

CHAPTER 5

DISTRIBUTION AND ABUNDANCE

5.1 Introduction

Distributional studies of freshwater mussels range widely in subject and consequently there is a large world literature ranging from surveys recording presence or absence and anecdotal notes on habitat preferences, to sophisticated multivariate descriptions of a species' niche requirements. Interest, both academic and commercial, broadly comprises three areas: to determine factors involved in broad geographical dispersal or to describe local or microhabitat requirements; to assess factors involved in the decline of valuable commercial species (especially of North America) through mismanagement of waterways; and using distributional information and/or shell character or chemical composition data, to assess freshwater mussels for their value in prehistory studies or as indicators of paleohydrology or of present day water quality.

The literature pertaining to distributional studies is comprehensively reviewed in Appendix 2, in relation to these three broad areas of interest, namely: factors affecting distribution of freshwater mussels, including broad geographical dispersal, biotic and abiotic (depth, hydrology and physicochemical limnology) relations - section A2.1; anthropogenic activities - section A2.2; and freshwater mussels as ecological indicators - section A2.3. In the light of the known or implicated factors affecting freshwater mussel distribution elsewhere, a comprehensive investigation of the distribution and abundance of

Velesunio angasi was undertaken in the Magela Creek billabongs.

Apart from determining distributional relationships, density data were sought in order to provide accurate measures of biomasses and production within billabongs. In addition, density data would contribute to baseline information upon which to detect potential environmental disruptions in the Magela Creek billabongs. In order to gain such information, distributional patterns (for both microhabitat and between-billabong) needed to be demonstrated and quantified in terms of environmental factors - that is, morphometry, hydrology and physicochemical limnology of the billabongs. Such study of within and/or between-site distributional patterns of freshwater mussels within a drainage system, has to a limited extent been demonstrated and occasionally quantified in relation to environmental factors elsewhere (Cvancara, 1967, 1970; Cvancara *et al.*, 1966; Salmon and Green, 1983) but rarely in Australia (Walker, 1981b) and never for the tropics. Investigation into the distributional relations of an Australian and tropical freshwater mussel therefore was of special appeal.

5.2 Sampling design and field procedure

Density estimates of Velesunio angasi in the Magela Creek billabongs were derived from sampling undertaken during 1980 and 1981.

In relation to the environmental variables that may influence mussel distribution, obvious features to consider were substrate and depth. Most sampling was performed during the mid to late Dry, and thus

precluded any measurement of stream velocity, another habitat parameter. However, substrate type is generally regarded as indicative of stream hydrology, and this correlation has been applied to billabongs of the Magela Creek (section 2.3.1). For Mudginberri billabong, data pertaining to velocity and flow patterns through the billabong are available; nevertheless the correlation between substrate type and stream velocity was still used here (Figs. 2.8 and 2.15, section 2.3.1.3).

Measurement of percentage vegetative cover was also precluded from the studies, as by the mid to late Dry much of the rooted vegetation had senesced and disappeared. The presence of macrophytic vegetation in the billabongs during the Wet and early Dry may have affected the observed patterns of mussel distribution. Vegetation, however, predominately occurred in quiet, shallow reaches of the billabongs - fairly abundant in backflow billabongs, common around the edges of the floodplain billabongs and scarce in channel billabongs (including Island). Generally, the same shallow reaches were those preferred by mussels, so that the often-described adverse effects of vegetation upon mussel density (see section A2.1.2) were not obvious. Such effects may nevertheless be felt, particularly in floodplain billabongs where plants may conceivably restrict Wet season water flow thereby interfering with oxygen availability. Here and elsewhere, however, water plants never occurred in such densities that could be considered restrictive either to water movement or to mussel distribution.

A stratified, random sampling procedure was adopted for Corndorl, Mudginberri and Buffalo billabongs - waterbodies with a variety of

substrate patterns. Sampling of mussels in these billabongs was undertaken during the mid-late Dry of 1980. Quantitative samples were allocated randomly to representative substrate and depth regions of the billabongs, derived from prepared maps of bathymetry and substrate type (section 2.3.1). This resulted in all regions of the billabong being sampled, thereby allowing for the detection of additional distributional differences along the billabong that may be related to other trends in physicochemical or other unknown factors.

The potential crocodile hazard precluded similar stratified, random sampling in floodplain billabongs. In Nankeen, the mussels along the banks of five evenly spaced sections of the billabong (Fig. 5.1) were sampled intensively during the late Dry of 1981. The billabong was similarly bathymetrically mapped prior to sampling (sediments of this billabong are reasonably homogeneous - section 2.3.1.4) and as before, quantitative samples were allocated randomly to each representative depth region. Densities in the other floodplain billabongs (Island, JaJa, Leichhardt and Jabiluka) were derived from the routine collections made during 1981 and 1982.

During the 1981 Dry, 8 transects evenly spaced along Bowerbird billabong were sampled for mussels, comprising a total sample area of 45 m². Ten transects evenly spaced along Gulungul billabong were similarly sampled during November 1981. Because of the small size of Georgetown billabong at the end of the Dry, and because all microhabitats of the billabong were represented in the two routine transects, density estimates were derived from monthly sampling during the late Dry (Oct-Dec) of 1980 and 1981. No quantitative sampling was

undertaken in Coonjimba billabong. (Mussels in Coonjimba were extremely scarce.) However, hand searching by systematically wading through this shallow billabong for over an hour in the late Dry of 1980, gave an approximate idea of the relative abundance of mussels.

Apart from Coonjimba and Georgetown billabongs, sampling of mussels for density estimates was done by hand from the confines of a quadrat. Usually, mussels below 19 mm were missed, collecting by this method. However, most collecting was done at times when growth of newly recruited mussels from the Wet season had surpassed this length (section 6.6.1). For the same reason, in Georgetown by the late Dry, few extra juveniles were incorporated into the density estimates by virtue of the more efficient sampling used then. Finally, recruitment in those billabongs sampled during 1980 (Georgetown, Corndorl, Mudginberri and Buffalo), showed similar patterns to those of 1981 (section 6.6.1) and therefore the abundance estimates in the two years between all of the billabongs of the Magela Creek can be compared.

Records of depth and substrate for all billabongs were made according to previous procedures (section 2.3.1). All depth measurements that were made at each site, were standardised to late Dry season levels.

5.3 The distribution and abundance of mussels along the Magela Creek

Mean densities per substrate and depth interval within the Magela Creek billabongs are shown in Tables 5.1-5.9. (Substrate subdivision does not appear in billabongs where the bottom type is reasonably

homogeneous.) No mussels occurred along any of the transects across Bowerbird billabong.

The spatial dispersion of the populations was determined using the method described by Elliott (1977). The null hypothesis of a random distribution of mussels over a homogeneous environment was tested by comparing the field population with a theoretical Poisson distribution. The departure from randomness gives an index of the degree of population aggregation. Values of variance (S^2)/mean(\bar{x}) greater than 1 indicate some degree of clumping, whereas in a Poisson series, the variance is equal to the mean. The significance of the departure from unity is assessed by the chi-squared test:

$$\chi^2 = \frac{(n - 1)S^2}{\bar{x}} \quad \text{where } n = \text{number of samples.}$$

Significant ($P < 0.05$) departure from unity ($S^2 > \bar{x}$), and hence contagious distribution is indicated in Tables 5.1-5.9.

From inspection of the tables, generally within a particular habitat there was significant clumping at high densities, but random dispersion at low densities. This is to be expected (Elliott, 1977). Further, no realistic inferences can be made where sample sizes were low, a factor contributing to nonsignificance of some observations. Finally, there was a suggestion that in deeper waters in some billabongs (Corndorl, Mudginberri and to some extent Buffalo), dispersion was random despite comparatively high densities and large sample sizes.

Total numbers of mussels per habitat area of a billabong were extrapolated using the mussel density data and the extent of habitat

areas derived from planimetry of the prepared bathymetric and substrate description maps. The estimated mussel totals for each habitat were then summed to provide a grand total for each billabong. From this figure, and using the total billabong area figures, mean density estimates of mussels averaged over the billabongs were derived and are shown in Table 5.10. Mean densities ranged widely between billabongs and no broad trends are apparent when geographic location of billabongs is considered.

5.4 Environmental determinants of distribution and abundance

5.4.1 Within billabongs

In relation to depth and substrate data, two-way analysis of variance was performed on the habitat density means wherever applicable to determine whether there were significant differences in population density among depths or in density among different substrates.

5.4.1.1 Depth

Apart from Georgetown, in all of the Magela Creek billabongs studied, an optimal, intermediate depth was found at which mussel densities reached a maximum. Henceforth this depth is referred to as the "preferred depth".

Backflow billabongs

In Georgetown billabong, no significant difference in density among

different depths was found. Mussel distribution in this billabong is strongly modified by the seasonal flooding and subsequent evaporation of the waters. Considerable recruitment occurs in the shallow waters of this billabong during the Wet and early Dry, in addition to significant migration here from deeper waters (sections 6.6.1 and 6.8.1 respectively). By the late Dry when densities were recorded, mussels have retreated and are concentrated in the remaining waters, with no discernible pattern of depth distribution.

Mussels were absent from the shallowest reaches of Gulungul billabong (<0.3 m) during the late Dry of 1981. Presumably the mussel distribution was affected by the previous Dry of 1980 at the end of which the billabong almost dried up. Peripherally inundated regions in late 1981 were presumably exposed over the same period in 1980. Mussel densities were maximal at 0.5 m. Although a quadratic relationship appeared an appropriate model of the depth distributional data for depths greater than 0.1 m, the fit was insignificant ($P > 0.05$) reflecting the few depth intervals sampled (Fig. 5.2).

Analysis of variance revealed no significant differences in mussel density among depths in Corndorl billabong when data were analysed with the two major substrate types of the billabong. However, partitioning of the sum of squares (SS) due to depths into linear, quadratic and residual components revealed a significant ($P < 0.05$) quadratic effect. (The residual component was also significant ($P < 0.05$) indicating possibly, that a more sophisticated model may have been appropriate had more depths been sampled.) As significant substrate effects were apparent in this billabong (section 5.4.1.2.1),

regression equations describing the relationship between densities and depth for both substrate types, and their levels of significance are shown in Table 5.11. The relationships are plotted in Fig. 5.2. Preferred depths are similar (1.0 m) for both substrate types.

Channel billabongs

No significant ($P>0.05$) and highly significant ($P<0.001$) differences were revealed in density among depths in Mudginberri and Buffalo billabongs respectively. As for Corndorl billabong, however, partitioning of the depths SS revealed highly significant quadratic effects in both waterbodies ($P<0.001$). As significant substrate effects were also revealed (section 5.4.1.2.1), regression equations were calculated separately for the different substrates (Table 5.11) and are plotted in Fig. 5.3. Preferred depths varied with substrate type, tending to be greater with decreasing organic content and softness of the sediments. This was revealed also from Fig. 5.4 which shows the combined sediment relationships for each billabong. The preferred depth in Mudginberri billabong with firmer, less organic sediments was greater than in Buffalo.

Floodplain billabongs

Data from Nankeen billabong for which large numbers of between-site observations were available (Table 5.9), were analysed for between-site and depth differences. Highly significant differences were revealed in mussel density among depths in this billabong ($P<0.001$). As homogeneous sediments are a feature of the floodplain

billabongs, the density data of each floodplain billabong were combined and analysed in a single AOV. This test revealed significant depth relationships ($P < 0.05$) when averaged over the billabongs and very significant differences in densities among billabongs ($P < 0.01$). Plots of densities and depths for each billabong suggested complex nonlinear relationships (Fig. 5.5). An appropriate exponential model of the form:

$$Y = Ae^{-\alpha x} - Be^{-\beta x} \quad \text{where } Y = \text{density, } X = \text{depth}$$

was chosen to describe the depth distributional relationship (see section 3.4). The regression equations are described in Table 5.12 and plotted for each floodplain billabong in Fig. 5.5. Although not always apparent (e.g. Island billabong with its low densities), a notable feature of the relationships between density and depth in floodplain billabongs was their skewed nature and shallow preferred depths in comparison to those of backflow or channel billabongs.

Depth relationships in all billabongs

Table 5.13 shows the preferred depth as derived from the predictive regression equations for each of the Magela Creek billabongs. Where two or more substrates were present in a billabong, the combined regression equation was used.

Of the factors previously suggested in the literature as restricting mussels from depth (section A2.1.2, Depth), in the relatively shallow and warm waters of the Magela Creek billabongs, finer and unconsolidated sediments and low dissolved oxygen levels with increasing depth are probably most relevant. Notable in the

distributional patterns was the skewed depth distribution of mussels towards shallower waters in the floodplain billabongs. The deep waters of these billabongs were particularly susceptible to Dry season stratification and deoxygenation (section 2.3.2.2), strongly suggesting that this factor was the direct cause of the observed, relatively shallow preferred depths. Mean dissolved oxygen levels of Nankeen averaged over 3 years of data and typical of the pattern in other floodplain billabongs (Walker *et al.*, 1983a) are plotted with density and against depth in Fig. 5.5. A correlation between decreasing density and mean dissolved oxygen was evident.

Both channel billabongs, however, do not stratify nor become deoxygenated to the extent of the floodplain billabongs. The preferred depths, presumably by way of the response of the mussels to the lack of deoxygenation, were notably greater, optimising in all likelihood the advantages of deepwater distribution. Also, as previously noted, the preferred depths tended to be greater with decreasing organic content and increasing consolidation of the sediments. This may also be related (at least partly) to microhabitat oxygen availability. Higher organic content of particular sediments presumably increases the oxygen demand of the surrounding waters, a factor accentuated with increasing depth and therefore likely to restrict mussels to shallower waters.

Some stratification and deoxygenation were evident in the backflow billabongs studied (section 2.3.2.2), factors that may have limited numbers of mussels in deep water regions. In addition, the sediments of these waterbodies are fine and unconsolidated (section 2.3.1.2);

from observations, the softness increased with depth (though not confirmed quantitatively). Mussels may sink and asphyxiate in such sediments.

It might also be argued that the actual depth of billabongs is important in determining the preferred depth of mussels. Figure 5.6 shows a scatter plot of preferred depth against mean depth of billabongs. Above a threshold depth (approximately 0.5 m), mussel density is apparently maximised at a depth proportional to the depth of the billabong. Nevertheless, the preferred depths of mussels in the two channel billabongs (Nos. 12 and 14 in Fig. 5.6) were disproportionately greater than the mean billabong depths. In the deeper billabongs where oxygen relations are likely to be most important, some correlation was also evident between preferred depth and mean dissolved oxygen (averaged over the seasons) (Fig. 5.6). Perhaps the relatively shallower preferred depth in Nankeen (No. 29) is a luxury afforded by the very turbid waters in this billabong at the end of the Dry (section 2.3.2.4) that may shelter mussels against high water temperatures at this time. Possibly the strongest evidence of the importance of low dissolved oxygen concentrations in causing the relative absence of mussels at depth is provided in the shape of the depth distribution curves. While the effect of high water temperatures and/or desiccation and predation should restrict mussels from shallow waters equally across the billabong types sampled, the skewed nature of the floodplain billabong relations strongly suggests that the stresses imposed by low concentrations of dissolved oxygen at depth here necessitates a bias to shallow water distribution. The skewed effect in floodplain billabongs is shown in the calculations of

preferred depths relative to mean billabong depth when viewed over all billabongs (Table 5.13). Significantly, in all (and in only these) the floodplain billabongs (Nos. 16 to 29), the preferred depths are shallower than the mean billabong depths.

5.4.1.2 Hydrological regime of the Wet

5.4.1.2.1 Substrate and stream velocity

Backflow billabongs

Analysis of variance revealed no significant differences in the density of mussels found among the different substrates within Georgetown billabong. Although densities were comparatively low on substrate 'D' (Table 5.1), this bottom type occurs at the edge of the billabong (Fig. 2.5), and by the late Dry, much of the population has moved away from these littoral regions (section 6.8.1). The bottom types in Georgetown billabongs are possibly the most diverse of any billabong on the Magela Creek ranging from very fine silt and clay to coarse, sandy sediments. Of relevance to mussels, however, is that all of the substrates are firm yet yielding.

In the Wet seasons of both 1980 and 1981, flood events (February 1980 and March 1981) displaced large numbers of mussels from Georgetown depositing them on a shallow, flooded meadow immediately downstream of the billabong. No censuses were undertaken, but hundreds and possibly thousands (1980) of mussels were believed to have been carried away. Some mussels burrowed into sandy patches amongst the grassed area and

presumably aestivated over the ensuing Dry but the vast majority trapped on impenetrable substrates and unable to burrow, succumbed either to intolerably high water or air temperatures as the shallow waters retreated. Such flood events are not uncommon in the region during the Wet season and thus must account for fairly regular and relatively significant mussel mortality in Georgetown. The Magela Creek's high water route through Georgetown has been previously described (section 2.3.1.2) and undoubtedly all substrates in the central portions are unstable during flood events. The sandy sediments, however, must be particularly unstable and shifting at such times. The Dry season density estimates therefore give no measure of the instability of the central and especially sandy sediments, as migration has occurred from the shallows into this region by this time.

While the bottom type of Gulungul billabong was relatively homogeneous (apart from observed differences in consistency, section 5.4.1.1), there were significant differences ($P < 0.05$) in the density of mussels occurring between the two major substrates of Corndorl billabong. Higher densities occur on the more inorganic and coarser sediments of the northern bank (Fig. 5.2). These sediments, being less silty and firmer than those of the other bottom type, may be more conducive to both post-larval settlement and maintenance of adult populations. As the silt and clay sediments of Gulungul are similar to those of Corndorl, the mussel population in Gulungul may also be reduced for the same reasons.

Channel billabongs

As previously mentioned, no mussels were found on the shifting, sandy sediments of Bowerbird billabong. No significant differences were found in mussel density among the major three substrate types in Mudginberri billabong. However, partitioning of the substrates SS revealed significantly fewer ($P < 0.05$) mussels occurring on sand than on the other finer and more organic sediments. In Buffalo billabong, highly significant differences ($P < 0.001$) were revealed in density among the four major bottom types. No significant differences, however, were found in densities between sand and the other finer and more organic sediments after partitioning of the SS.

Differences in density on the three finer, more organic sediments were tested for between both channel billabongs. No significant differences were found between billabongs, but a significant difference ($P < 0.05$) was revealed in density among the different bottom types. No sediment analyses were performed on the softest and most organic substrate type in Buffalo billabong. The three sediments were ranked on a scale of 1-3 in order of increasing organic content and decreasing particle size (also see section 2.3.1.3). The substrates SS was then partitioned into linear and residual components. This revealed a highly significant linear effect ($P < 0.001$) with densities declining with increasing organic content and decreasing particle size of the sediments (Fig. 5.7).

The significantly lower densities of mussels on clean swept sandy sediments in Mudginberri were undoubtedly due to the shifting nature

of the sediments, particularly during flood events in the Magela Creek (see section 2.3.1.3). Because of the branching of the creek as it leaves Mudginberri billabong, reduced stream velocities pass through Buffalo billabong. The densities of mussels in the corresponding sandy sediments of Buffalo, were notably higher (Table 5.5) as a result and, importantly, did not differ from densities occurring on the other sediments of the billabong.

Significantly fewer mussels occurred as the sediments of both billabongs increased in organic content and became siltier and increasingly unconsolidated. Two factors may be responsible for this. In the worst situations, mussels may be unable to maintain their station in the unconsolidated sediments of Buffalo billabong (substrate E, Table 5.5). Otherwise, the silty sediments may interfere with breathing or juvenile settlement. Alternatively or additionally, as mentioned earlier the organic sediments may also create microhabitat oxygen demands detrimental to maintenance of either juvenile or adult mussel populations. Finally, it was notable that the highest densities for the major bottom types occurred in sediments immediately out of range of the main Wet season stream flow; that is, in sediments that were neither too fine and silty nor too organic (substrate B, Table 5.4) and that occurred in Mudginberri, the best aerated billabong on the Magela Creek.

Floodplain billabongs

As in all of the floodplain billabongs, mussels were scarce at depth in Island billabong. Such parts of the billabong were subject to

oxygen depletions in the early Dry (section 2.3.2.2). In addition, however, much of the area was sandy and to some extent may be shifting and unstable during flood events. Further, the same area has been reported to be covered by an unconsolidated sediment floc on a past occasion (section 2.3.1.3). The detrimental effects of silt deposition upon mussels has already been mentioned. All three factors - oxygen depletions, shifting substrates and periodic silt deposition, have the potential to restrict mussels from the central, deep regions of Island billabong.

JaJa, Jabiluka and Nankeen billabongs each have reasonably homogeneous sediments although a sandy strip occurs along the eastern bank of Jabiluka billabong (section 2.3.1.4). Table 5.8 lists the densities occurring on the sandy sediments and those of the firm silt and dry sediments in Jabiluka. No significant differences ($P > 0.05$) were revealed in the density of mussels occurring between either sediment type.

Three sediment types occur in Leichhardt billabong: soft but firm silt and clay; extremely compacted clay; and extremely unconsolidated, silty vegetation and detritus. Significant differences ($P < 0.05$) were found in the density of mussels occurring among the three substrates, and further partitioning of the substrates SS revealed significantly more mussels ($P < 0.01$) occurring on silt and clay than on the other sediments.

All billabongs

Analyses of densities occurring on different sediment types of the Magela Creek billabongs revealed the unsuitability of some for maintenance of mussel populations. In the extreme, sediments comprising the sandy bottom of Bowerbird and the loose vegetation and compacted clay of Leichhardt billabong were completely unsuitable for mussels, being either shifting, too soft or too hard. To a lesser degree, the sandy sediments of Mudginberri (and occasionally Georgetown) and the gradient towards finer and more organic sediments in both channel billabongs also provided less suitable habitats. Such comments are applicable also to the even less consolidated organic, silt and clay sediments of Corndorl billabong and presumably Gulungul. Firm and yielding substrates, regardless of their texture and grain size had the highest densities. Such bottom types include sand, silt and clay, soft clay and sand with little silt or organic material.

5.4.1.2.2 Flow patterns in some floodplain billabongs.

Jabiluka billabong

Fig. 5.8 shows graphically the distribution and abundance of mussels in relation to depth along Jabiluka billabong. Clearly the southern end of the billabong had the highest density of mussels and, notably along the most southerly transect, densities reached a peak in the deepest regions. Mussels were generally absent from deep regions - particularly in floodplain billabongs, and as these deeper waters had lower oxygen tensions, dissolved oxygen status of the water appeared

to be clearly implicated in regulating densities of the mussels.

Entry of water into Jabiluka billabong during the Wet season has been previously described (section 2.3.1.4, Figs. 2.18 and 2.19). Water is effectively funnelled through the relatively narrow southern end, entering the billabong at depth and moving towards the surface as it moves northward through the billabong. Presumably, the Wet season bottom waters at the southern end of the billabong are reasonably well oxygenated as the water is moving (being funnelled) and has just left the relatively shallow floodplain. As the waters progress through the billabong, velocities presumably decline in wider reaches and importantly move to the surface, so that the bottom further northward must be relatively deprived of oxygen.

Some pertinent points from other parts of these studies (sections 6.6 and 7.10.1) can be made at this stage: 1) larval production in female mussels of the Magela Creek billabongs is correlated with availability of dissolved oxygen; 2) as a consequence, periods of low discharge through floodplain billabongs during the Wet lead to some oxygen depletion and resultant inhibition of larval production or even abortion of larvae from the female gills; 3) recruitment of metamorphosed juveniles in channel and floodplain billabongs is distinctly seasonal, occurring in the Wet season; 4) juvenile mussels are especially sensitive to low levels of dissolved oxygen (when compared with adult tolerances - see Appendix 6); and 5) recruitment of mussels from floodplain billabongs, as measured by strength of year classes, is significantly correlated with total Wet season discharges. Oxygen availability both during the Wet and early Dry is apparently

critical to successful recruitment of young. Larval development and juvenile survival depend upon an adequate oxygen supply during these periods when larvae are both produced and young recruited. The correlation between recruitment and Wet season discharge therefore is hardly surprising and is to be expected especially for floodplain billabongs where the effects of low dissolved oxygen would be most strongly felt. It is hypothesized therefore that the deepwater entry of presumably well oxygenated water into the southern end of Jabiluka during the Wet enhances both larval production and subsequent juvenile survival. This region therefore records comparatively high densities of mussels.

Nankeen billabong

From the findings of the distribution and abundance of mussels in Jabiluka billabong, a general hypothesis that Wet season flow is an important determinant of distribution and abundance of mussels in billabongs on the Magela Creek is proposed and argued as follows.

To provide adequate oxygenation, current velocities need to be of sufficient strength as waters in stronger currents presumably carry more oxygen. Assuming a constant discharge along a given section of stream, stream morphometry can determine current strength as a smaller cross-sectional area at a given point will result in stronger currents than a larger area.

From visual observations of the Wet season flow through Nankeen billabong, the course of peak flow (as might be expected) was through

the deepest section of the billabong (Figs. 2.14 and 5.1), along the left-hand or western bank. As mussels were virtually absent from the deepest portions of the billabong (Table 5.9), the billabong can be considered as comprising two distinct environments - a west and an east, separated by an uninhabitable deep portion. Thus, the 5 transects sampled along the billabong can now be considered as 10 sampling stations as at each transect, both east and west banks were sampled (Fig. 5.1).

On the premise that current strength may determine local distribution and abundance, the cross-sectional area, as a measure of current velocity, was estimated at each station. Cross-sectional area was calculated from the product of billabong width, from the bank to the deepest point of the transect, and the mean depth of the cross-section. A mean density for each cross-section was also calculated. All morphometric data were taken from the prepared bathymetric map (Fig. 2.14). Cross-sectional area and mean density for each sampling station are plotted in Figure 5.9. (Cross-sectional area has been converted to a reciprocal to provide a positive association.)

Analysis of variance revealed very significant ($P < 0.01$) differences in mussel density among the different stations in Nankeen billabong even prior to establishing a relationship between current strength and distribution and abundance. From Table 5.9 it is clear that mussel density along the west bank (even numbered stations) was considerably higher than that along the east bank. (A t-test applied to the two overall density means, averaged over either side of the billabong,

revealed a highly significant difference ($P < 0.001$). As Wet season flow passes alongside the west bank closely, it would follow that this bank would receive comparatively well oxygenated water via the stronger currents, so enhancing recruitment and survival of mussels. For the eastern bank, however, mussels were most numerous in shallower waters out of range of the peak current. It is conceivable that during periods of low discharge during the Wet, flow might be barely discernible in these reaches.

Unlike for Jabiluka, there is no knowledge as to the exact pathway of water flow into Nankeen billabong during the Wet. Because of this, interpretation of Fig. 5.9 could be unclear. However, a meandering and apparently relict channel exists between Nankeen and Jabiluka billabongs (Fig. 2.17). Nothing is known of its Wet season competence but because it represents the lowest ground on the floodplain in this region (being still filled with water towards the late Dry) it is tempting to suggest some flow at least must pass along it during the Wet. If this is the case, then at least some (perhaps most) water from the floodplain would enter the billabong via this right hand channel some distance downstream from the southern extremity.

Assuming this pattern of flow occurs, a reasonable interpretation can be made of Fig. 5.9. Firstly, the assumption of constant discharge along the billabong is invalidated, because in the extreme case of all Wet season flow entering the billabong via the described channel, then stations 9 and 10 (Fig. 5.1) are placed outside the main stream of flow. If similar subsurface entry of (presumably) well oxygenated water from the floodplain is the case for Nankeen, as it is for

Jabiluka billabong, then according to the hypothesised flow pathway (Fig. 5.1) the bottom regions to benefit from this water are those around station 8. Accordingly, for their given cross-sectional areas, stations 9 and 10 have fewer mussels than might be expected, while station 8 has far greater densities. If these three stations are considered anomalous for reasons of some peculiar water entry phenomenon, and are neglected from further calculations, a significant linear correlation ($P < 0.05$) is found between the reciprocal of cross-sectional area and mean density for the other stations (Fig. 5.9). That is, where stream flow is strongest (as measured by small cross-sectional areas) densities of mussels are highest.

As many assumptions have been made in the above interpretation of distributional patterns in Nankeen billabong, confirmatory evidence must await the collection of more hydrological data relating to the exact pathways of waterflow into the billabong. The significant differences in densities between east and west banks of the billabong at this stage, however, provide some evidence that the more turbulent and presumably better oxygenated environment of the west bank during the Wet in some way enhances recruitment of mussels. In relation to the anomalous patterns of distribution and abundance for stations 8, 9 and 10, some further comments are possibly valid. Well into the Dry season (July) flow continues to pass through the floodplain billabongs (N.T. Dept. Transport and Works, Water Division, 1980). Even if during the Wet, water entry into Nankeen via the meandering floodplain channel is not a significant source, by the early Dry it may well be the major channel source of the little water left flowing through the Magela Creek. In all likelihood, the retreating waters reach such low

levels that the only point of entry of water into Nankeen billabong can be via this route. If this is so, the subtle and perhaps unmeasurable early Dry season entry of water may enhance survival of newly recruited mussels at station 8 where the effects of the incoming trickle of waters would be most immediately and significantly felt. Further, presumably no flow would pass over the bottom regions of stations 9 and 10 at this stage.

Hydrological patterns in other billabongs may also explain local patterns in distribution and abundance. The highest densities of mussels in Mudginberri billabong are recorded on the stony and clay sediments (substrate D, Table 5.4) along the southwestern bank (Fig. 2.8). This site is well flushed during the Wet season (Fig. 2.15, section 2.3.1.3) enhancing the oxygen status until flow into the billabong ceases (about June). Larval production and recruitment must presumably benefit from the improved aerobic conditions here. Additionally, however, the stability and non-silty nature of these sediments must also benefit recruitment and consequent maintenance of adult populations. Another soft clay region in Buffalo, also has the highest densities of mussels for the billabong (Substrate F, Table 5.5, Fig. 2.9). No details of localised flow patterns are available for Buffalo billabong, other than that the bed of dense mussels was observed to lie close to (on the left-hand side) the main channel of flow. Flow from Corndorl Creek or from the Magela Creek has been observed to pass close to the gravelly sediments along the northern bank of Corndorl billabong (Fig. 2.7). This may account in part for the large population of mussels in these sediments, although significant flow in either direction through the billabong is probably

infrequent, considering the small catchment of Corndorl Creek and the relatively large discharges needed in the Magela Creek to create significant backflow events.

Finally, consideration needs to be given to the habits of host fishes in explaining the observed distributional patterns of V. angasi described above. It may be less the mussel's intolerance to low flow regimes and consequent low dissolved oxygen levels that determines distribution and abundance than it is the host fishes intolerance to these conditions. By seeking strong flowing and well oxygenated waters, the Wet season distribution of fish may inadvertently affect that of the mussel. Presumably, however, there are other areas to which a fish can move to avoid poor oxygen conditions. Avoidance may be affected by vertical and lateral movements into shallower waters for example. More information is needed on the Wet season distribution of fishes in billabongs. Finally, mussel shells have been found in the meandering channel between Jabiluka and Nankeen billabongs. Fish therefore occur in the channel during the Wet season. The presence of shells may reflect the relative permanence of water left at the end of the Dry for mussel survival or more likely, that the channel is used in relation to fish migration. The latter instance adds credence to the suggestion that the channel may be competent.

5.4.2 Correlates of distribution and abundance between billabongs.

Multiple regression analysis

Having examined several environmental influences on the distribution and abundance of mussels within billabongs, the identification of parameters responsible for broader distributional patterns between billabongs was sought. Under normal circumstances, between-site variation in physicochemical limnology of a perennial stream the size of the Magela Creek, might be expected to be minor or even negligible. However, strongly seasonal influences and geographic effects impart a marked heterogeneity to the water chemistry of the Magela Creek billabongs (section 2.3). Because of the large variation in between-billabong distribution and abundance of mussels and in water quality, and the substantial quantitative data base of both mussel densities and billabong limnology, the opportunity to assess the influence of environmental parameters on the distribution of freshwater mussels was presented.

A large array of physicochemical parameters was chosen for the analyses, representing monthly measurements over approximately three years of data collection. The chemical parameters are listed in Table 2.7 and were chosen, on the basis of previous descriptions in the literature, as having relevance to regulation of mussel species or to the physiological tolerances of mussels. Literature pertaining to these known or implicated effects has been reviewed in section A2.1.3; briefer reviews in relation to similar types of analyses have been

provided by Green (1971) and Sepkoski and Rex (1974). The chemical parameters comprised the following groups: relevant to shell formation and maintenance (pH, Ca, total hardness, carbonate hardness, bicarbonate concentration, total alkalinity); salinity (conductivity, K, Cl); trophic conditions (dissolved and total organic carbon, nitrate, ammonia, % organic matter of sediments, chlorophyll); other major ions (Mg, noncarbonate hardness); turbidity and suspended solids; and dissolved oxygen. Other relevant environmental parameters chosen were sediment characteristics (percent organic matter, mean sediment particle size) (Table 2.2) and mean depth (Table 2.1).

Stepwise multiple regression was used to assess the relationships between mussel abundance and the limnological variables. Sediment particle sizes were converted to phi units (Folk, 1968) as recommended by Green (1971) and the arcsine transformation was used to express percentage organic content of sediment. Scatter plots of each other environmental variable against the dependent variable, (mean billabong density) (Table 5.10) were made to determine the suitability of transformations. Log transformations were made and a quadratic term included where appropriate. The significance of a quadratic term would indicate a unimodal relationship between abundance and the relevant environmental gradient.

Unfortunately, because N.T. Water Division did not sample from Leichhardt billabong, some chemical data are missing (Table 2.7). Therefore, two multiple regression analyses were performed, one omitting all data from Leichhardt, and the other utilising data common to all billabongs. Few data are available also for Buffalo billabong.

Because of the close proximity of Buffalo billabong to Mudginberri and the similar characteristics of both billabongs, however, a similarity in physicochemical limnology was assumed. From comparison of chemical data collected over a year between both billabongs (Walker and Tyler, 1983b; Water Division data, N.T. Department of Transport and Works), this assumption appears reasonably well justified especially when the large total variation between all billabongs is considered. Thus, the values for 16 parameters were assumed common to both billabongs.

In terms of the relative importance of the independent variables in influencing and predicting densities of mussels between billabongs, only dissolved oxygen was significantly correlated with density in both analyses. With data from Leichhardt billabong omitted, dissolved oxygen accounted for 63% of the variation in density ($P < 0.01$), and when included, accounted for 53% of the variation ($P < 0.05$). The relationship between mean dissolved oxygen and mean billabong density of mussels is plotted in Figure 5.10. The linear regression equation is described:

$$Y = -13.518 + 5.702X \quad (P < 0.01, r^2 = 0.540)$$

where Y = mean billabong density (numbers/m²) and X = mean dissolved oxygen (mg/l).

Billabongs lying on the mainstream channel

The importance of dissolved oxygen (DO) in determining mussel distribution and abundance within and between billabongs, led to consideration of perhaps even better prediction of mussel abundance between billabongs.

It appeared conceivable firstly, that DO as manifested through Wet season flow patterns might influence mussel densities among billabongs. Flow patterns were at least already implied in the local distributions of mussels in two floodplain billabongs, Jabiluka and Nankeen. Wet season DO as a major factor in affecting successful recruitment among billabongs, could therefore be regarded as a possible determinant of mussel distribution and abundance. This is particularly pertinent to billabongs lying on the mainstream channel of the Magela Creek, where recruitment occurs in the Wet season and as such is presumably influenced by prevailing DO concentrations at this time. Accordingly, these billabongs are treated separately from those billabongs lying off the main channel of flow (backflow billabongs and JaJa billabong).

Rather than using spot monthly readings of DO, (which are presumably influenced to a considerable degree by fluctuating and highly variable daily discharges, section 5.4.1.2.2), mean cross-sectional area may be a more appropriate measure of current strength and associated DO concentration because it integrates the discharge characteristics of particular billabongs. (The rationale behind this statement has been argued previously.) Implicit in the use of such a morphometric index, is the assumption that discharge is constant over all billabongs. Although discharge is obviously proportional to catchment area and increases in a downstream direction, some compensation is made for by branching of the Magela Creek waters below Mudginberri billabong and some degree of dispersal of waters over the broad floodplain. Thus, while all Magela Creek water would not be channelled through the

floodplain billabongs, no measure of between-billabong variation in discharge is available. Regardless, a relationship exists between billabong morphometry and mean Wet season (January-April) DO (calculated from the data of Figs. 2.20 and 2.21) suggesting that slower flow rates through the larger billabongs are indicative of lower mean DO concentrations during the Wet (Fig. 5.11). While the Magela Creek waters branch downstream of Mudginberri, all water upstream flows through the billabong, contributing to the anomalously high mean Wet season DO level. Thus when Mudginberri is omitted from the regression analysis, the relationship between depth and Wet season DO in the remaining five billabongs is not significant, but there is a significant correlation ($P < 0.05$) between both mean width and mean cross-sectional area, and Wet season DO (Fig. 5.11). No further significance to the prediction of Wet season DO was obtained after addition of cross-sectional areas to the width/DO regression, but cross-sectional area accounted for 89%, in comparison to mean width which accounted for 78%, of the variation in Wet season DO. Cross-sectional area was retained therefore in further analyses, on the grounds that it has more underlying significance and stronger hydrological basis for influencing and predicting Wet season DO.

Both mean cross-sectional area and mean Wet season DO were regressed against mean density of mussels of each billabong (Figs. 5.12 and 5.13 respectively). Both linear regressions were significant ($P < 0.05$), Wet season DO accounting for 67%, and cross-sectional area 68%. of the variation in mean density (Figs. 5.13 and 5.12). Again, however, cross-sectional area was retained for further analysis, on the basis that it provides an integrated and quickly determined

measure of mean Wet season DO. The linear regression equation describing the relationship between cross-sectional area and density is:

$$Y = 26.094 - 0.107X \quad (P < 0.05, r^2 = 0.676)$$

where Y = mean billabong density and X = mean cross-sectional area.

The model (Fig. 5.12) thus far considers prediction of density in terms of billabong morphometry reflecting flow and oxygen, available for Wet season recruitment. However, from the multiple regression analysis, mean density over all billabongs is correlated with mean DO averaged over the year (Fig. 5.10).

It can be argued that adequate DO not only enhances larval production and recruitment, but also survival of newly recruited mussels that were found to be particularly susceptible to low concentrations of DO (section 5.4.1.2.2). Therefore the addition of mean DO averaged over both Wet and Dry seasons may improve the model. The morphometry of Leichhardt billabong for example might suggest a higher density than actually occurs there (Fig. 5.12). However, the low mean DO concentration in this billabong (Table 2.7) suggests that poor survival of recruits affects the distributional patterns.

Thus, a two-compartmental model of density prediction was evaluated: one component, billabong morphometry, considers Wet season flow characteristics and their influence on recruitment; and the other, mean DO averaged over the seasons, considers the survival of recruits throughout the year. As biological models may be expected to be multiplicative rather than additive, a simple model was constructed thus:

$$\text{Mean density} \propto \frac{\text{mean dissolved oxygen concentration}}{\text{mean cross-sectional area}}$$

for a particular billabong. A high value in the numerator, suggests a high density and vice versa. A low value in the denominator also implies a high density (and vice versa). Thus for example, a 'small' billabong with adequate DO should expect high mussel densities as opposed to a 'large' billabong with low DO values.

The predictive model of density for billabongs lying on the mainstream channel of the Magela Creek is shown in Figure 5.14. For predictive purposes a linear model provided a sufficient fit of the data, and the fitted regression equation is:

$$Y = -7.325 + 663.98X \quad (P < 0.001, r^2 = 0.978)$$

where Y = mean density (numbers/m²)

$$\text{and } X = \frac{\text{mean DO concentration}}{\text{mean cross-sectional area}} \quad (\text{mg/l/m}^2)$$

The derived model has significant predictive value, despite other factors not being fully considered. The model for example, assumes that the Wet season discharge through each billabong is the same. To what extent this assumption is invalidated however, is not known; regardless, however, Wet season DO and billabong morphometry were correlated. Inimical substrates affect the density figures in Mudginberri and Leichhardt billabongs respectively (section 5.4.1.2.1), so that as far as the model is concerned, the densities in these two billabongs were somewhat underestimated. Further, the relationship is extremely simplistic. While no environmental parameter other than dissolved oxygen was significantly correlated to density, some other unmeasured parameter (not yet implicated in the

literature) may be important. Fish relations for example are not considered; however, fish hosts are present throughout the year in all of the billabongs studied (sections 2.3.3 and 7.14). Nevertheless, the model makes good biological sense: dissolved oxygen is strongly implicated in mussel abundance throughout the Magela Creek billabongs (hardly surprising considering the characteristic low seasonal values in the billabongs); flow characteristics in billabongs lying on the mainstream channel of Magela Creek influence oxygen availability during the Wet, presumably therefore, affecting recruitment; and mean DO levels averaged over all seasons must presumably have a marked influence on survival of newly recruited mussels.

Finally, it is a significant observation that (although not shown on Fig. 5.14) only billabongs receiving constant flow from the Magela Creek fit the relationship, reflecting presumably, the importance of stream flow and oxygen availability to the Wet season recruitment that occurs in these billabongs. Backflow billabongs and JaJa, a floodplain billabong, do not receive regular flow from the Magela Creek and other factors presumably influence their patterns of mussel distribution and abundance.

Backflow billabongs

The significant correlation between mean DO and mean billabong density (Fig. 5.10) was derived from all the Magela Creek billabongs and therefore DO status presumably is as important in backflow billabongs as it is in other billabongs. Discharge, however, is not a critical factor in determining recruitment and the observed high densities of

some of these billabongs at least suggest they are adequately oxygenated when recruitment occurs (late Wet - early Dry season, section 6.6.1). The shallow waters of these billabongs must presumably enhance the DO levels when recruitment occurs especially as recruitment occurs in their littoral zones (section 6.6.1).

Depth is critical to the mussel populations of these billabongs in other ways, however. Shallow waters at the end of the Dry may leave mussels exposed to lethally high water temperatures, desiccation or predation. Deeper backflow billabongs then, might be expected to harbour a greater abundance of mussels. Presumably, however, a threshold depth is met which acts in an opposite direction, inhibiting recruitment as still, deep water during the Wet may become deoxygenated. (JaJa billabong is one example of this type, discussed below.)

On the premise that both mean DO concentration and water depth affect the recruitment and survival of mussels in backflow billabongs, and in the absence of any other significant environmental factor (see earlier 'Multiple regression analysis'), a model based on mean DO and water depth was proposed to explain density patterns among backflow billabongs. The model was constructed thus:

Mean density = mean DO x water depth, for a particular billabong. The model is based on the observation that deep, and adequately oxygenated backflow billabongs realise a greater abundance of mussels. A logarithmic model provided the best fit of the data (Fig. 5.15) and the fitted regression equation is of the form:

$$Y = 10.034 \ln X + 1.987 \quad (P < 0.05, r^2 = 0.932)$$

where Y = density (numbers/m²) and X = mean DO x depth (m.mg/l). Again, the derived model has significant predictive value and the theoretical basis for its validity is reasonable. However, the analysis is based on only a few billabongs. Further, some substrate effects were also observed to influence the distributional patterns in these billabongs (section 5.4.1.2.1). Shifting sands in Georgetown billabong, and soft, unconsolidated sediments in at least Gulungul and Corndorl billabongs supported a reduced abundance of mussels. No consideration, however, was given to the sediment characteristics of these billabongs towards predicting mussel densities. The derived equation, nevertheless, presents a reasonably adequate model. More backflow billabongs within the Region need to be studied to test its present validity.

Finally, it is a notable feature, that JaJa billabong was a misfit to both predictive models. It does not lie on the mainstream channel of flow of the Magela Creek, nor does it have the morphometric, hydrological and limnological characteristics of backflow billabongs of the Magela Creek catchment. Its location on the floodplain but off the mainstream channel, and relative depth in comparison to other backflow billabongs, means that it possibly does not receive adequate flow and oxygenation during the Wet to realise the higher densities expected from its morphometric appearance.

5.5 Discussion

Distributional patterns within billabongs

As might be expected in distributional studies of benthic organisms (Elliott, 1977), at higher densities, the local distributions of Velesunio angasi populations within specific habitats of the Magela Creek billabongs, are clumped. Demonstration of this distributional pattern in other freshwater mussel species, however, is uncommon (Kenmuir, 1980; Salmon and Green, 1983). Apart from being caused by differences in microenvironment, the clumped distribution of mussels may effectively enhance fertilization and reproduction as suggested by Tudorancea and Florescu (1968), in the lotic but also lentic phase of a billabong's seasonal cycle.

The depth distributional relationships of V. angasi follow the patterns reported elsewhere of an abundance maximised at an intermediate depth. However, the pattern elsewhere is invariably of a skewed relationship between depth and density, with a preferred depth occurring in relatively shallow waters in comparison to the overall depth distribution (Okland, 1963; Cvancara, 1972; Haukioja and Hakala, 1974; Lewandowski and Stanczykowska, 1975; Ghent et al., 1978; Kenmuir, 1980; Strayer et al., 1981). This pattern was repeated only in the floodplain billabongs of the Magela Creek. Presumably a number of factors, as reported, may inhibit colonisation of deeper waters in both lentic and lotic environments; in the generally shallow, warm water and low oxygen status billabongs of the Magela Creek, however, low dissolved oxygen, and in some instances siltier and less

consolidated sediments at depth, were considered most likely to restrict mussels.

A number of lines of evidence were found to support the idea that low dissolved oxygen concentrations restrict mussels at depth: the mean oxygen concentrations of the billabongs by world standards are low (Table 2.7); in all billabongs some deepwater oxygen depletion, to a greater or lesser degree is felt at some stage of the year; in floodplain billabongs where the effects of deoxygenation are most obviously felt, the depth distributional relationships are skewed with mussels preferring shallow depths especially when compared to the preferred depth of mussels in channel billabongs; a correlation between the decline in mean dissolved oxygen levels and mussel densities in one floodplain billabong, Nankeen, is shown (Fig. 5.5); it is argued that the cause of preferred depths tending to be greater with decreasing organic content and increasing consolidation of the sediments in channel billabongs is more likely to be related to microhabitat oxygen demand at depth in the more organic sediments; and finally, in the deepwater billabongs, a correlation is observed between preferred depth and mean dissolved oxygen averaged over the seasons (Fig. 5.6). In studies elsewhere, seasonal oxygen depletions in the deepwaters of Plover Cove in tropical Hong Kong were implied as the cause of the shallow water distribution of Anodonta woodiana (Dudgeon and Morton, 1983); mussels are absent from waters deeper than 11 m in tropical Lake Kariba because oxygen levels at greater depths could reach levels low enough to cause mortality (Kenmuir, 1980); and deepwater anoxia was similarly believed to be the cause of the shallow water distribution of mussels in Fort Loudon Reservoir, Tennessee

River (USA) (Isom, 1971).

Siltier, less consolidated sediments in the deepwaters of Gulungul and Corndorl billabongs may limit mussel distribution at depth. The smothering effect of silt was suggested by both Fisher and Tevesz (1976) and Ghent *et al.* (1978) as a possible factor restricting mussels from the deepest waters of certain lakes. However, some deepwater oxygen depletions have also been observed in these billabongs (section 2.3.2.2) and this factor may at least partly account for the observed distributional patterns.

As could be expected, populations of *V. angasi* were absent from, or scarce on, shifting sands, compacted, or extremely unconsolidated sediments. Even the gradient towards decreasing consolidation of organic and silty sediments showed a decline in mussel densities. This was observed in Mudginberri and Buffalo billabongs but whether the nature of the sediments *per se* or the presumed microhabitat oxygen demand of more organic sediments (or both) are inhibitive, is not known. The significantly lower densities of mussels on the unconsolidated silt and clay substrate than on the silt and gravel substrate in Corndorl billabong suggest that the nature of such sediments in both Gulungul and Corndorl billabongs is a restrictive factor to maintenance of mussel populations.

In the channel billabongs, the evidence suggests that the restrictive factor(s) of organic and silty sediments acts upon the young mussel, most likely the newly metamorphosed juvenile. Bronmark and Malmqvist (1982) believed that fine sediment particles might interfere with

feeding and respiration in Unio pictorum; and reduced growth rates of Elliptio complanata on muddy substrates have been observed (Kat, 1982). A significant increase in size, however, of V. angasi was observed with increasing organic content of the sediments. Although age also increased over the same gradient, growth rates were also higher (section 6.4.3.1). This suggests that the finer organic sediments at least do not interfere with normal growth and development of adult populations of mussels in the channel billabongs. Juveniles, however, may be particularly susceptible to silty environments, or to microhabitat oxygen deficiencies that organic sediments may render (Negus, 1966; Howard, 1922; Ellis, 1931).

Evidence as to the same age specific mortality induced by the sediments in the backflow billabongs is inconclusive: a significant decrease in mussel size was observed in Condor1 billabong but generally an increase in size was noted in Gulungul (section 6.5.2.1). No depth related growth rate data are available for either billabong, but older and larger mussels might be expected in the permanent deeper waters of Gulungul, as the billabong occasionally dries up. Apart from migrations away from the depths, higher mortality of mussels (and therefore reduced densities) in the depths of either billabong could arise from the smothering effects of the silty sediments upon adults (Fisher and Tevesz, 1976; Ghent et al., 1978). Substrate interference to maintenance, feeding and respiration of adults may also reduce the growth rates of mussels in at least Condor1, as found by Kat (1982). Thus, silty organic sediments described above have in common some degree of unconsolidation that is presumably inimical to juvenile settlement but in its extreme form is probably prohibitive to normal

growth and maintenance of adult populations. However, there is no evidence that sediment particle size per se is in any way restrictive to distribution and abundance of V. angasi. This was revealed from the multiple regression analysis of mussel densities between billabongs in which no sediment particle size effect was found. At the extremes of particle sizes, within some of the finest sediments (silt and clay) in Nankeen and the coarsest (sand) in Mudginberri (Table 2.2), comparable and high densities were recorded (Table 5.10). Both sediment types are firm and yielding and within these constraints no substrate preference of V. angasi could be shown. These observations support the contention of others that within the provisions of firm and yielding sediments, bottom type, whether muddy or gravelly, is unimportant in regulating distribution of mussels (section A2.1.3, Hydrology).

Apart from creating shifting sands or soft, silty and organic sediments in the backflow regions that are either conducive or inimical to mussels, water flow exerts other strong influences on distributional patterns of mussels in the Magela Creek. The localised distribution of mussels in at least two floodplain billabongs were attributed to wet season flow patterns which, through oxygen availability, enhance larval production and recruitment of mussels. Thus, wherever strongest flow occurred - at the southern end of Jabiluka billabong and along the west bank of Nankeen, highest densities of mussels were recorded. This pattern was also observed in Mudginberri and Buffalo billabongs where highest densities of mussels occurred in stable clay sediments exposed immediately to the side of the full force of current through the billabong. Elsewhere where

mussels have been reported as most commonly occurring near or on the full force of current, the optimal conditions of the locations for extracting food, soluble mineral materials and oxygen from the water are implied or suggested (Evermann and Clark, 1917; Cvancara *et al.*, 1966; Simmons and Reed, 1973; Brönmark and Malmqvist, 1982). In the Magela Creek, however, current strength is believed to provide optimal aerobic conditions for mussels during the Wet, enhancing recruitment in these regions. The higher densities found here are assumed to be a direct reflection of higher Wet season oxygen concentrations and better subsequent survival of metamorphosed young.

In summary, patterns of distribution and abundance of mussels observed within billabongs of the Magela Creek, are doubtless modified by hydrological and limnological events occurring during the lotic and lentic phases of the creek's seasonal cycle. Localised water flow may render some substrates shifting and unstable, or otherwise provide optimal aerobic conditions for mussel recruitment. In the absence of significant flow, other loose and unstable, silty sediments may develop that support more or less fewer mussels. Dry season events that presumably modify distribution of mussels, include: declining water levels and subsequent increases in water temperatures and predation in shallow waters; and while the location of fish hosts (from visual and fish collecting observations), is often over shallow waters, the lower densities of mussels from deeper waters is additionally, doubtless a function of the lower concentrations of dissolved oxygen occurring here. Each of the Dry season events modifies the preferred depths of mussels occurring in the billabongs.

Distribution and abundance of mussels between billabongs

In the very soft and acidic waters of the Magela Creek, any marked differences between billabongs in measures of chemical parameters important to shell formation and maintenance might be considered critical to the distribution and abundance of mussels. The absence, however, of any significant correlation between such measures and densities of mussels within billabongs, presumably reflects the small variation in mean concentrations when values are compared among billabongs, and of course, reflects the marked tolerance of Velesunio angasi to acid softwaters. This latter point is made even more remarkable when it is learnt that a negative (but insignificant) correlation was found between calcium concentration and mussel abundance. Mussel densities in Mudginberri for example, are amongst the highest of any billabong but mean calcium concentrations in this billabong (0.47 mg/l) are amongst the lowest (Table 2.7). Elsewhere, although considered important to mussel development, the interpretation of water hardness values is complicated by lack of data to show levels at which hardness determines presence or absence of any species (Fuller, 1974), and occasionally its assumed importance in restricting mussels from some regions has later been challenged (Harman, 1969; Harman and Berg, 1970). At least several species of freshwater mussel of the northern hemisphere are reported to be equally tolerant of softwaters: for example, Anodonta spp. (Green, 1980); Elliptio complanata (Strayer, 1981); and Margaritifera margaritifera (Hendelberg, 1960; Stober, 1972).

While no significant correlation was found between pH and mussel

abundance between billabongs, a noted feature of the shells of some mussels from Jabiluka billabong was their paper-thin consistency. The waters of Jabiluka are amongst the most acidic of any billabong (mean pH = 5.5). While there has been little evidence specifically relating the absence of mussels to the natural acidity of prevailing waters (Harman, 1969), valve erosion at low pH has been observed by a number of workers (Coker *et al.*, 1921; Jewell, 1922; van der Schalie, 1938; Tudorancea, 1972). As to whether low pH causes premature mortality of mussels in Jabiluka through this corrosive effect, however, is not known.

The absence of correlations between any measure of salinity and mussel abundance comes as no surprise. The waters of the Magela Creek are generally quite dilute, as gauged by the low mean conductivity levels between billabongs (Table 2.7). Specific measures of salinities (potassium, chloride) are low and well within upper levels thought responsible for the absence of mussels from regions in North America (Cvancara, 1967, 1970; Imlay, 1973) and Australia (Dean, 1968).

No trophic factor was implicated in the observed distributional patterns between billabongs. In fact, most trophic measures (chlorophyll, total organic carbon, percentage organic matter of sediments, nitrate and ammonia) were negatively (but nonsignificantly) correlated with mussel density, an observation contrary to the findings of others where increasing eutrophy is thought responsible for increased species diversity and abundance (Clarke and Berg, 1959; Okland, 1963; Sepkoski and Rex, 1974; Kenmuir, 1980; Strayer *et al.*, 1981; Brönmark and Malmqvist, 1982). Thus, food availability is not

limiting to mussel abundance. Rather increasing eutrophy realises fewer mussels, possibly partly explained by its effect on oxygen concentrations. Highly productive billabongs may experience overnight oxygen depletions, an observation for example, accounting in part for the low seasonal mean concentration in Leichhardt billabong (Table 2.7, section 2.3.2.2). In relation to its effect on DO concentration, it might be argued thus, that some billabongs are excessively enriched with nutrients (e.g. Leichhardt). This enrichment, however, is not reflected through any direct toxic effect of nitrogenous wastes. Ammonia levels for example, are well within the limits reported to be toxic or responsible for absence of mussels in other drainages in North America (Fuller, 1974; Horne and McIntosh, 1979).

Likewise, no significant adverse effects were observed from high turbidities and suspended solids. In fact, two billabongs, Georgetown and Nankeen become highly turbid during the Dry season and yet observe amongst the highest densities of mussels in the Magela Creek. While high turbidities adversely effect larval production (section 7.10.1), recruitment in all billabongs occurs at times when waters are reasonably clean (Wet- early Dry season). In other drainages, mussels are similarly unaffected by turbidity; high densities of mussels have been recorded in consistently and highly turbid waters both in North America (Cvancara, 1967, 1970) and Australia (Walker, 1981b). There was similarly no evidence of adverse siltation effects upon mussels in the Magela Creek. Siltation has been observed in Island billabong (section 2.3.1.3), and because of its close proximity to mining activities, might be expected in Coonjimba billabong. However, in neither billabong were dead shells observed in the substrates that

might indicate some past catastrophic event. The deepwaters of Island billabong normally experience Dry season oxygen depletions, a factor already strongly implicated as the main inhibitor of mussel distribution at depth in the billabongs. Apart from smothering effects, however, siltation may also indirectly affect benthic forms by its shallowing effect, resulting in increases in bottom water temperatures or early evaporation of waters (Chutter, 1969); or silt may retain organic matter and create oxygen demands immediately above the sediments (Ellis, 1936). Both factors may effectively reduce recruitment and survival of juvenile mussels at least. The waters of Coonjimba billabong are both shallow, and low in dissolved oxygen concentrations.

The concentrations of most heavy metals in the Magela Creek are naturally low (Fox et al., 1977) and even the increments in some metal concentrations over the Dry (copper, lead and zinc) in some billabongs are apparently not responsible for major fish kills. Freshwater mussels might be assumed to be more tolerant than fish to most pollutants and in fact V. anqasi has been shown to be markedly more tolerant than fish of the Region to some selected toxic metals (Skidmore and Firth, 1983). However, aluminium toxicity mobilised through highly acidic and sulphate-rich waters is believed to cause fish kills observed in some floodplain billabongs during early Wet season flushes (section 2.3.2.3). Some mussel deaths have been observed on a few occasions in these billabongs in association with fish kills and Morley et al. (1983) suggested that aluminium may be the similar toxicant. Considering the broad tolerances of mussels to associated acidity and anoxia that might occur with the kills

(unpublished observations) the same aluminium toxicity at this stage appears a plausible explanation for the deaths. Small numbers (<100) of dead mussels were observed on any one occasion and the events therefore, are assumed to have had an insignificant effect on mussel abundance in the affected billabongs, especially when related to total density figures.

In relation to other known adverse effects of low DO upon V. angasi - inhibited larval production and therefore recruitment (section 7.10.1), and relative juvenile sensitivity (Appendix 6) - it comes as no surprise therefore that mean DO concentration was significantly correlated with mussel abundance in the Magela Creek, the only physicochemical parameter in fact, to do so. The importance of low levels of DO in determining distributional patterns of mussels has received little attention in ecological studies, other than noting the broader tolerances to low DO of quiet water species (Horne and McIntosh, 1979; Walker, 1981b; Fuller, 1974; Kenmuir, 1980); the high sensitivity of young mussels to low DO (Ellis, 1931); the absence of mussels at depth in lentic environments (Coker et al., 1921; Bates, 1962; Isom, 1971; Fuller, 1974; Kenmuir, 1980; Dudgeon and Morton, 1983); or absence elsewhere wherever DO dropped occasionally to as low as 3 mg/l (Grantham, 1969; Isom, 1971) or 2 mg/l (Kenmuir, 1980).

Adult populations of V. angasi are exceedingly tolerant of low DO, surviving under experimental conditions for months in anoxic waters (Appendix 6). This tolerance appears even more remarkable in view of the large and apparently thriving populations inhabiting billabongs of generally low oxygen status, where for long periods DO concentrations

of waters may be consistently below 3 mg/l (section 2.3.2.2). These observations undoubtedly place V. angasi amongst the most tolerant species to low DO concentrations yet studied. Other tolerant species reported include Amblema plicata and some Anodonta spp., quiet water mussel species of North America (Fuller, 1974).

While juvenile V. angasi are particularly sensitive to low DO concentrations, the lower observed densities of mussels on some silty and organic sediments in channel billabongs at least, were attributed to a sensitivity by juveniles to the silty and unconsolidated nature of these sediments and/or to microhabitat oxygen demands that such sediments may create. This degree of sensitivity in agreement with the observations of others (section A2.1.3) indicates that the habitat requirements of juveniles are quite specialised. Isely (1911), Coker et al., (1921) and Kenmuir (1980) believed in fact, that any consideration of ecological factors inimical to mussel life should be directed towards the juvenile habitat, as adults could live in environments where young would perish. Thus, further analysis of distributional data was based on the observations that successful recruitment and survival of young are dependent upon adequate oxygen concentrations.

Because mussels occur in billabongs where no appreciable flow is present, stream flow per se is not regarded as essential to recruitment. Flooded peripheral zones in shallow backflow billabongs where recruitment occurs are presumably well oxygenated. In deeper billabongs, however, without the same shelving and shallow banks, recruitment is more dependent upon the supply of oxygen maintained

through water flow during the Wet season. At the depths that mussels are recruited, any significant respite in flow may quickly lead to some degree of oxygen depletion which in turn may adversely affect recruitment.

In billabongs lying on the main channel of flow of the Magela Creek, successful recruitment was argued to be related to adequate oxygen as manifested by stream discharges, while survival related to concentrations prevailing over the entire year. Distribution and abundance of mussels in these particular billabong types therefore, are effectively a function of Wet season flow patterns and mean seasonal oxygen concentrations. The resulting derived model was of exceptionally good predictive value. How fortuitous was the resulting goodness of fit of density data, however, remains for further study, yet in combination with known low dissolved oxygen effects, and within-billabong distributional patterns, a good case is presented to recommend V. angasi as a valuable indicator of stream flow patterns in the Magela Creek and perhaps in other monsoonal discharge systems of the Northern Territory or indeed throughout tropical northern Australia. Within the Magela Creek for example, its distribution and abundance in particular billabongs partly indicate a billabong's competence and channelling efficiency during the Wet. Within-billabong distributional patterns indicate local flow effects and the patterns observed within Nankeen billabong for example, strongly implicate at least partial competence of the 'relict' channel lying between Jabiluka and Nankeen billabongs. Such knowledge of hydrology and flow patterns of the Magela Creek is essential to future management, by way of a proper understanding of the likely pathways of

potential pollutants. Indeed the distribution and abundance of mussels over all of the Magela Creek billabongs are correlated with mean dissolved oxygen concentrations. Knowledge therefore of the abundance of mussels in a billabong indicates the general aerobic status of its waters. In pollutional terms, such knowledge is valuable in that poor oxygen relations, but especially persistent anoxia in a billabong, may have implications as to the likelihood of mobilisation of metals in a soluble and available toxic form under low redox conditions (Walker *et al.*, 1983a).

The sensitivity of juvenile *V. angasi* to low dissolved oxygen concentrations will undoubtedly make the species a particularly valuable indicator of the types of pollution in which oxygen concentrations are severely affected. Excessive organic enrichment is one such type, and in this respect the species might have value as an indicator of nonpolluted waters much as Horne and McIntosh (1979) advocated, as the presence of *V. angasi* indicates at least adequate oxygen concentration at a generally regarded critical time of the year for biota - the Wet-Dry interchange (Walker *et al.*, 1983a). Little is known of the sensitivity of *V. angasi* to other pollutants (Skidmore and Firth, 1983) but if juveniles are as sensitive to their effects as they are to low dissolved oxygen, populations of *V. angasi* may be sensitive pollutional indicators and may be used to mark the downstream area of full biological recovery in a polluted stream (Simmons and Reed, 1973).

In relation to the environmental determinants of distribution - dissolved oxygen and stream morphology, it is to the best of

knowledge, the first time attempts at quantifying distributional patterns of freshwater mussels between sites of a drainage system have been made, although previous surveys have eluded to obviously or at least potentially important determining factors (Cvancara, 1967, 1970; Walker, 1981b). Walker (1981b) also considered water flow, as a reflection of the supply of oxygen, the single most important factor governing the relative distributions of Velesunio ambiguus and Alathyria jacksoni in the Murray River in Australia. Both species have distinct preferences for slow-flowing and still waters, and river environments respectively and with the analysis of other such complementary animal-groups, Walker (1981b) suggested study may provide useful insights into the ecology of the Murray-Darling system with its characteristic river and floodplain environments. V. angasi like V. ambiguus is a species at least as tolerant of still waters, a factor borne out in consideration of its wider geographical range, in monsoonal seasonally flowing systems of tropical drainages. Analysis of its distributional patterns elsewhere could provide valuable insights into the aerobic status of waterbodies, which in deepwater billabongs may reflect regional and local Wet season flow patterns.