

CHAPTER 1

INTRODUCTION

The world fauna of freshwater mussels is divided into two superfamilies, the Mutelaceae and Unionaceae, according to larval features (Parodiz and Bonetto, 1963). The Unionaceae contains three families, one of which, the Hyriidae is found only in Australasia and South America. The Hyriidae again are distinguishable from other unionaceans by larval characteristics. Seventeen mostly endemic species from 6 genera occur in Australia; this fauna is presently thought to be composed entirely of freshwater mussels of the family Hyriidae (Walker, 1981a). The lower number of species found in Australia contrasts sharply with the fauna from other parts of the world, particularly North America where unionaceans of the family Unionidae number at least 227 species (Davis *et al.*, 1981). While the depauperate nature of the Australian fauna has been attributed to the long isolation and the arid climate of Australia, McMichael and Hiscock (1958) added that in compensation for this paucity of species, some forms are extremely abundant and widespread.

Nevertheless, despite their dominance in many Australian freshwater ecosystems (indeed, like freshwater mussels in benthic communities worldwide), biological and ecological information on the Australian hyriids has lagged well behind that for freshwater mussels from other parts of the world, notably European and North American forms. Even their meagre representation in terms of species numbers does not seem to have been a contributing factor facilitating research.

The paucity of work undertaken on Australian freshwater mussels can partly be explained by a lack of economic interest that has been a stimulus for their study in the United States in particular. Yet, worldwide, knowledge of the group still remains sufficiently minimal for Kat (1984) to have recently commented even in relation to the North American fauna: "Despite the diversity and abundance of unionacean bivalves in freshwater communities, they remain among the least understood of benthic macroinvertebrates, even with regard to such basic life-history attributes as reproduction, development, dispersal, competition, and habitat-selection".

The only extensive investigation on the biology and ecology of the hyriids of the Australasian region was completed by Walker (1981b), for two species of freshwater mussel from the Murray River in temperate Australia. The stimulus for this work was related to the potential of the two Murray River mussels for use as biomonitors of pollution.

While the specific findings of studies are reviewed elsewhere, the extent of other published material from the Australasian region can be summarised as follows. Systematic and taxonomic revisions were completed for the New Zealand fauna by Dell (1953) and later for the fauna of the Australasian region in general by McMichael and Hiscock (1958). McMichael and Hiscock summarised and reviewed much early and anecdotal material pertaining mostly to the taxonomy of the Australasian forms, and themselves provided some observations of general ecology and life histories. Hiscock (1950, 1953a, 1953b) had earlier studied certain aspects of the physiology and behaviour

of Velesunio ambiguus. McMichael and Iredale (1959) made some very general notes on the ecology and adaptations of the Australian fauna. Distributional patterns were studied regionally for the freshwater mussels in coastal streams of Victoria by Dean (1968), while Walker (1981a) discussed these aspects in a broader zoogeographical context for the entire Australian fauna. Aspects of the life histories of a number of species from the Australasian region have been investigated by Percival (1931), Hiscock (1951), Atkins (1979), and Jones and Simpson (in prep.).

The above studies comprise the extent of current knowledge on the biology and ecology of the Australasian hyriids. Viewed collectively, sufficient information of any comprehension is available for only two inland velesunionines, V. ambiguus and Alathyria jacksoni; the main contribution to this knowledge was the study by Walker (1981b). Further, all studies to date have been carried out entirely upon temperate Australasian forms. The range of V. angasi is restricted to tropical northern Australia (see Fig. 4.6). (An isolated occurrence of V. angasi, however, was reported by Walker (1981a), in the coastal drainage of the Fortescue River in central Western Australia. This location is not shown in Figure 4.6). Northward of a latitude of approximately 13°S in the Northern Territory, an area that incorporates the Alligator Rivers Region, the species occurs in isolation. It occurs sympatrically, however, with V. wilsonii, A. pertexta, Lortiella rugata and L. froggattii in other parts of its range (see Walker, 1981a). McMichael and Hiscock (1958) spoke of the range of V. angasi in northern Australia as "... a region not well known malacologically and poorly represented in

most collections." Up until the present investigation at least, this situation had changed very little.

With respect to freshwater mussels from tropical regions generally, there is a dearth of information. Although general life histories are well documented for unionids of the Indian subcontinent (Seshaiya, 1941, 1969; Lomte and Nagabhushanam, 1969; Ghosh and Ghose, 1972; Nagabhushanam and Lohgaonker, 1978), broader and more comprehensive ecological studies are shortcoming. Only two detailed studies have been documented for freshwater mussels of the tropics, that of Kenmuir (1980, 1981a,b,c) for forms from Lake Kariba, Zimbabwe, and that of Dudgeon and Morton (1983) for a unionid from Plover Cove, Hong Kong.

Thus there is generally a paucity of information on the biology and ecology of freshwater mussels of the Australasian region. No studies have been completed for tropical hyriids; further, studies on tropical mussels in other regions of the world are few. The study of V. angasi therefore was of considerable scientific interest because of the general lack of attention given to these groups of freshwater mussels. Also, investigation of the biology and ecology of V. angasi was particularly relevant to an understanding of the aquatic ecosystem of the region, because earlier surveys had shown that the mussels are a prominent member of the aquatic fauna.

Bivalve molluscs have been proposed as useful biological monitors for aquatic pollution. Assessment of their value in this role has concentrated mainly on marine bivalves, but there is also increasing

attention to the use of freshwater forms, particularly mussels of the superfamily Unionaceae. In relation to unionacean bivalves specifically, the attributes that make them suitable organisms for biological monitoring have been reviewed for the fauna of the northern hemisphere by Fuller (1974), Horne and McIntosh (1979), Forester (1980) and Cairns and van der Schalie (1980), and for the southern forms of Australia by Walker (1981b, 1984) and Simpson (1982).

These attributes were applied by Allison and Simpson (in press) to the freshwater mussel Velesunio angasi, in relation to its potential use as a biological concentrator of heavy metal pollution associated with the uranium mining ventures in the Alligator Rivers Region. The chief uranium deposits of this Region are located at Ranger, Jabiluka, Koongarra and Nabarlek (see Fig. 2.1), the former two deposits of which occur within the catchment of the Magela Creek.

If V. angasi is to be successfully employed as a biological monitor of pollution, then the variation in natural levels of elements in the flesh of mussels has to be understood in order to properly distinguish future, unnatural changes in metal concentrations. Apart from environmental conditions, this variation can be induced by different factors in the biology, ecology and physiology of the mussels themselves. An important objective of the present study therefore, was to provide such knowledge of the biology and ecology of V. angasi, from which variations in potential pollutant concentrations could be associated.

Other than as biological monitors for chemical pollution, freshwater mussels also have potential value as indicator organisms. The very presence or absence, shell form and size, and population structure and dynamics of mussel populations in particular environments may not only usefully indicate present day water quality, but also paleoenvironments and the activities of early man. Attributes that make mussels suitable as indicator organisms are reviewed and summarised elsewhere (section A2.1.3). Present assessments as to their worth in this regard are reviewed in terms of studies relevant to shell form, distribution, and population dynamics in Appendices 1-3 respectively. Similar indicator roles for V. angasi may be especially welcomed in an area such as the Alligator Rivers Region where efforts are presently concentrated on evaluating biological means for detecting future environmental changes brought about by pollution, and where signs of aboriginal prehistory by way of shell middens are plentiful.

The present investigation was carried out entirely in waterbodies lying in the catchment of the Magela Creek (Figs 2.1 and 2.4), and extended over a 27 month period from March 1980 to May 1982. Features of the biology and ecology of V. angasi studied, included shell shape and environment, distribution, abundance, population dynamics, reproduction, food ingestion, physiological condition, production, ecological tolerances, and seasonal changes in any of these. Information of this extent has not yet been presented for any hyriid or tropical freshwater mussel. (While details of ecological tolerances are not included in this thesis, brief mention is made of them where necessary in the relevant sections.) These

studies were undertaken concomitantly with other work measuring selected elements in the flesh of mussels from the Magela Creek, independently reported by Allison and Simpson (1983).

In relation to the format of the thesis, all tables and figures are presented in an accompanying volume. Their numeration parallels the same sequence in corresponding chapters of the text. The world literature on freshwater mussels is collectively a large one. Thus, because of the sheer volume of relevant material, extensive and comprehensive literature reviews appropriate to the material presented are provided in the appendices. While perusal of the material is not essential to the understanding and interpretation of the text, it is nevertheless an aid in this regard. Where necessary in the text, reference is made to the relevant literature in the appropriate appendix, sections of which are prefixed 'A'.

CHAPTER 2

THE STUDY AREA

2.1 Geography and climate

The Alligator Rivers Region is situated east of Darwin and abuts the prominent Arnhem Land plateau complex which occupies much of the northeastern portion of the Northern Territory. The Region mainly comprises the catchments of the East Alligator River and the eastern catchments of the South Alligator River, the tributaries of which were the concern of the present studies (Fig.2.1).

The Alligator River systems drain generally in a northwesterly direction to the Arafura Sea from headwaters which arise in the rugged sandstone plateau. After leaving the plateau, the major streams - largely confined to sandy and often braided channels - flow through extensive and extremely flat lowlands, to enter the broad, seasonally - inundated floodplains. The major tributaries including the Magela, Cooper and Nourlangie Creeks, spread widely on entering their floodplains with their drainage lines becoming fragmented. The larger Alligator Rivers however, maintain continuous stream channels. The floodplains finally merge with the tidal flats of the estuaries.

The climate of the Region is monsoonal, like much of far northern Australia, the dominant feature being the two distinct seasons - the 'Wet' and the 'Dry'. The seasons may be variable in length but generally the Wet season extends from November to March and the Dry from May to September, with April and October being transitional (Fox *et al.*, 1977). January, February and March are usually the wettest months (averaging around 300 mm each month), whereas June to September are normally completely dry.

As well as being highly seasonal in incidence, rainfall is also highly reliable (Christian and Aldrick, 1977) and there is little variation in amount throughout the Region, apart from some differences due to local topography. Long-term rainfall records for Oenpelli for example (kept since 1910 and used as representative for the Region), show an annual mean of 1343 mm (coefficient

of variation, 21 per cent). Rainfall at Jabiru in the lowlands of the Magela Creek catchment, over an eleven year period to the 1981-82 Wet season, averages annually at 1593 mm (Fig. 2.2). Details of the dynamics of the wet-producing systems are provided in Christian and Aldrick (1977) and Walker et al. (1983a). In short, these systems arise from the change to the humid north-westerly winds at the onset of the Wet, from the dry (continental) south-easterly winds of the Dry season.

Other features of the Region's climate are the high temperatures sustained throughout the year and the small seasonal range of mean monthly temperatures. The seasonal amplitude of mean monthly temperatures is only 5.6°C at Oenpelli (Christian and Aldrick, 1977) and further inland at Jabiru, 7°C (Walker et al., 1983a). A mean daily maximum of 37°C is reached in the period just prior to the Wet, while night temperatures may drop to a minimum of around 17°C in the Dry season between May and August (Oenpelli data).

Mean annual evaporation throughout the Region is estimated to be in the range of 2400-2700 mm, thus exceeding annual precipitation by 800-1200 mm. Mean evaporation is maximal late in the Dry season (about 260 mm in October) and minimal at the height of the Wet (about 100 mm in February) (Christian and Aldrick, 1977).

Day length varies little due to the latitude of the Region, with a maximum of 12.7 hours in January and 11.2 hours in June. Owing to the cloud cover in the Wet season, the least sunshine, 4.5 to 7.5 hours per day, occurs in this period while during the Dry it ranges from 9.7 to 10.2 hours.

2.2 The streams and waterbodies

Wet season flow of the streams in the Region is considerable and is highly variable both throughout the season and from year to year. In the Magela Creek for example, total flow past Jabiru averages about 250 million cubic metres per year, but may be three times this amount in a particularly wet year and only a quarter of the volume in a dry year (Fry, 1979). The annual

pattern in the streams, is one of a series of flood peaks following the more heavy periods of rain, superimposed upon a base flow (Hart and McGregor, 1980). Flow commences in an average year about mid December soon after the first substantial rains, declines in the early Dry season and ceases generally about the end of June. The flow pattern for the Magela Creek is shown in Figure 2.3. This figure displays monthly discharge data for the gauging station below Jabiru (GS 821009), over an eleven year period to the 1981-82 Wet season.

While the large rivers, including the Alligator Rivers, maintain a flow in lower sections and estuaries in the Dry season, all other streams including such major tributaries as the Magela, Nourlangie and Cooper Creeks, cease to flow for much of their length. In these streams, flow persists only in upstream sections fed by springs and seepage. During the Dry season, the lowland creek channels and the floodplains dry out, and the creeks contract to a string of small waterbodies. Some water remains until the next Wet season in rock pools on the plateau and in the small waterholes and swamps of the lowlands and floodplains. The small waterbodies left during the Dry season, are known locally in the Northern Territory, as billabongs. Pedantically, the word is somewhat of a misnomer (Walker *et al.*, 1983a), but because of its widespread usage, a billabong will be used here in reference to any waterbody of the lowlands and floodplains.

Three separate billabong classifications - "backflow", "channel" and "floodplain" - have been proposed for waterbodies in the Region; these classifications use geography, morphometry and hydrology (Davy and Conway, 1974; Walker and Tyler, 1979; Hart and McGregor, 1980). Backflow billabongs are situated near the mouths of tributaries to main stream channels of the lowlands and are formed as a result of the damming of the tributary at its mouth by the levee bank of the main stream; channel billabongs are located within actual main stream channels; and floodplain billabongs are depressions or remnants of abandoned channels on the floodplains.

2.3 Limnological features of the Magela Creek waterbodies

It is well known that environment can exert strong influences on freshwater mussels. There is a large literature in particular, describing the often strong relations between mussel morphology and distribution, and environmental factors (see Appendices 1 and 2 respectively). As background therefore to interpretation and to a proper understanding of the biology and ecology of V. angasi, pertinent limnological features of stream systems in the Region need also to be well known. The present study of V. angasi was confined to waterbodies of the Magela Creek - a system for which a great deal of other limnological information is available. The following descriptions summarise the relevant morphometry, hydrology and physicochemical limnology of the Magela Creek and its billabongs.

A feature of the billabongs of the Region, is the extraordinary and dramatic changes in hydrology and water quality between the Wet and Dry seasons. This confers on the waterbodies an individual dynamism and a between-billabong heterogeneity that precludes a generalised description of hydrology and physicochemical limnology for the Region. That is, a "typical" billabong cannot be described as might be the case for other waterbodies such as perennial streams and lakes.

2.3.1 Morphometry and hydrology

Figure 2.4 shows the location of the Magela Creek billabongs and Table 2.1 summarises their important morphometric and hydrological features. (The summary is a modified version of that prepared by Walker et al., 1983a.) Billabong area and mean depth are standardised to late Dry season conditions (1 November, 1981), the latter calculated from planimetry of prepared bathymetric maps. All bathymetric maps except those of JaJa and Jabiluka billabongs (source acknowledged in Figs. 2.11 and 2.13 respectively) were prepared from data collected during the study. Depth readings were taken at intervals of between 5 and 10 m apart, across transects spaced at 25 m

(Georgetown, Gulungul, Corndorl, Mudginberri and Buffalo), 50 m (Nankeen), 75 m (Leichhardt) or 200 m (Island) intervals along the billabong. Aerial photographs, and buoys and stakes aligned at set intervals throughout the billabong, aided with or without a need for compass bearings, were used to set the transects and to determine accurately the relative position of the billabong edge for final mapping. The bathymetric maps of the various billabongs are shown in Figures 2.5 to 2.14. Depths are mostly standardised to late Dry season levels.

At each site over which a depth reading was taken in the preparation of the bathymetric maps, sediment samples were collected by diving, and visually and subjectively assessed for textural character and organic content. These records, supplemented by the observations and some limited determinations of Thomas and Hart (1981) and Thomas *et al.* (1981) were used as the basis of descriptions of sediment texture. Particle size distributions and percent organic content in the billabong sediments, drawn from the data of the latter reports, are shown in Table 2.2. From these data, mean particle sizes of billabong sediments were estimated, and are also shown in that table. For the estimate of overall, mean particle size of billabong sediments, the particle size fraction greater than 63 μm was assumed (from visual observations) to represent very fine to medium sand, which has a mean particle size of 150 μm (Folk, 1968). The different and very distinct types of sediments in billabongs (where these sediments were markedly heterogeneous) are shown on the bathymetric maps. Bathymetric maps that are accompanied with sediment descriptions, are those of Georgetown, Corndorl, Mudginberri, Buffalo, and Leichhardt billabongs.

Gauging stations are located on two creek channel sites, but on only four of the billabongs, to measure discharge and flow rates. Of the billabong stations moreover, only two have been rated for conversion of stage height data to discharge. One of these (GS821023 at Jabiluka) is rated over the 2 km cross-section of floodplain at this point so that discharge cannot be

calculated specifically for the billabong. A shortcoming of the computed flow rates (derived from discharge and stage data) is that they represent a mean through the stream cross-sectional area and consequently underestimate velocities through the central channel regions.

Some data are available, however, to show the pattern of decreasing water velocity downstream of the Magela Creek. Table 2.3 displays this pattern, in measured water velocities during rhodamine dye experiments (1979-1980 Wet season) at sites and traverses along the creek (N.T. Dept. Transport and Works, Water Division, 1980).

Walker et al. (1983a) and Thomas and Hart (1981) claim respectively that billabong depth, and the type and distribution of the billabong sediments are good indicators of the current velocity and hydrological characteristics of the billabongs during the Wet. Bathymetry and study of billabong sediments are considered therefore as indirect but valid descriptors, in comparison to direct flow measurements, of the flow regime in billabongs during the Wet.

2.3.1.1 Lowland creek channel

Below Bowerbird and extending downstream to Mudginberri billabong, the Magela Creek flows through a well defined and braided channel. While flow persists throughout the year through Bowerbird and for some distance downstream (several kilometres), through-flow to Mudginberri billabong is accomplished shortly after the first substantial rains of the Wet season (generally between late November and mid December).

During the Wet, the base flow can be interrupted by a number of flood peaks. These spates can provide substantial discharge and with the confined nature of the channel, stream velocities can be considerable. In the Magela Creek below Jabiru for example, mean, cross-sectional flow rates have been recorded at up to 0.67 m/s (gauging station GS821009, 4 February 1980). As a consequence to the intensity of discharge over the period, the creekbed in this zone is well scoured, and has a mainly shifting, sandy substrate.

Stream flow through the creek channel ceases generally in the early Dry season (end of May) and the creek thereafter is reduced to a number of sandy pools which, depending on the duration of the Dry, may or may not persist until the following Wet. Regardless of their permanence, the creek pools are of no consequence to the present studies.

Vegetation along the banks of the creek channel is extensive and consists mainly of rainforest and some lowland flora. While some occasional Melaleuca and Barringtonia may colonise the actual creekbed, clumps of Pandanus are more common. The many branching roots of the latter are very much a stabilising influence on sections of sandy creekbed. During the Wet, macrophytes are common around the submerged banks of the channel in areas free from shifting, sandy substrates. These act, along with the root systems of the surrounding vegetation, to stabilise the muddy or loamy banks.

2.3.1.2 Backflow billabongs

The backflow billabongs are small, shallow and have shelving banks with mostly organic clay and silt sediments. During the Wet season, extensive wooded (Melaleuca) banks are submerged, and macrophytes grow prolifically in the open shallow waters. Bankside vegetation, however, is sparse during the Dry and macrophytes senesce, with the contracting of the waters. The waters are normally very shallow and turbid by the end of the Dry and over a particularly long Dry, some billabongs may in fact dry out completely.

Hydrologically, backflow billabongs are similar in that they are initially filled by 'backflow' at the commencement of the Wet, when water from the Magela Creek flows over the levee bank separating the billabong from the main creek channel, back up into the billabong. Subsequently, the direction of flow over the levee depends upon the relative flows in the Magela Creek and the billabong feeder stream. Backflow tends to deposit fine sediments and organic material in the billabongs. Flow down the tributary, however, tends to flush them.

Sediments in the backflow billabongs consist of fine grained silt and clay, rich in organic matter (about > 10%) (Thomas and Hart, 1981). Thomas and Hart (1981) attribute these characteristics to the poor flushing and high macrophyte biomass sustained in these billabongs during the Wet season. Observations on the shallowness of the waters (Table 2.1) and on the uniformity and unconsolidated nature of the sediments throughout the billabongs support these views.

An exception to the pattern, however, are the observations for Georgetown billabong. This billabong consists of two basins separated by a sill (Fig. 2.5). The sediments in each basin are mostly silt and clay, and those on the sill have a higher sand content (Fig. 2.5). As observed in the present study and also by Thomas and Hart (1981), as the Wet season progresses and water level in the billabong rises, the main flow pattern into Georgetown is from the Magela Creek at the southern end of the billabong (Fig. 2 of Thomas and Hart, 1981). This is particularly apparent when discharge in the Magela Creek is high, and during one major flood peak for example (March, 1981) very rapid water velocities were observed through the billabong.

Thus, Georgetown billabong can be well flushed during the Wet season, as observed visually, and as evidenced by the comparatively deeper water (Table 2.1) and marked differences in the proportions of sand and clay throughout the billabong. The lower content of organic material present, in comparison to other backflow billabongs - about 11% in sediments of the two basin regions, but as low as 0.1% on the sill (Thomas et al., 1981), further reflects effective flushing and the resultant lower macrophyte biomass sustained in this billabong.

2.3.1.3 Channel billabongs

The channel billabongs positioned in the main Magela Creek channel, are comparatively deep with steep and well-vegetated banks of mainly Pandanus with some Barringtonia and Melaleuca. Macrophytes are uncommon but occur in some

shallower waters around the billabong edges, away from strong currents. The sediments are very sandy (as evidenced by the larger sediment particles shown in Table 2.4) and together with the steep banks and overall depth ensure that the waters remain clear throughout the year. The channel billabongs apparently receive seepage input from the surrounding sandy aquifers for some time after the Magela Creek has ceased flowing (Hart and McGregor, 1978).

The sandy sediments which dominate these billabongs indicate that they are well flushed each year, and for the most part accumulation of fine sediments is prevented.

The Magela Creek at Bowerbird billabong is narrow (about 30-40 m wide) and well confined. Because of this and the comparatively steep gradient of the creek here in the escarpment region, stream velocities are exceedingly rapid, having been recorded at up to 1.72 m/s (gauging station GS821008, 4 February, 1980). The billabong, the deepest in the Magela Creek system, is thus well scoured each Wet season, and the sandy bottom here is shifting and unstable.

Mudginberri billabong is in a small transition zone between the lowlands and floodplain. It consequently marks a region of major change in flow characteristics as there is a dramatic reduction in slope of the creek bed at this point (N.T. Dept. Transport and Works, Water Division, 1980). Water velocities at the southern upstream end of this billabong can be considerable, particularly along the western side of the billabong where rapidly flowing water from the creek channel first meets the open water of the billabong. Rhodamine dye experiments have shown dead water and back-flow areas on the eastern side as water from the Creek enters the billabong at the southern end (Smith *et al.*, 1979). The experiments also revealed complex, local turbulence phenomena with depth of this end attributable to the sudden change in depth of the creek as it enters the billabong.

Measurements of stream velocity (under constant discharge) were undertaken during the 1982 Wet season of the present study across a number of transects

along the billabong. Figure 2.15 displays the results and clearly confirms that higher flow rates pass through the south-western end of the billabong than in any other part of the billabong until water becomes confined again and leaves through the narrower northern end. Further, under the prevailing flow regime at least, flow rates remained relatively faster along the western side until at least a third of the distance down the billabong. A measure of the stream velocity in the south-western end can be gauged from observation of the sediments in this region (Fig. 2.8). These consist of a fairly soft clay, found only in this reach of the billabong and indicating the prevention of sand deposition, and consequent scouring of the creek bed here. In contrast, sediment observations of a fairly large section of the eastern side of Mudginberri show deposition, the sediments here consisting of relatively high proportions of organic material and finer sediments (Fig. 2.8). Table 2.4 shows the particle size distribution and organic content of the sediments sampled across the transects or at the sites indicated in Fig. 2.16 at the southern end of Mudginberri billabong. These data show the increasing proportions of sand and decreasing organic content (from up to 16%) in the sediments away from the eastern side and immediate western edge of the billabong. From these data, the three major sediment types observed in the billabong (Figs. 2.8 and 2.16) were classified according to particle size distribution and organic content. The correspondence of textural character and organic content with the three sediment types is shown in Table 2.5. The highest Wet season flow rates through the billabong occur over those portions of the billabong with sandy sediments. To some degree, during flood events this sand bed is probably shifting and unstable.

There are two flow paths out of Mudginberri billabong. Both paths inflow to Island billabong, the right channel via Buffalo billabong. As a result of this branching, water velocity through Buffalo billabong is apparently reduced, though by what factor, is not known. From examination of the sediments, much of the billabong is sandy and hence well flushed, although like Mudginberri, a large depositional area exists, but on the western side

(Fig. 2.9). These deposits appeared to be similar to those of Mudginberri except for a region along the immediate western edge of the billabong (Fig. 2.9) where more silty and organic, and less consolidated sediments were present. While no analyses were carried out on the sediments to determine the relative fractions, of the major sediments in the billabong, the three coarsest and least organic in nature are assumed to be the same as those in Mudginberri (Table 2.5).

Island billabong is located at the junction of the floodplain and the lowland stream channel of the Magela Creek. During the Wet, the Creek changes from a confined, relatively fast flowing stream into a less defined stream dispersed over a broad floodplain, 1 to 2 kilometres wide, a short distance upstream from Island billabong. Walker *et al.* (1983a) consider Island billabong a 'hybrid', showing characteristics of a channel billabong but showing some affinities with the floodplain billabongs.

Although much of the surrounding weed-choked floodplain is inundated during the Wet, dye experiments have shown that at least under the prevailing flow conditions of the experiments most of the water passed through the open water areas of the billabong, and well ahead of that filtering through the adjacent floodplain (Smith *et al.*, 1979).

While no extreme, flood peak velocities are available, a relative measure of flow rate through the billabong can be obtained from Table 2.3. Water velocity through the billabong during the dye experiments (site 5) showed a considerable reduction over that measured only some 2.5 km upstream, the point at which the Creek channel enters the floodplain. Island billabong is the second deepest of the Magela Creek waterbodies (Table 2.1) and this depth together with observations of generally uniform sandy sediments, indicate that the billabong must nevertheless be reasonably well flushed during the Wet. From observations made during the study, sand over a grey, clay bed material dominated the sediments, in accordance with the observations of Thomas and Hart (1981), with increasing amounts of silt towards the banks.

Thomas and Hart (1981) however, over a period of two years regular monitoring of sediments in Island billabong, have noted their changeable character. A 10 to 20 cm deep layer of fine, unconsolidated sediment floc appeared after one Wet season (1979) to be apparently flushed out during a large flood in the following year, re-exposing the underlying sand layer. These authors considered that large flood events probably have a great influence on the distribution of sediments in the Magela Creek system.

2.3.1.4 Floodplain billabongs

The billabongs on the floodplains are relatively deep, less so than channel billabongs, however (Table 2.1), and generally have steep western banks with shelving eastern banks. Bankside vegetation is predominately Pandanus and Barringtonia, but this is variable and does not fringe the banks to the same extent as along the channel billabongs. During the Wet, macrophytes are common around the shallower edges. The deeper open water and some bankside vegetation are the only features which give the billabongs identity at this time, as water from the surrounding floodplain covers them.

Sediments of the billabongs, like the backflow billabongs, are generally composed of coarse silt and clay, but have considerably less (6 to 7%) organic content (Thomas and Hart, 1981). Because of the fine sediments, shelving banks, and being generally the most exposed of all the billabongs, the floodplain billabongs may become very turbid during the Dry.

Despite the width of the floodplain and a fall of only 15 cm in water level between the northern end of Island billabong and 35 km downstream to the East Alligator River (N.T. Dept. Transport and Works, Water Division, 1980), the floodplain billabongs effectively channel much of the water passing down the floodplain. According to the calculations of Thomas et al. (1981), more material is actually flushed from Jabiluka billabong for example, at the beginning of the Wet than could be deposited in it during the Wet season. The aerial photograph in Figure 2.17 shows the billabongs downstream of JaJa

during the Dry season, in relation to the broad surrounding floodplain. From this figure, distinct channels can be seen linking the floodplain billabongs (especially between Jabiluka and Nankeen). No studies, however, have yet indicated the extent to which the linking channels are operative during the Wet, or whether in fact they are relict.

Thus, while the floodplain billabongs cannot be considered depositional, dye experiments (Smith *et al.*, 1979) have shown that during the Wet season, Ja Ja billabong at least, is outside the main flow path of water passing through the plains. Observations made during the present study of the sediments around the billabong periphery also indicate a resemblance to those of backflow billabongs. The sediments are the least consolidated of the floodplain billabongs studied, and appeared to have a relatively high organic content. (No data are available, however, on the composition of the sediments.) These observations, in addition to its comparatively shallow nature (Table 2.1), indicate that Ja Ja billabong may be depositional in nature.

Other billabongs, however, effectively channel water passing over the plains. During dye experiments specific to Jabiluka billabong (Smith *et al.*, 1979) flow through the billabong (approximately 100 m in width) was estimated at 43 cumecs. As gauging at Jabiluka is rated over the 2 km wide section of floodplain here (Fig. 2.17), it is estimated from total discharge that 45% of flow across the plains passed through the billabong.

The same experiments showed that the main flow path through Jabiluka billabong is through the relatively narrow southern end. Water is channeled into the open section and does not spread onto the adjacent weed-choked floodplain areas as it moves through the billabong (Fig. 2.18). In addition to the 'funnelling' effect of water through the southern end, intrusion of water into the billabong is apparently subsurface, water entering the billabong during the experiment at a depth of 2.5 m (Fig. 2.19). However, the water moves towards the surface as it moves northward through the billabong (Fig. 2.19).

Thomas *et al.* (1981) provided additional evidence for the southern end being a "... more energetic environment" from sediment textural analysis, finding less fine silt and clay (69%) in the sediments in this zone than from a sample from the northern end (86%). The sediments of both Jabiluka and Nankeen are similar and are generally distributed uniformly throughout the billabongs. They are described by Thomas and Hart (1981) as being composed of coarse silt and clayey sediments low in organic matter (7%). An exception to the pattern, however, is the very sandy nature of the sediments along a narrow band (5-10 m in width) of the north-eastern edge of Jabiluka billabong. Presumably this reflects the very close proximity of the billabong here to the adjacent sandy lowland soils and reflects localised Wet season runoff from these soils.

Visual observations of Wet season flow through Nankeen billabong indicate that this billabong too, effectively channels floodplain waters. High flow rates, considerably faster than water movement through Jabiluka, were observed, particularly through the narrower northern end of the billabong. No discharge or flow rate data, however, are available for this billabong.

Unlike the other floodplain billabongs, from visual observations of flow and bottom type, there is evidence that Leichhardt billabong may be significantly scoured during the Wet season. This billabong is the narrowest on the floodplain (Fig. 2.12 and 2.17) and considerable water velocities were observed through the billabong during the present studies and have been observed by others (Thomas and Hart, 1981). Accumulation of fine sediments along the central channel section of the billabong is apparently prevented, unlike their uniform coverage throughout the other floodplain billabongs. This central channel region is composed of an extremely consolidated and very fine-textured clay (Fig. 2.12). Another notable feature of the substrate in Leichhardt is the extensive accumulations of deep and extremely unconsolidated detritus along the western edge of much of the billabong (Fig. 2.12). The sediments of the remaining shallower reaches differ from those of Jabiluka and Nankeen, in being composed of grey clay of a very sticky texture and lower in

organic content (5.6%) (Thomas and Hart, 1981). Because of the extensive areas of consolidated clays and accumulations of silt-free detritus, and its sheltered nature (bankside vegetation is extensive), the waters of Leichhardt billabong remain relatively clear throughout the year.

Hidden billabong is located to the immediate north of Island billabong and yet contains quite different sediments from the latter. The sediments are similar in texture and in size distribution to those of Leichhardt (Thomas and Hart, 1981); further, a compacted and fine-textured, grey clay layer also appears to dominate central portions of the billabong. As to whether the billabong is scoured to the extent of Leichhardt during the Wet however, is not known.

2.3.2 Physicochemical limnology

Since 1978 a large data base of physicochemical limnology has been collected pertaining to waterbodies of the Magela Creek. Work in the region has been carried out chiefly by four separate study groups: Water Studies Centre, Chisholm Institute of Technology; Environment Department, Pancontinental Mining Ltd; N.T. Department of Transport and Works, Water Division; and the Botany Department, University of Tasmania. Their data and reports provide the basis of the following descriptions.

2.3.2.1 Temperature

Figures 2.20 and 2.21 display spot monthly minimum temperature of bottom waters of the Magela Creek billabongs since May, 1978 up to and including the duration of the present studies. According to Walker *et al.* (1983a), these values lie approximately midway between the monthly mean maximum and monthly mean minimum air temperatures. While the seasonal fluctuations in water temperature are bimodal, minimum temperatures occur during the mid-Dry and maximum temperatures during the late-Dry.

Table 2.6 shows the surface maximum temperature and bottom minimum and maximum temperatures recorded over a four year period since 1978 for the Magela Creek

billabongs. The following generalisations can be drawn from these data: Generally, water temperatures are high and the seasonal range (of the shallower billabongs in particular) is considerable, from a winter low of 20.6°C recorded in bottom waters of Georgetown to a high of 40°C in surface waters of Gulungul during the late Dry.

In standing (still) waters there is generally a thermal stratification with observable differences between the warm surface waters and cooler bottom waters. In the more turbid billabong waters (during the Dry) this temperature differential can be considerable. In the deeper, turbid billabongs (e.g. Nankeen) the reduced penetration of radiation results in comparatively cooler maximum bottom temperatures whereas in very shallow turbid waters (e.g. Gulungul) appreciable heating of the bottom waters is evident. A notable feature of the deeper, turbid water billabongs is for their bottom water temperatures to reach maxima during the Wet and early Dry when waters are clearest and hence radiation penetration is deepest.

2.3.2.2 Dissolved oxygen

Dissolved oxygen concentrations in still waters are dependent upon atmospheric exchange at the water surface and from the reactions of photosynthetic organisms living in the waters. In still waters, changes in both water temperature and photosynthetic rate in particular, can result in considerable diurnal changes in the distribution of dissolved oxygen. Thus, during the day there is an increase in dissolved oxygen concentrations in waters containing dense populations of photosynthetic organisms, while during the night there is a depletion when these organisms respire. Further, if still waters become thermally stratified, bottom waters can become depleted of dissolved oxygen as a result of bacterial decomposition of organic material.

Figures 2.20 and 2.21 show the available dissolved oxygen values (1978-1982) for bottom waters of billabongs of the Magela Creek. The readings were taken in the early morning, the time of the daily minimum of dissolved oxygen. The

dawn readings show that most billabongs are considerably undersaturated. Even surface values are often below 50% saturation (3.5-4 mg/l) and according to Walker et al. (1983a), this is in contrast to the status of many temperate lakes whose surface waters always remain close to saturation.

From Figures 2.20 and 2.21 definite seasonal patterns in early morning values of dissolved oxygen are apparent, and these figures along with Walker et al.'s (1983a) accounts are used now to describe these trends.

The dominant feature of the seasonal patterns is the minima early in the Dry (April-June) that apparently pervades the entire water column. The chief cause of this oxygen deficit is the rapid bacterial decomposition of macrophytes, prolific during the Wet in the shallow waters surrounding the waterbodies, and on the floodplain. As water levels decline at the Wet/Dry interchange the large macrophyte biomass senesces and decays, causing a severe oxygen depletion that extends into the open waters of the billabongs.

After the annual senescence of macrophytes, wind-induced circulation patterns and the dynamics of phytoplankton populations in the billabongs determine the oxygen levels for the remainder of the Dry.

The diurnal range of oxygen values in the billabongs can be extreme, and can exceed the seasonal range. The magnitude of these diurnal changes is due mainly to the population densities of the macrophytes and phytoplankton. Phytoplankton levels are considerably higher in the Dry than in the Wet (section 2.3.2.5), and in deeper billabongs without extensive macrophyte beds, phytoplankton populations largely influence diurnal oxygen fluctuations. On 1/8/1979 for example between 0815 and 1520, an extreme range of 21-113% oxygen saturation was recorded by Walker et al. (1983a) in Leichhardt billabong, a waterbody where photosynthesis is chiefly algal. The diurnal fluctuations in the shallow backflow and floodplain billabongs, however, may be more influenced by their large macrophyte biomass, particularly in the early-mid Dry.

Of the Magela Creek billabongs, Jabiluka, Island and Gulungul frequently experienced a mid-Dry maximum of diurnal variation that coincided generally with the peak in chlorophyll levels at this time. The pattern in Leichhardt was typically irregular, involving a number of maxima and minima apparently related to the same erratic fluctuations of its phytoplankton populations (section 2.3.2.5). In other billabongs - Nankeen, Bowerbird and Georgetown, the magnitude of the diurnal flux was small and fairly constant throughout the Dry. Except for Nankeen, this was attributed to the lack of macrophytes and low chlorophyll levels sustained during the Dry in these billabongs. In Coonjimba billabong finally, the magnitude of diurnal variation was large, consistent with the large macrophyte population that persisted throughout the year in this billabong.

In lentic (still water) bodies of tropical regions, difficulties arise in recognising when stratification exists because of the very small temperature changes involved. Walker *et al.* (1983a) consequently, recognise a "de facto stratification" for billabongs of the Alligator Rivers Region: - at best, only partial mixing has occurred when both thermal and oxygen gradients are present at dawn (indicating that nocturnal mixing was incomplete), and this condition persists over a period of days or weeks, accompanied by a progressive decline in oxygen in the bottom waters.

In the Magela Creek billabongs, a continuum is recognised from transient periods of prolonged stratification, to stratification that is either broken down each night or in fact never develops.

Leichhardt, the most protected billabong on the floodplain, apparently experiences de facto stratification for much of the Dry with frequent periods of anoxia interspersed with periods of mixing. It was the only Magela billabong to experience periods of stratification other than briefly at the Wet/Dry transition. Considerable horizontal variation in oxygen concentrations at any one time was also a feature of the profiles in Leichhardt, and deepwater regions at sites only 10 m apart could differ by

more than 10% saturation. Moreover, on more than one occasion, an unexplained rise in oxygen status of deepwaters was observed during the Dry.

In most of the floodplain billabongs, brief periods of deepwater anoxia could also be experienced as the first floodwaters of the Wet reached the billabongs. The cause was attributed to the large amounts of organic material washed into the billabongs, creating a brief peak in oxygen demand before the billabongs were thoroughly flushed.

Jabiluka billabong is prone to periods of days of de facto stratification interspersed with considerable mixing. Periods of stratification, however, were generally limited to the beginning of the Dry when deepwater oxygen values could regularly fall to or close to zero. Walker *et al.* (1983a) demonstrated one such short period of persistent stratification at the beginning of the Dry (6 days during May 1981) when oxygen concentrations of the waters below 3 m were consistently below 30% saturation (about 3 mg/l).

Nankeen billabong, the most exposed of the floodplain billabongs was frequently well mixed in the early morning during the Dry. While on many occasions bottom waters could be depleted of oxygen, rarely did these values fall to zero. Ja Ja billabong similarly lacked any lasting stratification. This billabong is the shallowest of the floodplain billabongs studied, explaining why instances of stratification were only generally brief.

Although Island billabong was generally iso-oxic, occasional periods of stratification occurred during the early Dry, leading to significant oxygen depletion in the deepwaters.

Both channel billabongs, Mudginberri and Buffalo, as a rule experienced uniform distribution of oxygen throughout the waters. Oxygen was present at relatively high concentration throughout the year, and deepwater depletions were rare.

Periods of stratifications in the backflow billabongs were infrequent and

brief, these billabongs being the shallowest of the Magela Creek. Oxygen was generally homogeneously distributed throughout the billabongs and the values were relatively high. The exception to this pattern was in the early Dry for most billabongs, but only in Corndorl, however, was deepwater depletion of oxygen severe at this time or at other times such as during periods of static flow during the early Wet.

2.3.2.3 Chemical characteristics

According to Walker and Tyler (1983a) chemical differences between surface and deeper waters of billabongs in the Region are slight, and single surface samples describe sufficiently the characteristics of the waters at the time of collection. (The absence of any long-term stratification of the Magela Creek billabongs is used to support this claim).

Table 2.7 shows the seasonal means and standard deviations of an array of chemical characteristics of surface waters of the Magela Creek. Coverage is over a four year period (1979-1982) and the data were collated mainly from the N.T. Dept. of Transport and Works, Water Division, supplemented by data of Walker and Tyler (1983a) and those collected during the present studies. Figures 2.22 - 2.23, and 2.24 - 2.25 respectively display monthly values of conductivity (K) - the measure of the total concentration of dissolved inorganic salts in the water, and pH for waters of the Magela Creek billabongs from 1979 up to and including the duration of the present studies. The following description is a brief summary of billabong chemistry according to these figures and as related by Walker and Tyler (1983a).

During the Wet, the sheer intensity of discharge and effective flushing impart a uniform and common water chemistry to all the billabongs. Generally the waters are dilute (K below $20 \mu\text{Scm}^{-1}$), near neutral (pH's between 6.4 and 7.0) and are dominated by sodium bicarbonate. (The cationic dominance orders are $\text{Na} > \text{Mg} > \text{Ca} > \text{K}$ and anionic dominance, $\text{HCO}_3 > \text{Cl} > \text{SO}_4$). During the Dry as the waters in the billabongs evaporate, chemical changes occur but to varying

magnitudes, as solutes become concentrated, sediments are resuspended and groundwater enters the billabongs.

By the midpoint of the Dry (July), the uniformity of the Wet season ionic character had gone. Conductivities (17 to 145 μScm^{-1}) and pH's (5.8 to 7.1) now ranged more widely, and the billabongs could be separated into two groupings based on cationic proportions. One grouping, the channel billabongs, had more or less equimolar proportions of Na and Mg while the other, the backflow and floodplain billabongs, had an ionic order $\text{Na} \gg \text{Mg}$. A further subdivision was evident in anionic character in that the floodplain billabongs became chloride dominated.

By the late Dry (October/November), conductivities (18 to 2600 μScm^{-1}) and pH (a span of 3.8 units) ranged even more widely. Based on cationic proportions, the same groupings were present as during the mid Dry, but according to anionic proportions most billabongs had become chloride dominated while sulphate assumed dominance over bicarbonate in several billabongs.

Thus, while a common water chemistry dominated by sodium bicarbonate characterised the Wet, a diversity in ionic character of the billabongs arose during the Dry, but which could nevertheless be categorised according to particular characters. Some billabongs changed very little while most became sodium chloride dominated, of which some increased significantly in sulphate.

The sodium/magnesium bicarbonate billabongs are made up of the channel billabongs (with the exception of Buffalo). These billabongs are the least changed over the Dry: they maintain the ionic composition of the Wet throughout the year; remain dilute (K ranged from 15 to 30 μScm^{-1}); and pH fluctuations are slight with only a minor downward trend in pH evident. Their chemical stability is attributed to the reduced evaporation and concentration that most other waterbodies experience. This is a result of their low surface to volume ratios (being comparatively deep and narrow) and relative protection by the fringing vegetation.

The sodium chloride billabongs consist of all the backflow billabongs except Corndorl, one floodplain billabong (Leichhardt), and one channel billabong (Buffalo). In these billabongs, there is a change in ionic character over the Dry towards sodium chloride dominance. Where evaporative loss during the Dry is particularly high as in the shallow billabongs of this group, the waters concentrate considerably and conductivities range from 30 to 520 μScm^{-1} . pH values generally decline over the Dry to values as low as 4.0.

The sulphate billabongs include one backflow billabong (Corndorl) all of the floodplain billabongs (except Leichhardt) and Island billabong which in its physicochemistry is intermediate between channel and floodplain categories. In this group, there is the same change to sodium chloride dominance during the Dry (except in Island) but this is accompanied by significant concentration of sulphate. In all of the billabongs conductivity rises sharply during the Dry (except Island) and pH can become very low, particularly in the floodplain billabongs. The low pH values and the concentration of sulphate is apparently from groundwater aquifers, introducing both sulphates and sulphuric acid from the weathering of pyritic minerals (i.e. iron sulphide - a feature of the Region's geology) in the surrounding catchment. While this groundwater influx is considered to be gradual, sudden early Wet season flushes into the floodplain billabongs of runoff from the sulphate-rich and acidic crust that forms on the surface of floodplain soils during the Dry, may occur that are believed to be the cause of occasional, but often major fish kills that develop at the time (Pancontinental Mining Limited, 1981); the sulphate-rich and very acidic waters that result in the billabongs during such influxes, are believed to mobilise aluminium, a known toxicant to fishes, from the sediments.

2.3.2.4 Turbidity

Of the three factors most likely to affect light conditions in billabong waters of the Alligator Rivers Region, namely organic colour (gilvin), turbidity and chlorophyll, turbidity - the presence of suspended, finely

divided sediments, has been shown to be the dominant influence (Walker et al., 1983b).

In the Magela Creek, waterbodies can vary from non-turbid to very turbid during the Dry season, and from simple visual observations the billabongs can be so divided. An earlier table (Table 2.6) classifies the billabongs accordingly. The seasonal means of turbidity for the billabongs are similarly shown in Table 2.7 while the seasonal distribution is displayed as monthly values in Figures 2.26 and 2.27. From these data and the report of Walker et al. (1983b) the following generalisations can be drawn.

In most of the billabongs, maximum clarity occurs soon after the creek ceases to flow at the Wet/Dry transition (April-May) when suspended material is allowed to settle. Over the ensuing Dry, the channel billabongs do not experience much further change in triptonic turbidity (i.e. suspended, non-living particles), because of their narrow and sheltered nature, low surface area to volume ratios (as discussed in section 2.3.2.3), and coarse sandy sediments. For these billabongs, no other discernible trend in water clarity through the Dry is obvious though phytoplankton populations may contribute to the low turbidity (Walker et al., 1983b). Leichhardt billabong behaves similarly for reasons previously discussed (section 2.3.1.4).

By the mid-Dry in most other billabongs, however, namely all the backflow and most floodplain billabongs, more or less rapid deterioration in water clarity has occurred due to the rising turbidity. These rises are attributable to falling water levels permitting wind-disturbance of fine sediments, and probably from some additional disturbance by wallowing buffaloes. The influence of macrophytes in preventing turbulent mixing is important in the shallow backflow billabongs. Thus Georgetown with relatively fewer macrophytes becomes 'dirty' very early in the Dry (Fig. 2.26) in contrast to Gulungul and Corndorl, where the turbulent mixing occurs more or less later and as an abrupt event coinciding with the death of the dense stands of macrophytes in these billabongs.

At the Dry/Wet transition, previously clear and non-turbid billabongs become muddied whereas turbid billabongs are cleansed. During the Wet, water clarity in most billabongs fluctuates, depending on the rate of flow through the billabong. Between floodpeaks when the Magela Creek is not backflowing, Gulungul and Corndorl billabongs for example, can become extremely clear (e.g. Corndorl, February, 1982), whereas Mudginberri billabong in the main stream channel can experience relatively higher turbidities, particularly when the billabong is initially flushed and during proceeding flood events during the Wet (e.g. late December, 1981).

2.3.2.5 Nutrient status and phytoplanktonic productivity

If algal productivity in aquatic ecosystems is limited, the prime causes are most likely to be light and the availability of the two nutrients, phosphorus and nitrogen. Light availability has been discussed in the previous section. The reports pertaining to nutrient status (Walker and Tyler, 1983a), phytoplankton populations (Kessel and Tyler, 1983), and primary productivity (Walker and Tyler, 1983b) are the basis now for the following descriptions on nutrient status and productivity of phytoplankton in the Magela Creek billabongs.

During the Wet, nutrient levels are at their lowest. By world standards, however, total phosphorus levels are high and the billabongs can be regarded as mesoeutrophic to hypereutrophic. Nitrogen: phosphorus (N:P) ratios are low at this time, and the billabongs are ultra-oligotrophic in terms of inorganic nitrogen.

During the Dry, the nutrient status of the channel billabongs remains the same as during the Wet. This is attributed to the lower evaporative concentration that occurs in these billabongs, in addition to the coarse and largely inorganic nature of the sediments.

In the other billabongs, however, nutrient levels rise markedly and continuously as evaporative concentration and internal loading from

resuspended sediments proceeds over the Dry. The process is further accelerated by the congregation in, and use of, these waters by buffalo and large numbers of waterfowl. The rapid increase in nutrients occurs earlier in the floodplain billabongs than in the backflow billabongs, and in addition, inorganic nitrogen constitutes a much higher proportion of the total nitrogen than in the backflow billabongs.

With the exception of the floodplain billabongs, N:P ratios in other billabongs are low and nitrogen is suspected of limiting production, not phosphorus as is usually the case in aquatic ecosystems. Phosphorus levels in all the billabongs indicate hypereutrophy, while inorganic nitrogen levels suggest a range from mesoeutrophic to hypereutrophic on a world scale.

The seasonal distribution of both surface and bottom phytoplanktonic chlorophyll (a direct measure of algal biomass) is displayed as monthly values for the Magela Creek billabongs in Figures 2.28 and 2.29. In general, phytoplankton stocks and productivity increase in all billabongs as nutrient levels rise after the Wet. By the mid-Dry, however, in all backflow and most floodplain billabongs, the increase in chlorophyll concentrations and in productivity is arrested in response to increasing turbidity, even though nutrient concentrations continue to rise. Thus, underwater light conditions deteriorate, preventing phytoplankton productivities from reaching the levels they should on the basis of available nutrients. Only in those waters such as in Leichhardt billabong, where substantial rises in nutrient concentrations occur over the Dry, but where rise in turbidity is mild, do productivities increase for much of the Dry. In this case, phytoplankton is able to capitalise on the optimal nutrient conditions.

In terms of the trophic status and features of the phytoplanktonic populations of individual billabongs, Bowerbird was always unproductive as were generally all of the billabongs during the Wet, particularly when strong flow through the billabong was apparent.

Mudginberri billabong experienced a general rise in trophic status over the Dry, but as nutrient levels never reached the levels attained in the other billabongs, phytoplankton populations were generally checked, despite a suitable light climate. Buffalo billabong apparently behaves in a similar manner. Kessell and Tyler (1983) noted that during the Dry in Mudginberri, there was a general trend towards increasing phytoplankton along the north-south axis of the billabong. In addition, a regular daily pattern of migration of phytoplankton to intermediate depths by the afternoon was found, followed by their dispersion at night through convective mixing. The same phenomenon was found in Leichhardt billabong, and one assumes it is a pattern common to all of the billabongs. At the commencement of the Wet, heavy rains can wash detrital and other material of terrestrial origin into the billabong, producing short-lived but strong increases in chlorophyll (Fig. 2.28), a pattern previously observed in the same billabong by Hart and McGregor (1978).

Island and Leichhardt billabongs are the most productive of the Magela Creek billabongs and both observed the highest populations of phytoplankton biomass. Island billabong experienced maxima in trophic status in the early Dry, while for the remainder of the Dry algal populations fluctuated irregularly.

For reasons already discussed, in Leichhardt billabong there is a trend through the Dry towards higher chlorophylls. The levels attained in fact are the highest of any billabong. The monthly fluctuations in algal biomass, however, are unpredictable and even locally, extremely rapid temporal and spatial variation in the phytoplankton populations (apparently random) are notable and characteristic phenomena of this billabong (Kessell and Tyler, 1983). Like Mudginberri there can be considerable but far less predictable, horizontal heterogeneity of phytoplankton at any one time. (This same horizontal heterogeneity has been assumed for the other billabongs of the Region, and according to Walker and Tyler (1983b) precludes any determinations of whole billabong phytoplankton biomass or whole billabong productivity rates and production budgets from determination at one site).

In Ja Ja, Jabiluka and Nankeen billabongs, chlorophyll levels increased to maxima by the mid Dry, then declined (more or less) as turbidity increased, limiting the algal populations. The backflow billabongs behaved similarly although surface algal scums could produce late Dry season maxima as occurred too during the early Wet season when backflow conditions inputted detrital and other organic matter to the billabongs (e.g. Corndorl, December, 1981).

Finally, according to Walker and Tyler (1983b), the billabongs of the Region at their most fertile are placed in the lower-mid to middle of the range of measured productivities in tropical lakes, and high in comparison with many temperate lakes. Based on chlorophyll concentrations, the billabongs are oligotrophic to eutrophic.

2.3.3 Ecology of the freshwater fishes

The unionacean larva, the glochidium, develops in the marsupial demibranchs of the adult female. In order for further development and growth as a juvenile mussel to take place, a temporary period of obligate attachment to one or more species of fish (with only rare exceptions) is necessary, during which metamorphosis takes place. Dispersal occurs during this parasitic phase. Because of this reliance (and apart from anthropogenic interference), the most important biotic relationship of freshwater mussels is that of their glochidia upon fishes. The population structure and dispersal of Velesunio angasi therefore, are presumably dependent to some degree upon the habits and occurrences of its host fishes. Thus, a brief, background resume of some pertinent aspects of the ecology of freshwater fishes of the Magela Creek, particularly community structure in the various waterbodies and movements, is warranted.

While the Australian freshwater fish fauna is depauperate by world standards, the fish communities of northern Australia, in common with tropical regions generally, are the most diverse in the continent (Lake, 1971). Of the some 170 essentially freshwater fish species native to Australia (Lake, 1971), 45

species - over one quarter of the country's total - occur in the small Alligator Rivers Region of tropical northern Australia (Midgley, 1973; Pollard, 1974). Intensive and ongoing collection of biological and ecological data of the freshwater fishes of the Region, largely concentrating on the catchment of the Magela Creek, has been carried out by research staff of the New South Wales State Fisheries since December 1979. A comprehensive report provided information on various aspects of the biology of the fishes including ecological requirements, movements, community structures and fluctuations in numbers with time (Bishop et al., 1981). Both the latter report and a subsequent article (Bishop, 1983) provide the basis of the following summary.

Baseline information on the biology and ecology of 32 fish species were presented in Bishop et al. (1981); 21 of these species were found abundantly in waterbodies downstream of mining activities of the Ranger Uranium Project Area (Table 2.8). Dynamic seasonal and longitudinal changes were noted in the structure of fish communities in the Magela Creek. These changes are summarised in Table 2.8. Lowest homogeneity was shown between communities in the late Dry season and highest homogeneity in the mid Wet to early Dry seasons. During the Dry, refuge populations of fish species occur in either escarpment, or channel and floodplain zones. These populations may enter the lowlands from either zone following initial creek flow in the Wet season. Thus, the increased homogeneity of the fish community structure shown during the mid Wet to early Dry appeared to correspond to an increased homogeneity of the aquatic environment - Wet season flows relinked Dry seasons refuge areas thereby allowing a greater range of species to become more abundant and widespread. As environmental conditions deteriorated during the Dry season, well-adapted species that did not migrate back to refuge areas after the Wet, were thought to suffer high mortality thereby explaining the decreasing species diversity (or heterogeneity) found in the lowland communities. This was particularly marked in the backflow billabongs, and the unstable late Dry season environment of these billabongs realised both lowest species diversity and lowest abundances of fishes in comparison to the deeper channel and

floodplain billabong environments.

Specifically in relation to fish migrations in the Magela Creek, distinct downstream movements to the lowlands by characteristic escarpment species (those fewer species confined to the sandy creek channel shown in Table 2.8) were observed in the early Wet, followed by a return upstream at the end of the Wet season. Similar movements but in an opposite direction, and more obvious considering the larger numbers of species involved, were shown by species characteristic of the channel and floodplain zone. Communities in the lowlands hence, represent a species flux between communities in the upper and lower reaches of the catchment. Thus most of the species in the Region appeared to undertake potadromous migrations (i.e. movements within rivers and their floodplains or from lakes into rivers). At least several, moreover, are known to undertake catadromous migrations to brackish or saltwaters.

Although large concentrations of migrating fish were observed in the channel billabongs during the mid Wet, the abundances were primarily due to the billabongs lying in the mainstream channel of flow of the creek (i.e. migration route); thus aggregations occurred in quieter waters immediately downstream of the torrential input of the sandy creek channel. For most species, migration during the Wet was into the lowlands, particularly into the backflow and floodplain billabongs. Reasons for this response were explained by temporal and spatial patchiness of resources, since: 1) feeding activity was most intense in the Wet in backflow and floodplain billabongs; 2) while breeding activity peaked in the early Wet but declined through the Wet into the early Dry season, it was most intense in backflow billabongs followed closely by escarpment waterbodies, the sandy creek channel and floodplain billabongs; and 3) recruitment was greatest in the mid Wet season, and although more visible in the more downstream billabongs because of the physical displacement of juveniles, was noticeably high in backflow billabongs. Thus, the lowlands were argued to be valuable feeding, breeding and recruitment areas, exploited seasonally by freshwater fishes of the Region.

CHAPTER 3
MATERIALS AND METHODS

3.1 The study sites

Study of the biology and the ecology of Velesunio angasi was confined to the Magela Creek waterbodies. Sampling commenced in March 1980 and ceased in May 1982.

Populations from three billabongs were chosen initially for intensive study. As a wide range of habitat types were sought, the selection considered geography, morphometry and hydrology of the waterbodies, in addition to known sites where mussels occurred in reasonable numbers. Thus, in accordance with previous billabong classifications and because of their large mussel populations, Georgetown, Mudginberri and Nankeen billabongs were chosen, being representative of backflow, channel and floodplain billabongs respectively. The wide geographical range of these billabongs (Fig. 2.4) was an additional feature that lent support to their selection.

In July 1980, an additional site was added to the sampling routine. A population of mussels was found along the lowland sandy channel of the Magela Creek between Bowerbird and Mudginberri billabongs. As the creek dries out at the cessation of flow in the early Dry, the mussels in this reach are obliged to aestivate over the ensuing Dry until the creek flows again at the beginning of the next Wet season.

Mussels were collected monthly from the four waterbodies and except for mussels from the lowland creek channel (hereafter referred to as "creek" mussels), sampling in the billabongs over a two year period was done in a systematic and repeatable fashion. All age classes of mussels were collected quantitatively from defined areas (section 3.2.1) over a variety of habitat types.

Obvious habitat types within the billabongs were substrate and depth. (In

addition to any direct effect on mussels, substrate was also indicative of the Wet season flow regime in the mussels' immediate environment - see section 2.3.1). Distance along the billabong was also considered as a check for other subtle (but at that stage unknown) limnological gradients that could act upon the mussels.

With the above considerations in mind, two transects were established across Georgetown billabong (Fig. 3.1). The upstream or southeasterly transect was located largely on the shallow, sandy sill referred to previously (section 2.3.1.2) and the second transect was located across the comparatively deeper silt and clay basin downstream (to the northwest). Mussels were collected from 1m² areas at 5m intervals across the upstream transect, and at 10m intervals across the downstream transect. Both transects thus encompassed a wide range of depths and substrate types.

Five sites were established in Mudginberri billabong (Fig. 3.1) each with a regard to depth, substrate and distance along the billabong. Two downstream (northerly) sites were located in relatively shallow waters over predominately sandy sediments. Two sites were positioned upstream of these (in the southeast) in deeper waters, and over the chiefly detrital sediments of this backflow part of the billabong (section 2.3.1.3). The fifth site was established along the southwestern bank over a stony and clay bed that is well flushed during the Wet season (section 2.3.1.3). No sites were located over the sandy sediments totally free from silt and detrital deposits that occur in the central channel region of the billabong (Fig. 2.8), as mussels here were generally uncommon. Mussels were collected from 2 x 1m² plots at each site, except for the fifth site where 0.25m² was sampled.

The floodplain billabongs of the Region in particular, are renowned for their populations of saltwater crocodile, Crocodylus porosus that become increasingly conspicuous over the Dry season. Nankeen billabong on the Magela Creek floodplain has an especially large population in comparison to other freshwater billabongs of the Region, and because of this, routine sampling

here was restricted. One site only, located at the narrow, downstream (northern) end was established in this billabong (Fig. 3.1). Samples were taken along a transect beginning on the eastern shore across the shelving silt and clay bank, and finishing in the deepest waters approximately halfway across the billabong. A total area of 8m² was sampled across the transect, 1m² at each 3m interval. Sampling thus accounted for the variations in depth, while sediments throughout the billabong were found to be nevertheless reasonably homogeneous (section 2.3.1.4).

Routine samples of creek mussels were generally taken from the section of creek channel between Corndorl and Mudginberri billabongs. Because of their habitat (along loamy banks and amongst roots of trees and shrubs, particularly Pandanus) and its extremely variable nature, collections per unit area were not relevant to these populations.

Permanent transects and sites were established in the three billabongs. These were marked by metal stakes in Georgetown and Nankeen, and concrete blocks marked by floating buoys in Mudginberri billabong. Each month the transects and sites were moved 2m downstream (Georgetown) or upstream (Mudginberri and Nankeen) to ensure the same ground was not sampled twice.

By the end of 1980, a wide variation in biological patterns (e.g. growth, reproductive condition etc.) was evident between mussel populations of the four waterbodies, and no common trends were apparent. Consequently, from January 1981 a further four billabongs, Corndorl, Island, Leichhardt and Jabiluka, were added to the routine sampling in the hope that patterns might emerge with the addition of further variety in habitat types and environmental data. Mussels were sampled monthly from each billabong up until May 1981.

In Corndorl, collections were made at one site in the northeastern corner of the billabong (Fig. 3.1). In Island, Jabiluka and Leichhardt billabongs, mussels were sampled quantitatively across transects. These were regularly spaced along the billabong (Fig. 3.2), with one transect being sampled per

month, beginning at the first northern-most transect in January, 1981. Mussels were sampled from 1m^2 plots at regular intervals across each transect. A total area of at least 10m^2 (depending upon the billabong width) was sampled and depth and substrate type were recorded at each 1m^2 plot.

The mussel populations of a further two billabongs, Ja Ja and Buffalo, were sampled during 1981 and 1982 but not on a routine monthly basis. Ja Ja was sampled bimonthly from April 1981 and Buffalo billabong every third month from April 1981. Collections from Ja Ja billabong were taken in the same manner as those from Nankeen but at different sites per collection (Fig. 3.2), while samples from 1m^2 plots were taken from each of 10 sites (Fig. 3.1) in Buffalo billabong.

3.2 Field procedures

In studies of freshwater mussels to date, collecting has been achieved using a wide variety of sampling techniques - for example dredging, raking, dragging, brailing, tonging, wading and (comparatively recent), sustained diving with SCUBA. Quantitative collection of mussels is not essential to all studies. However, when estimates of abundance or density are needed, (for example when distribution, population dynamics and production are under investigation) an adequate quantitative capability is an important requirement of the sampling device.

It is well known for the marine environment, that most collecting devices including dredges, grabs and corers are at best semi-quantitative in so far as giving an accurate picture of the density and distribution of benthic fauna (McIntyre, 1971). In freshwaters similarly, apart from diving, most samplers are notoriously inefficient when quantitative collecting is required (Flannagan, 1970). Efficiency is more often dependent upon substrate type. Dredges and grabs for example are known to be ineffective over irregular beds especially hard-packed substrates and rock or debris-strewn bottoms (Stansbery, 1961; Stanczykowska, 1977), so that comparisons of distribution

between different habitats of a freshwater body are then often difficult to make. Even over sediments conducive to sampling by these devices, many mussels may be missed. Haukioja and Hakala (1974) found for example that per unit area an Ekman grab collected only one third of the number of mussels collected by hand.

A number of studies nevertheless, have used these supposedly "quantitative" collecting devices when good quantitative data were required (Hendelberg, 1960; Tudorancea and Florescu, 1968; Magnin and Stanczykowska, 1971; Mackie and Qadri, 1973). In other cases several techniques have been used such as hand-collecting and diving in combination with dredges, without any attempt to measure the efficiency of one technique over another (Okland, 1963; Negus, 1966; Lewandowski and Stanczykowska, 1975; Kenmuir, 1980). Even when the inefficiency is recognised in or between sampling techniques (e.g. Lewandowski and Stanczykowska, 1975; Stanczykowska, 1977) no estimates of the mean efficiency of the sampling equipment appear to have been calculated.

It is widely recognised that collection of mussels directly by hand, particularly when aided by SCUBA diving, is by far the quickest and most efficient sampling method. Even when SCUBA is involved, however, "intensive" or "exhaustive" searching by hand alone (Cvancara, 1972; Ghent *et al.*, 1978) is no guarantee of completely efficient sampling. Mussels, especially small specimens, may still be missed (Haukioja and Hakala 1974, 1978a; Coon *et al.*, 1977; Strayer *et al.*, 1981). In studies in which hand collecting alone is employed, only the studies by Haukioja and Hakala (1974, 1978a) have checked the efficiency, by sieving the substrate after handpicking to derive an estimate of the error involved. No mention, however, has yet been made of the size range of mussels that are too small to be collected by hand.

Although collection of small (young) mussels in some quantitative studies is not an important requirement - especially for production estimates where the biomass missed may be practically negligible, the collection of young mussels in studies of distribution and population dynamics is crucial to a proper

understanding of recruitment.

Only studies by Negus (1966), Brice and Lewis (1979), Kenmuir (1980) and Horn and Porter (1981) have combined hand collection of mussels by diving with subsequent sampling and sorting of the sediments using scoops for the remaining small mussels. Horn and Porter (1981) used in addition, a diver-operated suction-type dredge at quarterly intervals during the year to collect mussels. The study of Brice and Lewis (1979) was a 'point' sample in time, however, and nor did the studies by Negus (1966) and Kenmuir (1980) collect by this method on a routine seasonal basis. (In the above studies, this type of collecting is assumed totally effective, with no mussels being missed). The study by Horn and Porter (1981) is apparently the only attempt at systematic searching for all age-classes of mussels on a seasonal basis, using diving to collect mussels and sediments. Even when other methods that are apparently non-selective for size have been employed (e.g. dredges) that provide at least a relative measure of the population age structure, seasonal sampling has only been attempted by Negus (1966).

Thus, while it has generally been assumed in the past that young mussels are cryptic and have quite different habitat requirements to those of adults (Isely, 1911; Coker *et al.*, 1921; D'Eliscu, 1973; Walker, 1981b), nevertheless few studies have searched systematically for young mussels on a regular temporal basis. When breeding is highly seasonal, such as the case for much of the mussel fauna of temperate regions, young may only appear for a short period of the year, especially if juvenile mortality is high or growth is particularly rapid.

During the present study, diving was used to collect mussels. Virtually unlimited time was available for sampling through the acquisition of a petrol-driven, Hookah compressor; the characteristic and favourably high water temperature for diving; and the comparatively shallow waters (<10m) which never imposed limits upon submerged working times. This is contrary to other studies using diving as the sampling method, where SCUBA invariably

provides the air support. In these cases, tanks must be periodically refilled to the detriment of diving time. Limitations of distributional studies due to depth and low water temperature have been commonly cited in temperate regions.

3.2.1 Methods of sampling

Early surveys and collecting of freshwater mussels from the billabongs experimented with a dredge and a toothed, hand-held rake. While the latter was least time-consuming and more effective than the former, the rake was nevertheless inefficient over sandy and debris-strewn substrates and extremely labour intensive particularly under the prevailing hot and generally humid climate. No satisfactory quantitative sampling could be achieved by these methods.

Ultimately five types of sampling were employed to collect freshwater mussels during the present study. The first four methods are variants of diving; free diving with or without a snorkel in depths less than about 1m but aided by a petrol-driven Hookah compressor in deeper waters. The collecting methods are described as follows:

Type 1: Mussels were collected from a confined area, though not from the confines of a prescribed bounded area. The collecting area was roughly a semi-circle with radius the distance of the outstretched hands, with the diver in a kneeling position. Care was taken to sample all size classes of mussels, and to remove all the mussels from an area before moving a short distance and repeating the procedure. To effect this, once all the mussels were thought to have been removed from a locality (these having been placed in a collecting bag), the sediment was broken up in a systematic mulching fashion to a depth of about 7 cm, and the area rechecked by sight or by touch at least twice for remaining mussels.

In practice, all mussels above 27mm are assumed to have been collected by this method (section 3.2.2.). However, while no size-selection above this length was apparent, nor was any attempt made to relate numbers of mussels to area

for density estimates.

Type 2: Using this method, mussels were collected by hand from the confines of a metal-framed quadrat, of dimensions 0.5 x 0.5m (0.25m²) by 7cm in depth with an outer 2cm horizontal lip around the surface. The quadrat was pushed into the substrate as far as the lip (7cm) and all mussels within the frame removed. As in Type 1 sampling, the substrate was then thoroughly broken up to a depth of from 7 to 15cm (depending upon the firmness) and the area re-checked at least twice in a systematic fashion until no further mussels were recovered.

Type 3: Mussels were removed by hand from the confines of the quadrat, in the same manner as before (Type 2). Any debris such as coarse vegetation and sticks was carefully removed; macrophytes were pulled out by the roots, adhering sediment shaken off and the plant discarded; and the substrate was then collected into a scoop (a household plastic dustpan approximately 30cm in width). The contents of the scoop were then placed carefully into a large circular basket made of a rigid plastic mesh. Mesh size was 2.5 x 1.5mm. The basket was held over the quadrat, to ensure that spillages were re-directed into the confined area. Substrate collection was done in a systematic fashion working from one corner and side and finishing in the corner diagonally opposite. All sediment to a depth of 7 cm (the depth of the quadrat) was removed by this method. Care was taken to ensure that, as far as possible, no sediment remained adhering to the side, or collected in the corners of the quadrat.

At the water surface, the sediment and associated debris were thoroughly stirred and washed in the screen basket until all fine material had apparently passed through the mesh. The contents of the basket were then placed in plastic bags for later sorting and examination in the laboratory.

Type 4: This sampling was achieved using a diver-operated, air-lift pump. Mussels were again removed by hand, the sediment lightly broken up, and coarse

debris and vegetation removed. Air was then fed via a diving hose into a wide bore (7cm internal diameter) flexible but compressed and reinforced rubber hose, approximately 10cm from the mouth. A nozzle consisting of a 30 cm length of clear perspex or PVC tubing (50 mm internal diameter) was fitted to the mouth of the rubber hose. Water displacement with the resultant Venturi effect, acted to suck up water, sediment, associated debris and mussels through the hose via the inhalent nozzle to the surface where the material was directed by an assistant into the same screen basket as described earlier (Type 3). Sediment was collected in a systematic fashion, working from one side of the quadrat to the other, and to a depth of at least 7cm. The collected material was washed and treated in the same manner as before (Type 3).

Two hoses were used in the study, one of length 6m for deep (Wet season) waters and another of 4m used in the Dry. In shallow water (<3m), the hoses were replaced by PVC tubing (50mm internal diameter) of length appropriate to the depth of water. The pump principle is such that its drawing power decreases with decreasing depth. The pump used in the present study was ineffective in water less than 1m in depth. In water below this depth, the larger and heavier sand particles (and larger mussels) could not be lifted to the surface.

When diving, only for a few months of the year was visibility at the bottom of most of the billabongs sufficient to see more than a metre or so from the diver, and by the time the sediments had been disturbed (the routine practice), visibility was generally negligible in any case. Consequently, touch played a dominant role in the collection of mussels and performance of underwater actions. This did not impair the efficiency of collecting. Even in the clearest billabongs (e.g. Mudginberri) where the mussels were readily visible for much of the year, touch rather than sight was still responsible for most of the collecting actions.

Type 5: This type of sampling describes collection of creek mussels. During

the period of creek flow (about December to early June) mussels were collected from likely areas (described in section 3.1 by Type 1 sampling. Over the ensuing Dry the mussels burrow up to 20cm into the surrounding substrate to aestivate. This occurred usually as an abrupt event with the cessation of creek flow, and sampling then involved use of digging implements such as picks and mattocks in compacted soils, aided by the hands in the softer and friable sandy soils. Over the Dry season when digging was involved, care was taken as in Type 1 sampling, to thoroughly search a locality. This meant digging beyond the normal depth at which mussels burrowed, and searching through the exposed soils several times before moving onto the adjacent undisturbed region.

Collection of sediments for later sorting and collection of the small mussels missed by hand (Types 3 and 4 sampling) was limited to Georgetown, Mudginberri, Nankeen and Buffalo billabongs. This was particularly relevant to the first three billabongs, where mussel populations were under most intensive investigation. From July 1981 to the end of the Dry in Nankeen, but throughout the year in Georgetown billabong, sites became increasingly shallow for Type 4 sampling. Thus, as depth declined to below 1m, so too did Type 3 sampling (scooping) replace Type 4 (air-lifting) as the collecting method. By the end of the Dry, 3 of the 8 sites in Nankeen were so affected; in Georgetown only 4 out of 9 sites in the downstream transect, and none in the upstream transect, could be sampled using the air-lift.

In Nankeen billabong, there was some initial reluctance to spend long periods of time in the water with the knowledge of the attendant crocodile population and potential hazard. The time-consuming task of collecting sediments therefore, did not commence until January, 1981. From June, 1980 to the cessation of sampling, diving in this billabong was done within the confines of a large net as a safety measure. The net was laid in a semicircle about the diver, with both ends anchored to one shore. The net was multifilament and of the floating and sinking type with dimensions: mesh size 20cm

(stretched knot to knot); length 75m; and depth approximately 7m. The net was also used for protection in all of the floodplain billabongs during routine sampling.

While mussels were collected from defined areas (1m²) across transects in Island, Ja Ja, Leichhardt and Jabiluka billabongs, invariably the numbers so collected were insufficient for other biological studies. In these cases, Type 1 sampling was employed in the immediate vicinity of the transect but in the shallower water towards the banks, where mussels were most common.

Table 3.1 summarises the various collecting methods used in the Magela Creek waterbodies over the study period.

3.2.2 Sampling efficiency

As different methods were employed to collect mussels between waterbodies and even within the same billabong on any one occasion, it was necessary to check and find the efficiency of the various methods. This was deemed essential for accurate descriptions of distribution and population dynamics. Having found the mean efficiency of the sampling types, these could then be calibrated against one another and the necessary corrections made so that the pertinent features of the mussel's ecology were comparable over the Magela Creek system.

Efficiency was measured against air-lifting, which in the present study was assumed totally effective in so far as collecting all the mussels within a defined area. The basis of this claim were the observations made under optimal conditions of visibility (Mudginberri billabong during the Dry season) when the ability of the air-lift to draw up all substrate and debris within its path was unequivocal. A particular feature of the pump in this regard was its ability to effectively scour and draw up material from the corners and sides of the quadrat.

Apart from observations, an independent check of the efficiency of the air-lift pump was done in the following way: In April 1981, sediment and

mussels were air-lifted routinely from the 8.25m² of sites along Mudginberri billabong. No prior hand-collecting was attempted and all material to a depth of 7cm was collected. A further 7cm of the sediment was then air-lifted and collected separately (thus drawing up material over a total depth of 14cm). In the laboratory, the mussels were sorted and separated from the associated sediments and debris. In the upper 7cm of collected substrate 304 mussels were recovered including 43 below 23mm in length, while no mussels were recovered from the underlying 7cm of sediment. Hence, no mussels remained in the confines of the quadrat after collecting the top 7cm of sediment, and air-lifting was assumed a totally effective collecting method.

The above experiment also confirmed observations (by sight and touch) that the mussels did not burrow beyond the depth at which normal siphoning was not possible. This is a phenomenon common to mussels of temperate regions where winter burrowing and apparent "hibernation" are responses to low water temperatures (Stansbery, 1961; Walker, 1981b). Water temperatures were characteristically high throughout the year and never declined to such low levels as to induce the same response in mussels of the Magela Creek billabongs.

Having confirmed the total effectiveness of air-lifting as a collecting method, the effectiveness of hand collecting was then calculated on three occasions (September and October 1981, and May 1982) in Mudginberri billabong. Mussels were collected using Type 2 sampling (hand collecting from quadrats), then air-lifting was used to collect the substrate and remaining mussels. A total area of 24m² was sampled, representing a total of 589 mussels collected. The results are a direct check of the efficiency of Types 1 and 2 sampling which were the sampling procedures in other waterbodies (Table 3.1).

The results of the efficiency check are shown in Table 3.2. No mussels above 27mm in length were missed by hand collecting and over 60% of mussels between 20-27mm length could still be detected. Mussels below 19mm, however, were too small to be collected by hand.

The efficiency of Type 3 sampling (scooping sediments) was tested in Mudginberri (April and May 1982) and Buffalo (April 1982) billabongs. Mussels and sediments were collected using Type 3 sampling, prior to air-lifting a further 7cm of substrate. A total area of 26m² was sampled comprising a total of 50 mussels collected below 26mm. (Mussels above this size were collected by hand). In the laboratory the mussels were sorted and separated from the sediments according to scooped and air-lifted collection.

From the above experiment 36 mussels were found in the scooped sediments and 14 in those air-lifted. Thus scooping was found to have a mean efficiency of 72% in so far as collecting small mussels less than the size that could be collected by hand. A t-test was applied to the mean lengths of mussels collected by the two sampling methods. This revealed no significant difference ($P > 0.05$) between the two means ($t = 0.319$ on 22 DF). Therefore while scooping failed to collect all the small mussels from a defined area, the size distribution of small mussels so collected was nevertheless unaffected. For samples from Georgetown, Mudginberri and Nankeen billabongs then, a correction factor (of 1.39) was used to correct for numbers of small mussels missed when Type 3 sampling was used.

Although the experiments used to derive scooping efficiency were performed in the deep water of Mudginberri billabong, there was no reason to suspect that the efficiency would be any different in shallower water (<1m). As the methodology was similar over all depths of water, the correction factor is assumed applicable to the shallow sites of Georgetown and Nankeen billabongs where Type 3 sampling was performed. Similarly, the array of sediment types sampled in Mudginberri and Buffalo billabongs was sufficiently broad enough to represent the range found in Georgetown and Nankeen. Any discrepancy that could possibly arise would be from the selective efficiency of scooping between the heavier and more compacted sandy sediments and the lighter silt and detrital or silt and clay sediments. As two main types of sediments were collected from Mudginberri and Buffalo billabongs, a softer silt and detrital

sediment and a predominately sandy sediment, a chi-squared test was applied to the proportions of scooped mussels collected from the two sediment types. The test revealed no evidence for an efficiency bias of scooped mussels according to substrate ($\chi^2 = 0.386$, $P > 0.05$).

Presumably the effectiveness of the air-lift lay in its ability to draw up all the sediment from the sides and corners of the quadrat, places where the scoop could not always sample adequately. Further, in some instances it was not always possible to remove underlying debris such as sticks or buried logs, and these invariably interfered with scooping. This bottom type was typical of the two northern sites in Mudginberri billabong. Similarly sticky clay sediments were difficult to sample using the scoop, and at the fifth site in Mudginberri where this sediment was mixed with rocks and stones, air-lifting was virtually the only means of effectively collecting the sediment and small mussels.

3.2.3 Collection of limnological samples

Monthly sampling of mussels was immediately preceded in most instances (i.e. from January, 1981) by collection of limnological samples. (Prior to January 1981, collection and analysis of these samples was carried out by personnel from the Botany Department, University of Tasmania). Water samples were collected in the early morning generally between 0700 and 0830 and coincided therefore with minimum temperatures and importantly, minimum oxygen concentrations. As this was in accordance with the sampling rationale of Walker *et al.* (1983a) both data sets are comparable.

Collections were made from the bottom and surface waters, over a region where mussels occurred or where mussels were to be sampled. A fixed position in Georgetown, Corndorl, Mudginberri, Buffalo and Nankeen billabongs was sampled monthly but in Island, Ja Ja, Leichhardt and Jabiluka billabongs, water in the vicinity of the monthly transect was sampled.

Surface water samples were taken at 0.1m depth while bottom water samples were

collected by diving - that is, by swimming over the bottom sediments while holding and filling the bottles at a 45° angle immediately above the sediments. Constant swimming ensured that the waters from which the samples were taken had not previously been disturbed.

The limnological parameters to be measured from the collected water samples were bottom temperature and dissolved oxygen concentration, surface pH, conductivity and turbidity, and both surface and bottom phytoplanktonic chlorophyll. Of these, temperature and pH were measured directly in the field. The field procedure after collection was as follows:

One of the bottom water samples was fixed for later measurement of dissolved oxygen concentration. The water temperature of the other bottom sample was read by an accurate mercury thermometer, then between 250 and 500 mls of this water was filtered onto Whatman GF-C filters and stored on ice for later chlorophyll analysis. Similarly water from the surface sample was filtered and stored in the same manner for chlorophyll analysis. pH of the surface water sample was measured to the nearest 0.1 pH unit using a submersible glass electrode coupled to a portable Metrohm, Model E604 pH meter. The meter was calibrated against standard pH buffer solutions prior to collection of the water samples. The remaining surface water sample was taken back to the laboratory for measurement of conductivity and turbidity.

3.3 Routine laboratory procedures

All mussels used in routine reproduction and condition studies were processed on the day of collection. This involved excising the flesh and fixing the tissues for later histological examination, or otherwise cutting the mussels open (i.e. cutting the anterior and posterior adductor and protractor muscles) and storing them overnight in refrigerated water. Early experience proved that if mussels were kept any longer (e.g. overnight) before processing, mature females were liable to abort larvae from the inner gills. Hence, the routine laboratory procedure was as follows:

Mussels for reproduction and condition studies were randomly subsampled from the samples taken from the various habitats under study (section 3.1). Generally, mussels less than one year in age, however, were excluded from the subsamples and were dealt with separately. A number for later recognition was etched onto the shells of the selected mussels. The mark was made through the periostracum, with a small electric-powered hand drill (Dremel), fitted with a dental burr.

A number of external measurements of shell dimensions were made to describe the size and shape of mussels. Total length, maximum height and width were measured routinely, this system of measurements being the same as that used by McMichael and Hiscock (1958) except that maximum height was measured on the outside and not on the inside of the shell (Fig. 3.3). Each measurement was made to the nearest 0.5mm and was performed on a measuring board of plastic protected graph paper over a flat wooden base, bounded by two upright horizontal and vertical metal strips. Mussels were placed flush anteriorly and ventrally, or laterally to the bordering strips while another free, upright metal strip was placed flush to the mussel posteriorly, dorsally or laterally to read off the appropriate measurement. The measuring board was used only on mussels greater than 25mm in length. Smaller mussels were measured using Vernier calipers.

Three weights were performed routinely on mussels: total weight (expressed to the nearest 10mg); and flesh and dry weight (both to the nearest 1mg). All weights were taken on a top-pan balance precise to 1mg. Total weight refers to the weight of the whole, intact and live mussel. Flesh was shucked with a scalpel, care being taken to remove all the attached adductor and protractor muscles. Flesh weights were made after draining off the body fluids, and blotting the flesh of surface fluid with absorbent tissue paper. The blotting was performed in a consistent and repeatable fashion on all mussels. The further treatment of the flesh (i.e. fixation and oven-drying) and shells is dealt with in later relevant sections.

Collected substrate material from Georgetown, Mudginberri, Nankeen and Buffalo billabongs was sorted for small mussels on a large, shallow plastic tray. A pair of forceps was used to systematically move and sort the material from one end of the tray to the other, and having inspected all the material, the procedure was repeated in the same manner (i.e. the material was re-sorted).

Measurement of dissolved oxygen, conductivity, turbidity and chlorophyll were performed in the laboratory. Dissolved oxygen concentrations were measured by the Alsterberg azide modification of the Winkler technique (APHA, 1971). Conductivity was measured to the nearest $5\mu\text{Scm}^{-1}$ with a Metrohm, Model E518 conductivity meter. Turbidity was measured with a Hach 2100 turbidimeter, which gives a measure of the proportion of light scattered by the water at right angles to the incident beam. Filtered chlorophyll samples from field collection were frozen until processed. The determination of chlorophyll involved extraction with 90% acetone, followed by measurement of the absorbance at 750nm, 664nm, 650nm and 647nm (Jeffrey and Humphrey, 1975).

3.4 Data analysis

Where statistical procedures are described, analyses of variance were conducted using the NEVA programme (Burr, 1980); regression analyses using either the BAR3 programme (Chapters 4-6) (Burr, 1975) or the MINITAB statistical package (Chapters 7 and 8) (Ryan *et al.*, 1978); and complex exponential (Chapter 5) and logistic (Chapter 6) models were fitted using the BMDP statistical package for nonlinear regression (Dixon and Brown (Eds), 1979). The analysis of length-for-age data is described in section 6.4.1. Levels of significance of the statistical analyses in the tables, are indicated by the usual conventions of * for $P < 0.05$, ** for $P < 0.01$, *** for $P < 0.001$ or by ns for not significant (i.e. $P > 0.05$).

CHAPTER 4

SHELL SHAPE AND ENVIRONMENT

4.1 Introduction

A well recognised characteristic of unionacean bivalves is their high degree of phenotypic plasticity in shell shape. Explanations for why such high morphological variability amongst these forms can be maintained and can be adaptive, have been hypothesised as follows: Expanding largely on the review of Tevesz and McCall (1979), Tevesz and Carter (1980a) reiterated that inherent features of the environments that unionaceans inhabit are the low levels of competition and predation (by comparison with marine environments). Such low biotic selective pressures and the resultant lack of specialisation of freshwater mussels for particular resources such as food, substrate and space, were thought by Tevesz and McCall to have permitted the maintenance of variability; Eagar (1978) and Kat (1983c) added that high variability in shell shape might be adaptive in that it compensates for habitat unpredictability that results from the type of dispersal characteristic of unionids (i.e. via fish hosts). Such dispersal would preclude specialised habitat selection by juveniles.

Amongst the Australian hyriids, variability in shell shape within a single species is reportedly immense, a factor, according to McMichael and Hiscock (1958), accentuated by the vicissitudes of the Australian environment over large areas. For the hyriids (McMichael and Hiscock, 1958; Walker, 1981b), as in other unionacean families,

variability is a frustration to taxonomy and to other work in which high species integrity and ease of specific recognition is an essential prerequisite. For Velesunio angasi, the latter consideration has obvious implications for use of the mussel in pollution and biomonitoring work in the Magela Creek. No problems in this regard were expected for the freshwater mussels of the Alligator Rivers Region; according to McMichael and Hiscock, V. angasi is the sole species occurring in the area.

Within the catchment of the Magela Creek, a number of different and clearly distinguishable growth forms may be adopted by V. angasi. Of specific concern, early surveys produced isolated examples of shells from the billabongs that at cursory glance resembled those of a congener, V. wilsonii, a species which V. angasi more closely resembles than any other in the genus (McMichael and Hiscock, 1958). According to the taxonomic descriptions of McMichael and Hiscock, the shell of V. wilsonii is characteristically long with almost parallel dorsal and ventral margins, and an acuminate posterior end (Fig. 4.1); shells of V. angasi differ consistently from V. wilsonii in being notably higher, bearing a fairly pronounced wing and prominent and truncate posterior ridge (Fig. 4.1). For the taxonomy of the Australian fauna, specific recognition, which to date has relied almost solely upon conchological characters, McMichael and Hiscock stressed that specific, subspecific and ecotypic differences could only be discerned by studying large populations of mussels from as wide a range as possible. They believed nevertheless (reaffirmed later by McMichael (1967)), that despite variable shell form, the hyriid species of the Australian environment were discrete taxonomic

units that could be recognised easily by the student familiar with the group.

Considerable progress has been made in comparatively recent times in the taxonomy of North American unionaceans, with the use of electrophoresis and the resultant genetic identity that may now be ascribed to species and subspecies (e.g. Davis *et al.*, 1981; Kat, 1983b,c). This work marks a new era in the taxonomy of unionaceans that according to Kat (1983a,d) (and probably general opinion) has relied over-excessively on environmentally variable shell characters in the past for species determinations. Nevertheless, despite the anachronism that conchological investigation on its own is assuming, it remains an integral part of an approach in combination with soft-part morphology and electrophoretic techniques, that Kat (1983a,b) thought would be required to resolve taxonomic confusion in unionids. For congeners of some North American unionids not diverged long enough to accumulate genetic differentiation, dissimilarity of shell shape may be the only feature that allows for discrimination among species (Davis *et al.*, 1981; Kat, 1983b).

For species of a genus (such as Velesunio), whose taxonomic separation is based upon apparently distinct, conchological features, analysis of environmental relationships of variability of shell form in populations within a catchment, may provide for resolution and ultimately specific identification of the constituent forms. Populations so affected by environmentally induced changes (non-heritable) imposed directly on the phenotype, are referred to as ecophenotypes (e.g. McMichael and Hiscock, 1958). Such environmental

factors that may affect shell shape among unionaceans include temperature, water depth and flow rate, substrate type, trophic degree and size of the habitat, and water turbulence. These parameters and the resulting induced changes to shell forms that have been documented in the literature, are reviewed in Appendix 1.

The studies by Dell (1953), McMichael and Hiscock (1958) and Walker (1981b) represent the few ecological investigations to have identified ecophenotypic variation within the hyriids. The nature and extent of this variation in some cases has reconciled or amended existing taxonomic descriptions. No study in the Australasian region, however, has investigated thoroughly ontogenetic variability within a single species, which is critical to the present study in terms of characterising the species integrity of V. anqasi.

The limnological heterogeneity that prevailed within and between waterbodies of the Magela Creek, provided convenient environments in which to study the nature and extent of ecophenotypic variation in shell shape of the resident freshwater mussel fauna. Thus, the present investigation sought to describe this variation and its environmental determinants, in addition to describing ontogenetic variation in shell form of specific populations. As known soft-part (McMichael and Hiscock, 1958) and larval (Walker, pers. comm.) differences amongst members of the genus Velesunio are slight, conchological characters will no doubt continue to be important diagnostic features used for species recognition throughout the range of the constituent species. It was hoped from the present study, that apart from affirming the presence of a single species only (V.

angasi) in the Magela Creek, some additional insights into, and evaluation of, the present taxonomic distinction between V. angasi and the congener V. wilsonii, would result. These species are separated at present, chiefly by shell character.

Inherent in the evaluation mentioned above, is the extent to which shell description adequately distinguishes between ecophenotypes, and ultimately between species. Relative shell dimensions expressed by ratios, which partly demonstrate shape, were of considerable importance to the taxonomic work of McMichael and Hiscock (1958). Walker (1981b), however, made repeated reference to the inadequacies of relative dimensions (specifically relative height) towards detecting the presence or absence of wing development in particular, in hyriid mussels. Walker found that relative height showed trends in company with the degree of wing development in Alathyria jacksoni, but considerable variations in the relative height ratios (i.e. height/length) tended to conceal rather than to reveal any underlying patterns. While recognition of wing development is more dependent upon angular dimensions, both McMichael and Hiscock, and Walker, argued that their measurement was inappropriate for, and difficult to make upon, living mussels as fully opened valves are required. Relative shell dimensions between length, and height and width, expressed through allometric power functions over the size range of mussels considered in the present investigation, were used to describe variation in shape of mussels in the Magela Creek.

4.2 Methods

The relationships between length and height (i.e. relative height), and length and width (obesity) were chosen for analyses of environmental relationships of shell form variability in V. angasi. These dimensional relations have been most frequently mentioned as changing in predictable fashions from the headwaters of a stream in a downstream direction (section A1.1). If detected therefore, ecophenotypic variation in V. angasi should be evident in these relationships. Relative height most importantly, has been extensively used in taxonomic descriptions of members of the genus Velesunio (McMichael and Hiscock, 1958).

Length, height and width measurements of mussels collected from all of the Magela Creek waterbodies, were made according to the method described in section 3.3. Morphometric data derived from all mussels quantitatively sampled from the routine collections (made between 1980 and 1982, section 3.1), were used in the analyses. Unless otherwise indicated, only adult mussels were used for the analyses (>30 mm in length, section 7.7), as these mussels had been subjected to environmental influence for sufficiently long enough period of time to give a characteristic 'reaction form' for the local environment. The omission of juveniles was further justified in the observation that growth between the size dimensions approached isometry in juvenile mussels; indeed as shown below (section 4.3), some of the relationships between the size dimensions differed significantly between juveniles and adults of a given environment.

Plots of length against height and length against width of adult mussels, clearly indicated differential growth between the various size parameters. The appropriate size variables Y and X therefore were fitted to the allometric power function,

$$Y = AX^b$$

The constants A and b, were calculated using least squares regressions of the log transformed variables. The exponent b, the slope of the linear log-log transformed allometric equation, indicates the relative rate of increase or decrease of the dimension Y in relation to X. The value b therefore, provided a useful quantitative means of describing and comparing growth form variation in relative height and obesity, between different environments (i.e. between-waterbody comparison), and between habitats of the same environment (within-billabong comparison). Errors inherent in the measurement of size are assumed of the same order among each of the various size dimensions. Any biases introduced from measurement error should be consistent therefore, and should not alter or affect the comparisons of growth form variation between different environments. (For comparisons of relative height and obesity between populations, length (Y) is regressed against height and width (X) respectively.)

The approach used in the present study is a departure from previous analyses of ecophenotypic variation in unionaceans, that have relied entirely upon ratios calculated between the size dimensions for shell form comparisons. Ontogenetic variability inherent in these ratios may be minimised by including only data from mussels of a limited size range in the calculations - at the expense, however, of omission of data. As ontogenetic variability is accounted for in the allometric equation, study of ecophenotypic variation in shell form

of V. angasi using the slope of the equation, enabled most of the available data to be utilised. The order of increase in the slopes matched the order of increase in allometric intensity at mussel sizes only > 40 mm. (From the data of Tables 4.1 and 4.9, a negative correlation was found between the slope and intercept of the allometric equations describing the relationships between shell length and height, and length and width, among the populations.) For all populations nevertheless, size ranges > 40 mm comprised all or most of the material analysed (see Figs 6.23 and 6.24). Where tests of equality of slopes and intercepts between regression equations were required, analysis of covariance testing was performed.

Environmental parameters assessed as potential correlates of morphological variation in V. angasi were chosen on the basis of previous descriptions in the literature, as having relevance to shell form variation in unionaceans. From the review in section A1.1, these factors include water depth and flow rate, substrate type, trophic degree, and degree of water turbulence. The effect of turbulence upon shell form has been discussed in the literature mainly in relation to large lakes where stunting may result. This stunting reportedly affects overall size independently of relative changes in height and width (e.g. Green, 1972; Ghent et al., 1978). As variation in size of V. angasi is considered in chapter 6, minor consideration is given here to the relationship of water turbulence and shell shape. For between-waterbody comparison otherwise, standardised water depths were obtained from Table 2.1 while broad measures of relative stream velocities between waterbodies were inferred from substrate type (see sections 2.3.1 and 5.2). Sediment

characteristics, in terms of percent organic matter and mean sediment particle size, averaged broadly over each billabong are shown in Table 2.2. Trophic degree (as chlorophyll a), and a variety of physicochemical parameters considered, including dissolved oxygen and various measures of hardness, are given in Table 2.7 as averages over the seasons. For within-billabong study, records of depth and substrate at each sampling location were made according to previous descriptions (section 2.3.1). All depth measurements that were made at each site, were standardised to late Dry season levels (1 Nov. 1981). Stream velocities at each of the sampling sites in Mudginberri billabong were taken from the data of Figure 2.15. These measurements were determined for a specific stage of discharge (section 2.3.1.3) but nevertheless are assumed to represent a relative measure of flow rate that is constant between sites, for various intensities of Wet season discharge. The method of determination of mean chlorophyll concentrations averaged over the seasons for each of the sampling sites of Mudginberri and Buffalo billabongs (Tables 4.4 and 4.5), is given in section 6.4.3.1.

4.3 Variation in relative height

The nature of the allometric equations describing relative height and obesity of *V. angasi* for each of the populations in the Magela Creek waterbodies, was such that height increased relatively slower in relation to length, while width increased relatively faster. While ontogeny could explain this compensation of one shell dimension accompanied by a change in another within populations, among the populations no correlation was found between the same relative shell

dimensions. Thus for example, mussels from a population with relatively high shells were not necessarily less obese when compared with other populations. Averaged over all size classes of mussels, environmental influences affected relative height independently of obesity. To demonstrate this, regression analysis was performed between the slopes derived from the allometric equations for relative height and obesity, for the morphometric data of all mussels sampled in each waterbody (Tables 4.1 and 4.9). This analysis showed that the slopes of the respective equations were unrelated ($P > 0.1$).

4.3.1 Between sexes and waterbodies

The allometric regression equations describing the relationship between length and height of mussels, calculated for the sexes separately and combined from each waterbody, are shown in Table 4.1. Neither sex showed any tendency to be higher or lower in relative shell height than the other, and only in 4 out of the 12 Magela Creek populations were significant differences found between the regression coefficients of the equations derived for each sex. Only in one population (Nankeen) did the slopes differ significantly between the sexes. All further calculations and discussions therefore, are based on the equations derived from the data of the sexes combined. For 10 out of the 12 populations, the value of the slope b was greater than unity, indicating that length increases relatively faster than height.

Shell form description

In lateral outline, three shell forms were recognised in the Magela Creek. These are:

1) Billabong form - Except for one form found at a specific site in Mudginberri billabong (described below) the billabong form comprised, appropriately, shells from all billabongs. These shells were the true angasi form in that they were expanded posteriorly, where the elevated dorsal margin was abruptly truncated to produce a pronounced wing (Fig. 4.1). The larger shells in most populations, however, were truncated less abruptly and wing development was less obvious. A decline in relative height accompanied this trend. However, with increasing size of individuals from Nankeen billabong (particularly males), shells showed a tendency to become ovoid in lateral outline, with accompanying increase in relative height. As discussed below, no explanation for this increase in height of males could be advanced.

2) Creek form - These mussels were an ecophenotypic variant of the billabong or angasi form and inhabited the braided, sandy Creek channel above Mudginberri billabong - an environment exposed to rapid water flow during the Wet, with cessation of flow and evaporation of waters over the ensuing Dry. Creek mussels rarely occurred in shifting, sandy substrates; mussels would never survive in the hot, exposed sands during the Dry. Mussels invariably occurred in the rooted mat of aquatic or bankside vegetation, or amongst the roots of Pandanus that stabilised the shifting sands of the creek bed. While the Creek form was distinctly obese (section 4.4), in lateral outline

it resembled the billabong form in that, posterior to the beak, the dorsal margin was always elevated to produce a wing. However, unlike the billabong form, the dorsal margin was truncated less acutely and the postero-dorsal margin was slightly rounded. (In addition, the periostracum was dull and marked by fine growth lines, in contrast to the shiny periostracum of the billabong form.) This form is apparently widespread throughout the geographical range of V. angasi and was described and figured by McMichael and Hiscock (1958, Plate 3) as swollen shells of the holotype Aparchyria hemesa, an ecophenotypic variant of V. angasi from the Batavia River, Queensland (location 14, Fig. 4.6).

Although exposed to strong and turbulent currents, the microhabitats of Creek mussels were nevertheless stable, and there was no indication from the shape of these mussels to indicate that the shell morphology is an adaptation to anchorage and probing power of the foot for stability. The overriding environmental influence of shell form appears to be water recession, with the obligation by these forms to aestivate over the Dry season. According to the slope of the allometric equation (Table 4.1) height increased in the shells of Creek mussels faster than length. In company with increasing obesity, the increase in height with age results in an increase in shell volume. This would appear to be an adaptation whereby energy reserves, but particularly water content, are increased over the long and hot Dry season.

3) Non-winged form - Only at one location in Mudginberri billabong was this ecophenotype in its extreme form observed. Shells were of

the arcuate form with curved dorsal margins and reflected ventral margins. The location in the billabong was at site 5 (Fig. 3.1) that lay in direct contact with incoming turbulent and rapidly flowing Creek waters during the Wet season (Fig. 2.15). Mussels at this site were located on either sandy or stony-clay sediments. The characteristic shell outline was strongly reminiscent of the same form of Margaritifera margaritifera figured by Eagar (1977, 1978) and was undoubtedly, similarly associated with anchorage and resistance to displacement by strong water currents. The anterior ends of these shells were often strongly eroded. Relative height of the shells of this form was distinctly low, particularly in comparison with shells from other sites in the billabong.

Apart from the general description given above, the index of relative height b , the slope of the allometric regression equation, was found to adequately quantify the various growth forms and character gradients of V. angasi in the Magela Creek. This is demonstrated below.

Among the three growth forms just described, young shells were distinctly winged, and of the typical billabong or angasi form. However, at a size of only 20 mm, the postero-dorsal margin of the Creek form began to appear slightly rounded. Five young mussels (young of the year) from the Creek were transplanted to Leichhardt billabong in May 1981 to observe the ensuing morphological development of the shell. Mussels were placed in plastic containers filled flush to the rim with sediment. (The containers were the same as used to measure growth rates of mussels in the billabongs, and are

described in section 6.2. As no cage effects were observed with growth rates (section 6.3.3.4), shell shape is also assumed unaffected.) The lengths of these shells were 21, 22.5, 23.5, 33.5 and 35 mm. The rounded appearance of the postero-dorsal margin was discernible in all 5 mussels, but was especially evident in the two larger individuals. The mussels were recovered one year later, and had increased in size by an average of 23 mm. The 3 largest shells had assumed the Creek form (that included considerable inflation) while the two smallest had taken on the billabong form (that included relative compression laterally). The rounded postero-dorsal margin was absent in the 'new' billabong mussels and the margin was now abruptly truncated. Thus the distinct ecophenotype from the Creek is committed to its characteristic form only beyond a critical size. In addition to the observation that all young shells are winged, the transplant experiment just described indicates that the various shell forms are ecophenotypic variants only of a wider population of V. angasi in the Magela Creek, that has a common genetic identity.

Environmental correlates of relative height

Using the slope, b , of the allometric equation describing relative height of mussels from each of the waterbody populations (Table 4.1), environmental determinants of the variation in relative height between populations were sought. (A high value of b indicates that relative height of shells in the population is low, while a low value indicates the reverse.) Analysis of covariance testing showed that differences in the slopes and elevations of the allometric regression equations between the 12 Magela Creek populations were highly

significant ($P < 0.001$); there was a general trend toward decreasing height of mussels in a downstream direction.

The effect of increasing stream velocity upon shell morphology in the billabongs was to select for or induce growth of a non-winged form. The description of this form is given above. A decrease in height accompanies the progressive dorsal arching and ventral reflection of shells exposed to strong water currents (section 4.3.2). The two environments that experienced the most turbulent and strongest currents during the Wet season were the Magela Creek channel and Mudginberri billabong. The shells of mussels in the populations from these waterbodies, however, were amongst the highest in the Magela Creek (Table 4.1). Thus shell height was unrelated to water velocity and turbulence across all the waterbodies. Similarly sediment characteristics were unimportant; coarse and fine, organic and inorganic sediments contained high or low shells in equal proportions. Water depth and various physicochemical parameters (from Table 2.7) were similarly unrelated to shell height.

The single correlate of relative height that showed a progressive trend along the Magela Creek was apparently the trophic factor, chlorophyll, a measure of algal abundance in the waterbodies. With increasing eutrophy, relative height declined. The relationship between relative height and chlorophyll is plotted in Figure 4.2. A highly significant logarithmic regression equation was fitted to the data. The equation is:

$$Y = 0.887 + 0.0753 \ln X \quad (P < 0.001, r^2 = 0.769)$$

where Y = slope (b) of the allometric equation for relative height, and X = mean chlorophyll a averaged over the seasons ($\mu\text{g/l}$). This is a similar relationship as found between population growth rate and chlorophyll described in section 6.4.3.2, where growth rates of mussels were shown to be positively correlated to algal abundance as measured by chlorophyll.

Thus, increasing growth rate is accompanied by decreasing shell height. Just as within populations where height increased relatively slower in relation to length, it is tempting to suggest that the relationship just described and plotted in Figure 4.2, is merely an extension of this ontogenetic principle - i.e. shell height decreases with increasing size. However, there is evidence to suggest that it is growth rate per se and not merely size of mussels investigated that determines relative shell height. Allometric equations of relative height for juvenile (young of year) mussels (< 35 mm in length) for populations from Georgetown, Mudginberri, Buffalo and Nankeen billabongs are described in Table 4.2. Mussels in Nankeen billabong are the fastest growing of the populations shown in this Table (section 6.4.2), and it is apparent that juveniles from this billabong also have the lowest shells. Thus, the degree of change in relative height is generally constant between populations, at any given size.

The slope of the allometric equation for relative height of juveniles from Nankeen billabong (Table 4.2), indicated that length increased relatively faster than height and accorded with the relationship

plotted in Figure 4.2. Older mussels, however, showed a reverse trend of more rapid increase in height in relation to length. The slopes of the allometric equations of relative height, between juveniles and adults differed only in this population (Table 4.2), and the difference moreover, was highly significant ($P < 0.001$). Relative height therefore, plotted well below the value that could be expected for the given trophic level of the billabong. No explanation for these high shells, ovoid in lateral outline, can be given. They were peculiar mainly to male mussels; the slopes between the allometric equations of relative height of the sexes differed significantly ($P < 0.01$). A synergism between high late Dry season turbidities (and resultant low algal levels) and consistently low seasonal concentrations of dissolved oxygen could be responsible for the ovoid outline of male shells.

4.3.2 Within billabongs

Quantitative data for within-billabong study of variation in relative height were collected from Georgetown, Mudginberri, Buffalo, Leichhardt and Nankeen billabongs. The allometric regression equations describing the relationship between shell length and height for the various sites and depths of the respective billabongs sampled, are shown in Tables 4.3-4.7. The data within each billabong, are generally a composite of those used in the single regression equation averaged over each billabong (Table 4.1), and at all sites and depths morphometric data from a minimum of 50 mussels were used. Regression equations were calculated separately for the sexes of mussels from Nankeen billabong, where the slopes between the

respective equations combining all the data (Table 4.1) differed significantly.

In Georgetown billabong, relative height of shells was greater on the sandy, shallow transect located upstream (transect B) as opposed to shells found on the silty, clay and deeper transect downstream (transect A) (Table 4.3). On the same transects, occur younger and older mussels respectively (section 6.5.3.1). The shells of younger mussels are relatively higher in Georgetown billabong (as in most other billabongs) than adult shells. (Compare the slopes of the respective allometric equations of relative height for juveniles and adults shown in Tables 4.2 and 4.1.) Thus, the higher shells observed on transect B are presumably the result of this difference in age structure.

Given the relationship between relative height and trophic status as described above (section 4.3.1), and the observation of a low, dorsally-arched shell form at one sampling site, trophic status and Wet season stream velocity appeared to be obvious potential correlates of relative height in shells between sites in Mudginberri billabong. Relative height (as the slope b , of the allometric equation) is given in Table 4.4, in relation to stream velocity and chlorophyll concentration between sampling sites of Mudginberri. Given that the low relative height of shells (i.e. high value of b) at site 5 is unequivocally a response to rapid Wet season stream velocities (as discussed above), chlorophyll would otherwise appear to be unrelated to relative height. Stream velocity as shown below, however, was negatively correlated with relative height.

Eagar (1948, 1977, 1978) noted that unionaceans shared two contrasting patterns of growth between which there were often few intermediates; the first pattern, a dorsal arched form, was adapted for fast currents, and the second, a straight-hinged form was adapted for quieter waters (see section A1.1). He nevertheless proceeded to illustrate various stages and trends of dorsal arching with decline in relative height, of shells of Margaritifera margaritifera, associated with increase in water velocity of the habitat (Eagar, 1977, 1978). Eagar observed that bivalves with progressively more dorsally arched and ventrally reflected shells, tended to survive in stations of increasing water turbulence. Thus, the "progressive" "trends" but "contrasted patterns" with "few intermediates" are seemingly conflicting and contradictory ideas.

The same trend of shell form as described for M. margaritifera by Eagar (1948, 1977, 1978) was apparent in the mussels of Mudginberri, a billabong through which the waters of the entire catchment upstream of the floodplain are channelled during the Wet season. An extreme non-winged form with dorsal arching and reflected ventral margin, as described above, was characteristic of the larger mussel shells at a site exposed directly to incoming strong turbulent currents. Winging was also less pronounced in the shells of larger mussels occurring in some unstable sandy sediments exposed to relatively strong currents during the Wet. A decrease in relative height accompanied the progressive trend in loss of definition of the posterior wing. A similar trend by M. margaritifera was shown by Eagar (1977, Fig. 1; 1978, Fig. 8). A very significant ($P < 0.01$) negative linear

correlation was observed between relative shell height and stream velocity in Mudginberri billabong, indicating that more dorsally arched forms tend to survive in sites of increasing water turbulence. The relationship between relative height and stream velocity is shown in Figure 4.3, along with the fitted linear regression equation.

The Wet season waters emitting from Mudginberri billabong branch, so that water entering the neighbouring Buffalo billabong immediately downstream is considerably reduced in velocity. As a consequence, correlates of relative height of mussels in Buffalo billabong were more difficult to discern (Table 4.5). Both trophic status and Wet season flow rates (as discerned by substrate type) at the sites may influence relative height. Stream velocity (assumed greater over the sandy sediments) may be responsible for the lower shells found on sandy sediments to the north of the billabong (sites 1-4), whereas increasing eutrophy to the south (i.e. increase in site number) may be the cause of lower shells. In relation to height variation in other billabongs (as discerned by the magnitude of spread of the slope, b), differences between relative height of shells between the sites of Buffalo billabong are small.

An increase in relative shell height was found with increasing depth in the floodplain billabongs, Leichhardt and Nankeen (Tables 4.6 and 4.7 respectively). Although the slopes of the allometric equations describing relative height differed significantly between the sexes in Nankeen billabong (Table 4.1), relative height of both sexes increased with depth in a similar fashion (Table 4.7). The relationship between relative shell height and depth for mussels from

Nankeen was plotted therefore, for the data of the sexes combined. Plots of relative shell height and depth, with the associated fitted linear regression equations to describe the relationships, are shown in Figures 4.4 and 4.5 for Leichhardt and Nankeen billabongs respectively.

Growth rates for all size classes (Leichhardt) and in the younger ages (<13 years, Nankeen) decreased with increasing depth, presumably with decreasing eutrophy and increasing oxygen depletion at depth (section 6.4.3.1). Given the relationship found between billabongs, in which relative height declines with increasing eutrophy and growth rates (Fig. 4.2), it might also be assumed therefore, that increasing shell height with depth is also a result of declining eutrophy, and accompanying decrease in growth rate, with depth.

In Nankeen billabong, at approximately half-way through the lifespan of mussels (at about 13 years), growth rates are reversed so that older mussels (>13 years) grow fastest in the deepest waters (section 6.4.3.1). Nevertheless, relative height of shells increases with depth, independently of this growth rate reversal. As shown above (section 4.3.1), mussels are committed to a given growth form beyond a critical size. Presumably therefore, older mussels in Nankeen continue to grow and conform to the lateral outline prescribed them in younger years, and relative height therefore is relatively uninfluenced by trophic and growth rate phenomena.

4.3.3 Geographical variation in juvenile Velesunio

In the Magela Creek, morphological variability recorded in the relative height of shells of juvenile V. angasi was slight. Although analysis of covariance testing showed that differences between the slopes and elevations of the allometric regression equations of relative height, for juveniles from 4 populations investigated (Table 4.2), were highly significant ($P < 0.001$), compared to adult populations these differences were minor. Within populations, variation between length and height as denoted by r^2 values of the allometric equations, was low for juveniles ($r^2 > 0.97$, Table 4.2) as compared to adults of the same populations ($r^2 > 0.86$, Table 4.1). Moreover, the range in the values of the slopes of the equations for the 4 juvenile populations, was less than 60% of the range recorded in the adult populations from the same waterbodies.

Relative shell height of V. angasi from the Magela Creek as shown above, progressively declined with increasing age, and with the environmental influences of increasing eutrophy and (more locally) increasing stream velocity over relatively unstable sediments. These changes to relative height brought about by ontogeny and environment were demonstrated by allometry and by variation in the slopes of the allometric equations between populations respectively. The progressive decline in relative height was generally accompanied by progressive loss of definition of the posterior wing.

According to McMichael and Hiscock (1958) the shells of V. angasi and V. wilsonii are clearly distinguishable. The shells of V. angasi are

winged and truncated posteriorly, while the shells of V. wilsonii are never more than slightly winged, being acuminate posteriorly so that the dorsal margin is straight and almost parallel to the ventral margin. Accompanying these features, the maximum height index (MHI = height/length) is reportedly lower in V. wilsonii (46-53%) than in V. angasi (50-60%).

All shells of young V. angasi in the Magela Creek (<35 mm) without exception were strongly winged. This feature was borne out in calculations of relative height of juveniles. Despite significant differences between the slopes of the allometric equations of relative height for the 4 populations investigated (Table 4.2), actual differences in relative height between the populations were minor; the minimum MHI values for example, predicted for the populations from the regression equations, ranged between 59-61 percent.

Thus, the evidence from the present study indicated that the clearly distinguishable outline of the shells of V. angasi, is best exemplified in those of the young mussels relatively uninfluenced by the environment. Low variability in lateral outline of shells of V. angasi in the Magela Creek further, suggested that the young stages provide the most suitable material for which interpopulation comparisons of shell form, without the effect of environment (such as for taxonomic study), may be made. These same virtues were assumed to characterise the young shells of V. wilsonii, after examination of some limited material from a site outside of Mary Kathleen, Queensland (location 9, Fig. 4.6). These shells were

characteristically non-winged, and contrasted sharply in form to the winged young shells of V. anqasi from the Magela Creek (Fig. 4.1). Both species were clearly distinguished by relative height alone; the MHI values for young of V. anqasi ranging from 59-61% (at the least) in the Magela Creek, and of V. wilsonii from Queensland ranging from 44-45% (Table 4.8). These limited observations stimulated enquiry as to whether such differences in relative height between juvenile V. anqasi and V. wilsonii were consistent over the broad geographical ranges of both species. Put another way, the question was posed: is relative shell height without the influence of environment, sufficiently bimodal throughout the ranges of both congeners, to clearly separate the species? If this was the case, then morphometry of young shells could provide useful taxonomic differentiation of the two species in regions where doubt was expressed in the species composition.

All records of shell length and height of small V. anqasi and V. wilsonii (< 40 mm length) throughout the entire ranges of both species, were kindly forwarded by curatorial staff of the Australian Museum (Sydney). Unfortunately the shells were not personally inspected and thus the relative ages of the constituents, and the environments from where they were collected were unknown. Museum collections for example, may be assumed to be biased toward those from shallow waters. Such environments may include variable habitats such as small, ephemeral creeks that are inhabited by stunted mussels. Some of the V. anqasi material forwarded (for example, location 14, Table 4.8) was known to comprise the Creek form, which in the Magela Creek is a relatively high and slow growing shell.

Nevertheless, the very nature of the collections, i.e. probably from similar environments, likely inferred a relative constancy in shell form between the various locations, so that comparisons should still be valid. The morphometric data with respect to species and location are given in Table 4.8, while the locations with respect to geography, species and mean annual rainfall, are shown in Figure 4.6. With the reservations concerning the unknown ages of the constituents and their environments, nevertheless, some points may be made from the data of Table 4.8 and Figure 4.6.

No plots of MHI frequencies were drawn to discern bimodality. However, reasonable separation of the species by relative height alone is apparent from the data of Table 4.8. In regions where the species are sympatric or where the species ranges border, possible misidentifications may have occurred (indicated for locations 1 of V. angasi and 4 of V. wilsonii respectively, Table 4.8). V. angasi for example, has been reported to occur in the catchment of the Victoria River (N.T.) (location 13), suggesting that the individual V. wilsonii reported at location 4 in the same catchment was misidentified. Apart from this exception, the MHI values of V. wilsonii are consistently low.

Relative height of V. angasi is more variable, but apparently much of the variation is accountable for. Despite the fact that the extent of ecophenotypic variation is unknown in the data, it nevertheless appears possible that a geographical cline in relative height of V. angasi exists; individual shells are apparently higher in northern and wetter parts of the range of the species. At more southern and

drier parts of the range, however (e.g. locations 11, 12 and 13, N.T.), shells are lower. More thorough investigation, controlling for the environments, will be required to affirm the presence of such a cline.

High species integrity of V. angasi otherwise, is assumed in far northern locations of the Northern Territory, including the Magela Creek (location 16, Fig. 4.6), where MHIs are consistently high. Low variability in relative shell height within and between populations of young mussels, and the high nature of the young shells (MHIs ranging in the very least between 59 and 61%) which are consistently winged and truncate in appearance, leads to the unequivocal conclusion that V. angasi is the sole species occurring in the Magela Creek. If a cline throughout the species range in relative height is actually confirmed, however, species determination may be difficult in more southern latitudes, particularly in areas of sympatry of V. angasi and V. wilsonii or in areas where the ranges border.

4.4 Variation in obesity

Allometric regression equations describing the relationship between length and width of mussels, calculated for the sexes separately and combined from each waterbody, are shown in Table 4.9. In 9 of the 12 Magela Creek populations, females were found to be more obese than males (-indicated by the larger slopes of the regression equations derived for males, as opposed to females). However, only in Georgetown billabong did the slopes of the regression equations differ significantly between the sexes (Table 4.9). In only 3 other

populations, moreover, did the intercepts of the equations differ significantly between the sexes. As variation in obesity between populations is described by way of the slope, b , of the regression equations, all further discussions and calculations therefore are based on the equations of the sexes combined. In all populations, the value of b was less than unity, indicating that width increases relatively faster than length.

In terms of obesity, two shell forms were recognised in the Magela Creek, the billabong form and the Creek form. These are the same forms as those described for lateral outline, except that the billabong form here includes both winged and non-winged shells. The Creek form was clearly distinguishable, in being remarkably more obese compared to shells from the billabongs. The causes of this inflation are considered further below.

As found above (section 4.3), averaged over all size classes of mussels and over all waterbodies, variation in obesity occurred independently of changes in relative height. The single most important environmental correlate of obesity was clearly apparent when all data, both within and between populations were amassed. For within-billabong study, quantitative data were collected from Georgetown, Mudginberri, Buffalo, and the floodplain billabongs, JaJa, Leichhardt and Nankeen. The allometric regression equations of obesity for the various sites and depths of the respective billabongs sampled, are shown in Tables 4.10-4.13. Morphometric data from a minimum of 50 shells at each site and depth was used to calculate the regression equations. Both within and between billabongs, obesity

was found to increase with increasing water depth. So direct was the relationship across the billabongs in fact, that a single analysis of the data both between and within billabongs was possible. Obesity (as measured by the slope, b , of the allometric regression equations) is plotted with respect to depth, for the data of each billabong in Figure 4.7. (Decreasing values of the slope, b , indicate increasing obesity.) A highly significant ($P < 0.001$) linear regression equation was found to describe the relationship between obesity and depth. The equation is:

$$Y = 0.986 - 0.097X \quad (P < 0.001, r^2 = 0.801)$$

where Y = slope (b) of the allometric equation describing the relationship between shell length and width,
and X = water depth (m).

Thus 80% of the variation in obesity of mussel shells recorded in the Magela Creek billabongs, was accounted for by water depth.

A positive correlation was found between age of mussels and depth within most billabongs (section 6.5.3.1). Using mean age and mean billabong depth data (Tables 6.37 and 2.1 respectively), a significant linear regression ($P < 0.05$) was also found between age and depth across all billabongs. (Thus for example, older mussels are found in deeper billabongs.) Given the depth/obesity relationship above and the depth/age correlation, obesity therefore was also linearly correlated with age when the data were regressed across the billabong averages. The linear regression equation found to describe the relationship between obesity and age is:

$$Y = 0.974 - 0.0138X \quad (P < 0.01, r^2 = 0.654)$$

where Y = slope (b) of the allometric equation describing the relationship between shell length and width,

and X = mean age of mussels (years).

This correlation in fact, is a better one than that calculated using values of obesity and depth averaged over each billabong. Using billabong averages, only 50% of the variation in obesity was accounted for by variation in depth, as opposed to 65% accounted for by variation in age. Thus rather than a direct effect of depth upon obesity (that could only be explained through associated changes in hydrostatic pressure or temperature for example), the most likely explanation for increasing obesity with depth is an ontogenetic one; with increasing age, mussels become more obese. Because older mussels are found in deeper waters of the Magela Creek, the relationship between obesity and water depth may be associative only.

Of other limnological and hydrological factors considered as correlates of obesity in the billabongs, substrate type appeared to be the only influence apart from water depth. Softer and less consolidated substrates tended to support more inflated shell forms. Thus as a general rule, data points lying below the regression line of Figure 4.7 represent more obese forms found on soft organic sediments; noteworthy are the soft and relatively unconsolidated sediments of Gulungul, Corndorl, the shallowest waters of JaJa, and site 2 (Table 4.12) of Buffalo billabong. Conversely, firm sediments supported generally more compressed forms that plotted above the

regression line of Figure 4.7; these sediments, for example, characterised Georgetown and Island billabong. Increasing obesity of *V. angasi* in soft, unconsolidated sediments of the Magela Creek billabongs could be a morphological adaptation enhancing buoyancy and preventing shells from sinking and asphyxiating.

The shells of mussels from the Magela Creek channel, were by far the most inflated of those of any population found in the Magela Creek (Table 4.9). As Creek mussels live in the most shallow sites and are amongst the youngest (Table 6.37) of any population, the degree of inflatedness of their shells therefore, is in direct contradiction to both the depth-obesity and age-obesity relationships just described for billabong mussels. According to Eagar (1978), increase in relative height and obesity provide the most functionally efficient means of increasing bivalve shell volume at the expense of its surface area. Shells of Creek mussels are both the highest and widest in relation to length, than shells of any other population. As discussed previously (section 4.3.1), the resulting increased volume would seem to be an adaptation whereby energy reserves, and especially water content are maximised for the period of aestivation during the hot Dry season.

For comparison with the Creek form from the Magela Creek catchment, mussels were collected from running waters of the East Finnis River, some 280 km west of Jabiru (location 4, Fig. 4.6). Because of possible clinal effects (section 4.3.3), comparison of shell forms over broad geographical areas should be approached with some reservation and caution. Nevertheless, even in relation to

neighbouring billabong mussels in the East Finnis River catchment (similar in general appearance to billabong forms from the Magela Creek), the shell form from running waters of the river were notably strongly winged and laterally compressed. The slopes of the respective allometric equations of relative height and obesity for these river shells are given in Tables 4.1 and 4.9. Thus from these Tables, the shells from the East Finnis River are also relatively high and compressed by comparison with populations from the Magela Creek. Compared to the Creek form from the Magela Creek in particular, the river mussels are much less inflated. The two environments differ in that the Magela Creek below Jabiru is ephemeral, whereas the East Finnis River at the site of mussel collection flows all year round. Like the Creek mussels, the microhabitat of the river mussels was relatively stable, with mussels being lodged generally amongst rooted macrophytic and bankside vegetation. As there is no obligation for the river forms to aestivate, the relatively compressed shells are probably an adaptation enabling mussels to orientate themselves better to withstand strong (Wet season) currents. Because of the stable microhabitat presumably, dorsal arching was not observed in the river shells. Thus in two very similar (flowing waters) and yet contrasting environments of ephemeral and permanent streams respectively, occur two contrasting shell forms; one obese and adapted to aestivation, the other compressed and adapted to stability in strong water currents.

4.5 Discussion

Ontogenetic and sexual variability in shell shape

Allometric relationships were found between shell length and height, and shell length and width of V. angasi in the Magela Creek; relative height declined but obesity increased with size. Among unionaceans, allometry is apparently commonly observed between standard shell dimensions (Eagar, 1978) and relative height and obesity may either increase or decrease with age (Eagar, 1948). Agrell (1949) and Crowley (1957) also reported for example, that juvenile unionids were less obese than adults, but the reverse allometry for the same relationships was reported by Ortmann (1920) and Ball (1922). Stream-forms, including the Australian hyriid Alathyria jacksoni (McMichael and Hiscock, 1958; Walker, 1981b) generally decrease in relative shell height with age with progressive dorsal arching of the shell (section A1.2). Changes in relative height of V. angasi were not accompanied by compensatory changes in obesity as have been reported for other unionaceans (Eagar, 1948; Agrell, 1949; Hendelberg, 1960).

Invariably, studies of ecophenotypic variation in unionaceans have relied upon ratios calculated between the size dimensions for comparisons of shell form. Isometric growth is assumed in comparisons of ratios. Thus as also noted by van der Schalie and van der Schalie (1950) and Cvancara (1963), if shells of variable age are compared, even considering only those shells of the adult population, variability caused by allometry is introduced. In the present study

allometric equations describing the relative growth dimensions of the adult population were used to study ecophenotypic variation. Ontogenetic variability was thereby accounted for. The extent of departure from unity of the slope of the allometric equations in some extreme populations, indicated that considerable error in comparisons would have occurred had isometric growth between the size dimensions been assumed.

No obvious sexual dimorphism in shell shape was observed in V. angasi from the Magela Creek. While females tended to be more obese than males, the differences found between the sexes were generally not statistically significant. Similar, inconspicuous tendencies only have been reported for other unionaceans (Johnson, 1946; Heard, 1975; Dudgeon and Morton, 1983) including hyriids (McMichael and Hiscock, 1958; Walker, 1981b), for the shells of females to be more inflated than males. In these groups, it is generally assumed that ecophenotypic variation in shell form is sufficient to mask any tendency for dimorphism between the sexes. Marked sexual dimorphism in shell features, however, characterise lampsiline unionids (section A1.2). Amongst other features, females are more obese than males particularly over the marsupial regions, an adaptation according to Coker et al. (1921) and Anderson and Ingham (1978) allowing for large numbers of eggs to be held in the outer gill marsupia.

Shell shape and environment

Three shell forms of V. angasi in lateral outline and obesity were recognised in the Magela Creek: a winged, billabong or true angasi

form, and two ecophenotypic variants of the true form, a non-winged and dorsally arched form, and a high, moderately winged and swollen Creek form. Indications from descriptions and figures of McMichael and Hiscock (1958) are that the swollen Creek form is an ecophenotype, distinctive in morphology, that is widespread throughout the geographical range of the species. This study, however, is the first to identify such shells as a discrete form of V. angasi and to interpret the functional morphology of such a form. Experiments on transplanting young Creek mussels to a billabong confirmed that the distinctive Creek shell was a phenotypic morph only of the true angasi form, when young shells developed according to the typical form of the resident billabong mussels.

The only immediately apparent environmental trend that accompanied the progressive decrease in relative height of mussels in a downstream direction of the Magela Creek was increasing eutrophy. Increasing eutrophy was also correlated with increasing growth rate of mussels (section 6.4.3.2). Thus with faster growth and increase in size, relative height declined, in company with a progressive loss of definition of the posteriorly expanded wing.

As summarised by Eagar (1948) (see section A1.1), unionacean form is often reported to become more arcuate in terms of lateral outline in swift-flowing waters as opposed to increasingly straight-hinged and winged in slower flowing or still waters. Generally a decrease in relative height accompanies the trend to more arcuate form and increasing stream velocity (e.g. Altnoder, 1926; Dell, 1953; Cvancara et al., 1978; Walker, 1981b). Wet season stream velocities through

the Magela Creek waterbodies do not correlate with the relative position of the waterbodies along the Creek, mainly because backflow billabongs occurring upstream do not receive significant flow compared to channel and some floodplain billabongs lower downstream. Thus the trend downstream of decreasing relative height of V. angasi is not correlated with decreasing stream velocity. Moreover the mussels of two populations only, those of the Magela Creek channel and Mudginberri billabong, were affected by rapid stream velocities. Compared with the other populations the shells of these mussels were amongst the highest. The decline in relative height of V. angasi found in the downstream direction of the Magela Creek therefore, is in direct contrast to other reported ecoclines in relative height in riverine mussels (see above references) where an increase in relative shell height can be expected in the downstream direction.

Apart from V. angasi, trophic factors alone were also suggested by Agrell (1949) as affecting various shell dimensions of Swedish unionids including relative height, while Cvancara et al. (1978) implicated nutrient availability as one of a number possible factors affecting relative height of North American unionids with respect to location along a stream. Both studies, however, observed a positive correlation between eutrophy and relative height. The correlation observed for V. angasi was a negative one. Among marine intertidal gastropods, Vermeij (1980) summarised a number of reports for species in which relationships between growth rate and intensity of allometry have been noted. Other than V. angasi, there has been no direct report of this phenomenon in unionaceans although one might ask whether the results of Agrell and Cvancara and co-workers are not

suggestive of this. Regardless, no obvious functional advantage can be implicated from the eutrophy/relative height relationship. For V. angasi it is more easily interpreted in ontogenetic rather than environmental terms; with increasing growth rate, relative shell height declines.

Within habitats, such as sites and depths of the same lake, attempts at demonstrating relationships between shell morphology and environment have generally met with little success (Fisher and Tevesz, 1976; Ghent et al., 1978; Horn and Porter, 1981). In relation to lateral outline, Cvancara (1972), however, found a significant decrease in height of two unionid species with increasing depth in lake environments. No causal explanation was offered. Harman (1970) also observed that Anodonta grandis was higher in the littoral than the profundal waters of various lakes studied, and implicated a temperature decline with depth as a possible cause. In contrast to these observations, relative height of mussels in floodplain billabongs of the Magela Creek, increased with increasing depth. The likely cause of this trend to increasing shell height with depth, was argued to be the same factor that determined variation in relative height between waterbodies, namely decreasing eutrophy. Evidence for this association was substantiated in the observation that growth rates of mussels (and thus partly food availability) declined similarly with increasing depth in the same billabongs.

The increase in relative height of male mussels in particular, with age in Nankeen, was exceptional amongst the billabong populations

where the pattern was for a general decline in height. This tendency for increased height, however, was not accompanied by more pronounced wing development but with development of a more ovate outline. No causal explanation for this unusual ontogeny can be offered. Thus, these shells became more ovate with increasing depth. Harman (1970) also noted that Lampsilis r. radiata become more ovate in lateral outline with increasing depth in the Finger Lakes of central New York State (U.S.A).

In Mudginberri billabong through which relatively rapid flowing waters pass each Wet season, a negative correlation was observed between relative shell height and stream velocity amongst various sites exposed to more or less strong currents. Associated with the decrease in height of mussels was the development of more dorsally arched and ventrally reflected, and non-winged shells. The correlation between stream velocity and shell height indicated that more dorsally arched forms tend to survive in sites of increasing water turbulence. Eagar (1977, 1978) first provided a functional explanation for this relationship, widely observed amongst stream-dwelling unionaceans (see section A1.1). Dorsally arched and ventrally reflected shells provide a larger pedal gape, which in turn allows a stronger anchorage for the foot in unstable substrates. Shells with curved ventral margins on the other hand were argued by Eagar to have functional advantage over the dorsally arched shells, in providing active movement over the surface of the substrate in quieter environments. In relation to the respective dorsally arched and straight-hinged growth patterns, Eagar (1948, 1977, 1978) referred to these as "contrasting" growth forms between which there

were often few intermediates. He nevertheless noted that bivalves with "progressively" more dorsally arched and ventrally reflected shells tended to survive in stations of increasing water turbulence. The same continuum of form was observed for shells of mussels in Mudginberri billabong and progressive dorsal arching (culminating in ventral reflection at one site) was accompanied by decrease in relative height and progressive loss of definition of the posterior wing.

In addition to V. angasi, arcuate shell forms in environments of fast water currents have been noted for various other hyriid unionaceans (Dell, 1953; Walker, 1981b). Walker observed two distinct shell forms of the riverine mussel Alathyria jacksoni, a winged (straight-hinged) and non-winged (dorsally-arched) form, characteristic of mussels from moderate and fast water currents respectively. Few intermediate forms were observed between these two growth patterns. Although a decrease in relative height accompanied development of the arcuate form, Walker emphasised that the relative height dimension (height/length) was not particularly sensitive to revealing the distinct, dual growth patterns. A continuum of form of V. angasi at sites in Mudginberri billabong, however, was observed with progressive dorsal arching and loss of definition of the posterior wing, in response to increasing current velocity. Relative height as measured by the slope of allometric regression equations relating length and height, revealed this continuum. The same observations are relevant to between-waterbody comparisons in the Magela Creek where increasingly less obvious wing development in association with increasing eutrophy of the environment, was detected

by associated changes in relative height. No comparable arcuate form of the congener V. ambiguus in the Murray River in southeastern Australia was reported by Walker (1981b). Walker believed that the mussel was absent from fast-flowing waters because it was unable to maintain a strong anchorage.

As a very general rule, shells of unionaceans tend to become obese in quieter waters such as prevail downstream in streams and in lakes, as opposed to being laterally compressed in more turbulent environments such as in the headwaters of streams and in exposed lake sites (see section A1.1). The functional advantage of increased obesity in quiet waters has generally been given as enhanced buoyancy that prevents shells from sinking into soft, muddy sediments that invariably prevail in these waters (Eagar, 1978; Ghent et al., 1978; Anderson and Ingham, 1978; Tevesz and McCall, 1979; Walker, 1981b; Stern, 1983). Eagar (1978) added that greater obesity would increase the volume of living tissue thereby providing improved metabolic and functional activity to forms from quieter waters. Functional interpretation as to why less inflated and more compressed shells occur in unstable and shifting substrates has been variously offered as adaptations enabling mussels to orientate themselves better to withstand strong currents, and to plough deeper and more supportive furrow paths (Wilson and Clark, 1914; Grier and Mueller, 1926; Clarke, 1973; Anderson and Ingham, 1978; Ghent et al., 1978; Stern, 1983). Clarke (1973) nevertheless, found L. r. siliquoidea to be more obese on shifting and unstable lake sediments than elsewhere. He suggested that these obese forms might be better able to remain in place without being dislodged by turbulent wave action and currents

during storms. Other than hydrological factors, increasing eutrophy has also been implicated as a cause of greater obesity of some unionids (Agrell, 1949; Cvanara et al., 1978).

Three environmental correlates of obesity in V. angasi were identified in the present study, namely water depth, substrate type and exposure of mussels due to water subsidence. Only the latter two factors apparently, have functional interpretation. Eighty percent of the variation in obesity found in billabong mussels, was accounted for by variation in water depth. Mussel shells across all billabongs, were found to increase in obesity with increasing depth. The most reasonable explanation for this relationship, however, was forwarded in ontogenetic rather than environmental terms; across the billabongs, mussels become more obese with increasing age, while age of mussels generally, increases with increasing water depth both within and between billabongs. No depth related factors have been implicated in the literature as affecting obesity of unionacean shells, other than the report by Harman (1970) that Elliptio complanata decreased in obesity from shallow to deeper waters in lakes in central New York state (U.S.A.). This is the opposite trend to that observed for V. angasi in billabongs of the Magela Creek.

Softer and less consolidated substrates tended to support more inflated shell forms of V. angasi among and within the Magela Creek billabongs. Relatively more compressed forms, however, tended to occur on firmer sediments. Increasing obesity of mussels on softer and muddier sediments is presumably an adaptation enhancing buoyancy and preventing shells from sinking and asphyxiating. This

observation is in accordance with similar interpretation given above, to the functional advantage of swollen shells of unionaceans in general on soft, muddy substrates. The shell form of the congener, V. ambiguus, is also characteristically swollen on unconsolidated, muddy substrates of lagoons according to Walker (1981b). Sediment type has been related to obesity in only one other study of within-habitat shell form variation in unionaceans. Horn and Porter (1981) found that obesity of a lake population of Lampsilis sp. was correlated with percent organic matter of the sediment. No mention was made, however, as to whether the more organic sediments were softer and less consolidated in nature.

The high and swollen shells of the Creek form inhabiting the braided, sandy channel above Mudginberri billabong, represented a distinct, ecophenotypic variant of V. angasi in the Magela Creek. The microhabitats of these forms were stable enough that the shell morphology did not appear adaptive to anchorage and stability; shells of V. angasi in a permanent stream from another geographical location seemed better adapted to this function in being generally laterally compressed. Dorsal arching and ventral reflection of the shells were also absent in the Creek form, that would suggest increasing stability in flowing water environments. Almost certainly the increased volume resulting from increases in relative height and obesity of the Creek form, are adaptive to aestivation, where the amount of energy reserves and water content are maximised for the dormant period over the hot Dry season. By nature of the tropical, monsoonal climate, small streams in the geographical range of V. angasi are ephemeral. The apparent, widespread occurrence of the

Creek form throughout the range of V. angasi therefore (deduced from the figures and descriptions of McMichael and Hiscock, 1958) suggests that the ecophenotype is adapted broadly to life in streams of annually variable discharge. This study is the first to recognise in an ecophenotype, adaptive morphology to aestivation in unionaceans.

Considerable interest has been held in regard to analysing the environmental relationships of the variability in shell form of present day unionaceans, to provide paleoecological and paleolimnological reconstructions. A general review of this work, including the thorough appraisal and review of the topic of Tevesz and Carter (1980a), is presented in sections A1.1 and A1.2. Indications from the present study are, that relative height only of V. angasi may prove useful for inferring environmental changes in paleoenvironments, or for that matter for inferring present day hydrological or limnological patterns in environments as yet unstudied by man. A distinctive low, non-winged and arcuate shell form is characteristic of environments of unstable, shifting sediments where waters are swiftly flowing for some part of the year at least. Conversely, the relative height of shells with curved ventral margins (as opposed to ventrally reflected margins of the arcuate form) are generally indicative of the degree of eutrophy of the environment from which these mussels were found. This correlation would hold presumably in most environments, despite the fact that no obvious functional advantage can be implicated from the eutrophy (or growth rate)/ relative height relationship. The association is apparently more closely related to ontogeny rather than to any environmentally induced change to shell form.

In spite of a strong correlation found between obesity and depth, it is unlikely that shells of V. angasi will prove to be useful indicators of depth in any broad context. A correlation was found between obesity and age of mussels in the Magela Creek, and because of this ontogeny, depth segregation of different age classes resulted in morphologically distinct groupings correlated but not causally related to any environmental factor. The extent to which the age/depth relationship of mussels between waterbodies of the Magela Creek is fortuitous is not known. Only if age was found to be consistently correlated to depth among populations and causal relations identified, could shells be used to indicate water depth.

Indeed, it would be of interest to learn the extent to which ecoclines reported in the literature, are nothing more than gradients of ontogeny. For example, if obesity was found to correlate with age in unionaceans other than V. angasi, and age was found to increase downstream in a given catchment, functional interpretations given to Ortmann's (1920) 'Law of Stream Distribution' (which states that in a given species, shells tend to become more obese in a downstream direction), may be entirely spurious. Previous studies have largely neglected to account for the effect of ontogeny. The extent of ontogenetic variability found in the length/width relationship of V. angasi, sounds a cautionary warning to future studies of unionacean shell form, to carefully consider its effect before offering interpretations of functional morphologies. Similar advice was offered by Tevesz and Carter (1980b) in relation to the distinction between ontogenetic, and environmentally induced variability in

unionacean shell form (see section A1.2).

While the obesity of billabong forms may not be so usefully employed as environmental indicators, the Creek form may provide some value in this regard. The outline and swollen nature of this form is unmistakable and therefore may be usefully employed as an indicator of seasonally ephemeral, stream environments.

Species integrity of *V. angasi* in the Magela Creek: shell morphometrics and taxonomy

Low variability found in the lateral outline of shells of juvenile *V. angasi* both within and between populations of the Magela Creek, indicates that these young stages provide the most suitable material for which interpopulation comparisons of shell form, without the effect of environment, can be made. Because *V. angasi* and the congener *V. wilsonii* are distinctive in relative height, comparison of relative heights of the young shells of both species, should indicate whether a bimodality of form is present. This in turn would suggest whether or not the species occur alone or in sympatry with one another.

More material in addition to that compiled in the present study will be needed before conclusions regarding the taxonomic value of the young shells can be made. Early indications are, that while the young shells of *V. wilsonii* are consistently low, relative height of *V. angasi* is more variable. Some of this variation may be caused by a geographical cline in relative height; shells are apparently higher

in northern (wetter) parts of the species' range as opposed to more southern (drier) parts of its range. Latitudinal (McMichael and Hiscock, 1958; Cvancara, 1963; Clarke, 1973) and longitudinal (Clarke and Berg, 1959) clines have previously been detected in unionacean form (section A1.1). Thus determinations of these two Velesunio may be difficult in more southern latitudes, particularly in areas where the ranges of both border or overlap. More morphometric data pertaining to juveniles from regions of sympatry of the two species should enhance future criteria for separation of the two species.

Importantly, high species integrity of V. angasi is assumed in the 'Top End' of the Northern Territory. V. angasi is the sole species occurring in the Magela Creek, on the evidence that amongst juveniles (1) inter- and intrapopulation variation in relative shell height is low; (2) the shells are characteristically high; and (3) the shells are consistently winged and truncate in nature.

Although differences in soft part morphology among congeners of Australian hyriids are too minor for species determinations, McMichael and Hiscock (1958) reported that the siphons of V. wilsonii were lightly pigmented as opposed to the siphons and postero-ventral border of the mantle of V. angasi which were brick-red with black blotches. The pigmentation reported for V. angasi was present in all mussels from the Magela Creek dissected for tissue examination. This feature may prove to be a useful taxonomic discriminant and doubtful determinations using shell features may yet be resolved upon inspection of the siphons and mantle.