the proprietary brand "Tetramin" aquarium fish food and wheatgerm, and the optimum temperature for *Atya innocous* was 27°C. Unless otherwise indicated, larval *Australatya striolata* were raised at 27°C and fed daily with "Tetramin"™ and wheatgerm. The water used for the experiments was a mixture of stream water, distilled water and seawater known to be free of metal ion contamination, and was changed every two days unless otherwise indicated. The experimental designs were as follows and the number per treatment is indicated in Figure 4.6. Modifications were made to the design of successive experiments to overcome perceived problems.

Experiment 1 A maximum of 10 larvae were placed in 5, 10, 15, 20, 25, 30, and 35‰ salinity water in 100 ml glass bowls at laboratory temperature (approximately 22 to 25°C). The larvae were fed with cultured *Dunalliella* sp. The experiment ran between 21 May 1984 and 7 June 1984.

Experiment 2 The egg masses were removed from two females on 18 December 1984 and a number hatched on 19 December 1984. The larvae were reared in 0.5 l plastic containers at 0, 10, 15, 20, 25, 27, 30 and

32‰ salinity water. Each container had mild aeration and was placed in a water bath to control the temperature. A further egg mass was removed from another female on 20 December 1984. The experiment ran until 28 January 1985.

Experiment 3 Eight ovigerous females were held in an aquarium with 1mm plastic mesh dividing the aquarium into two sections. Hatched larvae were attracted to a light near the section without adults, then collected. The larvae were placed in 0.5 l plastic containers as for experiment 2, but with salinities of 29, 30, 31, 32, 33, 34, and 35‰. The experiment started on 9 February 1985 and was terminated on 3 March 1985.

Experiment 4 The larvae were collected as in experiment 3. The water used was autoclaved, and acid washed 0.5 l glass containers were used. The containers were aerated and held in a water bath. The experiment ran from 11 March 1985 to 24 March 1985 and the salinities used were 27, 28, 29, 33 and 34‰.

Experiment 5 The chelipeds were removed from several ovigerous females before they were placed in 0.5 l plastic containers through which stream water was circulated. The females tended to remove the eggs from their pleopods before they had hatched. The larvae obtained from the females were held in 100 ml cylindrical, plastic containers with a 62 µm mesh bottom and two 250 µm meshed holes approximately 2x3 cm in the side wall. These containers were floated in three aerated, 12 l aquaria filled with 27, 30 and 33‰ salinity water

respectively. The larvae were fed with a mixture of *Chlorella* sp. and *Isochrysis* sp. The experiment ran from 24 January 1986 to 17 February 1986.

Experiment 6 The system used for experiment 5 was used again between 18 March 1986 and 31 March 1986.

Experiment 7 An under-gravel filtration system was fitted to each of the above aquaria, and the larvae were fed with *Isochrysis* sp. only. The experiment started on 6 May 1986 and the aquaria were heated to 30°C until 10 May when the heaters were switched off and the aquaria were held at room temperature (approximately 25 to 27°C) until the experiment finished on 27 May 1986.

Experiment 8 Twelve ovigerous females were collected from Yuccabine Creek with dip nets and 6 ovigerous females were collected by electrofishing on 15 May 1987. A large hatch from both groups of females on 20 May 1987 allowed 300 larvae to be placed in each of two 0.5 l plastic containers for each salinity treatment. The containers were held in a water bath and mildly aerated. The salinities used were 27, 30 and 32‰, and the larvae were fed with micro-encapsulated egg yolk and cod-liver oil. The experiment was terminated on 9 June 1987.

Experiment 9 100 larvae from the hatch on 20 May 1987 were placed in each of two of the small larval containers of experiments 5 to 7, and 200 in another container. These were placed in an aquarium filled with 30‰ salinity water with under-gravel filtration. The aquarium was

covered with smoked glass and placed in the open under 50% shade cloth without artificial heating. The larvae were not fed and algae were allowed to grow in the aquarium. Interference was kept to a minimum. The experiment was terminated on 9 June 1987.

The larval stages were separated on the basis of morphological differences as exuviae were difficult to detect and tended to fragment in the experimental containers. Representative specimens of each larval stage were preserved in 70% alcohol when there were sufficient numbers.

Sampling for drifting larvae in Yuccabine Creek was carried out on two occasions. On 12 to 13 March 1986, a 250 µm meshed conical net, 2 m long with a 0.5 m diameter opening was placed immediately downstream of the pipe used for discharge measurements (see Chapter 2), so that it filtered more than 90% of the stream flow. The cod end of the net was changed at 2 hr intervals for a 24 hr period from 1400 hrs on 12 March. The samples were preserved in 70% alcohol and sorted in the laboratory. Eggs and larvae of *A. striolata* were counted in each sample. On 4 to 5 April 1987, a similar net, but with 62 µm mesh was used. It clogged within 0.5 hr when placed below the pipe, so it was positioned at the site used for physico-chemical measurements (see chapter 2) where it sampled approximately 8% of the stream flow.

Sampling for larvae in the estuary of the Murray River was carried out during the 1984/1985 and 1985/1986 adult breeding seasons when larvae were likely to be most abundant. A conical net of similar dimensions

to those used in Yuccabine Creek was towed for 5 mins at approximately 2 Knots at each site. In 1984/1985 a 90 μm mesh size was used, while in 1985/1986 a 250 μm mesh was used. The samples were preserved in 10% formalin and a top and bottom salinity reading was taken using an American Opticals optical salinometer. During 1986 the surface and bottom temperatures were measured using a YSI Instruments Dissolved Oxygen Meter. The samples were sorted in a 30×20 cm Bogorov tray under a dissecting microscope. Large samples were sub-sampled by pipetting sufficient matter from the bottom of the settled sample to fill three trays. Preliminary examinations showed that no new types of caridean larvae were found in the third tray. Sub-sampling was only required for samples from 1984/1985. All caridean larvae found were counted.

4.3.2 Results

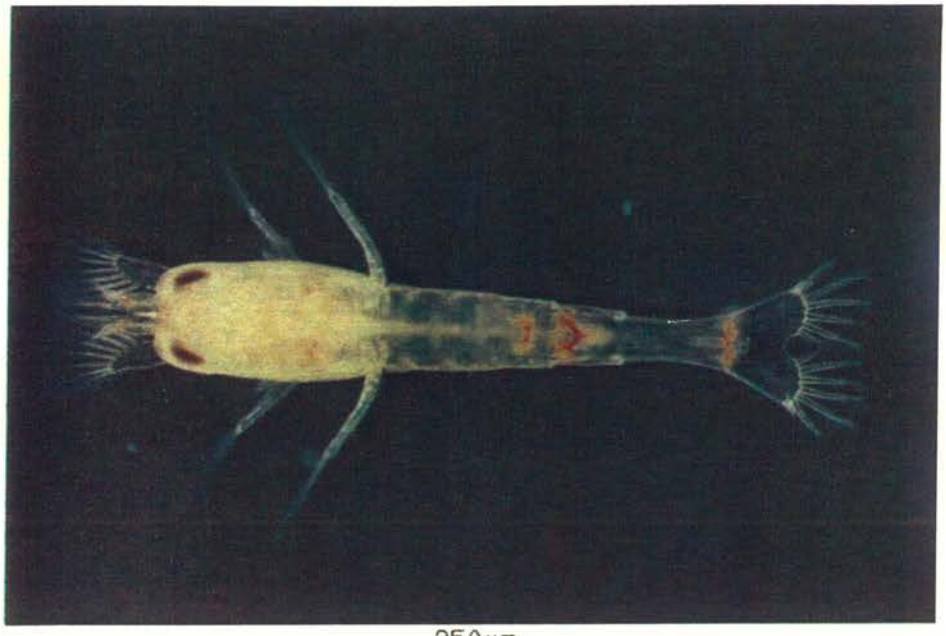
Survival of the larval stages of *A. striolata* in the nine rearing experiments is shown in Figure 4.6 (pp. 95-102). In Experiment 1, stage 2 larvae eventually predominated in the treatments with salinities of 20‰ or more. Only one individual moulted to stage 2 in each of the 10 and 15‰ treatments. In the 5‰ treatment, eight of the original ten larvae survived for 30 days without moulting. Stage 2 (and higher) larvae had complete guts and were observed to feed, while stage 1 zoeae had large yolk supplies within the cephalothorax which obscured the gut (Plate 4), and they did not feed.

Plate 4 Representative larval stages of *Australatya striolata*.

(a) Stage 1

(b) Stage 6

(a)



250μm

(b)

250μm

Figure 4.6 Survival and development of reared larvae in each treatment in each experiment.

● stage 1

▲ stage 2

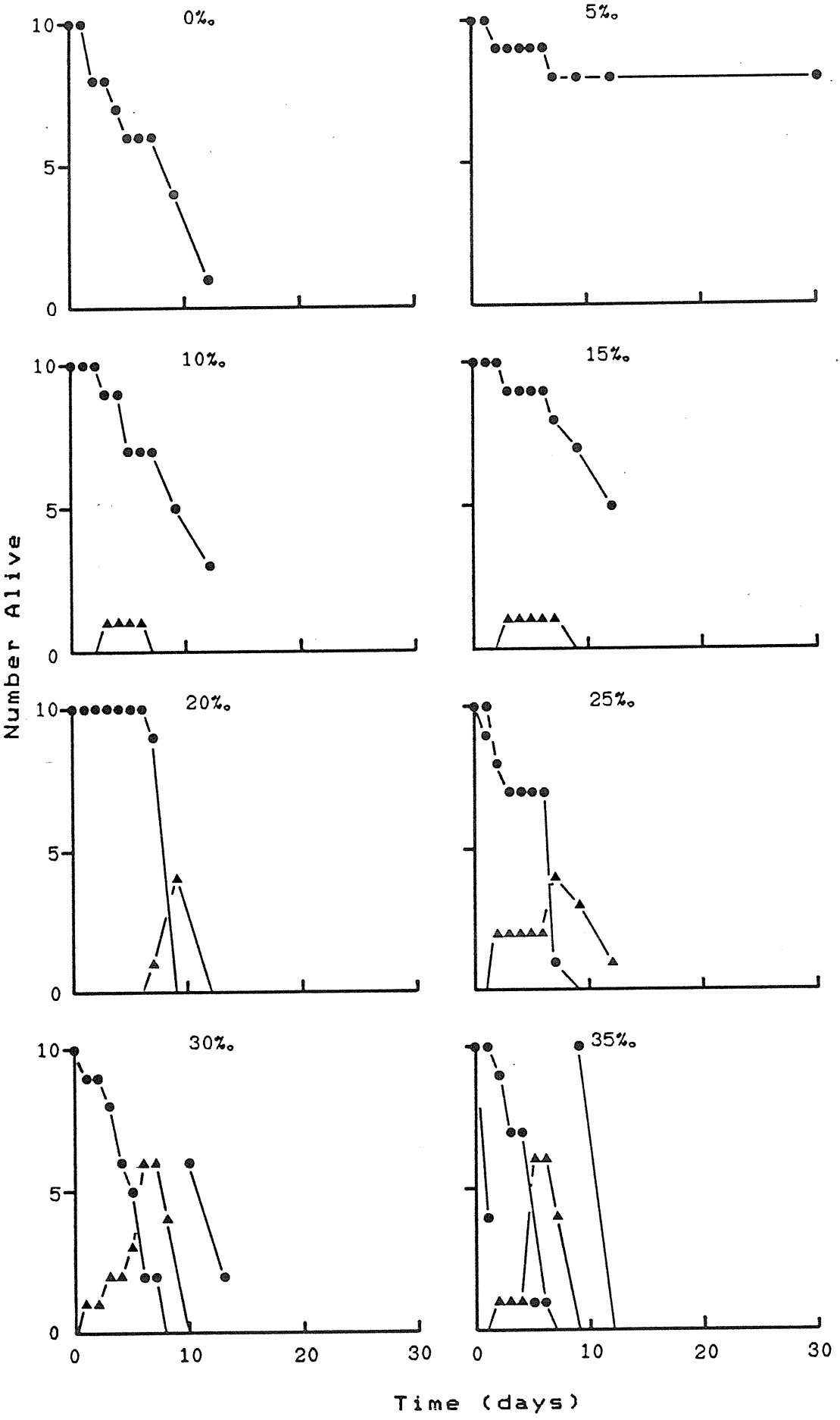
○ stage 3

△ stage 4

□ stage 5

☆ stage 6

□ unknown composition


0‰
5‰
10‰
15‰
20‰
25‰
30‰
35‰
Number Alive
Time (days)
0
5
10
20
30

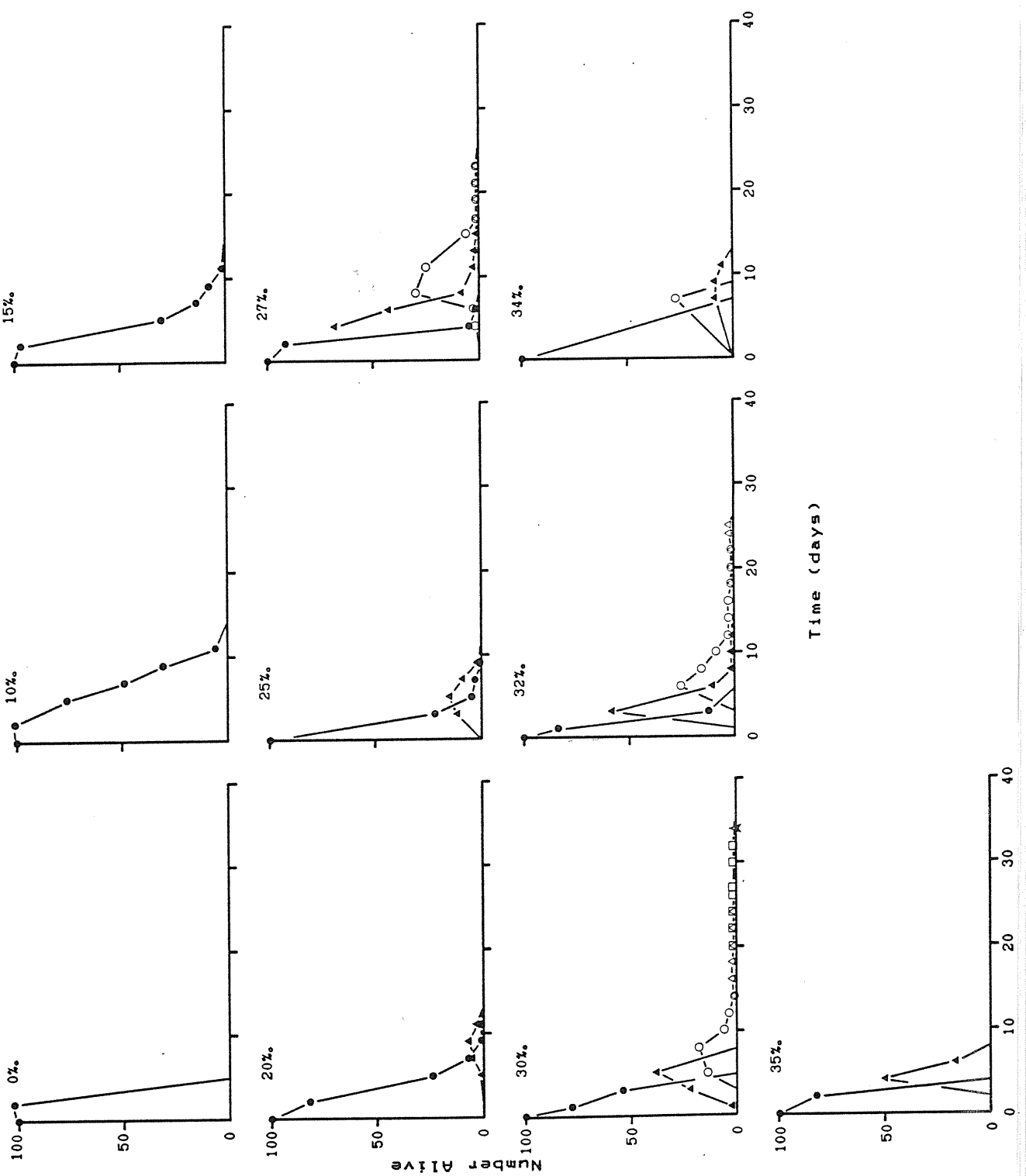


Figure 4.6 continued

Figure 4.6 continued

Experiment 3

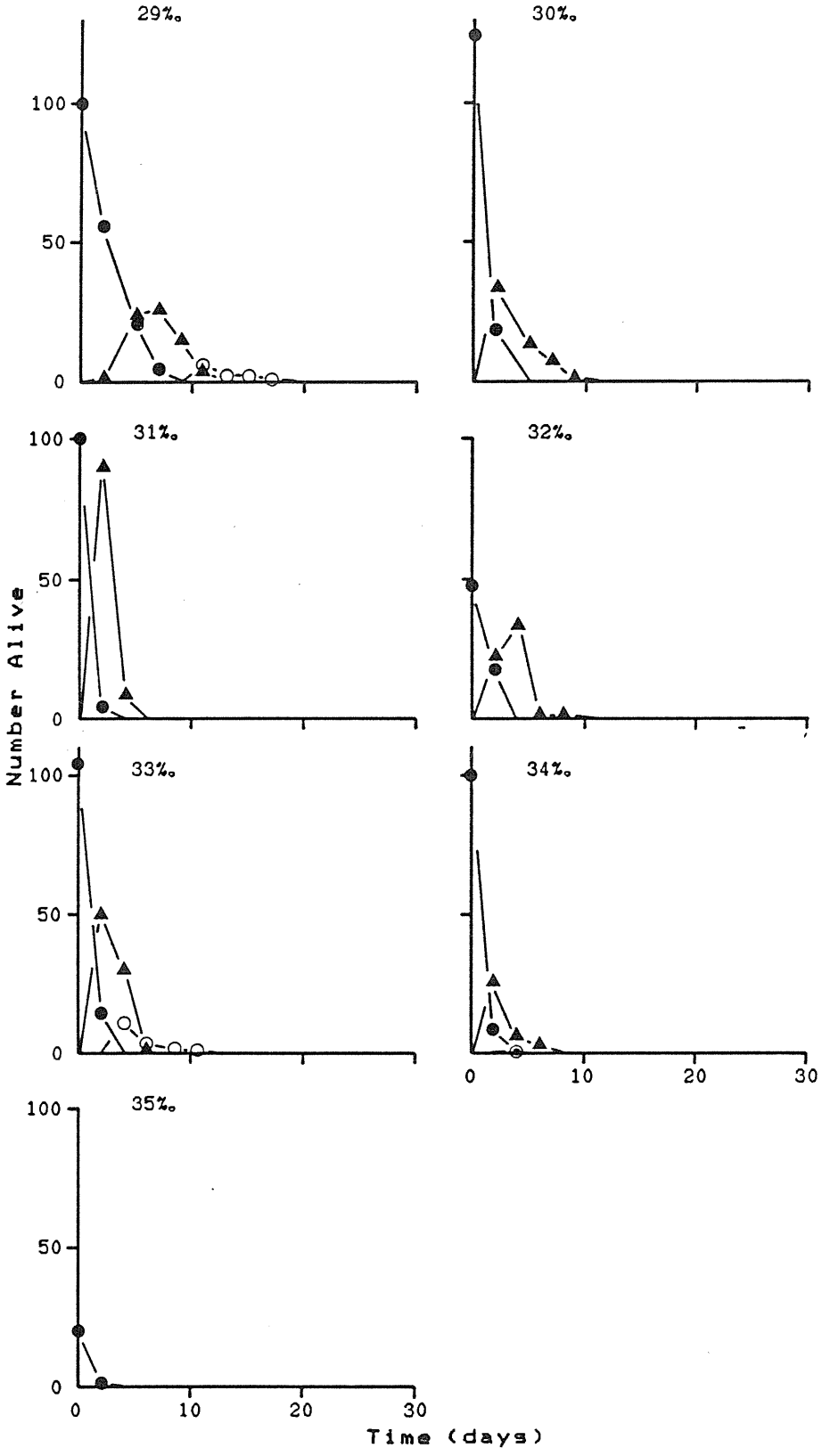


Figure 4.6 continued

Experiment 4

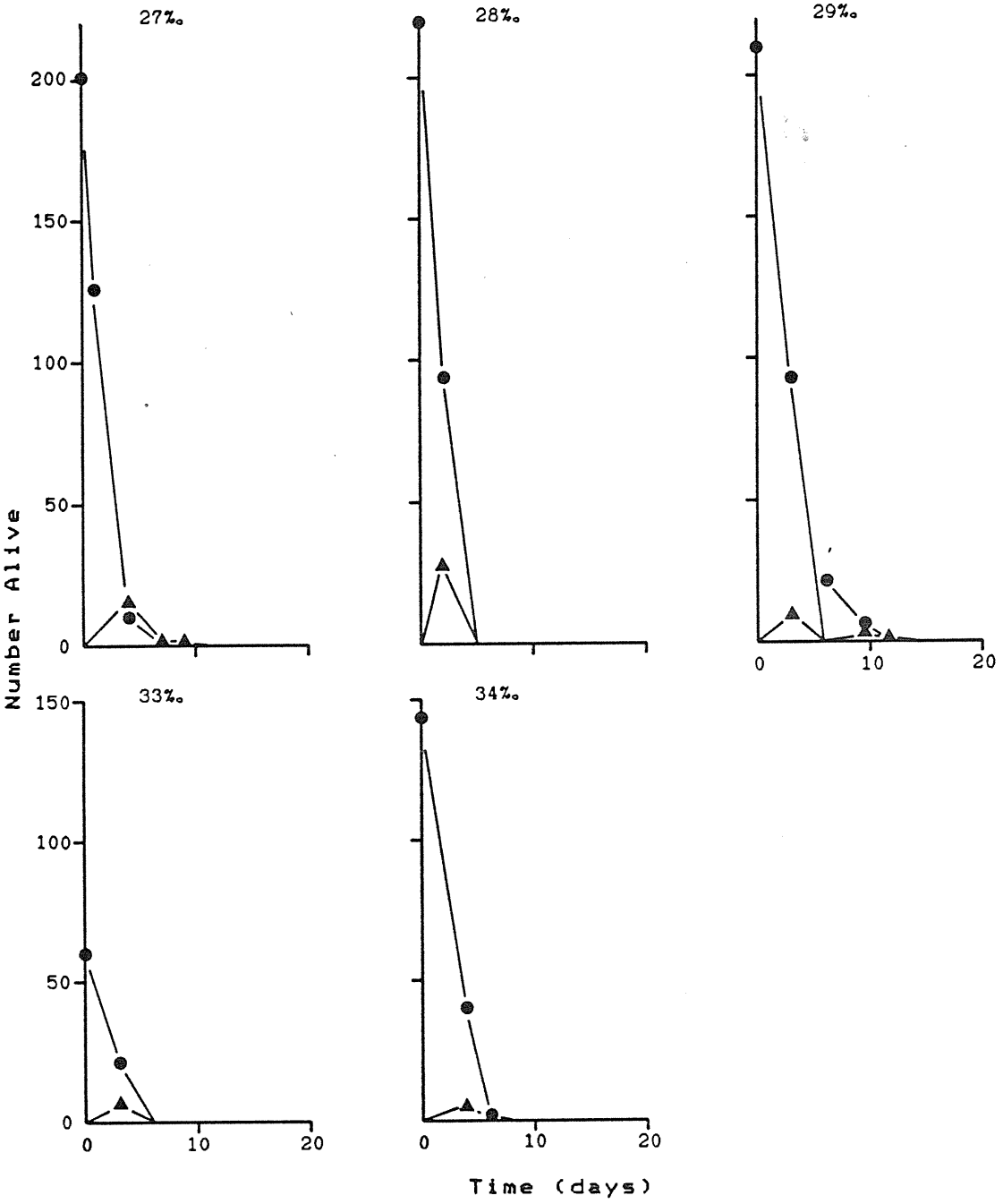
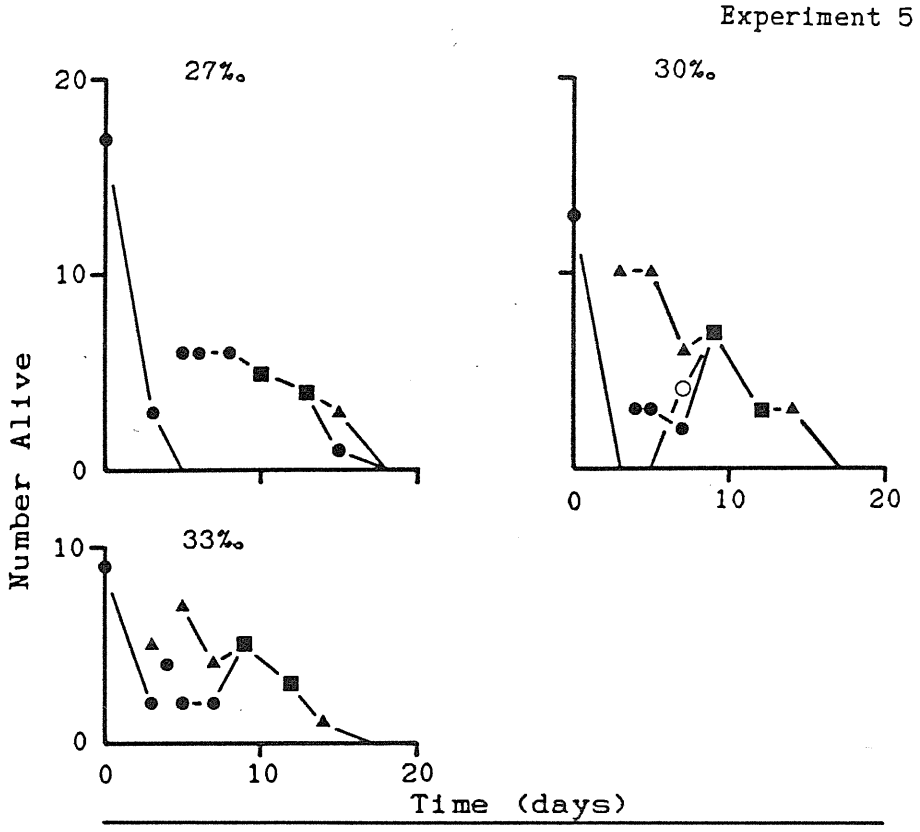


Figure 4.6 continued



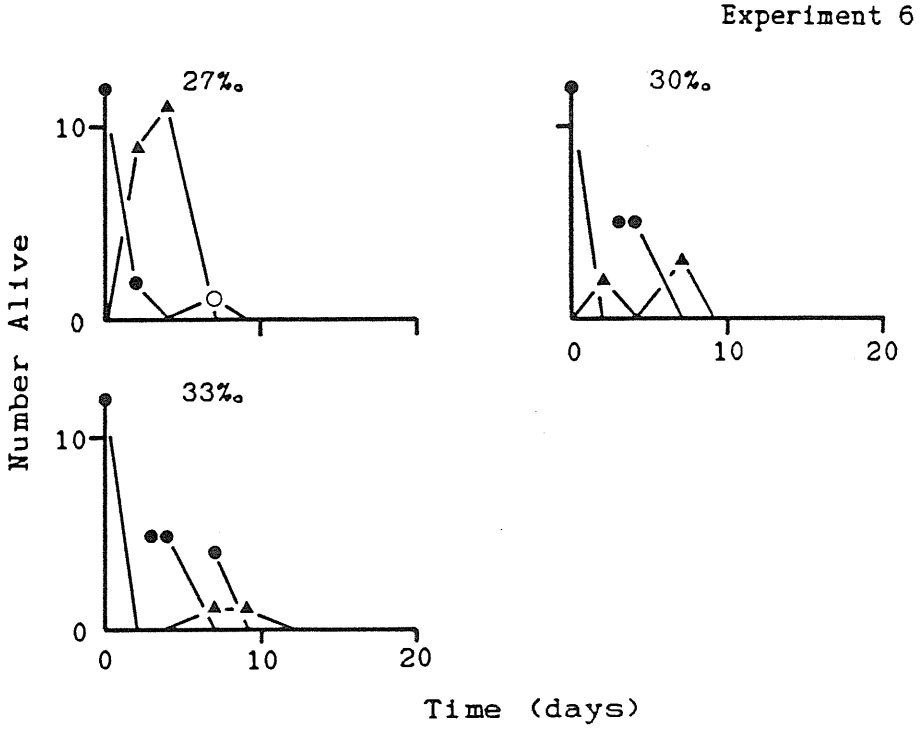


Figure 4.6 continued

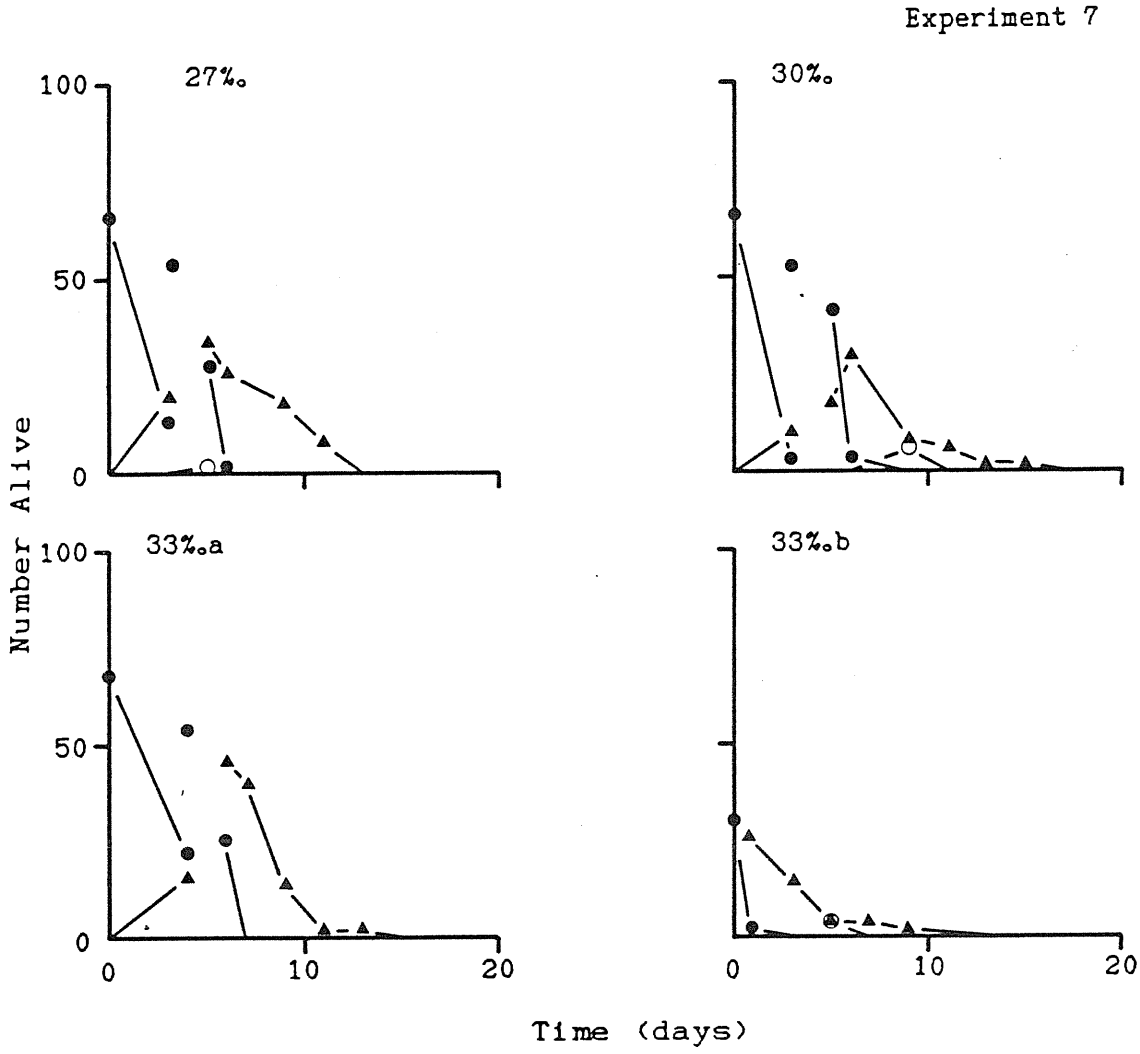


Figure 4.6 continued

Experiment 8

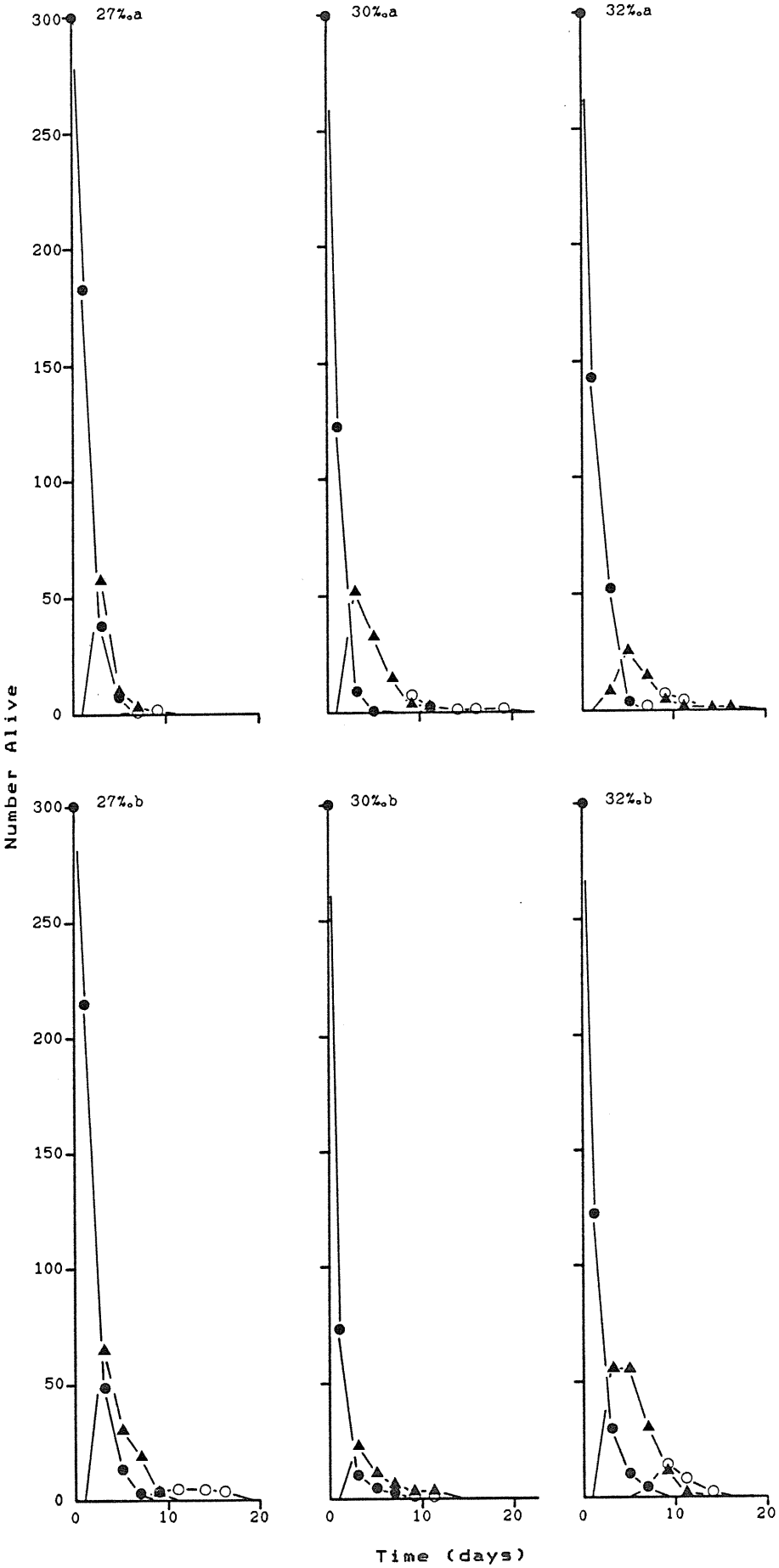
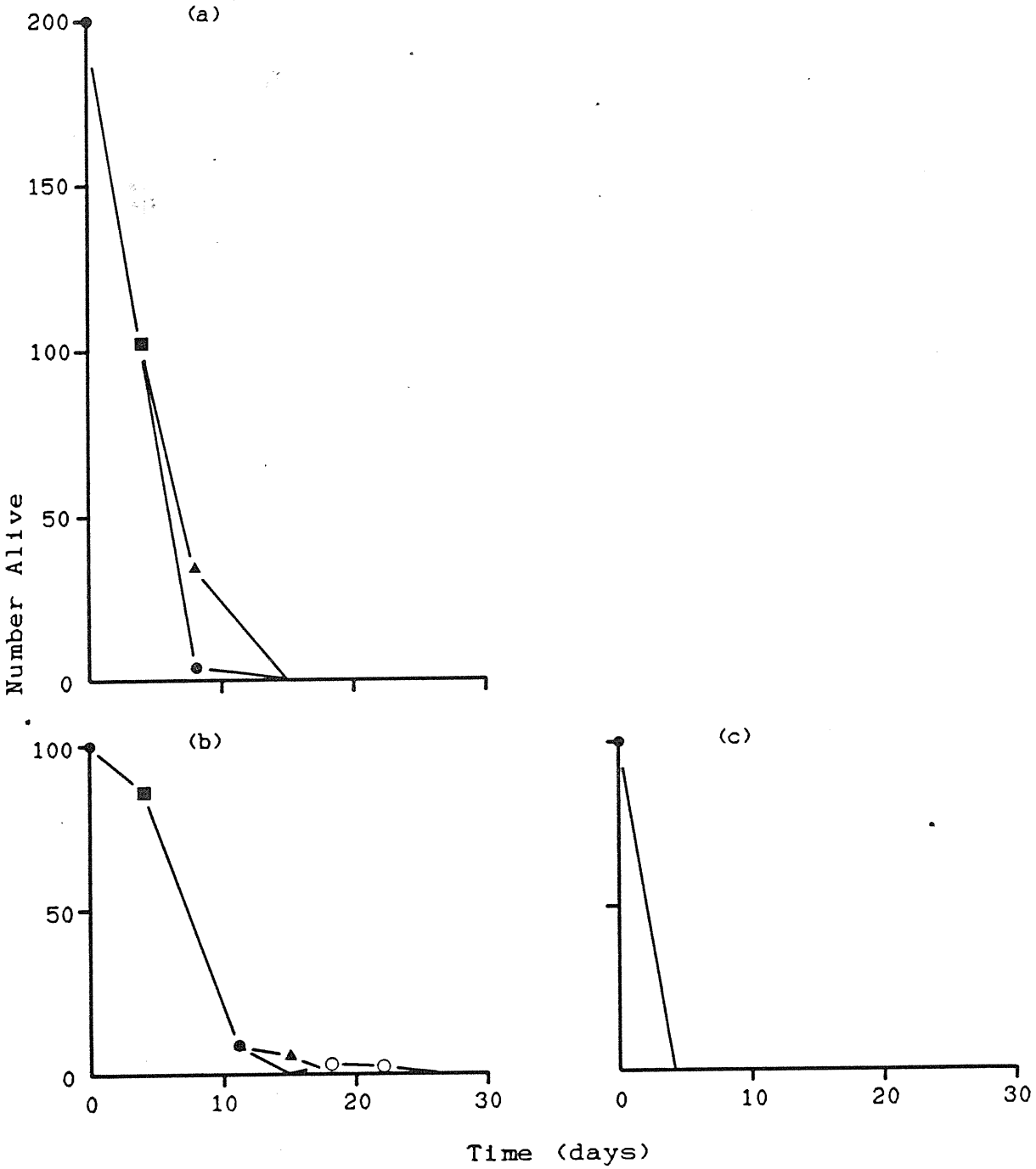


Figure 4.6 continued

Experiment 9



In the second experiment, stage 2 zoeae only occurred in treatments of 15‰ or more. Again, only one individual successfully moulted to stage 2 in the 15‰ treatment. Survival was markedly better between 27 and 32‰, with one individual in the 30‰ treatment dying while moulting from stage 5 to stage 6. The stage 6 larva had developed pleopod buds (Plate 4) and was equivalent in development to the seventh larval stage of *Micratya poeyi* (Hunte, 1979a) and the ninth larval stage of *Atya innocous* (Hunte, 1979b).

Survival in Experiment 3 was poor, and stage 3 larvae only developed in the 29 and 33‰ treatments. Despite improvements in the design of the experiments, survival remained poor for Experiments 4 to 7. Even with the large initial numbers in Experiments 8 and 9, no larvae survived past stage 3. Survival in Experiment 9 was initially better than that in the more controlled environment of Experiment 8, but the onset of cold weather over the weekend of the 23 and 24 May increased the mortality rate. Examinations of the larvae in each experiment under a dissecting microscope indicated that their guts were only partially full of food at best except in Experiment 9. It was found that powdered "Tetramin"™ and wheatgerm tended to promote fungal and bacterial blooms within the experimental containers, while cultured algae did not survive in the experimental salinities. The design of Experiment 9 allowed more tolerant species of algae to grow in the experimental aquarium, which were fed on by the larvae. The guts of the larvae in that experiment were distended with algal cells. These "uncultured" algae may be the most suitable food for future studies.

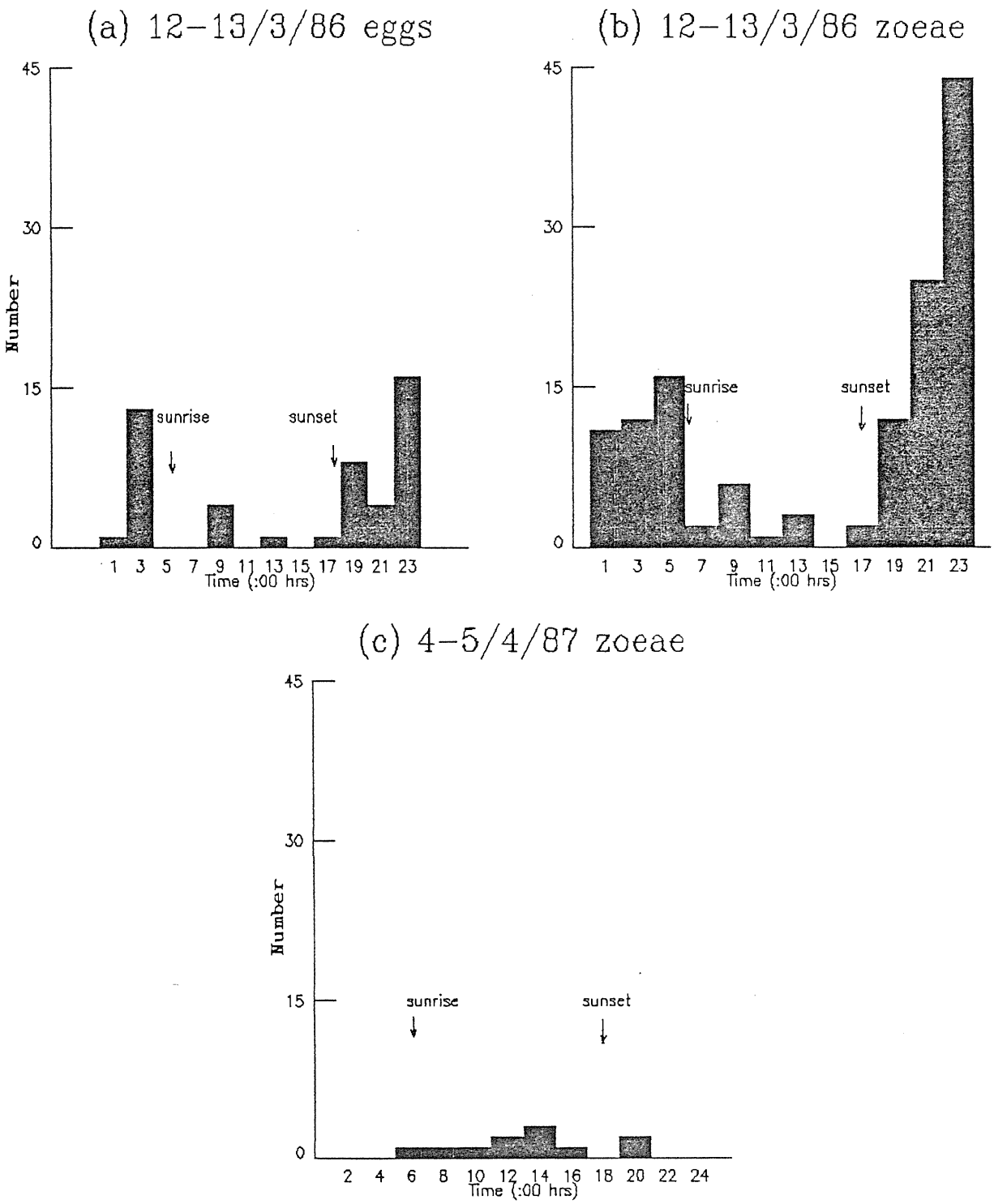
Certainly the success of fish food and wheatgerm in Experiment 3 could not be repeated, even with added precautions against infections.

It is unlikely that electrofishing was the cause of the low hatch rates as the numbers of larvae released from netted females was similar to the number released by electrofished females at the same time. The large hatches on 19 December 1984 (Experiment 2) and 20 May 1987 (Experiments 8 and 9) both occurred soon after the females had been brought to the laboratory. The smaller hatches occurred up to 3 weeks after arrival in the laboratory. Although only eggs with visible eye spots were selected for transport to the laboratory, this was not a reliable measure of the time before they hatched.

Despite the problems described above, the results of these experiments demonstrate that *A. striolata* larvae require salinities of at least 20‰ for development to occur, and that the first larval stage is capable of surviving on its reserves of yolk for up to 30 days if the salinity is too low for development.

The number of eggs and zoeae caught drifting in Yuccabine Creek are shown in Figure 4.7. Both eggs and zoeae showed a nocturnal peak in drift on 12 to 13 March 1986, while zoeae drifted during the day on 4 to 5 April 1987. The numbers found drifting were low on both occasions, especially when it is considered that the March 1986 samples represent virtually the total drift for the stream. That the larvae were going through the mesh of the net is unlikely as *A. striolata* zoeae are 250 µm across the cephalothorax (see Plate 4). It is

Figure 4.7 Numbers of eggs and zoeae collected in a drift net over two separate 24 hour periods.



possible that the larvae collected were released by a single female on each occasion. The presence of eggs in the 12 - 13 March 1986 drift samples increases this possibility as they were likely to have been released by a female a short distance upstream of the net.

Table 4.4 lists the number of caridean larvae counted in the estuarine samples. No larvae of *A. striolata* were found in these samples. The salinities within the estuary were frequently below the salinities required for development of *A. striolata*, particularly following spates in the Murray River system (Table 4.5). The observed temperature range of 26 to 31°C (Table 4.6) encompassed the temperatures used for the rearing experiments.

4.4 Juvenile Life History

4.4.1 Methods

Juveniles were collected during the population sampling in the Yuccabine Creek and Douglas Creek sites, and have been considered in that context in Chapter 3. Sampling for juveniles was also carried out on a monthly basis at five sites in the lowland sections of the Murray River (see Figure 2.1) between 15 June 1984 and 6 July 1986 except for MR5 which was sampled once on 4 December 1984 (see section 2.2.2).

Sampling at all sites was by electrofishing around snags, rocks, vegetation and the river banks. The time spent electrofishing was

Table 4.4 Number of caridean larvae (C) and *A. striolata* larvae (A) collected from samples in the Murray River estuary.

Date	Bluff Landing		1st Inlet		Roundabout		Bedford Ck		Mouth	
	C	A	C	A	C	A	C	A	C	A
5/11/84	5	0	-	-	-	-	-	-	107	0
5/12/84	74	0	-	-	63	0	-	-	18	0
5/1/85	3	0	15	0	3	0	5	0	0	0
5/2/85	5	0	0	0	2	0	16	0	6	0
6/3/85	27	0	1	0	3	0	6	0	0	0
3/4/85	76	0	111	0	58	0	23	0	378	0
5/12/85	28	0	1	0	2	0	1	0	0	0
7/1/86	1	0	45	0	23	0	4	0	-	-
11/2/86	4	0	27	0	27	0	3	0	3	0
15/3/86	18	0	0	0	4	0	7	0	42	0
19/4/86	104	0	298	0	93	0	1068	0	35	0

Table 4.5 Surface (S) and bottom (B) salinities at the Murray River estuary sites during the sampling periods. Salinities are in parts per thousand.

Date	Bluff Landing		1st Inlet		Roundabout		Bedford Ck		Mouth	
	S	B	S	B	S	B	S	B	S	B
5/12/84	14	-	-	-	17	-	-	-	34	-
5/1/85	26	27,5	28,5	34	34,5	34,5	34,5	35	35,5	35
5/2/85	28	28	26	26	30	29	30,5	31	30,5	32
6/3/85	14	15	22	25,5	18	25	26	26	30	30
3/4/85	0	0	0	0	0	0	2	2	3	5
5/12/85	2	2	8	14	14	18	23	25	28	30
7/1/86	22	24	28	30	26	32	34	34	-	-
11/2/86	<1	<1	<1	<1	2	7,5	3	26	27,5	28
15/3/86	0,5	0,5	0,5	1	2,5	7	11	25	17	30
19/4/86	0	0	0	0	0,5	0,5	2	7	7	15,5

Table 4.6 Surface (S) and bottom (B) temperatures (°C) at the Murray River estuary sites during the 1986 sampling period.

Date	Bluff Landing		1st Inlet		Roundabout		Bedford Ck		Mouth	
	S	B	S	B	S	B	S	B	S	B
7/1/86	31	31	31	31	30	31	30,5	30,5	-	-
12/2/86	-	-	31	-	29	-	30	-	30,5	-
15/3/86	27	27	28	28	28	28	28	28	28	28
19/4/86	27	26	26	26	26	26	26,5	26	26,5	26

noted from the instrument's display. In January 1985 the instrument failed, and a back-up, generator powered electrofisher (constructed at James Cook University) was used. This instrument did not have a time display. All shrimp other than large *Macrobrachium* spp. were either preserved in 70% alcohol or frozen until sorted in the laboratory. The carapace lengths of juveniles of *A. striolata* collected were measured using an optical micrometer.

4.4.2 Results

The catch per 10 secs of electrofishing effort (CPUE) for juveniles at the Murray River sites is shown in Table 4.7. Generally, the CPUE was much lower than at the adult sites (see Figure 3.1), and MR3 was the only site with regular catches. *A. striolata* juveniles were only seen to be collected from rocks and large snags, but the number noticed while sampling was usually lower than the number sorted from the sample. Juveniles were only collected from MR4 after the sand and rock riffle was exposed. This apparent preference for rocks is consistent with adult behaviour in aquaria and in the field.

Figure 4.8 shows the relationship between juvenile size and distance from Bluff Landing. The regression equation is:

$$CL = 4.1 + 0.015 \times \text{distance} \quad (p<0.01)$$

where CL is the carapace length in mm and the distance is in km. Figure 4.9 shows the mean size of juveniles collected from MR3 during

Table 4.7 Catch per 10 seconds of electrofishing (C) and total number caught (N) at each Murray River site during the study. - indicates no sample. n.d. indicates not determinable.

Date	MR5		MR4		MR3		MR2		MR1	
	C	N	C	N	C	N	C	N	C	N
15/6/84	-	-	-	-	0,0	0	0,10	3	0,30	3
20/7/84	-	-	-	-	0,0	0	0,0	0	0,03	1
25/8/84	-	-	0,0	0	0,0	0	0,03	1	0,09	4
8/10/84	-	-	0,0	0	0,27	5	0,0	0	0,07	2
6/11/84	-	-	0,0	0	0,40	6	0,0	0	0,0	0
4/12/84	0,20	6	0,0	0	0,70	11	0,0	0	0,14	3
3/1/85	-	-	n,d,	0	n,d,	2	n,d,	0	n,d,	11
6/2/85	-	-	0,0	0	0,0	0	-	-	-	-
7/3/85	-	-	0,0	0	1,90	28	0,55	5	-	-
4/4/85	-	-	0,0	0	0,0	0	0,0	0	0,0	0
1/5/85	-	-	0,0	0	2,12	32	1,07	16	0,0	0
4/6/85	-	-	0,0	0	0,33	5	0,0	0	0,0	0
3/7/85	-	-	0,0	0	1,43	22	0,0	0	0,0	0
9/8/85	-	-	0,0	0	0,32	6	0,0	0	0,12	4
9/8/85	-	-	0,0	0	0,85	14	0,08	1	0,04	1
9/10/85	-	-	0,0	0	0,0	0	0,0	0	0,0	0
14/11/85	-	-	0,0	0	0,18	3	0,0	0	0,0	0
6/12/85	-	-	0,0	0	0,33	4	0,0	0	0,0	0
8/1/86	-	-	0,0	0	0,07	1	0,0	0	0,0	0
11/2/86	-	-	0,0	0	0,0	0	-	-	-	-
16/3/86	-	-	0,0	0	0,0	0	0,0	0	-	-
20/4/86	-	-	0,16	3	2,59	37	0,0	0	-	-
11/6/86	-	-	0,08	1	0,52	5	0,0	0	-	-
6/7/86	-	-	0,11	1	0,19	2	0,0	0	0,0	0

the study. The mean size increased with time at this site, between spates in the river (February/March each year). When a regression analysis was applied to each between-spate section, significant fits were found for the second and third sections, *viz.*:

1 May 1985 to 6 December 1986

$CL = 4.2 + 0.005 \times T$ $(p<0.01)$ n=86

20 April 1986 to 6 July 1986

$CL = 4.2 + 0.018 \times T$ $(p<0.01)$ n=44

where T is the time in days from 1 May 1985 and 20 April 1986 respectively, CL is carapace length in mm and n is the number of individuals in each case.

4.5 Discussion

This study has shown that the life history of *A. striolata* does not involve a migration of ovigerous females to the estuary contrary to the suggestion by Smith and Williams (1982) as tagged females were observed to become ovigerous, brood and release their larvae within the upland sections of the study streams. Also, no adults were captured in the lowland sections of the Murray River, and larvae were collected from the adult habitats. However, it is apparent that the larvae do require high salinities for development. All larvae that hatched in freshwater were non-feeding, phototactic zoeae, and no demersal mysis

Figure 4.8 Relationship between juvenile size in the Murray River and distance upstream of Bluff Landing.

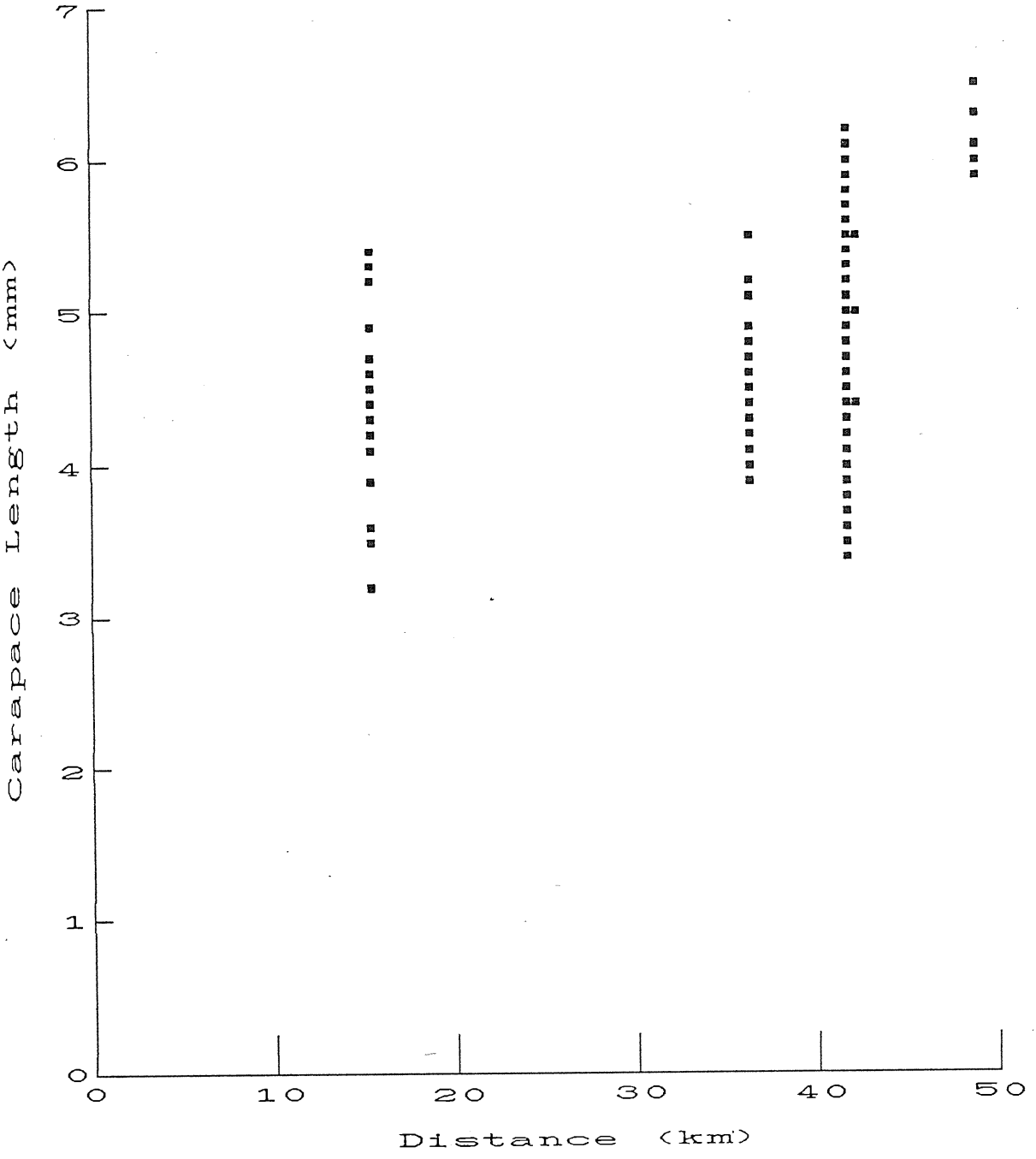
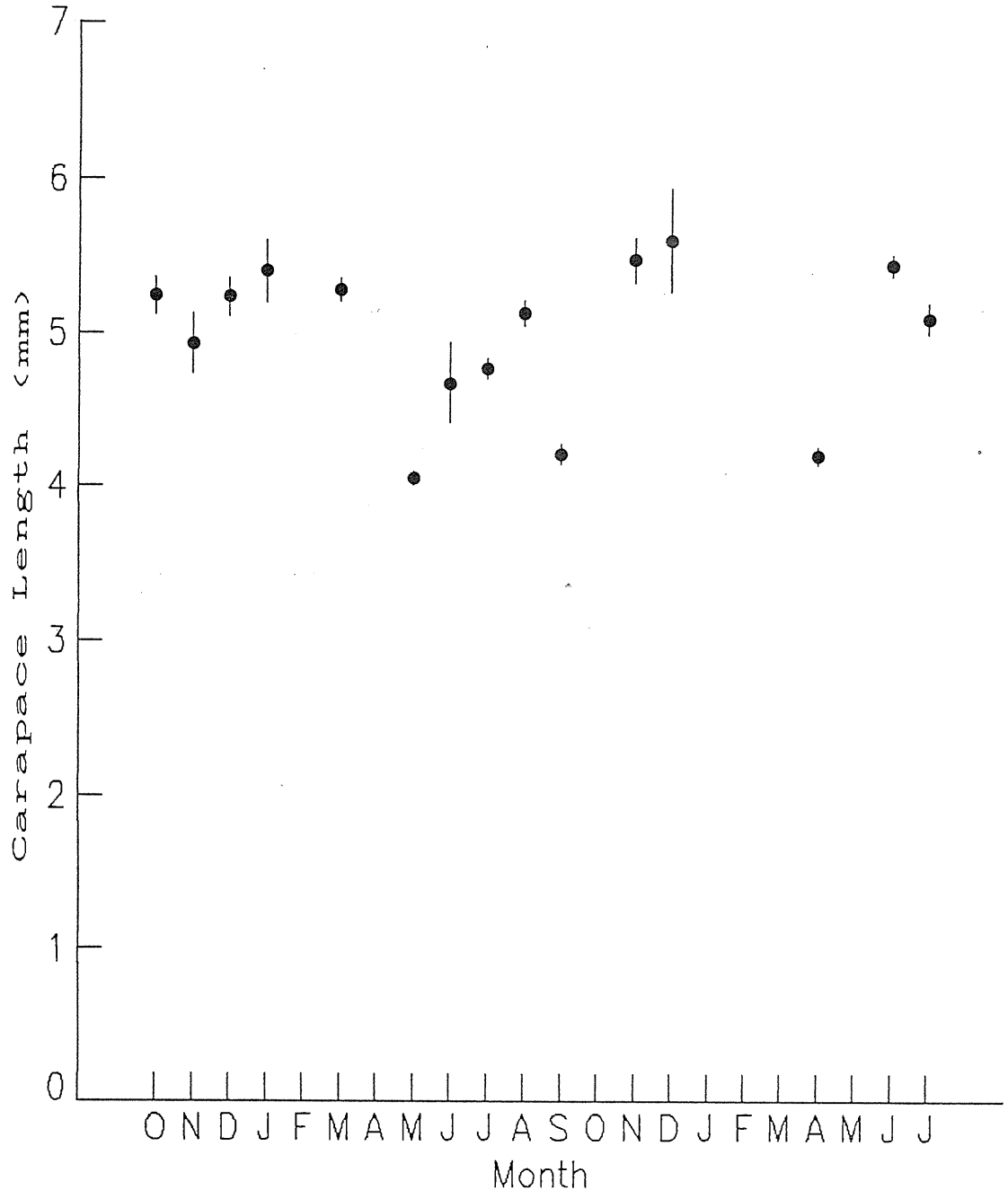


Figure 4.9 Mean monthly carapace length ± one standard error for juveniles collected from MR3.



such as those of *Atyoida bisulcata* (Edmondson, 1929) were ever found either in the field or in the strongly aerated aquaria used to hold ovigerous females. The first stage zoeae of *A. striolata* were shown to survive for 30 days without development in water of 5‰salinity. The 0‰ treatments used distilled water which may have been too dilute for larval survival.

The reproductive season encompassed the summer wet season, and the development of mature gonads was restricted to this period. It is not known what triggers this reproductive effort, as three aquarium specimens became ovigerous at the start of the breeding season, even though the aquarium had been heated for 4 months. It is possible that photoperiod may be the cue. The importance of breeding during the wet season for a species which inhabits upland streams, but which has larvae which require high salinities for development, is obvious. Having more than one brood per season would also be very advantageous in the seasonal wet tropics, where the timing of spates is unpredictable. Considering the distances from the adult habitats to the estuary in the study streams and the hazards such as waterfalls on the way, it is likely that zoeae carried by spates have a higher chance of surviving the journey than zoeae carried by the normal, much smaller discharges. If the mean current speed between the adult habitats and the estuary was 10 $cm.s^{-1}$, the time required for the larval journey would be approximately 17 days in Yuccabine Creek, and 8 days in Douglas Creek. Since during spates the mean current velocity could be greater than this, the ability of the larvae to survive for 30 days is more than adequate for migration to the estuary.

The numbers of larvae collected in drift nets in Yuccabine Creek were very low, and could not represent the reproductive output of the entire population of *A. striolata* upstream of the net. It is possible however, that larvae remain in pools within the stream until a spate, or that the females release larvae in response to spate conditions. The ability of larvae to survive for 30 days on yolk reserves would give them the ability to await spates, while the second hypothesis is consistent with the poor hatch rates for captive females.

During much of the wet season, particularly following spates when *A. striolata* zoeae were most likely to have been carried downstream, the Murray River estuary was much more dilute than the larvae require for development. It is likely therefore that they develop outside the estuary. This does not support Hunte's (1978) hypothesis that larval salinity preferences allow the selection of suitable rivers. Although Douglas Creek is a high gradient stream, the Murray River is a low gradient stream in the lowland regions with an extensive estuary 13 km long. In north Queensland, full marine salinities may only be found some kilometres offshore following the high rainfalls which would favour the downstream transport of *A. striolata* larvae (J.D. Collins, pers. comm.). The sixth larval stage was similar to the seventh larval stage of *Micratya poeyi* Hunte (1979a) in both morphology and age. If the complete larval development of *A. striolata* is similar to that of *M. poeyi* then the likely total duration would be about 55 days (Hunte, 1977). That could be sufficient for dispersal between streams on the north Queensland coast.

The observed increase in juvenile size with increasing distance upstream from the estuary is consistent with the hypothesis of upstream migration of the juveniles after development in the estuary or offshore. However, the increase in juvenile size with time at the one site (MR3) indicates that at least some juveniles remain at one site for some time. In view of their preference for rocky substrata, which are uncommon in the lowland Murray River, migrating juveniles may rest in such habitats and increase their energy reserves before continuing their migration. They would be especially likely to congregate below waterfalls until conditions were suitable for negotiating these barriers. The arrival of juveniles at Douglas Creek during the wet season and at the Yuccabine Creek sites shortly afterwards indicates that high rainfall may be required for this. Following rainfall, shrimp could walk around the waterfall or up the moist sides of the fall away from the mainflow of water. McCulloch and McNeill (1923) commented on the walking abilities of the species (see Chapter 1) and I found that smaller specimens were the most active out of water.

The migration of larvae downstream and the subsequent migration of juveniles back upstream must result in high mortalities. It is therefore important that the reproductive strategy of the adults compensates for this. Ghiselin's (1969) hypothesis that protandry is favoured when increased size imparts a greater advantage to females than to males is supported in this case. Increasing female size is correlated with an increase in the number of eggs produced. The high variability of egg numbers for females in the predominantly female sizes is probably due to shedding of infertile or diseased eggs by the

female as the brood develops. Darnell (1956) noted that a single female *Atya scabra* with developed eggs had fewer eggs than was expected on the basis of the relationship between female size and the number of eggs carried for three females with undeveloped eggs. Females of *Australatya striolata* were observed to shed their eggs when held in captivity. Thus, by being protandrous, *A. striolata* increases the potential output of larvae from the population.

The relationship between egg volume and female size is more complex, and its advantage, if any, less obvious. It is reasonable to assume that larger zoeae, with larger yolk supplies, would survive better between release in fresh water and arrival in appropriate salinities. Therefore, increased egg size would increase larval survival. However, there would need to be a trade-off between egg size and the number of eggs produced by each female. It is possible that the smaller, and therefore generally much younger females, may be able to favour a slightly larger egg size, but are restricted to a smaller number of eggs by gonad size or some other constraint.

Chapter 5 Trophic Relations

5.1 Introduction

As a consequence of the general lack of studies of the ecology of the *Atya*-like shrimp, there have been few accounts of the feeding of the group other than of an anecdotal nature, despite the extremely good studies of the functional morphology of the feeding appendages by Fryer (1977) and Felgenhauer and Abele (1983). Both studies stated that *Atya innocous* has two feeding modes, the typical filter-feeding mode, and sweeping the substratum with the cheliped fan. The later method was suggested to collect algae, including diatoms, from the substratum. Fryer (1977) also observed these two modes for *Atya scabra*. Cowles (1915) stated that *Atyopsis moluccensis* only fed when exposed to a current, and then only by filter-feeding. Felgenhauer and Martin (1983) found that *Atya abelei* Felgenhauer and Martin (1983) was primarily a filter-feeder as it lacked scraping setae on the chelipeds.

The lack of ecological studies on the *Atya*-like shrimp has also precluded any studies of predation on them, or of any close interspecific associations. An examination of sources of mortality, especially predation, is important for an understanding of the population biology of a species.

Early collections of *A. striolata* showed the presence of a commensal temnocephalid (Platyhelminthes: Temnocephaloidea) living on the

maxillipeds of freshly caught shrimp. Some effort was put into examining this relationship.

5.2 Methods

5.2.1 Feeding

Observations of the feeding of the *Atya*-like shrimp have been restricted to observations in aquaria (e.g. Fryer, 1977; Felgenhauer and Martin, 1983). However, the relatively sedentary nature of feeding individuals, and the clarity of the water in their natural habitats makes them very suitable for *in situ* observations. One problem associated with this for *A. striolata* was its tendency to feed within crevices in the substratum, making finding individuals in relatively open positions a difficult task.

Preliminary observations of aquarium specimens showed that *A. striolata* employed three modes of feeding, *viz.* filter-feeding, scraping, and a combination of the two. The latter was usually accomplished by filter-feeding with the first peraeopods and scraping with the second peraeopods, although sometimes only one chela was involved in a particular feeding mode. Thus the feeding of *A. striolata* is much more flexible than has been previously reported for any *Atya*-like shrimp. It was decided to investigate the relative importance of the feeding modes under natural conditions by direct observation. This was accomplished by snorkelling. Individual shrimp, when found in an observable position, were observed for 15 minute periods. The time

spent in each of the three feeding modes, or not feeding, was recorded, and the relative current speed in the vicinity of the shrimp was scored on a simple five-point scale, from still water (1) to high current (>50 $cm.s^{-1}$) (5).

An experiment was carried out to examine the availability of food in the natural environment. Use was made of an artificial stream channel constructed as part of the on-going studies by R.G. Pearson. This channel is situated in the tributary which marks the upstream limit of Yuccabine Upper (see Figure 2.1) and consists of a 3 × 0.3 × 0.2 m sloping aluminium channel supported by a timber frame. It is gravity fed with water from the tributary stream via a 50 mm diameter, plastic irrigation pipe. Output from the pipe can be split into two sections, one into the channel and one falling clear ("pipe").

Measurements taken from photographs of the cheliped fan in the filter-feeding position indicated that the mean, mid-distal sieve size was 35×115 μm (hole area 3844 μm^2). Of the available synthetic mesh sizes, a 62 μm mesh was chosen as being of comparable size to the cheliped mesh size (hole area 4025 μm^2) but capable of sieving the discharges of the artificial channel system. The channel was scrubbed clean and then filled with scrubbed rocks from the stream bed to simulate the natural substratum. Two conical nets 2 m long with a 0.5 m diameter opening and a mesh size of 62 μm were positioned over the "pipe" and "channel" outputs of the system after the discharge rates had been determined in each case. The nets were cleaned at 6 hour intervals from 1800 hrs on 26 August 1986 until 1800 hrs on 5 September 1986.

During this time the channel was stocked with shrimp at densities of 0, 25.5, 50, 100 and 200 shrimp m^{-2}, with each treatment being maintained for two days. In the absence of an accurate estimate of natural densities, 200 m^{-2} was judged to greatly exceed natural conditions (the greatest Fisher-Ford estimate of density for Yuccabine Normal was 9 m^{-2}). At the end of the experiment, the channel and the rocks in the channel were again scrubbed clean and all particulate matter thus removed was collected for weighing.

Samples collected from the nets were preserved in 10% formalin until returned to the laboratory where they were split into 60 to 1000 µm and greater than 1000µm fractions. The smaller size fractions were dried at 60°C for 24 hours and their dry weights were determined and converted to grams dry weight per m^3 of water filtered. Samples from the two highest shrimp densities and their corresponding "pipe" samples were then burnt in a muffle furnace at 500°C for a minimum of 4 hours, and ash-free dry weights were determined.

Two male and two female *A. striolata* were selected at random from each of the December 1985 and June 1985 samples from Yuccabine Upper and Log Crossing, and from the April 1985 samples from Yuccabine Normal and Douglas Creek, for gut contents analysis. The gastric mill was removed from each specimen and the contents spread in water on a microscope slide. Each preparation was then examined under a compound microscope at 400× magnification and the percent cover of each food type estimated for 5 random fields (450 µm diameter).

5.2.2 Predation

There are only three potential predators of *A. striolata* in the streams in Kirrama Range. The most abundant was the eel *Anguilla reinhardtii* Steindachner (1867), while the freshwater turtle *Elseya latisternum* Gray (1867) was seen on occasions in Yuccabine Creek. Kingfishers, mostly azure kingfishers *Ceyx azurea* (Latham, 1801), were seen near Yuccabine Creek but not Douglas Creek. However, they are widespread in Kirrama State Forest. The purple-spotted gudgeon, *Mogurnda adspersa* (Castelnau, 1879) occurs in Yuccabine Creek, but is a small species and Whitehead (1985) found no evidence for it feeding on *A. striolata.* During the population sampling of *A. striolata* the number and size of eels was recorded for each study site, and the presence of any other potential predators noted.

A total of 41 eels were collected for gut contents analysis, 39 from Yuccabine Creek and 2 from Dunn Creek, a tributary of Douglas Creek. Seventeen, including the two from Dunn Creek, were collected during the day, 2 at night, and 22 at dawn. The contents of the entire guts were examined as stomach and "intestine" (post stomach) fractions. Crustacean and fish were identified to species and all other food items to family.

5.2.3 Ecto-commensal

All shrimp sampled at Yuccabine Normal and Douglas Creek from 17 May 1984 to 3 May 1985 were examined for the presence of temnocephalid

commensals. The taxonomic status of the species of temnocephalid found on *A. striolata* is currently being investigated.

5.3 Results

5.3.1 Feeding

A total of 32 shrimp were observed feeding *in situ* at current rankings of 2, 3 and 4. No shrimp were found feeding in observable positions in still water or high current. Table 5.1 summarises the proportion of time spent in each feeding mode for each current rank. The proportion of time spent filter-feeding increased with current speed, while the proportion of time spent in the other feeding modes decreased from current rank 2 to 3. Spearman rank correlation coefficients for percent of time spent in each feeding mode with current are as follows:

filter-feeding	0.93 ($p<0.01$)
sweeping	-0.85 ($p<0.01$)
both	-0.50 ($p<0.01$)
none	-0.79 ($p<0.01$)

Filter-feeding was the only feeding mode used in moderately high current (rank 4), but some time was spent not feeding even at current rank 4. Time not spent feeding was used either for cleaning the body surface with the fifth peraeopods, or the branchial chamber with the third maxillipeds, or for finding new feeding positions. Thus, filter-feeding is the preferred feeding mode of *A. striolata* provided current speed is sufficient to facilitate it. Most of the observations of shrimp in currents of ranks 2 and 3 were made between November 1985

and January 1986 when the discharge of Yuccabine Creek was low (see Chapter 2) and there were few sections of high current deep enough for observations. *A. striolata* individuals tend to congregate in sections of high current as a general rule, and so would maximise the time spent filter-feeding where possible. Shrimp in slow flow would at times sweep vigorously with three cheliped fans while holding one open in the filter-feeding position. Disturbed specimens in aquaria often hold three chelae closed while holding one of the first pair open or partially open. This "testing" position and the use of both feeding modes would enable the shrimp to rapidly detect favourable changes in food availability.

Interactions between individuals were limited and usually consisted of a larger individual pushing a smaller individual away from a preferred position. This was accomplished by the larger individual moving forward from a posterio-lateral position relative to the smaller individual, and pushing with its cephalothorax against the posterior part of the cephalothorax of the smaller individual. Sometimes the latter would move before actual contact and generally settled down to feed a short distance away. *A. striolata* tended to shy away from individuals of *Macrobrachium australiense* Holthuis (1950) before physical contact, and were at times disturbed from feeding positions by large objects such as leaves being carried near them by the current.

The mean duration of each feeding mode is shown on Table 5.2. The shrimp tended to spend far longer filter-feeding without interruption than in any other mode. *A. striolata* stopped feeding for less than

Table 5.1 Times spent in each feeding mode by *A. striolata* in the stream as total time in seconds and percent of the total time observed at that current rank.

Current rank	filter-feeding secs	%	sweeping secs	%	both secs	%	none secs	%	total secs
2	328	8.7	1980	52.7	751	20.0	700	18.6	3759
3	3634	57.7	1700	27.0	454	7.2	512	8.1	6300
4	15297	99.8	0	0.0	0	0.0	3	0.2	15300

Table 5.2 Mean and standard error of duration of each feeding mode.

Feeding Mode	Mean Duration (secs)	Standard Error
Filter	393	58.7
Sweep	63	9.6
Both	38	8.1
None	28	4.0

half a minute on average, and employed both feeding modes together for slightly longer periods.

A peculiarity of the feeding experiment in the artificial stream channel was that the rate of output of particulate matter from the "pipe" discharge was generally lower than for the channel discharge (mean difference, pipe-channel, of -0.0041 gm^{-3} for treatments without shrimp). This may be due to the hydrodynamics of the T-piece used to split the pipe discharge in two. The following analyses were performed on the difference in particulate matter discharge rates (PMD=pipe-channel).

Figure 5.1(a) shows the relationship between PMD and the density of shrimp in the channel. There was no significant effect of the density of shrimp on PMD for this experiment ($p>0.05$). It was noticed that at a density of 200 m^{-2}, the shrimp appeared unsettled, with many crawling actively over the substratum at night, some even emerging above the water level in the channel. However, when the 200 shrimp.m^{-2} treatment was excluded from the analysis, there was still no significant effect.

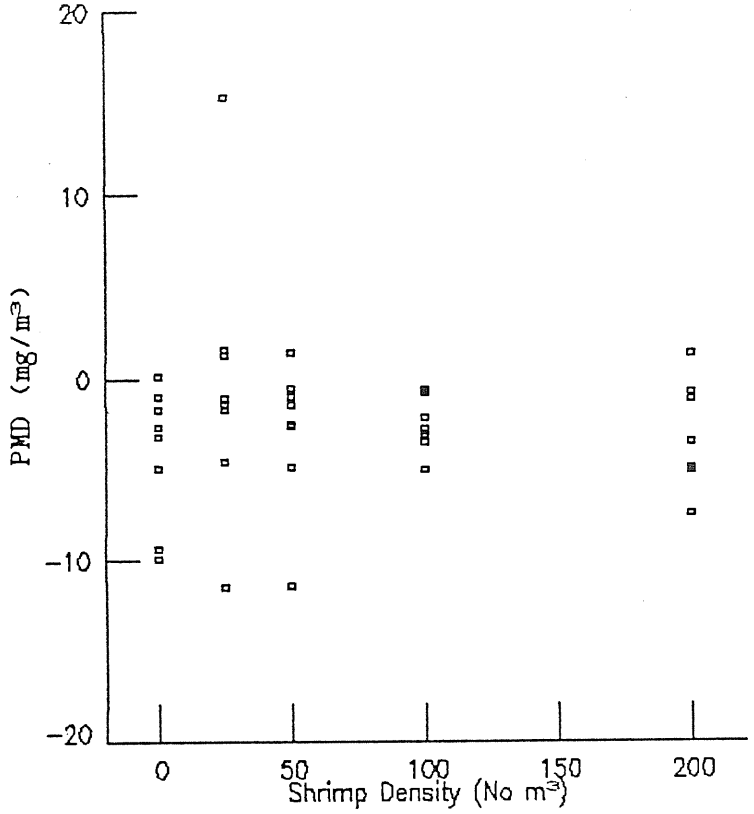
An analysis of variance of PMD for time of day was significant for shrimp densities greater than or equal to 100 m^{-2} ($p<0.01$). Figure 5.1(b) shows that PMD was higher during the day than at night for these treatments. This may be due to greater feeding rates during the day reducing the discharge of organic matter from the channel, or to

Figure 5.1 (a) Relationship between net channel effect on particulate matter output (PMD=pipe-channel) and shrimp density in the artificial stream channel.

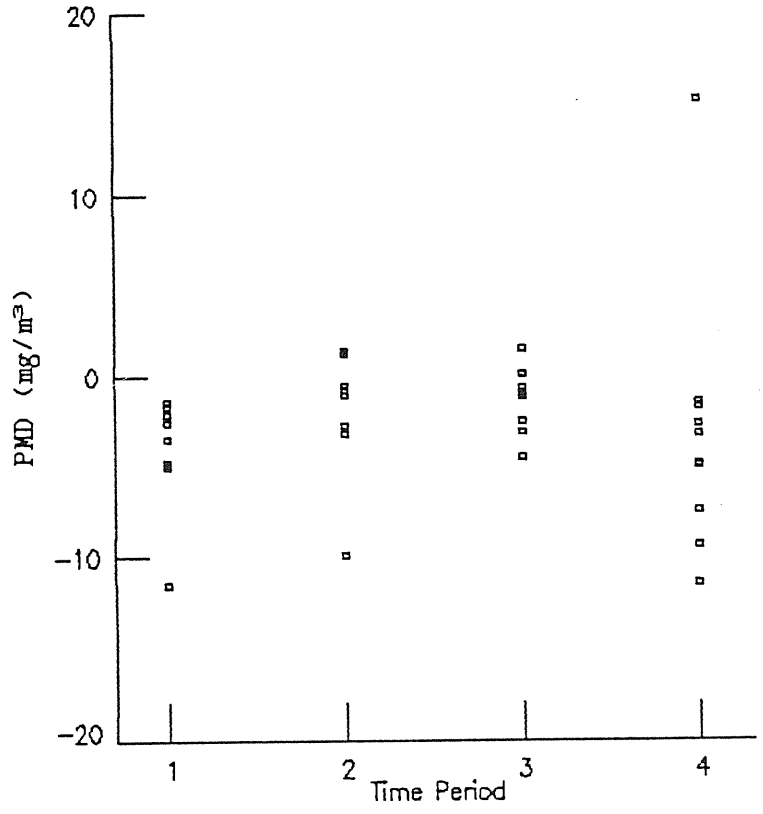
(b) Relationship between PMD and time of day.

Time period	Time of day
1	2400-0600
2	0600-1200
3	1200-1800
4	1800-2400

(a)


20
10
0
−10
−20
PMD (mg/m³)
0
50
100
150
200
Shrimp Density (No m⁻³)

(b)


20
10
0
−10
−20
PMD (mg/m³)
1
2
3
4
Time Period

greater activity of the disturbed shrimp suspending settled sediments at night.

A recognised problem of the experimental design was that if the weight of faeces was not significantly different from the weight of food ingested, then the effect of shrimp on their food would be masked. Therefore, the organic content of the food supply as determined by ashed dry weights was compared with the organic content of the particulate matter discharged from the channel, on the assumption that some of the organic content of ingested particles would be digested. However, a means test of pipe versus channel organic content was not significant ($p>0.5$).

Table 5.3 lists the relative abundances of the food items found in the gastric mills of the shrimp examined. Diatoms, algae (mostly portions of filaments) and inorganic matter (mostly sand grains) are all indicative of sweeping, and the low abundance of these items demonstrates a low importance of this mode of feeding. Particulate organic matter (POM) predominated in all shrimp, irrespective of date, site or sex, as would be expected for a filter-feeding organism. A single egg (probably of an insect species), and a single piece of woody material were also found. Setae from the cheliped fan were common items in the gut (although not listed in the table), which presumably were removed from the chelipeds by the maxillipeds during the cleaning process.

Table 5.3 Mean percent of total food cover per field for all food items found in the gastric mill. Figure in parentheses is standard error in each case. Size is carapace length (mm). POM is particulate organic matter.

Date	Site	Sex	Size	POM	Algae	Diatoms	Bacteria	Inorganics	Egg	Wood
2/12/85	Yuccabine Upper	Female	15.0	96.3(1.03)	2.8(0.81)	0.9(0.61)	-	-	-	-
		Female	14.7	95.8(2.09)	2.9(2.15)	1.4(0.86)	-	-	-	-
		Male	10.6	90.4(5.90)	3.1(3.08)	1.5(1.54)	5.0(5.00)	-	-	-
		Male	10.6	100.0(0.0)	-	-	-	-	-	-
	Log Crossing	Female	15.1	94.6(1.71)	0.3(0.27)	5.1(1.78)	-	-	-	-
		Female	14.3	99.0(0.27)	-	1.0(0.27)	-	-	-	-
		Male	10.1	98.2(1.82)	1.8(1.82)	-	-	-	-	-
		Male	9.6	88.3(9.60)	-	10.0(10.0)	-	1.7(0.87)	-	-
2/6/85	Yuccabine Upper	Female	14.5	96.0(2.10)	1.8(1.82)	2.2(1.76)	-	-	-	-
		Female	14.3	97.3(0.52)	2.2(0.11)	0.5(0.48)	-	-	-	-
		Male	9.9	98.8(0.92)	0.5(0.48)	0.2(0.25)	-	0.5(0.48)	-	-
		Male	10.3	96.7(3.33)	-	3.3(3.33)	-	-	-	-
3/6/85	Log Crossing	Female	15.8	96.6(1.51)	0.6(0.34)	1.7(0.52)	-	0.6(0.61)	0.6(0.61)	-
		Female	13.5	98.4(0.87)	-	0.7(0.42)	-	1.0(0.95)	-	-
		Female	10.5	95.6(1.54)	2.3(1.76)	1.2(1.18)	-	1.0(0.59)	-	-
		Juvenile	7.8	100.0(0.0)	-	-	-	-	-	-
2/4/85	Douglas Creek	Female	14.9	98.3(0.66)	0.7(0.42)	1.1(0.50)	-	-	-	-
		Female	14.3	89.0(5.82)	-	1.0(0.95)	-	6.7(3.16)	-	3.3(3.33)
		Male	9.8	94.5(3.05)	-	1.0(0.95)	-	4.6(3.26)	-	-
		Male	10.3	77.9(7.96)	2.3(1.43)	3.08(2.81)	-	16.7(5.86)	-	-
1/4/85	Yuccabine Normal	Female	15.3	93.6(2.72)	3.5(3.29)	1.7(0.73)	-	1.1(0.69)	-	-
		Female	14.8	94.8(1.60)	0.9(0.63)	4.3(1.98)	-	-	-	-
		Male	10.3	90.6(5.00)	1.0(0.95)	-	3.8(2.77)	4.7(2.61)	-	-
		Male	9.9	94.7(1.10)	1.3(0.78)	4.0(1.48)	-	-	-	-

5.3.2 Predation

No turtles were seen at the sample sites during this study despite the fact that turtles are stunned by the electrofisher used, and sightings in Yuccabine Creek as a whole were rare. While azure kingfishers were sighted frequently, particularly at Log Crossing, they were only seen to feed in the pools, and the only food item I observed them to capture from the stream was *Mogurnda adspersa*. Turbulence in riffle sections greatly reduces visibility from above, and this coupled with the cryptic nature of *A. striolata* would make it difficult for birds to feed on them. Thus, turtles and kingfishers would be of limited importance as predators of *A. striolata* .

Figure 5.2 shows the length-frequency distributions of eels at each site during the study. Most eels present at the sites were in the 20 to 40 cm size range, and abundances were generally low. Table 5.4 shows that *A. striolata* was not found in any eel gut examined, and that insects, particularly Ephemeroptera, Trichoptera and Odonata, were the predominant food items. Notably, fish (*Mogurnda adspersa*) were present in only two eels, 31 and 33 cm long, while larger eels (≥50cm) fed mainly on large Odonata and terrestrial insects. The only crustacean food item was a single specimen of *Macrobrachium* sp. found in the gut of a 61 cm eel. In an unsuccessful attempt to capture *Anguilla reinhardtii* by fishing, I used *A. striolata* as bait. The bait was taken on several occasions and the tangled, mucus covered condition

Table 5.4 Occurrence of food items in eel guts. Data are the number of stomachs or intestines each food item was found in.

Item	Stomachs	Intestines	Total gut		Eel size (cm)	
			mean	SE		
Ephemeroptera	14	8	20		38.7	3.35
Odonata	11	2	12		37.5	3.34
Trichoptera	9	10	17		40.4	3.39
Nematoda	6	1	6		36.6	2.71
Anura adult	3	1	3		48.0	1.00
larvae	1	0	1		44	0
Diptera	2	1	3		31.3	1.45
Terrestrial insects	2	2	4		53.0	9.58
Megaloptera	2	1	3		40.7	4.91
Mogurnda adspersa	2	0	2		32.0	1.00
Coleoptera	1	0	1		34	0
Insect remains	0	6	6		39.0	8.05
Arachnida	0	1	1		29	0
Macrobrachium	0	1	1		61	0
sand	0	1	1		39	0
Empty	20	25	9		25.9	3.56
Total examined	41	41	41		34.6	2.24

Figure 5.2 Length frequency distributions of eels sighted at each site on each sampling occasion

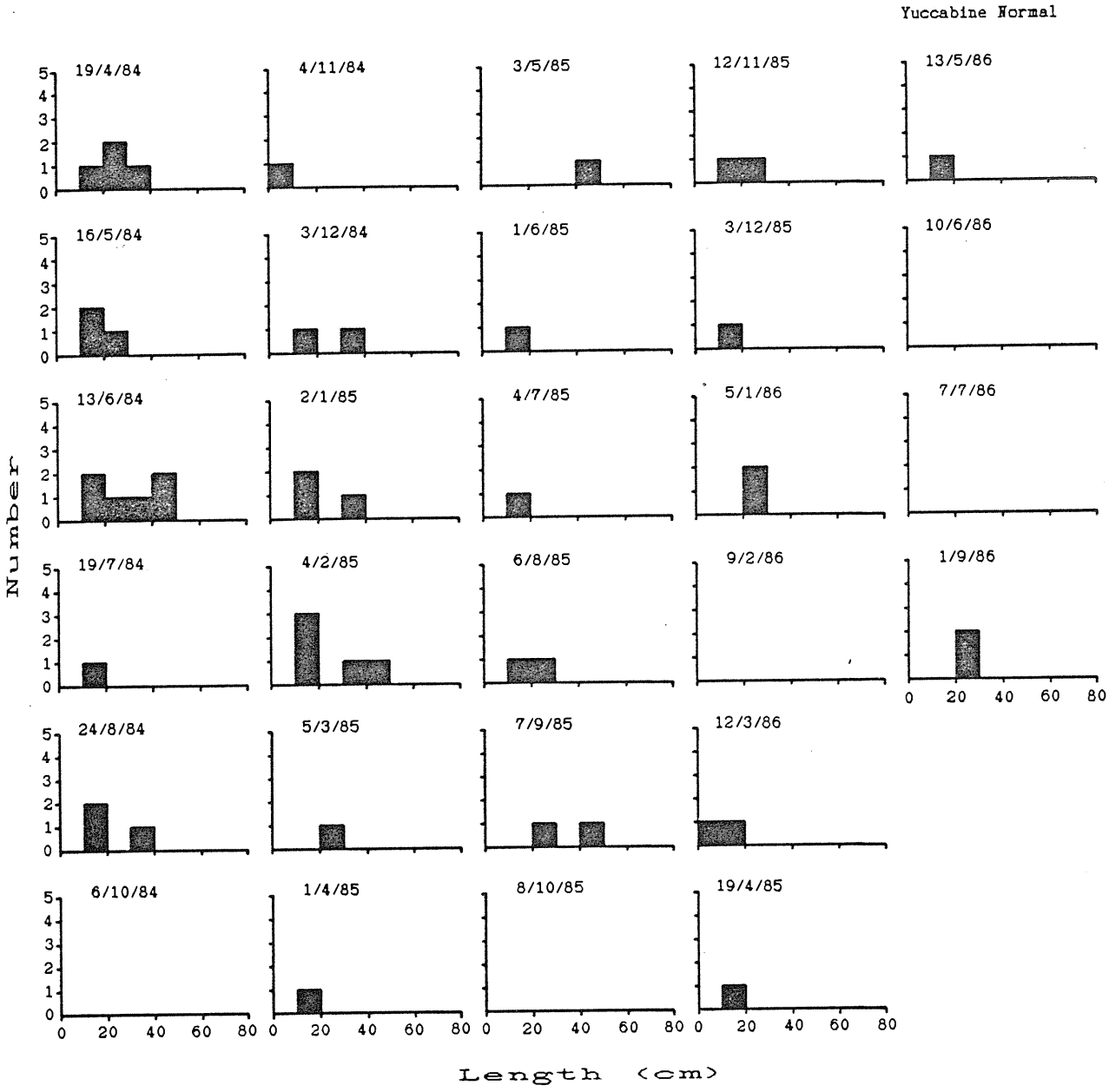


Figure 5.2 continued

Douglas Creek

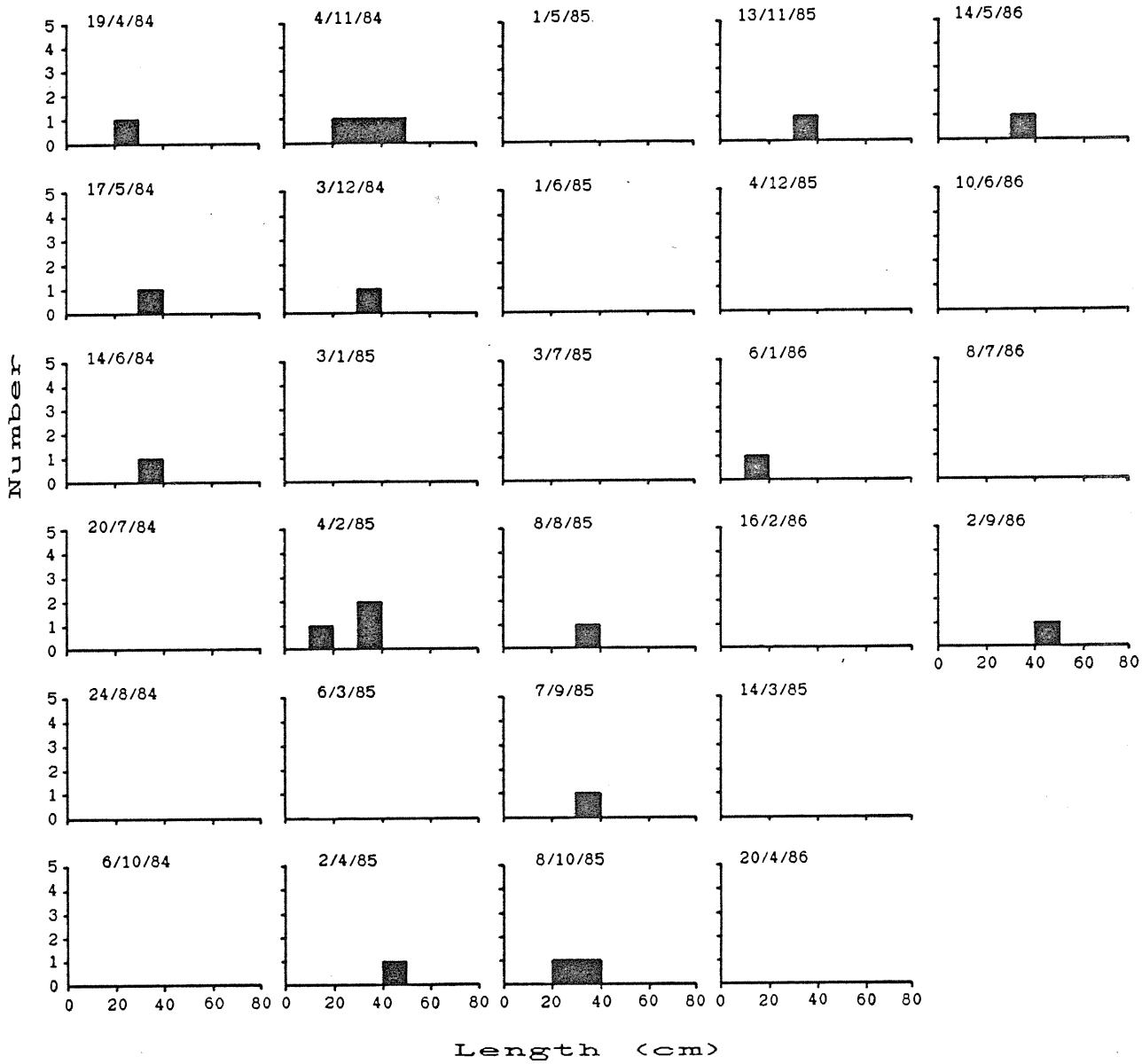


Figure 5.2 continued

Yuccabine Upper

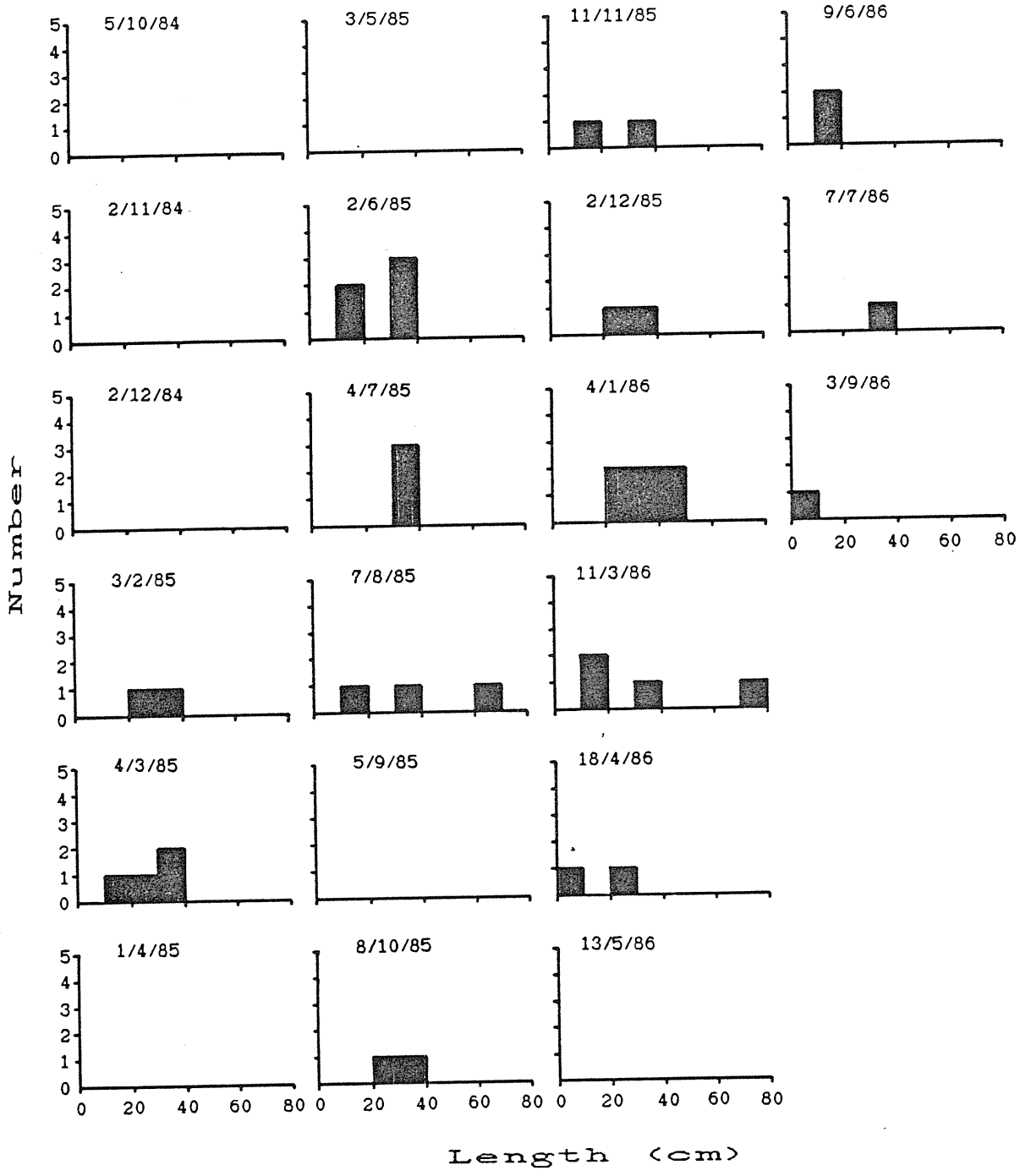
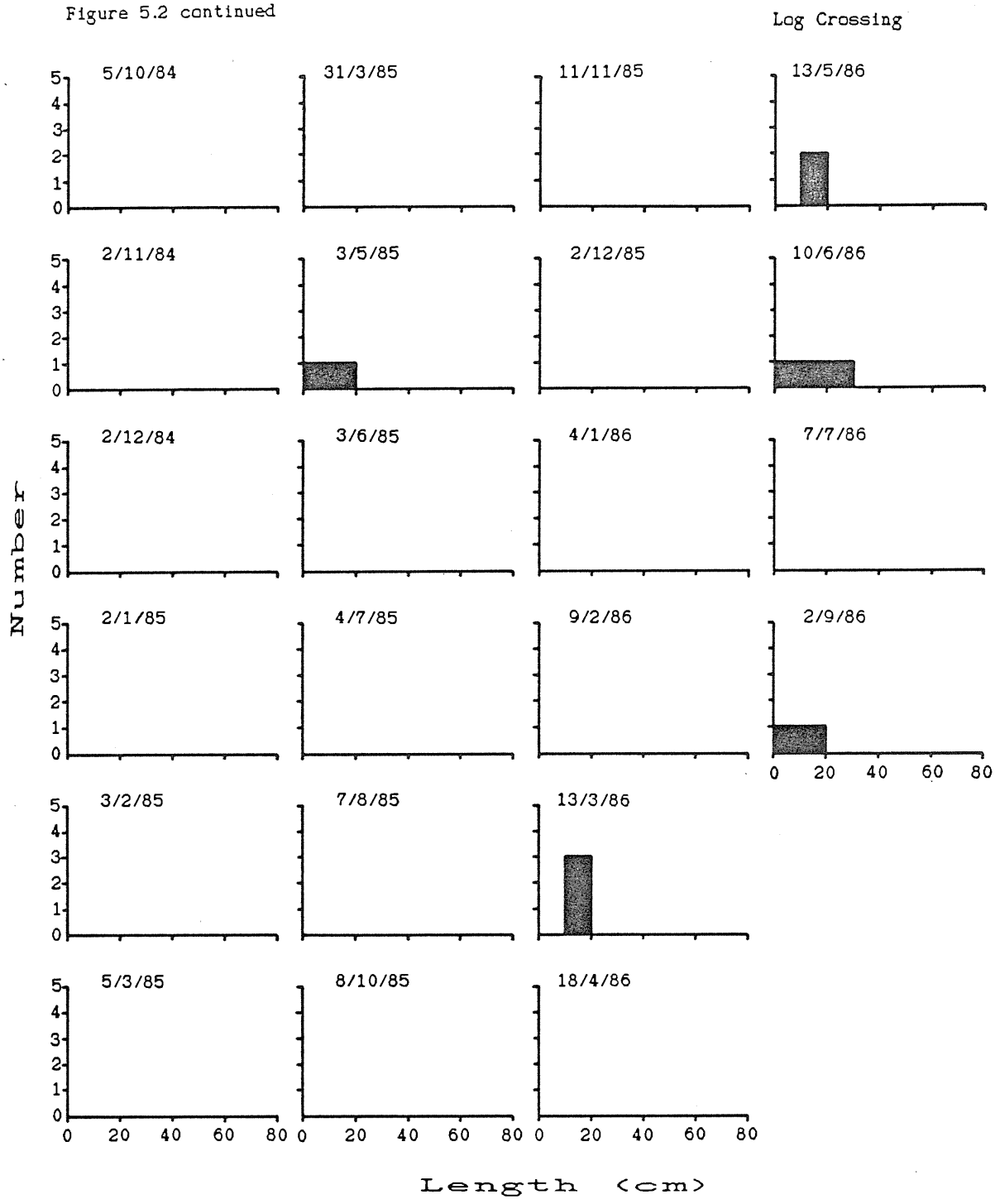


Figure 5.2 continued

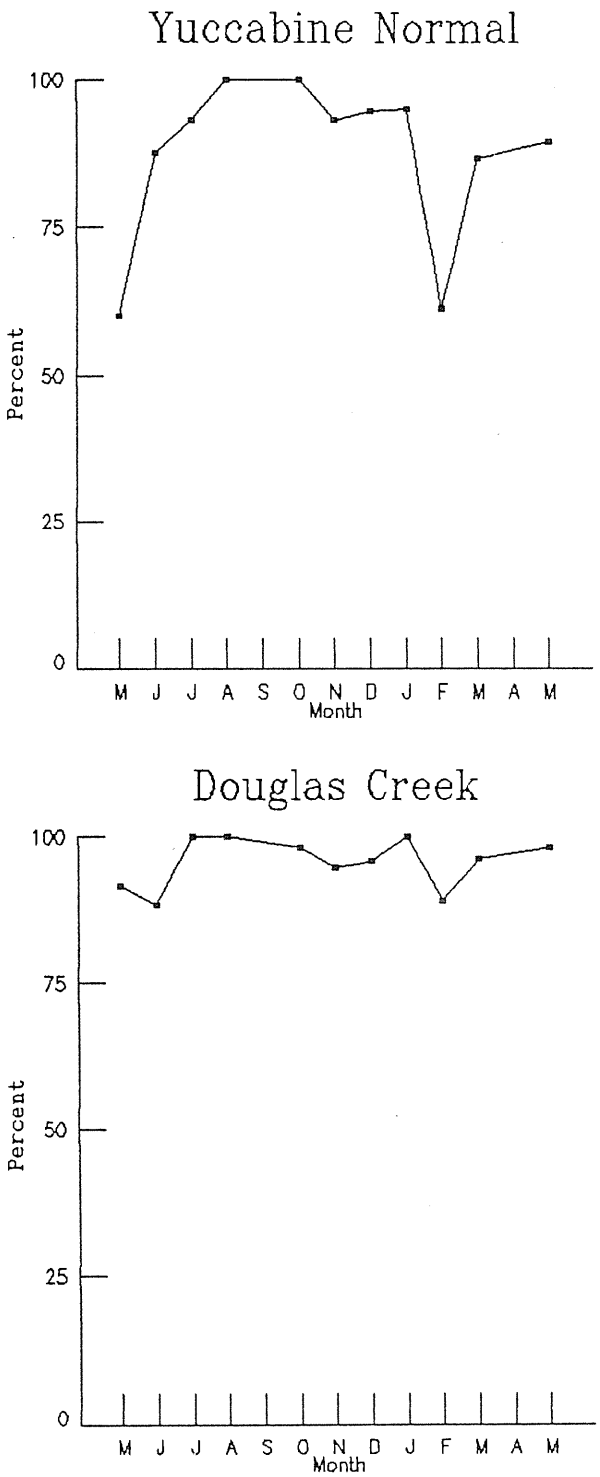


of the line indicated that an eel was responsible each time. An eel kept in an aquarium was quite willing to eat *A. striolata*.

5.3.3 Commensal

The species of temnocephalid occurring on *A. striolata* belongs to the genus *Temnocephala*, but its specific status is still under examination. Accumulations of *Temnocephala* sp usually occurred at the proximal ends of the penultimate segments of the third maxillipeds, but in cases of high infestation they were sometimes found on the bases of the antennae and the anterior margin of the carapace as well. Adults were not observed within the branchial chambers, although eggs were only found on the branchial chamber wall. *Temnocephala* sp did not remain on shrimp held in aquaria and readily left the host while the shrimp were held in a bucket for measuring. It was therefore not possible to observe feeding of *Temnocephala* sp, and the records of occurrence on shrimp may be underestimates in some cases. It was this tendency for the commensal to leave the host that precluded accurately counting the number per host. The observed proportion of *A. striolata* with *Temnocephala* sp for Yuccabine Upper and Douglas Creek are presented in Figure 5.3. Infestation rates were very high for both sites, although more variable for Yuccabine Normal. In general it was only recently moulted shrimp that did not carry *Temnocephala* sp. In view of the sensitivity of the commensal to host captivity, the higher variability of occurrence on shrimp in Yuccabine Creek may be related to the greater physico-chemical variability of that stream.

Figure 5.3 Monthly percent of *Australatya striolata* individuals with *Temnocephala* sp. at Yuccabine Normal and Douglas Creek.



5.3.4 Disease

No evidence of infection was found in any individuals of *A. striolata* collected from natural habitats. Even tagged individuals showed no sign of infection around the entry and exit wounds from the tags. It is therefore apparent that adult populations of *A. striolata* are remarkably disease free.

5.4 Discussion

The ability of a passive filter-feeding organism to exploit an alternative feeding method would be very important in regions such as the Kirrama Ranges with distinct wet and dry seasons, and therefore seasonal flow rates of streams. *A. striolata* is predominantly a filter-feeder, which is also capable of feeding by sweeping the substratum. The latter technique is only used in conditions of low to moderate flow. The dominance of filter-feeding is further evidenced by gut contents analysis as items indicative of sweeping represented only a small proportion of the gut contents. Since filter-feeding is obviously the method of choice, it would be important for individuals to rapidly detect suitability of conditions for that method. Therefore, in low flow conditions it would be advantageous to occasionally 'test the waters' for the return of favourable conditions for filter-feeding. The simultaneous use of both modes for short periods of time at regular intervals would be the most efficient way of achieving this.

Unless *A. striolata* feed mostly on food particles between 35 and 62 μm diameter, then the results of the feeding experiment suggest that the most preferred food (i.e. particulate organic matter) is not a limited resource, at least for normal densities of shrimp. Whilst this experiment served to examine food availability in the environment, quantitative determination of the processing rates of *A. striolata* would need much more rigid control.

The feeding habits of *Anguilla reinhardtii* examined in this study are quite different from those found by other authors. In the Black River near Townsville, Beumer (1976) found that orthopterans, fish and *Macrobrachium* spp were the most important food items, while in Macleods Morass in Victoria, Beumer (1979) found that large eels (>50 cm) fed predominantly on fish, and that crustaceans, including atyids, were common food items. Sloane (1984) found that eels 20cm or more long fed predominantly on *Paratya australiensis* in the Douglas River in Tasmania, fish not being numerically important food items. Hortle and Pearson (in press) observed that large eels fed mainly on fish and palaemonids, while smaller eels (<23 cm) fed on aquatic insects. In this study, eels fed mainly on aquatic insects for all size ranges. Thus, although the eels seen at the study sites (Figure 5.2) were usually in the 20 to 50 cm size range, for which crustaceans are reported to be common food items, and the densities of *A. striolata* were high in the study streams, the eels did not feed on *A. striolata*, even though they would eat shrimp presented visibly. Possibly, individuals of *A. striolata* are too cryptic in their natural habitat, or are too difficult to capture for eels to successfully feed on them.

Alternatively, the density of aquatic insects in the study streams may be high enough for it to be energetically advantageous for eels to feed mostly on insects.

As there does not appear to be any important source of predation for adults of *A. striolata*, and there is a minimal incidence of disease, the survival rate of adults should be very high. This would facilitate the longevity of the species, and would greatly help to compensate for high mortality of the immature life stages.

The consistent position of *Temnocephala* sp on the third maxillipeds, and the high infestation rate on *A. striolata* indicate a close relationship between the two species which may involve supplementary feeding. Jennings (1968) found that two species of *Temnocephala* were both carnivorous, capturing food from the water with their tentacles, and Cannon and Jennings (1987) found that *Temnocephala minor* fed similarly. The species occurring on *A. striolata* may feed on animal matter ejected by the shrimp when removing food from the chelipeds with the maxillipeds. The concentration of *Temnocephala* sp. on the maxillipeds, or at least the anterior of the shrimp, and not the bases of the legs, branchial chamber or general body surface as is usually reported (eg. Jennings, 1968, 1971; Williams, 1981 and Cannon and Jennings, 1987) indicates the relationship between the temnocephalid and its host is closer in the present case than has been previously reported. Whether or not this species of *Temnocephala* is unique to *A. striolata*, or indeed if it is a new species, is not yet known.

Chapter 6 Distribution and Geographical Variation

6.1 Introduction

Smith and Williams (1982) examined the distribution of *Australatya striolata* and the extent of morphological variation over its range, from both museum specimens and their own collections. However, the number of specimens available to them was limited, especially for north Queensland. Only 51 specimens from Queensland including 16 from north Queensland were examined by the authors. It was desirable therefore to re-examine the geographical variation in morphology with more specimens from the northern part of the range. Also, in the light of the knowledge of the population structure in Yuccabine and Douglas Creeks, it would be useful to undertake a preliminary examination of the population structure over the geographic range of the species.

As there existed some confusion over the southern limit of distribution (see Chapter 1) and the known northern limit of distribution did not fit the existing theory of the colonisation of Australia by the Atyidae from the north (Bishop, 1967), it was decided to investigate the geographical limits of the distribution.

6.2 Methods

I undertook two collecting trips to examine the northern and southern distribution respectively. The time available was restricted to 15

days (17 August 1985 to 31 August 1985) for the former, and 30 days (22 September 1986 to 22 October 1986) for the latter. Preliminary samples had been made in the Nerang River catchment, south Queensland on 4 July 1984.

Sites were chosen from topographic maps and from discussions with local residents in each area. Samples of up to 200 individuals were collected from each site by electrofishing. Specimens were preserved in alcohol and returned to the laboratory for analysis. The altitude of the sites was determined where possible from topographic maps.

The shrimp were measured (carapace length) and sexed in the same way as for samples from the population biology study sites (see Chapter 3). In order to examine geographical variation in morphology, six sites were selected to cover the range of the species. Twenty specimens each were selected randomly from Yuccabine Creek, the Nerang River, Heckey Creek, and Bugong Creek for measurement. For the sites near the northern and southern limits of the distribution, there were fewer available specimens, so seven were selected from the Leo Creek collection and two from the Genoa River sample. For each specimen 34 characters were determined (listed in Table 6.2).

6.3 Results

6.3.1 Distribution

Figure 6.1 shows the distribution of *A. striolata* , including data from other studies. The complete list of sites examined is given in Table 6.1. Thus the known limits of distribution have been extended north to the Claudie River, Iron Range, on Cape York Peninsula (12° 45'S, 143° 12'E), and south to the Genoa River, Victoria (37° 29'S, 149° 35'E). Iron Range is the most northerly extension of the Great Dividing Range, and is therefore the most northerly montain region in eastern Australia. My collections in Victoria were restricted by permit limitations to four sites, so the species could be more widespread in this state than Table 6.1 indicates.

Figure 6.2 shows the lowest altitude observed for adult populations of *A. striolata* over the geographic range of the species. The available data are insufficient to determine the altitude range of adult populations for each catchment. Nevertheless, there is a tendency for the minimum altitude to decrease with increasing latitude. The lowest altitude inhabited by *A. striolata* in each region will ultimately be determined by the availability of suitable habitat. Table 6.1 shows that sampling at altitudes less than 300 m in north Queensland at best produced only juveniles of the species, even in otherwise suitable habitat, whereas in the southern portion of the range, adults were found at very low altitudes. At Currowan Creek, the adult population was less than 1 km from tidal influence.

Figure 6.1 Geographical distribution of *Australatya striolata*. ○ Data from Smith and Williams (1982). □ Data from Richardson (1985). ● Data from this study.

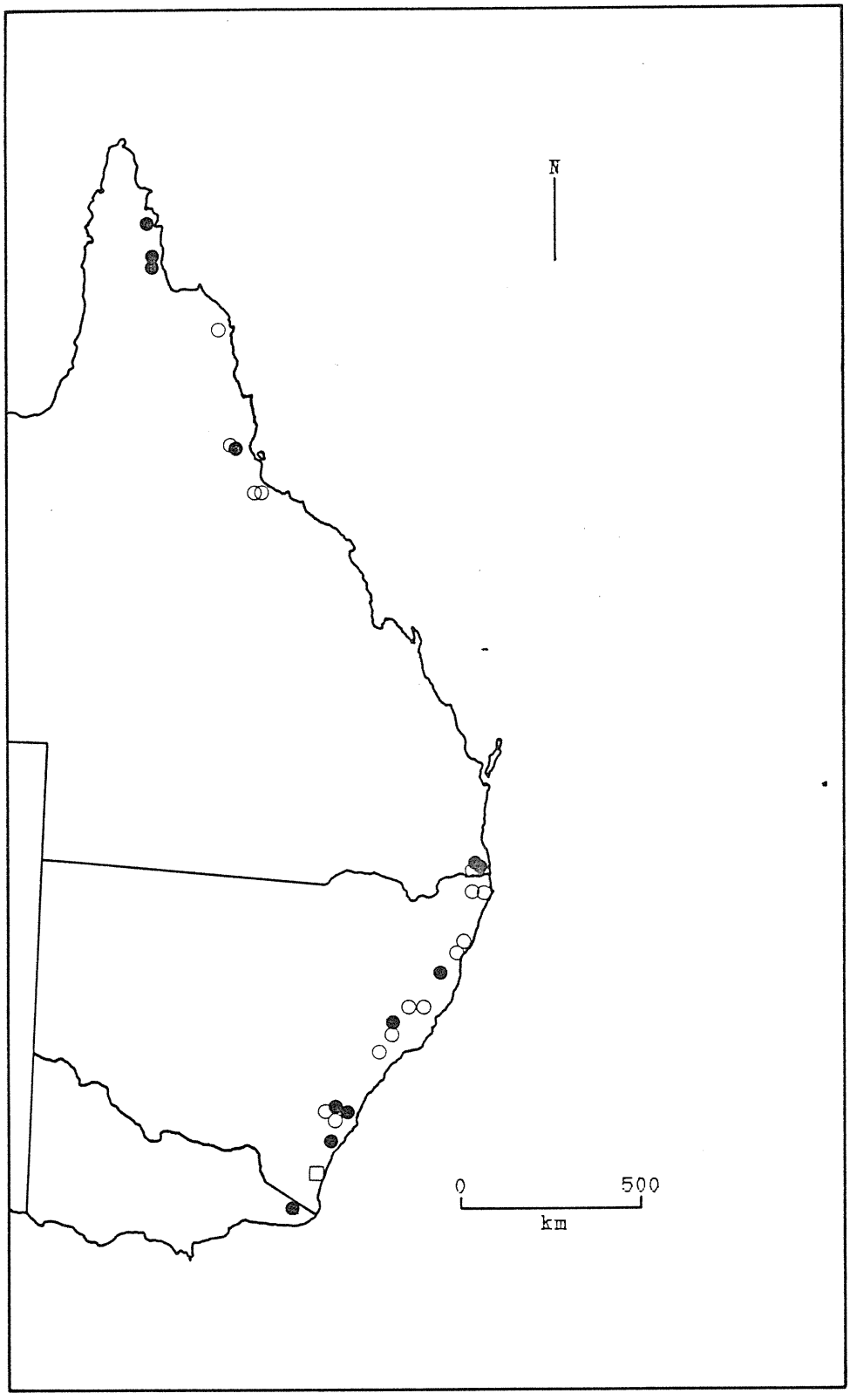


Table 6.1 Sites sampled for presence of *Australatya striolata* . Sites are listed by catchment or area and locality.

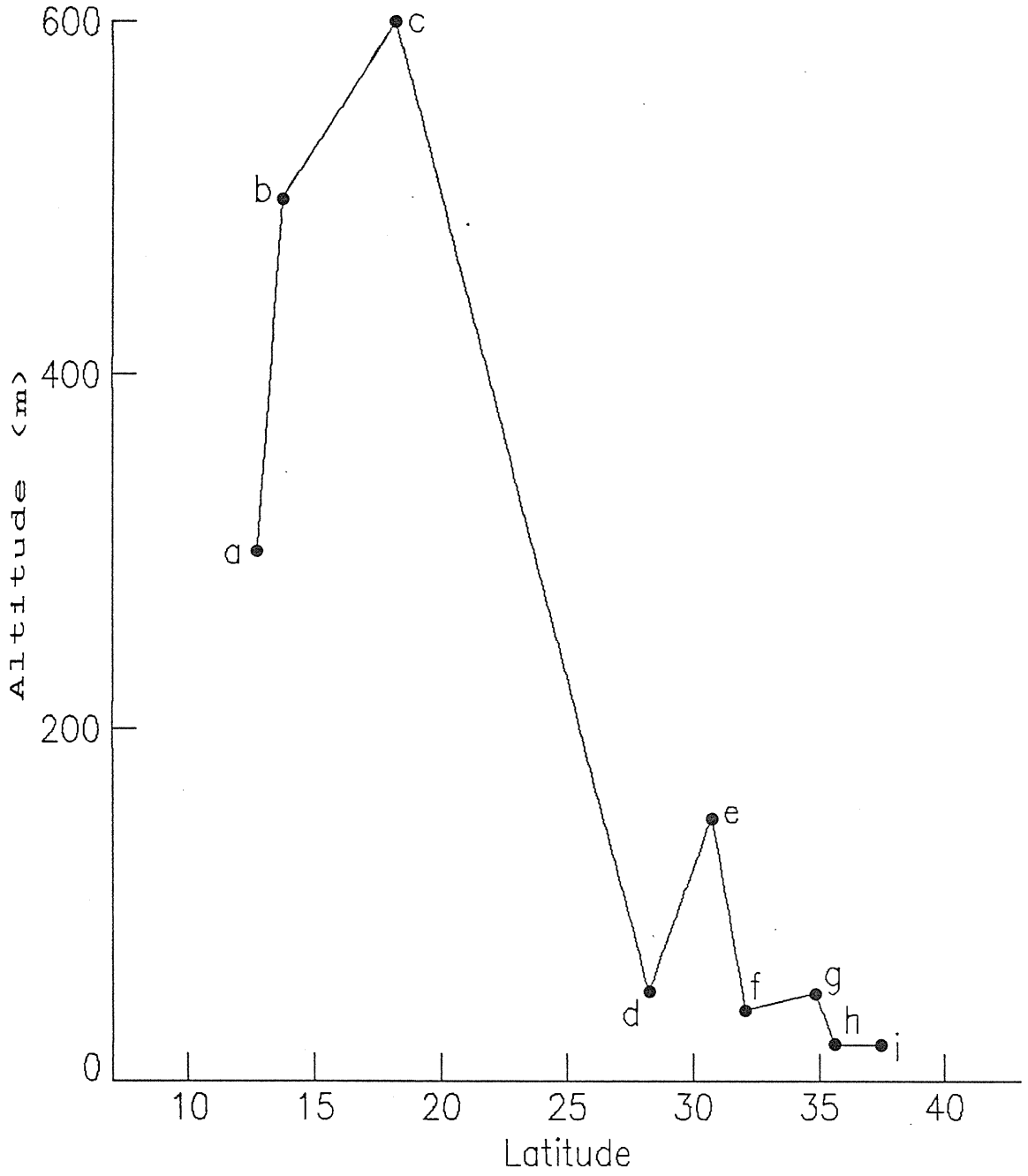
Site	Latitude	Longitude	Altitude (m)	*A. striolata*
Cape York area				
Polo Creek	10° 45'	142° 33'	38	-
Big Creek	10° 45'	142° 31'	75	-
Laradeenya Creek	10° 46'	142° 27'	30	-
Cowal Creek	10° 58'	142° 22'	30	-
Jardine River				
main crossing	11° 8'	142° 22'	<40	-
Heathlands				
Meenum Hill Creek	11° 38'	142° 44'	120	-
Claudie River				
Tozers Gap	12° 45'	143° 12'	300	+
McIlwraith Range				
Rocky River	13° 48'	143° 27'	50-120	juveniles
Leo Creek	13° 45'	143° 23'	500	+
Byfield				
Stony Creek	22° 53'	150° 38'	40	-
Nerang River				
Hinze Dam	28° 3'	153° 17'	100	+
Tallebudgera Creek	28° 12'	153° 20'	50	+
Macleay River				
Heckey Creek	30° 45'	152° 32'	150	+

Table 6.1 continued

Site	Latitude	Longitude	Altitude (m)	*A. striolata*
Hunter River				
Allyn River	32° 22'	151° 32'	<50	+
Shoalhaven River				
Talowa Dam	34° 47'	150° 21'	24	-
Bugong Creek	34° 49'	150° 27'	110	+
Good Dog Creek	34° 50'	150° 32'	50	+
Clyde River				
Currowan Creek	35° 35'	150° 9'	<20	+
Tuross River				
Reedy Creek	36° 15'	149° 58'	100	-
Mumbulla State Forest				
Mumbulla Creek	36° 34'	149° 53'	150	-*
Bega River				
near Bega	36° 44'	149° 48'	30	-
Tatawangalo Creek	36° 44'	149° 38'	130	-
Genoa River				
Genoa	37° 29'	149° 35'	<<50	+
Cann River				
near Cann River	37° 30'	149° 9'	110	-
Snowy River				
Tara Creek	37° 31'	148° 14'	50	-
Betebelong Creek	37° 33'	148° 16'	70	-

* *A. striolata* collected from this stream by Richardson (1985)

Figure 6.2 Lowest observed altitude of adult populations of *Australatya striolata* over the geographical range of the species. *a* Claudie River. *b* Leo Creek. *c* Yuccabine Creek. *d* Tallebudgera Creek. *e* Heckey Creek. *f* Allyn River. *g* Good Dog Creek. *h* Currowan Creek. *i* Genoa River. All data from this study.



It was noted that there were several fish species present at most sites from the Nerang River south, where *A. striolata* was present, while in north Queensland the only fish found in association with *A. striolata* were eels, *Anguilla reinhardtii*, and the gudgeon *Mogurnda adspersa*.

6.3.2 Geographical Variation

Morphology

The mean value and standard error for each morphological character for each site are given in Table 6.2. Of these measurements, six showed clinal variation and are depicted in Figure 6.3. With increasing latitude, the rostrum tends to become more elongate as does the telson, the extent of the excavation of the carpi of the first two peraeopods decreases, while the propodus of the second peraeopod tends to become more elongate, and the merus of the third peraeopod tends to become shorter relative to the propodus length. Fryer (1977) found that in *Atya* the excavation of the carpal cup is used to lock the position of the filtering chelae. Therefore, the trends associated with the carpus excavation of peraeopods 1 and 2 and the propodus of peraeopod 2 may relate to changes in feeding over the range. Most of the other measurements made exhibited variation which was not clinal.

The results of a discriminant analysis and a principal components analysis of these data are presented in Figure 6.4 and Figure 6.5 respectively. The discriminant analysis demonstrated that the populations could be discriminated *a posteriori* with 100% accuracy on

Table 6.2 Means and standard errors for the characters used to examine morphological variation. Sites are listed by catchment or area, and location. The number of specimens for each site is indicated. NA denotes measurements not made.

Character	Catchment	McIlwraith Range		Herbert River		Nerang River		Macleay River		Shoalhaven River		Genoa River	
	Location	Lee Ck		Yuccabine Creek		Kirra Dam		Hickey Creek		Bugong Creek		Genoa	
	Number	7		20		20		20		20		2	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Carapace depth/carapace length		0.41	0.070	0.64	0.006	0.58	0.003	0.62	0.006	0.62	0.004	0.58	0.011
Rostrum length/carapace length		0.40	0.072	0.19	0.003	0.26	0.002	0.26	0.004	0.27	0.004	0.27	0.016
Rostrum length/rostrum depth		1.94	0.837	4.14	0.161	4.28	0.106	4.62	0.119	4.70	0.130	4.25	0.452
Scaphognathite length/carapace length		2.60	0.784	0.38	0.006	0.36	0.006	0.33	0.006	0.34	0.003	NA	NA
Telson length/carapace length		0.34	0.007	0.35	0.006	0.35	0.003	0.35	0.006	0.35	0.004	0.41	0.017
Telson length/telson width		1.10	0.355	2.17	0.050	2.08	0.020	2.23	0.027	2.26	0.044	2.57	0.092
Antennule seg.1 length/carapace length		1.24	0.370	0.18	0.002	0.17	0.002	0.17	0.002	0.18	0.003	0.18	0.001
Antennular peduncle length/antennule seg.1 length		0.46	0.141	0.83	0.022	0.94	0.011	0.97	0.013	0.90	0.012	0.83	0.016
Maxilliped 3 penultimate seg. length/CL		0.57	0.136	0.19	0.003	0.18	0.002	0.19	0.002	0.19	0.003	0.18	0.003
Peraeopod 1 propodus length/width		2.18	0.936	5.36	0.123	5.41	0.071	5.54	0.111	5.99	0.160	5.39	0.324
Peraeopod 1 carpus length/width		2.87	0.660	1.06	0.019	1.06	0.013	1.09	0.017	1.16	0.022	1.08	0.017
Peraeopod 1 carpus excavation/length		1.00	0.021	0.99	0.014	0.94	0.006	0.95	0.008	0.90	0.010	0.94	0.056
Peraeopod 1 carpus length/propodus length		0.75	0.113	0.43	0.009	0.44	0.005	0.41	0.020	0.44	0.004	0.44	0.011
Peraeopod 1 merus length/propodus length		0.65	0.092	0.89	0.008	0.92	0.007	0.86	0.007	0.88	0.008	0.96	0.063
Peraeopod 2 propodus length/width		2.59	0.805	4.96	0.082	5.33	0.092	5.41	0.106	5.49	0.094	4.88	0.000
Peraeopod 2 carpus length/width		3.05	0.709	1.08	0.021	1.05	0.015	1.06	0.011	1.11	0.018	1.05	0.017
Peraeopod 2 carpus excavation/length		0.97	0.145	0.95	0.013	0.89	0.010	0.89	0.011	0.88	0.010	0.83	0.016
Peraeopod 2 carpus length/propodus length		0.72	0.106	0.40	0.006	0.42	0.004	0.39	0.004	0.41	0.004	0.41	0.000
Peraeopod 2 merus length/propodus length		1.06	0.013	1.00	0.011	1.00	0.011	1.00	0.009	1.03	0.009	1.11	0.058
Peraeopod 3 propodus length/width		4.82	0.107	5.85	0.104	5.87	0.072	6.02	0.149	5.76	0.082	5.17	0.017
Peraeopod 3 propodus length/dactylus length		2.99	0.148	3.65	0.075	2.90	0.046	3.18	0.065	3.16	0.064	3.05	0.052
Peraeopod 3 carpus length/width		3.41	0.101	3.97	0.067	3.44	0.042	3.88	0.071	3.83	0.072	3.65	0.015
Peraeopod 3 merus length/width		1.97	0.015	5.67	0.110	4.78	0.058	5.33	0.084	5.23	0.091	5.26	0.323
Peraeopod 3 merus length/propodus length		4.95	0.123	1.84	0.017	1.78	0.015	1.71	0.024	1.76	0.019	1.78	0.025
Peraeopod 4 propodus length/width		6.05	0.135	7.80	0.156	6.49	0.094	7.03	0.176	7.48	0.379	6.81	0.188
Peraeopod 4 propodus length/dactylus length		3.70	0.115	4.63	0.122	3.28	0.066	3.77	0.118	3.81	0.092	3.76	0.026
Peraeopod 4 carpus length/width		3.66	0.098	4.33	0.082	3.70	0.039	4.11	0.069	4.14	0.074	4.15	0.150
Peraeopod 4 merus length/width		5.13	0.087	5.89	0.066	5.13	0.053	5.67	0.085	5.69	0.109	5.78	0.024
Peraeopod 4 merus length/propodus length		1.47	0.021	1.36	0.024	1.35	0.010	1.29	0.013	1.29	0.017	1.35	0.006
Peraeopod 5 propodus length/width		7.06	0.227	11.01	0.211	8.48	0.104	9.91	0.178	9.81	0.222	9.61	0.464
Peraeopod 5 propodus length/dactylus length		4.14	0.145	5.39	0.115	3.69	0.064	3.97	0.072	4.32	0.138	4.34	0.070
Peraeopod 5 carpus length/width		3.75	0.093	4.80	0.082	3.83	0.052	4.38	0.078	4.31	0.095	4.11	0.105
Peraeopod 5 merus length/width		4.73	0.105	5.55	0.096	4.49	0.046	5.19	0.098	5.37	0.011	4.89	0.069
Peraeopod 5 merus length/propodus length		0.86	0.012	0.78	0.008	0.81	0.006	0.82	0.008	0.82	0.011	0.82	0.010

Figure 6.3 Mean values ± one standard error of the morphological measurements found to show clinal variation.

(a) Rostrum length/carapace length.

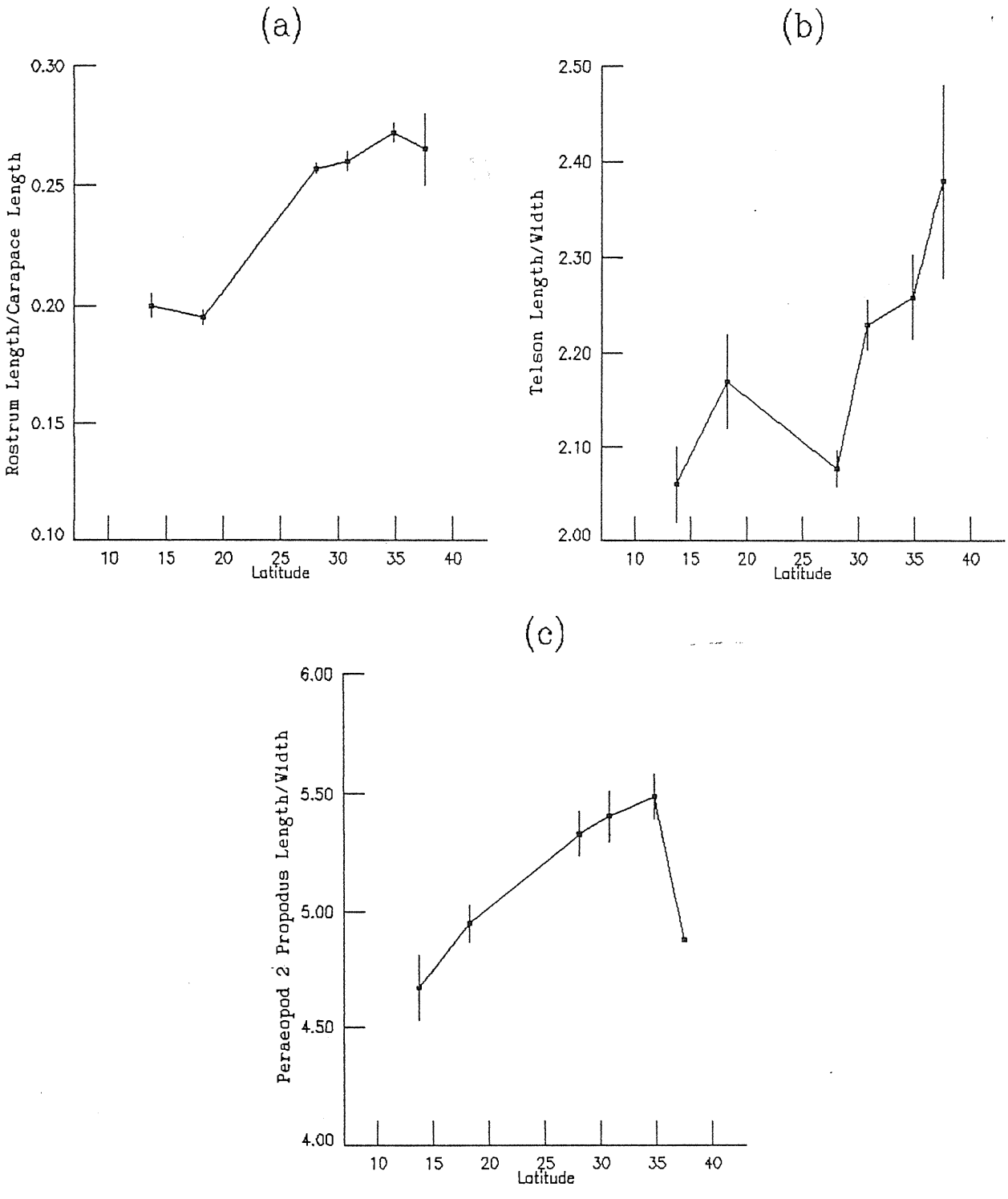
(b) Telson length/telson width.

(c) Peraeopod 2 propodus length/propodus width.

(d) Peraeopod 1 carpus excavation/carpus length.

(e) Peraeopod 2 carpus excavation/carpus length.

(f) Peraeopod 3 merus length/merus width.


(a)
Rostrum Length/Carapace Length
0.30
0.25
0.20
0.15
0.10
10
15
20
25
30
35
40
Latitude
(b)
Telson Length/Width
2.50
2.40
2.30
2.20
2.10
2.00
10
15
20
25
30
35
40
Latitude
(c)
Peraeopod 2 Propodus Length/Width
6.00
5.50
5.00
4.50
4.00
10
15
20
25
30
35
40
Latitude

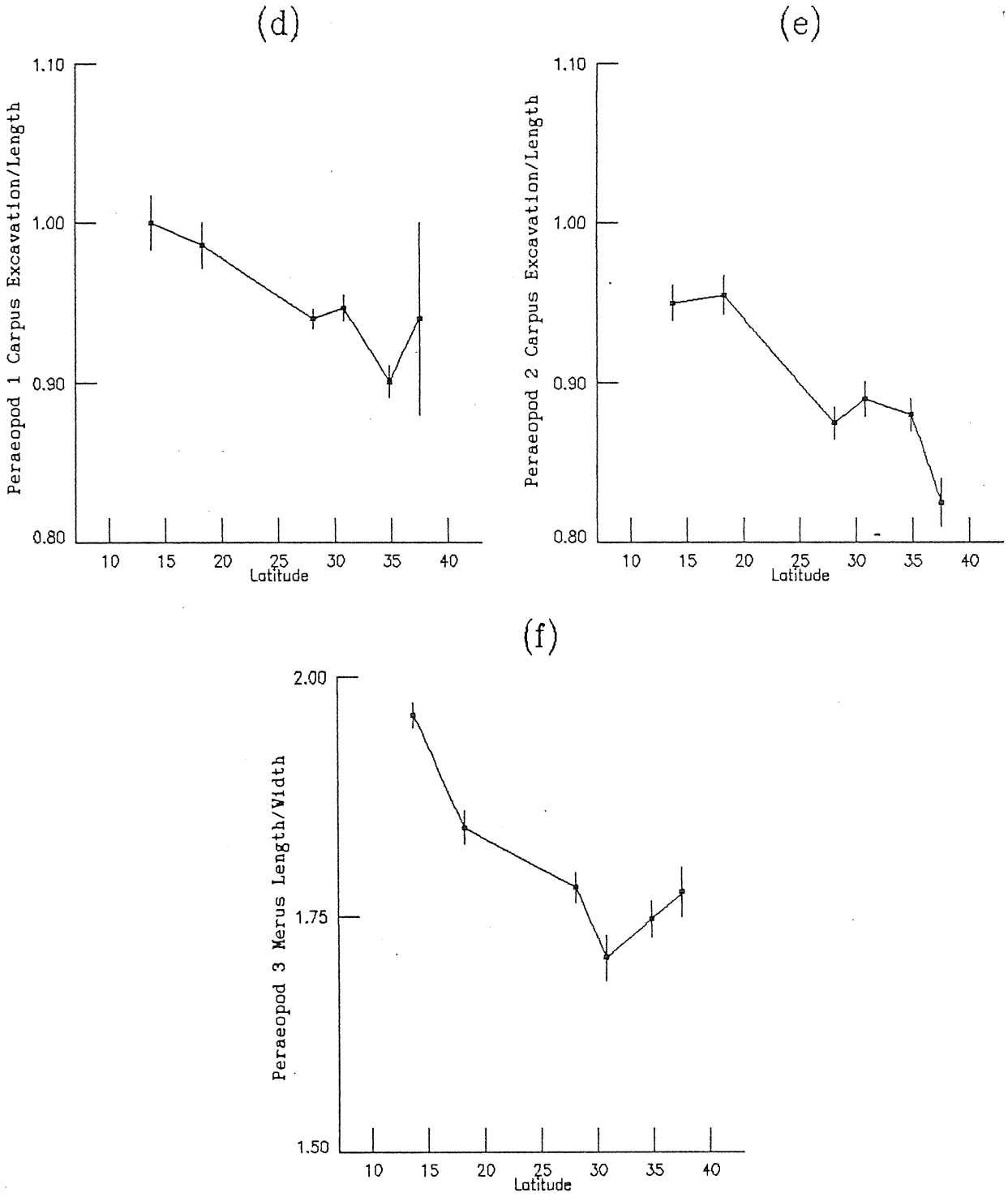

(d)
Peraeopod 1 Carpus Excavation/Length
1.10
1.00
0.90
0.80
10
15
20
25
30
35
40
Latitude
(e)
Peraeopod 2 Carpus Excavation/Length
1.10
1.00
0.90
0.80
10
15
20
25
30
35
40
Latitude
(f)
Peraeopod 3 Merus Length/Width
2.00
1.75
1.50
10
15
20
25
30
35
40
Latitude

Figure 6.4 Canonical discriminant function values of the centroid for each site for the first three canonical discriminant functions. *L* Leo Creek. *Y* Yuccabine Creek . *N* Nerang River. *M* Heckey Creek, Macleay River. *S* Bugong Creek, Shoalhaven River. *G* Genoa River.

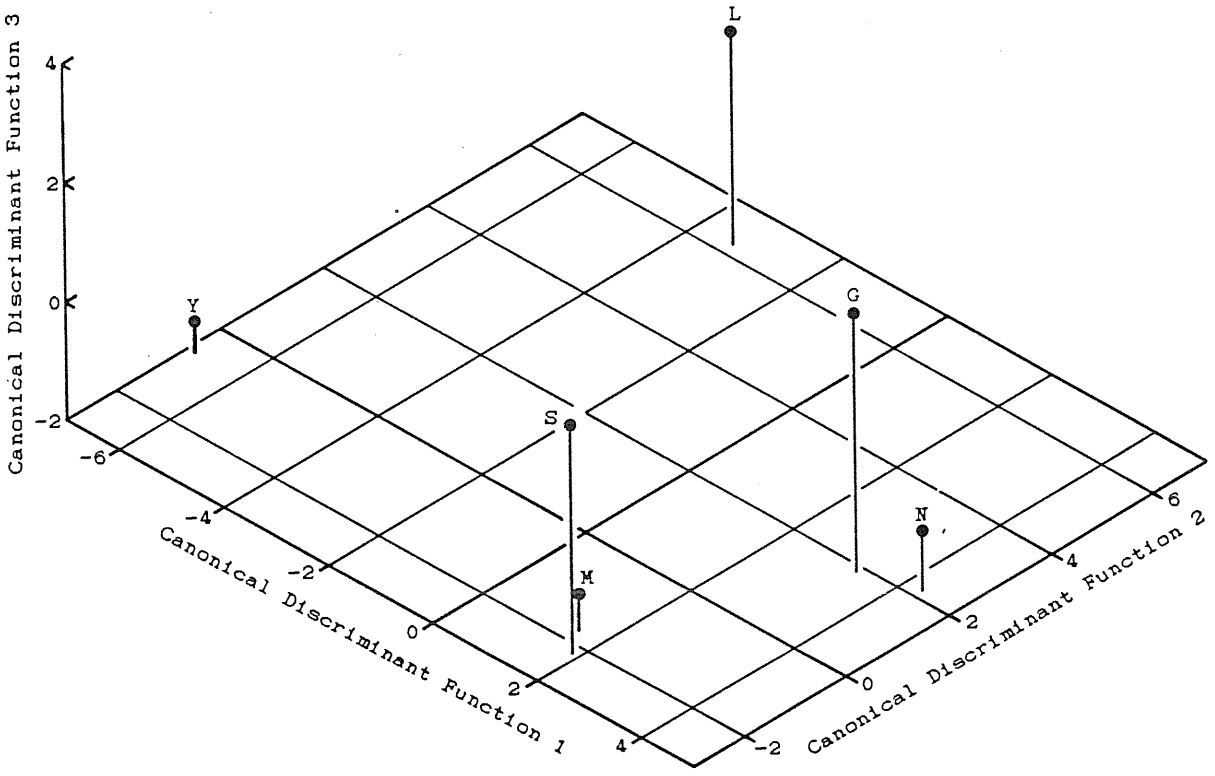
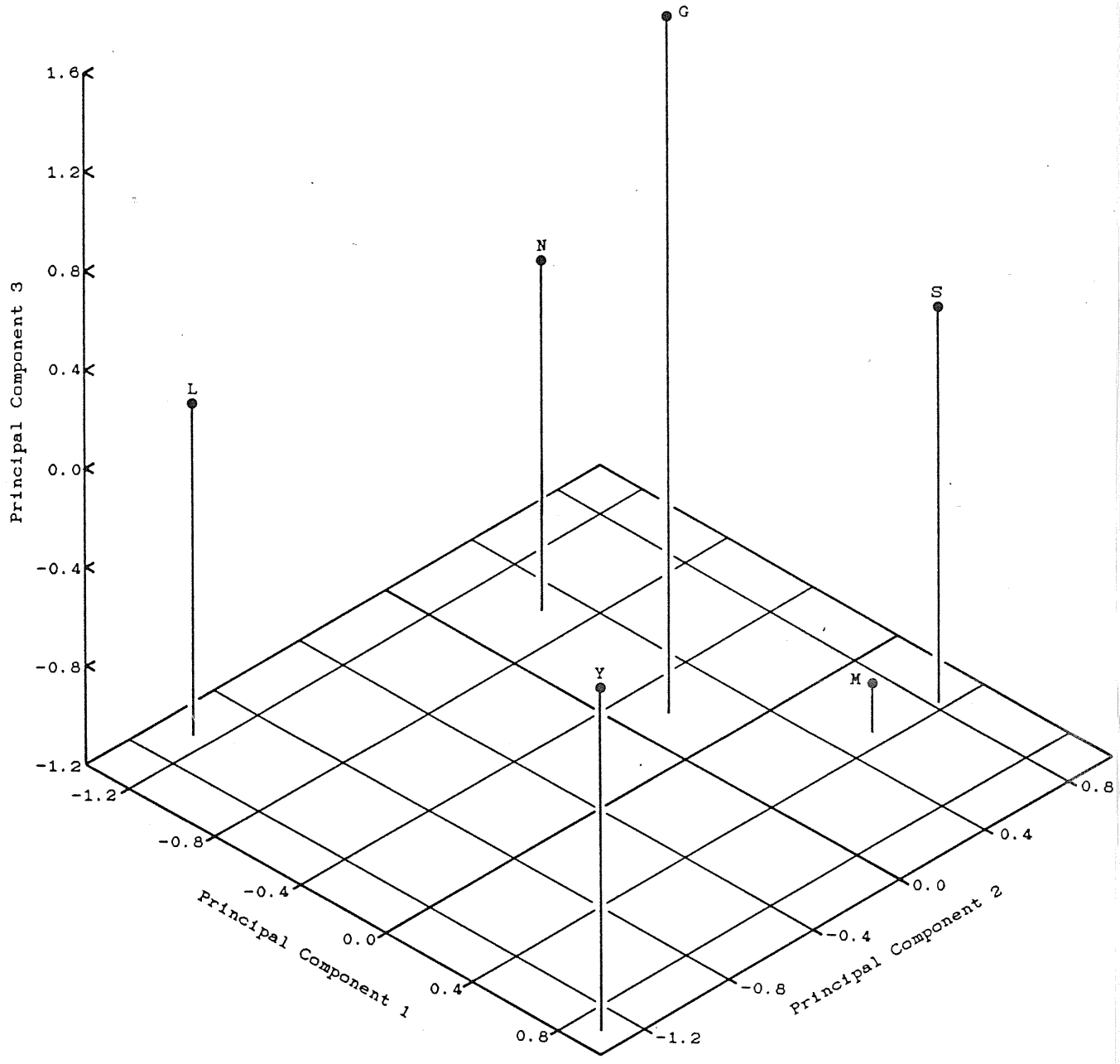


Figure 6.5 Principal component scores of the centroid for each site for the first three principal components. *L* Leo Creek. *Y* Yuccabine Creek. *N* Nerang River. *M* Heckey Creek, Macleay River. *S* Bugong Creek, Shoalhaven River. *G* Genoa River.

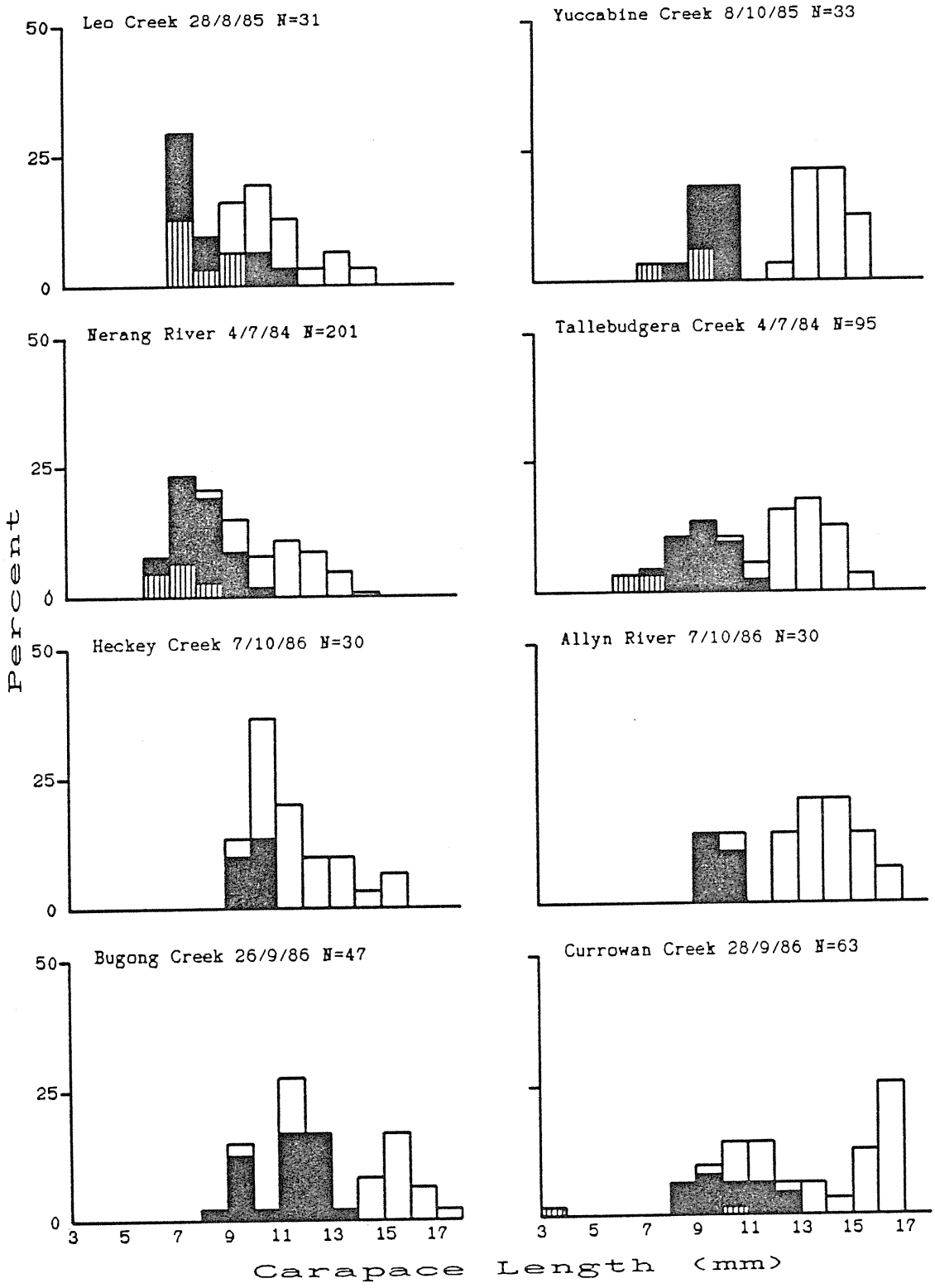


the basis of the morphological measurements. Figure 6.5 shows that the sites were widely separated in principal component space. The separation of the sites is clinal for the first canonical discriminant function except for Leo Creek and the Nerang River, and for the second principal component except for Leo Creek and the Genoa River. These two functions loaded highest for the measurements which varied clinally and therefore suggest that while there is clinal variation between populations it is to some extent reduced by non-clinal variation.

Population Structure

Size frequency distributions for the seven catchments where sufficient numbers were available are presented in Figure 6.6. The bimodal distribution found at Yuccabine Creek was also found at Tallebudgera Creek, the Allyn River, and Bugong Creek. For the other sites, there was considerably more overlap of the size ranges of the sexes, and the distribution tended to be skewed toward the left. Further, the modal size classes for each sex were shifted to the left of the Yuccabine Creek "standard" for the Leo Creek and the Nerang River populations, and to the right for the Clyde River and Bugong Creek populations. However, all the observed populations were apparently protandrous, and apart from the Heckey Creek sample had bimodal size-frequency distributions. Heckey Creek had almost dried out at the time of sampling as a result of drought in the region and thus may represent an unusual situation.

Figure 6.6 Size frequency distributions for sites where the sample size was 30 or more individuals. Bar patterns as for Figure 3.2.



6.4 Discussion

This study has shown that *A. striolata* occupies streams at greater altitude with decreasing latitude and that its distribution extends to the mostly northerly montain region of eastern Australia. There was not sufficient data to determine the reason for this altitude requirement, but probably a combination of adult temperature tolerance and preference for high gradient streams is involved. Thus, the northern limit of its distribution is restricted by habitat availability, which is consistent with the hypothesis that the Atyidae invaded Australia from New Guinea (Bishop, 1967). The presence of planktonic larvae requiring high salinity provides a means of dispersal from New Guinea and down the east Australian coast.

This study has also shown that the species is found in eastern Victoria. It is possible therefore that Von Mueller did find *Atya*-like shrimp in Victoria, and that he may indeed have sent specimens to the Muséum D'Histoire Naturelle (see Chapter 1). Since Von Mueller was unlikely to have been able to obtain specimens of *Atya scabra* or *A. margaritacea*, it is more likely that if he did lodge specimens of *Atya*-like shrimp that they were actually *Australatya striolata*. *Australatya* is sufficiently similar to *Atya* in appearance for the specimens and or labels to have been confused at the museum. Such an accident seems the most likely explanation for Von Mueller's name being associated with Central American atyids.

Contrary to the results of Smith and Williams (1982), this study has demonstrated clinal variation in morphology for this species, although it is relatively minor and in multivariate space is partly obscured by non-clinal variation. Major variation between populations of a species with a planktonic larval stage would not be expected, but the variation that exists is sufficient to be able to discriminate between specimens from different river systems on the basis of morphology alone. It would be of value to examine the extent of genetic variation between populations to determine whether the observed variation, particularly clinal variation, is due to genetic or environmental differences.

A preliminary survey of size-frequency distributions over the geographic range of the species suggests that these distributions are more stable in time at one site (as evidenced by the study of the population biology of the species in Yuccabine Creek and Douglas Creek, Chapter 3) than geographically. The variation over the range of the species is probably due largely to variation in ease of recruitment of juveniles to the adult habitat, which would be affected over the geographic range of the species by the distance from the adult habitat to the estuary, and the amount of rainfall. In particular, the higher rainfall in the McIlwraith Range area would greatly facilitate migration of juveniles past barriers such as waterfalls (see Chapter 4). Also, the density of juveniles in the lowland sections of the Claudie and Rocky Rivers was considerably higher than that in the Murray River while the adult densities sampled in Leo Creek were lower than those in Douglas creek (data not presented here), indicating greater survival rates for the early life stages in the far north. Such an increase in

recruitment success would be expected to skew the size structure of the population towards the smaller sizes. In the long term, such an improvement in recruitment would reduce the selective advantage of the high longevity found at the Kirrama sites, and this may account for the decrease in the male and female sizes at Leo Creek. Conversely, lowered larval survival in the cooler estuaries of the higher latitudes would favour increased longevity, and therefore may result in the observed increase in size of males and females. The effect of greater potential predation from fish in the lower altitude sites cannot be determined from such a brief investigation, but has the potential to greatly alter the dynamics of the populations.

Chapter 7 General Discussion

7.1 Review of Findings

This study has shown that the life history strategy of *Australatya striolata* populations in Yuccabine Creek and Douglas Creek is highly unusual, and possibly unique in the recorded literature. Adult *A. striolata* inhabited rocky riffle sections in low order, upland streams, and exhibited remarkably stable bimodal length frequency distributions. The shrimp is a protandrous hermaphrodite, with the left mode of the length frequency distributions consisting primarily of males, and the right of females. Because recruitment was found to be seasonal, the most likely mechanism for maintenance of this bimodal distribution was a two-stage growth curve with little growth of mature male and female individuals, relatively rapid growth of juveniles and a relatively rapid transition from male to female size.

This explanation was well supported by the available evidence. Analysis of length frequency distributions through time indicated very little growth of mature males and females during the two and a half years of sampling, and showed that juveniles attained male size approximately 61 days after entering the adult habitats. The slow growth of individuals within the modal size classes was also shown by a mark-recapture programme and a caging experiment.

A modification of the mode plotting method of Carpenter (1983) demonstrated a sigmoidal growth curve for individuals between the

modal size classes, and indicated a time of approximately 200 days was required for the transition from male to female size. A single tagged individual was observed to take 534 days to grow through half of this transition. It was not possible to determine whether the tag had reduced its growth rate, or whether the growth rates derived from the mode plotting technique over-estimated the actual growth rates. Thus, the relatively rapid transitional growth spurt represents an increase of approximately 3 mm carapace length (9 mm total length) in slightly less than 1 year (based on the derived estimate), or 3 years (based on the observed growth of the tagged individual).

The difficulties found in examining this growth pattern were not due to inadequate sampling, but to the idiosyncrasies of the life history of the species. The remarkable consistency of the length frequency distributions through time, at all sites where samples were adequate, clearly shows that the populations were well sampled, and that there were no adult stages that were not sampled. Negligible or slightly negative growth was demonstrated for the dominant size classes by all techniques used. The two-stage growth curve hypothesis is supported by all the available evidence, and is therefore the best model which can be derived under the circumstances. In order to further refine this model, sampling and tagging over a much longer time scale than was available for this study would be required, preferably in conjunction with long term caging or artificial stream experiments.

It was in some ways fortuitous that this study was carried out during a prolonged drought. If recruitment had not been reduced by the poor

rainfall, the observed gradual increase in some of the sexually mature size classes and reduction of others may not have occurred. The remarkable stability of the length frequency distributions, and the anomalous life history which generated it prevented the derivation of most of the population parameters which are the standard goals of population studies. Therefore, no life table could be constructed for the populations studied.

The reproduction of *A. striolata* has been shown to be seasonal, and to coincide with the summer wet season in north Queensland. The first larval stage was shown to be lecithotrophic, and to require salinities in excess of 20‰ for further development. It was demonstrated that the first zoeal stage could survive for up to 30 days on its yolk supplies if kept in low salinities. It was calculated that this time period was more than would be required for moderate stream flow to carry the larvae the required distance to the estuary. As the numbers of larvae drifting in Yuccabine Creek during the breeding season were very low, it was suggested that larvae may be released by the females in response to spates, or that larvae congregate in pools and await spates. The transport of larvae to the required salinities would be greatly facilitated by high stream flow. That juveniles subsequently migrate upstream to the adult habitats was evidenced by field collections, and it was shown that this migration took 12 to 18 months in the stream systems studied.

A. striolata was shown to feed predominantly on particulate organic matter filtered from the water column. A field experiment demonstrated

that this food source was not limiting (in terms of abundance) for the densities of shrimp found naturally. The nutritional value of this food is not known.

Predation and disease were shown to be minimal sources of mortality for adult *A. striolata* in Yuccabine Creek and Douglas Creek. Since the time spent as male or female seemed comparable and was at least 870 days, high adult survival was also indicated by the maintenance of near 1:1 sex ratios at the study sites, despite the greater age of females.

The distribution of *A. striolata* was shown to extend from the Claudie River, Cape York Peninsula, to the Genoa River, Victoria. The northern distribution was limited by habitat availability. Presumably temperature tolerances determine the southern distribution. Observed differences in length frequency distributions over the geographic range of the species were probably related to different rates of recruitment. Adult populations were found to occur in the presence of potential predators at some sites, but the effect of predation on population dynamics could not be assessed.

7.2 Conclusions

This study has highlighted the unique life history strategy of *A. striolata*, but this very uniqueness has precluded the development of definitive answers to many of the more interesting questions that arise from the study. Obviously there is a great deal of scope for further

study of this peculiar shrimp, but some light can be shed on some of the broader implications of the above observations.

The population densities of *A. striolata* in the two streams studied seem to be limited by recruitment rates. The mortality rates of the adults were very low, and there is no evidence of a limited food supply. It should be noted that other filter feeding species such as Simuliidae and some species of Trichoptera are abundant in these streams (see Pearson *et al*, 1986). Since there was evidence that there had been higher recruitment rates at some time before the period of this study, and the rainfall during the study period was well below the long term average, the density of *A. striolata* in the streams may reach much higher levels when conditions favour greater recruitment.

An obvious question arising from this study is why do individuals grow so slowly for so long? There are at least two possible reasons for this. If the nutritional quality of the food is low, then the growth rates of reproductive individuals would be restricted by their need to produce reproductive material. If this is the case, since mature gonads were only found during the breeding season, it would be expected that lipid stores would build up in reproductive individuals during the dry season. No deposits of fatty tissue were found in dissected specimens, but oil droplets were common in the alcohol-based preservatives used to store specimens.

Alternatively, the slow growth of mature females may simply be because they approach the asymptotic maximum length of the species, and if the

sex change mechanism is linked with size, then it would be very disadvantageous for mature males to continue to grow as such growth would lead to a reduction in the number of males available for breeding. Unpredictable stream discharge would favour individuals remaining as males for more than one year, to compensate for poor recruitment.

It is possible that sex change may be under density-dependent controls, i.e. that males change sex to replace females lost from the population. Such mechanisms have been demonstrated for some fish species (e.g. Robertson, 1972; Fricke and Fricke, 1977). Experimental manipulations of the sex ratio may shed some light on this question, but the difficulty of maintaining good condition in aquarium specimens and the long time span required for transition from male to female size indicate that long term, artificial stream channel experiments would be required. Also, the slight difference in sex ratio in Douglas Creek compared with Yuccabine Creek and the different length frequency distribution found at Leo Creek may indicate that density-dependent controls do not exist.

Perhaps the most important question arising from this study is what are the advantages of this life history strategy over the more conventional patterns, and how did it arise? The keys to the strategy adopted by *A. striolata* are undoubtedly the high salinity requirement for larval development and the preference of adults for fast-flowing, low order streams. The preference of the adults may be related to their use of a passive filter which requires an externally produced

water current. However, it is difficult to explain why they do not live in the lower reaches of streams where their offspring, which also are passive filter feeders when juveniles, manage to obtain sufficient energy input for growth and migration. Perhaps the answer lies in the lack of effective predation in the more upland sections of the streams.

This preference for low order streams does not conform with the prediction of the "River Continuum Concept" of Vannote *et al.* (1980) that the relative abundance in terms of biomass of filter feeding organisms should increase with stream order. *A. striolata* is both a relatively large and numerically abundant invertebrate species, and even when collected with a dip net, a technique which has been shown to be very inefficient at capturing this species, it accounted for the majority of the biomass of filter feeding organisms in Yuccabine Creek (R.G. Pearson, pers. comm.). The presence of large populations of this species in low order streams must skew the distribution of collector biomass toward lower order.

The reason for the high salinity requirement of the larvae is also not obvious. The Atyidae are considered to be ancient freshwater fauna, having been in fresh water since the Jurassic (Hunte, 1978), and a number of species have freshwater larvae. These include several Australian species which occur in the same stream systems as *A. striolata* (e.g. Glaister, 1976; Williams, 1977; and unpublished data), and some of its more closely related species such as *Atyoida serrata* (Bordage, 1908, 1909) and *Atyoida bisulcata* (Edmondson, 1929), both of which are suspected of being protandrous hermaphrodites (Carpenter,

1978). Hunte (1978) pointed out that the retention of marine planktonic stages by many atyids suggests that there are strong advantages for doing so, and that the main advantage was the dispersal ability of such stages.

In eastern Australia where rainfall is highly variable, the low order streams inhabited by *A. striolata* are subjected to periodic if irregular droughts, a point particularly pertinent to this study (also see Pearson *et al*, 1986). During the Pleistocene glacial periods, the climate of Australia was cooler and drier than at present, and resulted in the contraction of rainforests in north Queensland (Keto and Scott, 1986) and presumably also in the reduction of habitat for *A. striolata*. Therefore, the history of the species must contain many cases of local extinction as the adults' habitats dried out. Marine larvae from other catchments could recolonise streams which had dried out, when conditions became more favourable. Therefore, in Australia, any populations of *A. striolata* which evolved a freshwater larva would be at a considerable disadvantage, and in the long term would vanish. It would seem, however, that a freshwater larva could have evolved in the more southerly parts of its distribution where the drying out of the stream systems is currently much less frequent. Since it is thought that the atyids invaded Australia from the north (Bishop, 1967), the southern extension of the distribution may be a relatively recent event.

Given that the adults live in low order streams, and the larvae require high salinities, then the observed life history strategy is highly adaptive. The breeding season is limited to the wet season when larvae

are most likely to be carried to the estuary. As recruitment is variable and dependent on the climate, a strategy of high longevity and multiple breeding periods for each individual would increase the chance of effective recruitment. Protandry maximises the reproductive output of each individual, and the low adult mortality means that most individuals which reach adulthood reproduce as females. Therefore, in order to maintain the population density, each individual would on average need to produce only about one adult offspring in its life time. The effectiveness of this system may be such that it has precluded the evolution of freshwater larvae in the more favourable sections of the distribution.

This study indicates that there is considerable scope for further study of this remarkable species, and I have endeavoured to provide testable models where possible. Whilst these models could not be considered to be complete at this stage, in the words of Bradley (1985, p.85) "In the real world, where organisms are variable, idiosyncratic and interesting, imperfect agreement has to be accepted if any estimates are to be obtained."

References

Anderson, C. (ed) (1926) Footnote 22. In J. Roux, An account of Australian Atyidae. Rec. Austr. Mus. 15: 253.

Barclay, M.H. (1966) An ecological study of a temporary pond near Auckland, New Zealand. Aust. J. Mar. Freshw. Res. 17: 239-258.

Begon, M. (1979) Investigating animal abundance: capture-recapture for biologists. Edward Arnold, London.

Beumer, J.P. (1976) The fishes of a tropical river with emphasis on the spangled perch, *Therapon unicolor* Gunther, 1859, and the East Queensland rainbowfish, *Nematocentris splendida* Peters, 1866. Ph.D. thesis James Cook University of North Queensland.

Beumer, J.P. (1979) Feeding and movement of *Anguilla australis* and *A. reinhardtii* in Macleods Morass, Victoria, Australia. J. Fish. Biol. 14: 573-592.

Bishop, J.A. (1967) The zoogeography of the Australian freshwater decapod Crustacea. In A.H. Weatherley (ed.) "Australian Inland Waters and their Fauna" ANU Press, Canberra. pp. 107-122.

Bordage, E. (1908) Recherches expérimentales sur les mutations évolutives de certains Crustacés de la famille des Atyidés. Compt. Rend. (Paris) 147: 1418-1420.

Bordage, E. (1909) Mutation et régénération hypotypique chez certains Atyidés. Bulletin Scientif. France et Belgique 43: 93-112.

Bouvier, E.L. (1905) Observations nouvelle sur les crevettes de la famille des Atyidés. Bulletin Scientif. France et Belgique 39: 57-132.

Bradley, J.S. (1985) Comparative demography of four species of grasshopper on a Common site. In L.M. Cook (ed) "Case studies in population biology." Manchester University Press, Manchester pp. 61-100.

Brey, T. and D. Pauly (1986) Electronic length frequency analysis. A revised and expanded user's guide to ELEFAN 0, 1 and 2. Berichte Aus Dem Institut Fur Meereskunde an der Christian-Albrechts-Universitat Kiel Nr. 149: 1-50.

Bright, G.R. (1982) Secondary production in a tropical island stream. Limnol. Oceanogr. 27: 472-480.

Cannon, L.R.G. and J.B. Jennings (1987) Occurrence and nutritional relationships of four ectosymbiotes of the freshwater crayfishes *Cherax dispar* Riek and *Cherax punctatus* Clark (Crustacea:Decapoda) in Queensland. Aust. J. Mar. Freshw. Res. 38: 419-427.

Carpenter, A. (1978) Protandry in the freshwater shrimp, *Paratya curvirostris* (Heller, 1862) (Decapoda: Atyidae), with a review of the phenomenon and its significance in the Decapoda. J. Roy. Soc. N.Z. 3: 343-358.

Carpenter, A. (1982) Habitat and distribution of the freshwater shrimp *Paratya curvirostris* (Decapoda: Atyidae) in North Canterbury. Mauri Ora 10: 85-98.

Carpenter, A. (1983) Population biology of the freshwater shrimp *Paratya curvirostris* (Heller, 1962) (Decapoda: Atyidae). N. Z. J. Mar. Freshwat. Res. 17: 147-158.

Caughley, G. (1977) "Analysis of vertebrate populations". J. Wiley & Sons, Brisbane.

Chace, F.A. Jr. (1983) The *Atya*-like shrimps of the Indo-Pacific region (Decapoda: Atyidae). Smith. Contrib. Zool. 384. 54 pp.

Cowles, R.P. (1915) The habits of some tropical Crustacea: II Philippines J. Science 10: 11-18.

Darnell, R.M. (1956) Analysis of a population of the freshwater shrimp *Atya scabra* (Leach). Am. Midl. Nat. 55: 131-138.

De Silva, K.H.G.M. (1982) Aspects of the ecology and conservation of Sri Lanka's endemic freshwater shrimp *Caridina singhalensis*. Biol. Conserv. 24: 219-231.

Dudgeon, D. (1985) The population dynamics of some freshwater carideans (Crustacea: Decapoda) in Hong Kong, with special reference to *Neocaridina serrata* (Atyidae). Hydrobiologia 120: 141-150.

Edmondson, C.H. (1929) Hawaiian Atyidae. Bernice P. Bishop Museum Bulletin 66: 1-37.

Felgenhauer, B.E. and L.G. Abele (1983) Ultrastructure and functional morphology of the feeding and associated appendages in the tropical freshwater shrimp *Atya innocous* (Herbst) with notes on its ecology. J. Crustacean Biol. 3: 336-363.

Felgenhauer, B.E. and JW Martin (1983) *Atya abelei* a new atyid shrimp (Crustacea, Decapoda, Atyidae) from the Pacific slope of Panama. Proc. Biol. Soc. Wash. 96: 333-338.

Fisher, R.A. and E.B. Ford (1947) The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* (L). Heredity 1: 143-174.

Fricke, H. and S. Fricke (1977) Monogamy and sex change by aggressive dominance in coral reef fish. Nature 266: 830-832.

Fryer, G. (1977) Studies on the functional morphology and ecology of the atyid prawns of Dominica. Philos. Trans. Roy. Soc. London 277(952): 57-129.

Ghiselin, M.T. (1969) The evolution of hermaphroditism among animals. Q. Rev. Biol. 44: 189-208.

Glaister, J.P. (1976) Post embryonic growth and development of *Caridina nilotica aruensis* Roux (Decapoda: Atyidae) reared in the laboratory. Aust. J. Mar. Freshw. Res. 27: 263-278.

Goodman, D. (1981) Life history analysis of large mammals. In C.W. Fowler & T.D. Smith (eds.) "Dynamics of Large Mammal Populations" John Wiley & Sons, New York. pp. 415-436.

Gulland, J.A. and S.J. Holt (1959) Estimation of growth parameters for data at unequal time intervals. J. Cons. Perm. Int. Explor. Mer. 24: 47-49.

Hart, R.C. (1981) Population dynamics and production of the tropical freshwater shrimp *Caridina nilotica* (Decapoda: Atyidae) in the littoral of Lake Sibaya. Freshwater Biol. 11: 531-547.

Hartnoll, G. (1985) Growth, sexual maturity and reproductive output. In A.M. Wenner (ed) "Crustacean issues 3. Factors in adult growth" A.A. Balkema, Rotterdam. pp. 101-128.

Hoagland, K.E. (1978) Protandry and the evolution of environmentally-mediated sex change: A study of the Mollusca. Malacologia 17: 365-391.

Hobbs, H.H. Jr. and C.W. Hart Jr. (1982) The shrimp genus *Atya* (Decapoda: Atyidae). Smith. Contrib. Zool. 364. 143 pp.

Hortle, K.G. and R.G. Pearson (in press) The fauna of the Annan River system, north Queensland, with reference to the impact of tin mining. I. Fishes. Aust. J. Mar. Freshw. Res.

Hunte, W. (1977) Laboratory rearing of the atyid shrimps *Atya innocous* (Herbst) and *Micratya poeyi* (Guerin-Meneville) (Decapoda, Atyidae). Aquaculture 11: 373-378.

Hunte, W. (1978) The distribution of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. Zool. J. Linn. Soc. London 64: 135-150.

Hunte, W. (1979a) The complete larval development of the freshwater shrimp *Micratya poeyi* (Guérin-Méneville) reared in the laboratory (Decapoda, Atyidae). Crustaceana Suppl. 5: 153-166.

Hunte, W. (1979b) The complete development of the freshwater shrimp *Atya innocous* (Herbst) reared in the laboratory (Decapoda, Atyidae). Crustaceana Suppl. 5: 231-242.

Jennings, J.B. (1968) Feeding, digestion and food storage in two species of temnocephalid flatworms (Turbellaria: Rhabdocoela). J. Zool. Lond. 156: 1-8.

Jennings, J.B. (1971) Parasitism and commensalism in the Turbellaria. Adv. Parasitol. 9: 1-32.

Johnson, D.S. (1958) Some aspects of the distribution of freshwater organisms in the Indo-Pacific area, and their relevance to the validity of the concept of an Oriental region in zoogeography. Proc. Cent. Bicent. Congr. Biol., Singapore 1958: 170-181.

Johnson, D.S. (1965) A review of the brackish water prawns of Malaya. Bull. Nat. Mus. (Singapore) 33: 7-11.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration - stochastic model. Biometrika 52: 225-247

Keto, A. and K. Scott (1986) "Tropical rainforests of north Queensland. Their conservation significance." Australian Government Publishing Service, Canberra.

Khalaf, A.N. and L.J. MacDonald (1975) Physicochemical conditions in temporary ponds in the New Forest. Hydrobiologia 47: 301-318.

Kynaston, E. (1981) "A man on edge. A life of Baron Sir Ferdinand Mueller." Penguin, Melbourne.

McCulloch, A.R. and F.A. McNeill (1923) Notes on Australian Decapoda. Rec. Austr. Mus. 14: 49-59.

McNeill, F.A. (1929) Studies in Australian carcinology No. 3. Rec. Austr. Mus. 17: 144-156.

Moore, W.C. (1970) Limnological studies of temporary ponds in south eastern Louisiana. South West. Nat. 15: 83-110.

Morton, D.W. and I.A.E. Bayly (1978) Studies on the ecology of some temporary freshwater pools in Victoria with special reference to microcrustaceans. Aust. J. Mar. Freshwat. Res. 28: 439-454.

Pearson, R.G., L.J. Benson and R.E.W. Smith (1986) Diversity and abundance of the fauna in Yuccabine Creek, a tropical rainforest stream. In P. De Deckker & W.D. Williams (eds) "Limnology in Australia." CSIRO, Melbourne. pp. 329-342.

Perrin, W.F., J.M. Coe and J.R. Zweifel (1976) Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull. 74: 229-269.

Perrin, W.F., D.B. Holts and R.B. Miller (1977) Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris*, in the eastern tropical Pacific. Fish. Bull. 75: 725-750.

Radir, P.L. (1930) An interpretation of the taxonomic status of *Atya bisulcata*, Randall, and *Ortmannia henshawi*, Rathbun. Ann. Mag. Nat. Hist. series 10 5: 351-354.

Reik, E.F. (1953) The Australian freshwater prawns of the family Atyidae. Rec. Austr. Mus. 23: 111-121.

Riek, E.F. (1959) The Australian freshwater Crustacea. In A. Keast R.L. Crocker and C.S. Christian (eds) "Biogeography and ecology in Australia." W. Junk, The Haag. pp. 246-258.

Richardson, B.A. (1985) The impact of forest road construction on the benthic invertebrate fauna and fish fauna of a coastal stream in southern New South Wales. Aust. Soc. Limnol. Bull. 10: 65-88.

Robertson, D.R. (1972) Social control of sex reversal in a coral-reef fish. Science 177: 1007-1009.

Roux, J. (1926) An account of Australian Atyidae. Rec. Austr. Mus. 15: 237-254

Seber, G.A.F. (1965) A note on the multiple-recapture census. Biometrika 52: 249-259.

Sloane, R.D. (1984) Distribution, abundance, growth and food of freshwater eels (*Anguilla* spp.) in the Douglas River, Tasmania. Aust. J. Mar. Freshwat. Res 35: 325-340.

Smith, M.J. and W.D. Williams (1982) Taxonomic revision of Australian species of *Atyoida* Randall (Crustacea: Decapoda: Atyidae) with remarks on the taxonomy of the genera *Atyoida* and *Atya* Leach. Aust. J. Mar. Freshwat. Res. 33: 343-361.

Smith, R.E.W. and R.G. Pearson (1987) Community dynamics of the fauna of an intermittent stream in tropical Australia. Hydrobiologia 150: 45-61.

Tramer, E.J. (1977) Catastrophic mortality of stream fishes trapped in shrinking pools. Am. Midl. Nat. 97: 469-478.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing (1980) The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

Webb, L.J. (1959) A physiognomic classification of Australian rainforests. J. Ecol. 47: 551-570.

Whitehead, M.D. (1985) Ecology of the purple-spotted gudgeon *Mogurnda adspersa* (Castelnau) (Pisces: Eleotridae) in a tropical upland rainforest stream. Honours thesis James Cook University of North Queensland.

Williams, J.B. (1981) Classification of the Temnocephaloidea (Platyhelminthes). J. Nat. Hist. 15: 277-299.

Williams, W.D. (1977) Some aspects of the ecology of *Paratya australiensis* (Crustacea: Decapoda: Atyidae). Aust. J. Mar. Freshw. Res. 28: 403-415.