CHAPTER 8

FOOD INGESTION, CONDITION AND ANNUAL PRODUCTION

8.1   Introduction

Despite the often reported dominance of freshwater mussels from the second trophic level benthic fauna in lakes and streams, and hence their implicated importance in the processing of energy and nutrients, comparatively few studies have been undertaken to investigate the contribution made by mussels to the nutritional dynamics of freshwater ecosystems. Feeding relationships, the incorporation of ingested material into the body, and the relative contribution of the assimilated tissues to the overall economy of freshwaters in fact, are the least well understood aspects of the ecology of freshwater mussels.

From the standpoint of such basic information as to what freshwater mussels feed upon, only a limited number of attempts have been made to determine specifically the nature of the particulate organic matter strained from the water by these filter-feeding forms, and the dynamics of this filtration process. Apart from a number of general statements that appear in the literature based mostly upon cursory observations of the food items observed in the guts of freshwater mussels, the only comprehensive investigations were undertaken 60 to 70 years ago - for North American unionids by Allen (1914, 1921), Coker et al. (1921) and Churchill and Lewis (1924). Annual variations in the composition and abundance of the ingested particulate matter have never been investigated in freshwater mussels.

Similarly, seasonal fluctuations in body weight i.e. condition, as a part measure of the availability of food resources, are poorly understood. Although annual variation in the weight of the soft parts of freshwater mussels have been noted to be high (Haukioja and Hakala, 1978b), minor fluctuations are more generally assumed (e.g. Cameron et al., 1979). Huebner (1980) emphasised, however, that seasonal changes in body weights must be accounted for in the estimates of biomass of mussel populations for population and community energetics studies. Huebner's study in fact is the only one to date to have investigated seasonal body weight fluctuations in populations of freshwater mussels. Condition indices, however, have been derived by Tudorancea and Gruia (1969) and Haukioja and Hakala (1978b) for between-population study of body weight variations.

Studies of the contribution of production and biomass of various species of freshwater mussel to the functioning of ecosystems have been completed by Negus (1966), Tudorancea and Florescu (1968) and Tudorancea (1972), Magnin and Stanczykowska (1971), Lewandowski and Stanczykowska (1975), Coon et al. (1977), Kenmuir (1980), and Strayer et al. (1981).

In at least several billabongs of the Magela Creek, the standing crop of Velesunio angasi is considerable. Studies of the benthic macroinvertebrates apart from V. angasi conducted currently with those of the present, indicated that V. angasi was the major constituent of the benthos, dominating in terms of biomass by over 95% (P. Outridge, unpublished data). As basic information required for estimating the

role and importance of the large standing crop of V. angasi in the economy of the freshwaters of the Magela Creek, studies of food ingestion, condition and annual production were undertaken in the waterbodies. No comparable studies have been undertaken on any hyriid unionacean, and the only study for other tropical freshwater mussels is that of Kenmuir (1980) who estimated annual production of the mussels of Lake Kariba, Zimbabwe.

A. FOOD INGESTION

The present investigation sought to determine: what Velesunio angasi ingested; the seasonal changes in the composition and abundance of the ingested particles; and whether or not selectivity of the ingested materials could be ascertained.

8.2   Materials and methods

Material for dietary study was collected from Georgetown, Mudginberri and Nankeen billabongs. Rationalising the time required for investigation, 5 monthly collections from each billabong, taken over the period 1981 and 1982 were used for study. The choice of the time intervals at which mussels were collected was made in order to maximise observed peaks and lulls in body condition (Figs 8.2 and 8.3). Thus, mussels were sampled at mid-Dry and early-Wet season peaks, at late-Wet and late-Dry season lulls and at early-Dry season increases in condition (Figs 8.2 and 8.3). The collection dates for each billabong are given in Table 8.1. An additional collection was made from Mudginberri billabong during June 1980, for selectivity

studies (section 8.4).

Mussels to be used in dietary studies were taken from the routine sampling sites of the billabongs during the monthly collections (section 3.1). After collection, mussels were immediately placed in 50% ethanol that was kept on ice both in the field and for some period of time back in the laboratory. Such treatment after collection ensured that digestion or the passage of food materials through the digestive system was prevented. The collection times at which mussels were preserved was constant for each sample, and were always within one or two hours prior to midday.

Fifteen adult mussels randomly selected from each collection provided the material for study. In bivalve molluscs including unionaceans (Allen, 1914), digestion is virtually completed in the stomach. According to Morton (1970), food in the stomach of Anodonta is subjected to extracellular digestion by fragmentation spherules from the digestive diverticula and enzymatic breakdown by the crystalline style, and intracellular digestion as the food is passed into the digestive diverticula itself. For studies of relative digestibilities of the ingested particles therefore, the respective contents of both stomach and intestine were processed. The shucked visceral mass of each individual was dried at room temperature for an hour, prior to longitudinal dissection through the centre of the firmed mass. The relative amount or fullness of ingested material present in both the bulbous stomach and the first loop of the intestine was scored from 0 (empty) to 5 (full). The contents of both stomach and intestine were removed and stored in 70% ethanol.

To determine the relative organic and inorganic fractions present in the ingested material, the stomach and/or intestinal contents of 5 mussels from each sample were combined and dried to a constant weight at 40° C. The ash content was then determined by burning off the organic matter in a muffle furnace at approximately 500° C for 20 hours. It must be stressed that the organic fraction determined by this method is an underestimate, as alcoholic preservation is known to chemically alter organic material. By what factor the fraction is underestimated is not known. The relative weight loss nevertheless, is assumed constant between all samples.

To determine and identify the relative algal fractions of the ingested material, a portion of gut content from each of 10 individuals from each monthly sample, was mounted on a glass slide according to the method of Prescott (1980), for microscopic inspection. Identification of the phytoplankton was based upon the regional key of Ling and Tyler (in press) and the key of Prescott (1980). Working in a systematic fashion across the slide, the first 50 algal units were identified under high power microscopy to genus, but mostly to species. This numerical limit was chosen because often no further plankton could be found on the slide. The algal fraction of the ingested material was determined from areal proportions. Using a 1 mm² gridded eyepiece graticule, the number of grid squares (out of 100) at each of 10 fields located at random on each individual slide, superimposed upon algal units and unidentified material (both organic and inorganic) were counted. The number of grid squares containing algal units and unidentified material were summed respectively over the 10 fields. A

mean proportion of phytoplankton was then averaged over the 10 individuals from each sample.

8.3   Seasonal changes in the composition and abundance of the gut contents

Composition of ingested material

The relative fractions of the ingested material for each sample are given in Table 8.1 and relative to various environmental parameters in Table 8.2. In general, the proportions of the ingested fractions − phytoplankton, organic detritus, and inorganic material are considered approximate only. The dominance and absence of various algal taxa in the ingested material can be explained by either differential digestibility and/or possible selectivity of some groups (see section 8.4). Thus overall, the algal fraction is almost certainly underestimated and a proportion of the organic detrital fraction probably comprises some broken down and digested algal cells. Further, the total organic fraction is likely to be underestimated because of error involved in the ashing procedure (see above). Between samples nevertheless, biases are assumed to be constant, and comparisons may still be made.

From the data of relative fractions of the ingested material (Tables 8.1 and 8.3-8.5) and from the relationships between the stomach contents of mussels and various environmental parameters (Table 8.2), some general statements may be made:

1) No zooplankters were observed in the guts of V. angasi.

2) As observed by Coker et al. (1921) for unionids (for which the only comparable data are available), the algal fractions in the stomachs of V. angasi are generally low. In V. angasi the values range from 1 to 27% of the ingested materials. While Coker et al. (1921) observed that the phytoplankton normally found in natural waters rarely amounted to more than 20% of the suspended organic material, partial and complete digestion of some algal forms in the stomachs of V. angasi are almost certainly responsible in part for the low representation of algae (see below).

3) As graphically portrayed in Figure 8.1, a correlation is observed between the amount of phytoplankton in water samples and the proportion found in the stomachs of mussels collected simultaneously. The phytoplankton observed in Georgetown during August 1981, considering the high turbidity of the waters (Table 8.1), was presumably restricted to the surface waters (see section 2.3.2.5) and may not have been accessible to mussels. Under such circumstances, a low proportion of algae found at this time in the stomachs of mussels from this billabong could be expected.

4) The only other pattern apparent for the remaining ingested organic and inorganic fractions observed in the stomach contents over the seasons was that the inorganic fraction overall was higher in Georgetown than the other billabongs. This billabong also had the highest turbidities (Table 8.2).

Gut fullness

The fullness indices of ingested material present in the stomach and

first loop of the intestine averaged over the individuals of each monthly sample, are shown in Table 8.2. As relative fullness is a measure of feeding intensity, the indices calculated in Table 8.2 are assumed to be synonymous with 'ingestion rates' (Winter, 1978). To discern the effect of the environmental variables shown in Table 8.2 upon ingestion rates of mussels, multiple regression analysis was performed over the data of all billabongs, with either stomach or intestinal fullness as the dependent variable, and chlorophyll, turbidity and dissolved oxygen as the independent variables.

Using stomach fullness as the dependent variable, the only significant relationship was observed in an untranformed regression equation where the partial regression coefficient of dissolved oxygen was (positively) significant (P < 0.05). Presumably this reflects an immediate suppression to feeding caused by overnight and early morning oxygen depletions such as were commonly recorded in Nankeen (April, June, August) and occasionally in Georgetown (April) (Table 8.2).

Intestinal fullness is likely to be a better integrated measure of the daily ingestion rate, because the contents are less likely to be voided (vomited) in response to preservation as might be the stomach contents, and further, are less likely to be influenced by the immediate limnological environment prevailing prior to collection. In a multiple regression analysis using log transformations of the independent variables, relationships (but not particularly strong ones, P < 0.1) were found between ingestion rate, and dissolved oxygen and chlorophyll. Increased concentrations of either dissolved oxygen or chlorophyll are suggestive of increased ingestion rates. In the

same regression equation, turbidity had a negative (but negligible) effect upon food ingestion.

In the floodplain billabongs specifically, however, the sustained effect of anoxia during the early Dry season must have a profound effect upon food ingestion. From Table 8.2 it is evident that in Nankeen billabong, despite high algal concentrations during June 1981, feeding is suppressed probably because of low (sustained) dissolved oxygen concentration. Multiple regression analysis was performed over the data of all billabongs, using intestinal fullness as the dependent variable, and omitting the data from Nankeen during June. In a linear model, all three partial regression coefficients proved significant and Student t values were a follows: chlorophyll, 4.11 (11DF, P < 0.01); turbidity, -2.25 (P < 0.05); dissolved oxygen, 2.58 (P < 0.05). Needless to say, the linear regression equation between intestinal fullness and chlorophyll with the omitted Nankeen data, also proved significant (P < 0.05). This indicates that ingestion rates increase with increasing algal concentration; the effect, however, is overridden during periods of low sustained oxygen concentration, when feeding is suppressed. (The inclusion of temperature data to the above analyses indicated that temperature had a negligible effect upon ingestion.)

Food value of the organic fractions

There are indications from the above data, that both the algal fraction of the diet and overall ingestion rates increase in response to increasing phytoplankton in the waters. No seasonal measures of

suspended organic detritus are available, but similar cycles in suspended detritus to those of phytoplankton might be expected. More data would be required to discern whether it is the algal populations alone, by some influence upon a preferential feeding behaviour of mussels, that are responsible for the amounts of food ingested. Nevertheless, to affect ingestion rates, food concentration is presumably at submaximal levels (Jorgensen, 1975; Winter, 1978).

Regardless of the influences of ingestion rates, there are good indications that phytoplankton is the chief utilisable food source of V. angasi. The strongest evidence of this relies upon the general observation that growth of bivalves normally varies with food levels present in the environment (Jorgensen, 1975). Growth of V. angasi in the Magela Creek, is directly related to algal concentrations (section 6.4.3.2). The other utilisable food source is suspended organic detritus, which appears to comprise the main bulk of the ingested material of mussels (see above). An averaged measure of suspended organic detritus over the seasons and between the billabongs, is provided in Table 2.7, as total organic carbon. Growth rate of mussel populations as measured by L_∞ of the von Bertalanffy growth equation (Table 6.20), was not correlated with this parameter.

Further indications of assimilation efficiencies between algae and detritus are provided in Table 8.1. A decrease in carbon content of the ingested fractions is observed with the passage of food through the gut. From analysis of the data in Table 8.1, the loss of organic material between the stomach and intestine varied from 0 to 16% in the four samples that were processed. During August 1981 in Mudginberri,

data pertaining to the algal and organic detrital fractions of both stomach and intestinal contents were available. Approximately 14% of the organic material was lost between the stomach and intestine; of this proportion, a 46% loss of algae was recorded, but only an 8.3% loss of organic detritus. Whilst this might indicate preferential digestibility of algae, nevertheless, presumably a proportion of the wastes from algal digestion in the intestine may now comprise the unidentified organic detrital fraction, thereby underestimating to some degree loss of the organic detritus. Data on relative fractions of algae and detritus between sites of the gut are inconclusive, and proper feeding experiments using a variety of different diets would be required to estimate properly the assimilation efficiencies of algal and detrital food sources. As far as these studies are concerned, growth rate data suggest that the chief utilisable food source of _V._ _angasi_ is unicellular algae. This accords with the general case that living phytoplankton has a higher food value than either bacteria or detritus in the diets of suspension feeders (section A5.1). In terms of ingestion nevertheless (as opposed to digestion), _V._ _angasi_ may be regarded as a phytophagous and detritivorous filter-feeder.

8.4   Composition and selectivity of ingested phytoplankton

Species composition

The combined percentage composition of phytoplankton genera observed in the stomachs of the 10 individuals of each monthly sample was calculated, and is shown in Tables 8.3-8.5 for Georgetown, Mudginberri and Nankeen billabongs respectively. Highest to lowest species

diversity of phytoplankton in the guts of mussels from the 3 billabongs was found to be in the following order: Georgetown, Mudginberri, and Nankeen billabongs.

Two studies relating to phytoplankton populations in the Magela Creek billabongs have been completed: that by Pancontinental Mining Limited (1981), and by Kessell and Tyler (1983). Unfortunately neither source provides comprehensive information upon seasonal changes in the composition and abundance of phytoplankton populations within any of the billabongs. Kessell and Tyler (1983) recorded that motile flagellates especially, but also passively floating desmids (Zygnematales), Chlorococcales, and diatoms dominate the phytoplankton of the Magela Creek. Their studies were mainly confined to the Dry season, and no seasonal data were presented. Pancontinental Mining Limited (1981) provided some limited information on seasonal changes in phytoplankton in the floodplain billabongs of the Magela Creek. They recorded representative species occurring in blooms in the billabongs, and noted in general that 46 species or 36% of the total flora recorded in the billabongs belonged to the Zygnematales. (This is apparently consistent with most Australian freshwater systems where desmids are the dominant taxa.) Pancontinental Mining Limited (1981) noted no apparent differences in taxonomic composition of phytoplankton populations inhabiting billabongs during either Wet or Dry seasons.

Seasonal patterns, however, were apparent in the species composition of phytoplankton ingested by mussels of the Magela Creek. The number of species ingested by mussels was highest in all billabongs during

the Wet season (Table 8.3-8.5). Motile flagellates (Dinophyceae and Euglenophyceae) dominated the ingested photoplankton during the Dry. Desmids (Zygnematales) and Chlorococcales were underrepresented in the material from the turbid billabongs during the Dry (i.e. months prior to December 1981, Tables 8.3 and 8.5), but generally dominated in the material from all billabongs collected during the Wet. Assuming that ingestion in V. angasi is unselective (see below), these major shifts in species diversity between the seasons were a feature of the dynamics of the phytoplankton populations of the billabongs over the study period. Such patterns, however, have apparently been previously undetected in the plankton of the billabong waters.

Selectivity of ingested phytoplankton

Unfortunately, no water samples were taken with the mussel collections from the billabongs to allow for direct comparison of phytoplankton composition in the guts of mussels and in the surrounding waters. Kessell and Tyler (1983), however, sampled the waters of Mudginberri billabong intensively, over an 11 day period from 24 June to 4 July 1980, recording species present on each consecutive day. Their results in terms of the number of days over which genera were present in the waters (out of 11 days), in relation to the generic composition of the phytoplankton observed in the stomachs of mussels collected on 15 June 1980 are shown in Table 8.6. From the 11 day record of Kessell and Tyler reasonable stability of the phytoplankton populations was apparent with no major shifts or trends in species composition over the period. It is unlikely therefore, that the species composition observed in the waters should have differed to any

marked degree from that present 9 days earlier at the time that mussels were sampled.

The water samples of Kessell and Tyler (1983) were taken by towing a net in the open waters of the billabong. Thus, while these samples were not taken from immediately above the benthos, nevertheless a uniformity between different depths of the billabong in algal species composition is assumed. This assumption is justified in that the shallow waters of the Magela Creek billabongs including Mudginberri (section 2.3.2.2) are generally well mixed. Further, algae are not restricted to the surface of the clean waters of Mudginberri and Kessell and Tyler noted regular daily patterns of migration of algae in the billabong, including dispersion at night.

From comparison between the algal composition present in the plankton and in the stomachs of mussels (Table 8.6), it is immediately apparent that the ingested phytoplankton is a poor representation of that present in the water. The phytoplankton of the Magela Creek is diverse and from a water sample from any of the billabongs, 80-100 species can generally be expected (Kessell and Tyler, 1983). The number of species (27) found in the stomachs of mussels from Mudginberri billabong during June 1980, amounted to only one third of that which could be expected from the surrounding waters (Table 8.6). With the same counting procedure (i.e. a total of 500 phytoplankton units) from monthly samples from the billabongs, the total number of species of algae recorded in the stomach varied but rarely exceeded 80 (Tables 8.3-8.5).

The low numbers of algal species observed in the stomachs of mussels, compared to the high numbers found in the plankton could be the result of either 1) differential digestibility or 2) selection against certain algae by mussels.

Evidence of differential digestibility is as follows. The composition of phytoplankton in the stomachs of mussels is characterised by very dominant genera (Tables 8.3-8.5); notable are Trachelomonas, Peridinium and Cosmarium spp. Almost all of the Trachelomonas comprised T. oblonga, which apparently is consistently represented in algal blooms throughout the Magela Creek (Pancontinental Mining Limited, 1981; Kessell and Tyler, 1983). None of the individual species of the preceding listed genera, however, dominate in the plankton to anywhere near the extent that they are represented in the stomachs of mussels. Analysis of intestinal contents also shows that the dominant taxa are consistenty represented, unchanged in form, in the digested material (see August 1981 in Mudginberri billabong, Table 8.4). Their dominance in the stomach contents of mussels therefore, indicates that these forms are resistant to digestion. The cell wall of Peridinium is an armoured thecate; the cell wall of Cosmarium is surrounded by a gelatinous sheath; and the Trachelomonas cell is enclosed in a rigid, mineralised and nonliving lorica. As also noted by a number of authors therefore (e.g. Allen, 1921; Ten Winkel and Davids, 1982), these spherical algae may pass through the alimentary canal of freshwater bivalves undigested, because of resistant cell walls.

Although species identifications with the material at hand were

reliable, with preservation and digestion, the subtlety of form of some algae may have been lost, resulting in some inadvertant misidentification, or lumping of species of similar appearance. This error, however, is assumed minimal and with proper perusal, it is more likely that phytoplankton with naked cell walls will be found to be underrepresented amongst the ingested algae; this would indicate that these forms are rapidly digested in the stomach of V. angasi. In the warm waters of the Magela Creek, this is almost certainly the case and overall, algae should tend to be underrepresented in the stomach contents. Comparison of the phytoplankton composition between that of the stomach content and that suspended in the environment therefore, is unlikely to yield satisfactory results in selection studies, and to properly determine whether V. angasi selects its food, controlled feeding experiments would be required.

Evidence for selection against certain algae is as follows. The number of diatom species in the plankton of the Magela Creek waters is reportedly low, by comparison with the high species numbers of green algal forms. The normally digestion-resistant diatoms are apparently underrepresented in the stomach contents (Table 8.6). Even considering that many broken frustules (presumably of the larger ci nate forms such as Asterionella) were observed (but not recorded because they were unidentifiable), tests of the smaller diatoms (e.g. Eunotia) were rarely seen, even though they were commonly recorded in the plankton (Kessell and Tyler, 1983). Gale and Lowe (1971) concluded that Sphaerium transversum fed unselectively, despite the fact that diatoms were underrepresented amongst the ingested phytoplankton. Further, it is quite probable that very large

phytoplankton forms (e.g. *Netrium*, *Asterionella*) are omitted from the diet of *V. angasi*, and that a size range (but a large one) of algae is preferred.

Because the number of diatom species (and the taxa of very large algae) represented in the plankton are small in relation to the green algae, selection by *V. angasi* against diatoms and large algae may account for only minor underrepresentation of algae found in the guts of mussels. The weight of evidence therefore, favours the view that *V. angasi* generally feeds unselectively, and that algae are underrepresented in the stomachs of mussels because some species are digested much more rapidly than others. Apart from a size selection – if indeed present at all and an unexplained absence of diatoms, further evidence of unselective feeding is presented in that *V. angasi* includes a large inorganic fraction (silt) (Table 8.2) in the diet. On this criterion alone, i.e. the failure to discriminate between organic and inorganic ingested materials, other authors have decided that respective bivalve species are unselective in their feeding (e.g. Churchill and Lewis, 1924; Nasr, 1984). Further strength to unselective feeding in *V. angasi* is advanced, given that a wide array of algal taxa at some time or another are represented in the stomach contents (Tables 8.3-8.5).

That the proportions of inorganic particles are not even higher in the guts of mussels from turbid environments (e.g. Georgetown and Nankeen during the Dry season, Table 8.2) is probably explained by the efficiency of retention of particles by the gills. Bivalves can generally retain particles no smaller than 1 μm in diameter

(Jorgensen, 1975). The suspended particles that comprise the turbidities observed in the Magela Creek billabongs, however, are generally less than 0.45 μm in size (Walker et al., 1983b).

B CONDITION

8.5   Wet/dry weight conversions

The flesh of 50 individuals from each of the routine monthly samples from the billabongs (30 individuals from each of the routine samples from the Magela Creek channel) was weighed (section 3.3), and oven dried at 65° C to a constant weight. All dry weights were made to the nearest 1 mg.

Plots of flesh (or wet) weights against dry weights clearly indicated nonlinear relationships within the sexes and waterbodies and showed that water content of mussels decreased with increasing size. Log-log transformed regression equations therefore were calculated to describe the relationship between wet and dry weight. The linear transformed equations are shown for each waterbody, and for sexes separate and combined in Table 8.7. Within any one waterbody, there are generally no significant differences found between the slopes and intercepts of the regressions for each sex (Table 8.7). However, using an analysis of covariance test, very strong evidence (P < 0.001) was found against the hypotheses of equal slopes and means of the combined-sexes regressions of each waterbody. A single regression equation using the data from all billabongs therefore, cannot be used to describe the wet/dry weight relationship of mussels from the Magela Creek.

8.6   Length/weight relationships between sexes and waterbodies

Of six external shell dimensions (length, height, inflation, profile, girth and circumference) used to predict biomass of a number of unionid species, it was concluded by Golightly and Kosinski (1981) that functions with the variable shell length as the independent variable, provided accurate and adequate models. Thus even early results using the theoretically ideal dimension, inner shell volume, were quickly abandoned in the present study when it was learnt that as accurate (if not better) prediction of biomass could be obtained using shell length alone. In addition to its virtue of accurate prediction, length has been argued to be the best dimension for field use because of its ease of measurement, and because it is the largest dimension, thus minimising measurement error. Further, its extensive use in the literature facilitates comparison of biomass estimates between various environments (Golightly and Kosinski, 1981).

Using dry weight as the dimension of biomass in the present investigation, log-log transformed regression equations were calculated to describe the relationship between shell length and dry weight. The linear transformed equations are shown for each waterbody, sexes separate and combined in Table 8.8. Only in 3 out of 10 waterbodies were significant differences found between the slopes and/or intercepts of the regressions for each sex (Table 8.8).

To follow changes in the length/weight relationship or condition of the sexes of V. angasi between seasons and locations of the Magela

Creek, the relationship between length and dry weight for all data of
the Magela Creek, sexes, locations and seasons combined, were used as
a baseline to which the weight of individual mussels of a specific
size and from any season and location could be compared. The linear,
tranformed regression equation for all mussels combined, is described
in Table 8.8.

8.7   Relative condition

The condition of individual mussels, relative to the entire Magela
Creek community sampled over the study period, was calculated
according to the method of Le Cren (1951) for fish studies, using the
formula:

$$K = \frac{W_0}{\hat{W}} \qquad (1)$$

where   K = relative condition,

             W_0 = observed weight,

             $\hat{W}$ = expected weight.

$\hat{W}$ was calculated by substituting the length of individual mussels into
the regression equation determined for the combined Magela Creek data
(Table 8.8).

8.7.1   Between sexes and waterbodies

Relative condition is shown for male and female mussels (means   95%
confidence   limits)   from   Georgetown,   Mudginberri   and   Nankeen
billabongs, and the Magela Creek channel at monthly intervals in

Figure 8.2; from Corndorl, Island, JaJa, Leichhardt and Jabiluka billabongs at bimonthly intervals, and from Buffalo billabong at intervals of three months, in Figure 8.3.

In waterbodies where condition was determined at monthly intervals, a diphasic annual cycle of condition is apparent (Fig. 8.2). A major peak in condition during the mid-Dry season (July-September) and a minor peak during the early Wet season (January-February) are observed. Condition is lowest at the end of the Dry (December) and again at the end of the Wet (March-April). Generally speaking, the peaks in condition coincide with periods when food availability (phytoplankton and organic detritus) is greatest, while the lulls correspond to periods of lowest food concentration (see below). In billabongs where condition was determined bimonthly, only a Dry season peak in condition was immediately discernible. Nevertheless, food availability again, appeared to be chiefly responsible for the patterns observed.

Generally, the condition of females was lower than males at any one time and location (Figs 8.2 and 8.3). Rarely however, were the disparities between the sexes significant. The lower condition of females is probably best explained by the repetitive spawning observed in V. angasi, which can be assumed to be more taxing upon the physiology and energy reserves of females than males. Nevertheless, periods were observed when the condition of females exceeded that of males. These periods were associated with either less intensive spawning of females (e.g. late Dry season in Nankeen, Fig. 8.2) or with lag phases in which the condition cycle of females was

occasionally observed to fall behind that of males (e.g. January-March 1981 in Mudginberri and the Magela Creek channel; August-December in JaJa). The latter is possibly the result of the lag that would be observed in the weight of females (as opposed to males) retaining brooding larvae.

While the condition cycles appeared to be broadly associated with seasonal abundances and deficiencies in food availability, other climatic and limnological factors from the literature (sections A5.1 and A5.2) have been implicated as affecting either condition or feeding activity of bivalves. Chief amongst these factors are temperature, turbidity, and dissolved oxygen. As was the case for larval production therefore (section 7.10.1), attempts were made to model the condition cycle over all billabongs, or at least within the billabongs, using a mutliple regression approach. Just as was found for larval production the analyses can indicate at least, the contribution of the various climatic and limnological factors towards determining the cycles of condition.

Dry weights and thus condition, were measured and only determined bimonthly in most billabongs. To utilise all of the available data for analysis therefore, the individual wet weights of mussels examined every other month in these billabongs, were converted to dry weights by using the appropriate regression equation (Table 8.7). Relative condition was then calculated for the data in question using the formula (1) described above. Within the alternate months when condition was determined by actual dry weights, condition was also calculated using the conversion of wet to dry weight, for comparison

of the estimates. Condition (males and females combined) as derived by the two methods is plotted monthly for the appropriate billabongs in Figure 8.4. The closeness of fit generally observed between the estimates at any one time and location was sufficient justification for including the condition data from all months in the analyses.

The same independent variables as were chosen for larval production were included in the analyses performed on condition, namely chlorphyll, turbidity, dissolved oxygen, temperature and time. (The basis for the inclusion of time in the analyses was the same as presented in section 7.10.1.) Appropriate transformations were decided according to the criteria given earlier (section 7.10.1). Log transformations of chlorophyll, turbidity and dissolved oxygen were used. No multiplicative combinations of the variables were suggested for the analyses. For the dependent variable, condition, the data of both sexes combined were analysed, as differences in body weights between the sexes of V. angasi were generally not significant (Figs 8.2 and 8.3).

Multiple regression analyses were performed on the five independent variables against monthly condition of mussels from each billabong, and on the data of the billabongs combined. The resulting regression equations are shown in Table 8.9. Results of AOVs of the regression coefficients over the billabongs and over groups of hydrologically similar billabongs showed very strong evidence, in both cases, against the assumption that all the regression equations estimated the same population regression (P < 0.001). The absence of consistent and significant correlations between condition and environmental factors

within billabongs and groups of billabongs indicated that the effects of the various factors were either minimal, masked by other environmental factors, or mediated and controlled more by internal physiological mechanisms rather than realised by an immediate response of body weight to any of the factors.

As noted for larval production (section 7.10.1), the equation derived from the data of the billabongs combined, is a useful descriptive model, giving a general indication of the importance of the various environmental parameters studied, to condition averaged over the Magela Creek. Because condition was calculated relative to the entire Magela Creek data, however, the values of condition at the peaks and lulls do not necessarily correspond between the billabongs. To some extent therefore, the correlations using the combined equation may be expected to be low for independent variables such as temperature and dissolved oxygen whose range in values is similar between billabongs. The results of the regression equations may be summarised as follows:

1) Turbidity - With respect to the regression equations derived from the data of individual billabongs, the sign of the partial regression coefficient of turbidity in the turbid billabongs, Georgetown and Nankeen is positive (significant at $P < 0.01$ in Georgetown, Table 8.9). From the evidence given below, these relationships are assumed associative only, and the seasonal trends of both condition and turbidity are merely coincident. In several billabongs, turbidity and chlorphyll are intercorrelated (Table 8.10) and as shown below, turbidity may obscure the relationship between condition and chlorophyll within these billabongs.

Averaged over all billabongs, the sign of the partial regression coefficient of turbidity is negative (Table 8.9), indicating that increasing turbidity is inhibitive to weight gain. In highly turbid billabongs, food availability (phytoplankton at least) might be expected to be low owing to reduced light penetration through the water column. However, as discussed below, this effect in the Magela Creek billabongs, might only be felt during the late Dry season. In highly turbid waters, additional energy might be expended by mussels in sorting and rejecting the suspended solid load from the surrounding waters. Across all billabongs, nevertheless, the influence of turbidity upon condition is apparently not a strong one.

2) Temperature - The significant, negative partial regression coefficient of temperature (P < 0.05) in the regression equation from Nankeen billabong suggested merely coincidental, seasonal trends of both condition and temperature. However, given the correlation between spawning intensity of mussels and temperature in Mudginberri billabong (section 7.10.1), the significant, negative coefficient of temperature (P < 0.01) for Mudginberri suggests that condition declines directly in response to increasing reproductive activity. Over all billabongs, the effect of temperature upon condition is nevertheless negligible.

3) Dissolved oxygen - The availability of sufficient oxygen is doubtless conducive to weight increase, and a consistently positive sign of the partial regression coefficient was observed among the billabongs. During June 1981 in Leichhardt billabong, a decrease in

weight of mussels was observed (Fig. 8.3) in association with deoxygenation of the billabong at the time. The suppressed condition of mussels observed between April and June 1981 in Island might similarly be explained in terms of the relative anoxia found in the billabong over this time. Presumably filtering and feeding activities cease during periods of anoxia. Nevertheless, over all billabongs, the influence of dissolved oxygen upon condition is apparently minimal.

4) Chlorophyll - Averaged across all billabongs, trophic conditions are apparently the only significant influence of the magnitude of weight variations of mussels. Thus food availability as measured by chlorophyll, was the only significant partial regression coefficient (P < 0.001) in the regression equation using the combined Magela Creek data. Within billabongs, the relationship between chlorophyll and relative condition is partly obscured by intercorrelation between turbidity and chlorophyll (Table 8.10). However, in 5 out of the 8 billabongs, significant regressions were found between seasonal chlorophyll concentrations and condition (Table 8.10).

Weight increment and decline of V. angasi in the Magela Creek, are depicted as smoothed and averaged responses to food availability. The monthly measure of food availability (algae) for mussels, however, is not necessarily highly correlated with monthly measurements of chlorophyll. Algal concentrations in the Magela Creek are highly variable both temporally and spatially (Kessell and Tyler, 1983). While the chlorophyll value averaged over the seasons might be a good indicator of the trophic status of the particular environment

generally, the spot monthly readings measured in each billabong might not necessarily be the best measure of algal abundance from a month to month basis. This may explain the poor correlations observed between seasonal condition and chlorophyll within billabongs (Table 8.10). (Indeed the weight variation observed in $\underline{V}$. angasi might be a good integrated measure of seasonal trends in the trophic status of the waterbody in question.)

Thus, with increasing algal production over the Dry season, a weight increase of mussel flesh is generally observed (Figs 8.2 - 8.3). As stated above, this increase is depicted as an integrated response to food availability. That the period generally coincides with a decline in water temperature, would indicate that respiratory and maintenance costs also decline, thereby availing more energy for growth. Condition peaks during the mid-Dry season in most billabongs.

An ensuing decline in weight is found until the end of the Dry (December) in turbid billabongs (Georgetown, Corndorl, JaJa, Jabiluka, Nankeen) and one non-turbid billabong (Mudginberri) (Figs 8.2 - 8.3). Suppressed algal production due to increasing turbidity is depicted as the cause of weight loss of mussels in turbid billabongs, while a temperature increase and associated spawning intensity are probably the cause of the decline in condition of mussels from Mudginberri. Apparently algal abundance is high enough in the non-turbid billabongs, Island and Leichhardt, that no discernible weight loss occurs with spawning intensity over the Dry season. Weight variations of mussels in these billabongs may be more directly related to oxygen and food availablity.

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During the early Wet season, a minor peak is again observed in
condition, most evidently in waterbodies where condition was
determined monthly (Fig. 8.2). With major early Wet season flushes
into the billabongs, dramatic influxes of nutrients into the
billabongs occur with associated major peaks in algal production
(section 2.3.2.5). These nutrient fluxes apparently decline in
intensity, with each major ensuing spate of the Wet season. Thus
significant, but nevertheless sporadic and short-lived increases in
algal production, in addition to detrital material, probably
characterise the waters of the early Wet season. The measurements of
chlorophyll taken during the early Wet (December – January) in the
present study do not necessarily depict this. (Note, however, the
high chlorophyll value recorded for Corndorl billabong during early
flushes in December 1981, Fig. 2.28.) The weight gain of mussels
observed during the early Wet season, is undoubtedly associated with
significant but short-lived increases in algal concentrations. As
nutrients are flushed through the catchment with the progression of
the Wet, the flowing waters become increasingly oligotrophic and
mussel condition reaches a seasonal low at the end of significant Wet
season discharge.

Seasonal increases and declines in condition of mussels correspond
broadly to the same patterns of fluctuations in algal production
observed in the Magela Creek billabongs. Using the data of the
respective variables averaged over the seasons for the billabongs, a
significant linear regression equation (P < 0.05) was found to
describe the relationship between mean condition and mean chlorophyll

concentration. The relationship is plotted in Figure 8.5 and the regression equation is:

$$Y = 0.595 + 0.046X \qquad (P < 0.05, \; r^2 = 0.575)$$

where   Y = mean relative condition

and   X = mean chlorophyll concentration (μg/l).

Thus, relative condition of mussels averaged over the seasons is clearly dependent upon the trophic status of the waters. This relationship is taken as further independent evidence that phytoplankton is probably the main utilisable food and energy source for V. angasi.

From Figure 8.5, it is interesting to note that condition of mussels from the non-turbid billabongs (Mudginberri, coded 12; Buffalo, 14; Island, 16; Leichhardt, 24) plotted above the regression line, while the values of the other, non-turbid billabongs plotted below the line. This suggests that energy is expended (at the expense of somatic growth) by mussels in clearing the filtering apparatus of inorganic particles and/or that ingestion in V. angasi may cease or be reduced under conditions of high turbidity. The observation is in agreement with the negative influence of turbidity upon weight increase suggested in the negative sign of the partial regression coefficient from the combined multiple regression equation (Table 8.9).

The mean condition value averaged over the seasons, of mussels from the Magela Creek channel, was not included in the above regression

equation describing the relationship between seasonal condition and algal abundances. Of the populations from the Magela Creek waterbodies, the shells of these mussels are exceptionally inflated (section 4.4), and flesh weights therefore, are disproportionately high in relation to mussel length. These mussels consequently, have the highest conditions relative to the other Magela Creek populations (Figs 8.2 and 8.3).

In terms of annual patterns, a diphasic cycle of condition as shown for other populations, is shown for mussels from the Magela Creek channel (Fig. 8.2). An early Wet season peak in condition corresponds presumably to nutrient (and detrital) flushes in the Creek. A seasonal low in body weights occurs at the end of the period of major discharge (March). However, as the Creek is reduced to a trickle and eventually to a series of lentic pools (from March to August), algal populations apparently build up in sufficient concentration for condition of mussels to improve. Condition peaks just at the period when mussels are obliged to aestivate with water subsidence. Energy reserves are depleted over the dormant phase of the mid-late Dry, until feeding recommences at the onset of the Wet season.

8.7.2   Between age classes

Mean condition with respect to age is plotted in Figures 8.6 and 8.7 for each of the Magela Creek waterbodies. Both linear and quadratic weighted regression equations were fitted to the data. Significant regression relationships as described in Table 8.11, were found in 9 out of the 10 populations. In the Mudginberri, Island, JaJa and

Jabiluka populations, the quadratic model was appropriate whereas the linear model was used in the Georgetown, Corndorl, Buffalo, Island, Leichhardt and Nankeen populations. In particular billabongs, mussel condition increased over the earliest ages, peaked at an intermediate age, and declined over the oldest age classes (Mudginberri, Buffalo, Island, JaJa, Nankeen - Figs 8.6 and 8.7). In Buffalo billabong, the decline in condition was noted only amongst the oldest age classes (> 25 years). In other billabongs, a decline in condition was observed over the entire life-span of mussels (Georgetown, Corndorl, Leichhardt).

The increase in condition observed amongst the younger age clases of mussels in several billabongs (and the Magela Creek channel) can be attributed in part at least, to the allometric relationship between length and width of mussels in the Magela Creek (section 4.4). Larger mussels are more inflated than smaller mussels and therefore tissue weight is proportionately greater in the larger individuals of a population.

Senility (Comely, 1978) or the increased energy requirements for basal metabolism that would result in less food being made available for growth (Hickman and Illingworth, 1980), have been suggested as causes of a decline in condition observed amongst the older age classes of respective marine bivalve species. The decline in condition invariably observed amongst the older age classes of mussels of the Magela Creek populations (Figs 8.6 and 8.7), corroborates the evidence of section 7.8, that reproductive functioning of V. angasi, declines with age. That this decline is at least one factor contributing to

the relative weight decrease of mussels, is shown by the fact that in female mussels at least, gravidity and oogenic activity decline in intensity with age (section 7.8). Relative weight loss can be assumed to accompany these changes therefore, as significantly fewer oocytes and subsequent larvae are produced.

8.7.3   Within billabongs

The mean condition of mussels sampled in Georgetown (Fig. 8.8), and Leichhardt and Nankeen billabongs (Fig. 8.9) was plotted according to depth. As was found for within-billabong study of larval production (section 7.10.2), the relationships shown in Figures 8.8 and 8.9 could generally be explained in terms of the known condition-age relationships as discussed above (section 8.7.2) and the age-depth relationships as described in section 6.5.3.1. Some exceptions to the expected patterns, however, were noted. At shallow depths, the condition of mussels in Georgetown and Nankeen billabongs was the reverse of the patterns that could be expected if they were to accord with known condition-age and age-depth relationships. Thus, the youngest mussels occur at the shallowest depths (< 0.5m Nankeen, < 1.5m - Wet season levels - Georgetown) in these billabongs yet their condition was amongst the lowest observed and not the highest as might be expected from section 8.7.2 above (Figs 8.8 - 8.9). To some extent, the anomalous patterns observed in Georgetown may be explained in terms of the seasons that mussels were collected. Waters less than 1m in depth represented the peripherally inundated shallows of the Wet season. The condition of mussels collected at this time was generally low (Fig. 8.2). As discussed in an earlier section (section 6.4.3.1)

nevertheless, at the shallowest depths in either Georgetown or Nankeen billabong, wave-induced resuspension of the silty sediments during the Dry season might interfere with the normal filtering processes. Extra energy may be expended by mussels feeding in highly turbid waters (see above, section 8.7.1). For greater depths (> 0.5m Nankeen, > 1.5m Georgetown) and all depth intervals of Leichhardt billabong otherwise, condition accords with the patterns as could be expected from known condition-age and age-depth relationships.

No depth relationships could be shown for the condition of mussels within Mudginberri and Buffalo billabongs. Although age and depth relationships have previously been shown for mussels from these billabongs (section 6.5.3.1), condition does not vary greatly over the life-spans of mussels from either billabong (Fig. 8.6). Nevertheless, in both billabongs relationships were found between mean condition of mussels at the particular sampling sites and mean chlorophyll concentration (calculated for these sites as described earlier in section 5.4.3.1). The relationships between mean condition of mussels and chlorophyll concentration are plotted in Figure 8.10 for Mudginberri and Buffalo billabongs. Condition of mussels clearly improves with increasing chlorophyll concentration.

Thus, between relatively widely spaced sampling sites of a billabong such as in Mudginberri and Buffalo, trophic conditions may be expected to affect relative condition. Otherwise, age and local turbidity effects may influence the patterns of relative condition observed over a depth range at a sampling station, such as were observed in Georgetown, Leichhardt and Nankeen billabongs.

C   ANNUAL PRODUCTION

8.8   Biomass

The lengths of individuals that were used to determine the density estimates of mussels in each billabong (section 5.3, Tables 5.1-5.9), were converted to dry weights, using the appropriate length/weight regression equation (Table 8.8). The mean shell free, dry weight of mussels per unit area was then calculated according to habitat types within the billabongs (Tables 8.12-8.19).

From the data of Tables 8.12-8.19 no overall mean biomass (per unit area) was calculated for each billabong. Cursory but reliable approximations, however, range as follows: <5 g dry weight/m^2, Jabiluka $<$ Gulungul $<$ Island; 5-10 g/m^2, Georgetown; 10-15 g/m^2, JaJa $<$ Leichhardt $<$ Corndorl; 15-20 g/m^2, Buffalo $<$ Mudginberri $<$ Nankeen. The biomass ranking thus, is similar to the billabong density ranking (Table 5.10), except that the high density of mussels in Georgetown (second highest of the billabongs) realises a small biomass (fourth lowest) because of the slow growth rates exhibited by mussels in this billabong (section 6.4.2).

8.9   Annual production in selected billabongs

Annual production of $\underline{V}$. $\underline{angasi}$ was estimated in several billabongs of the Magela Creek - Georgetown, Mudginberri, Leichhardt and Nankeen. The choice of billabongs was made according to the variety of hydrological and trophic types represented in the Magela Creek.

Biomass and production estimates were computed from the population data using method 1 of Crisp (1971). This is the method used by other workers (Table A5.1) to estimate biomass and production in respective freshwater mussel populations. Biomass was obtained from the product of density (n) and mean weight (b), and production from the product of density and change in mean weight (b) (where b at age n = b_n - b_{n-1}) of each age class. Density of mussels of each age class was obtained from the product of the grand, mean density of mussels (per m^2, Table 5.10) and the proportion of the total age structure that individuals of the respective age class comprised (Figs 6.29 and 6.30). Biomass of individuals of each age class was calculated by converting age to length according to the appropriate von Bertalanffy growth equation (Table 6.20), and converting length again to dry weight using the appropriate length/weight regression equation (Table 8.8). Step by step computations (following Lewandowski and Stanczykowska, 1975) used to calculate annual production and biomass of the various age classes of V. angasi in the respective billabongs, are presented in Tables 8.20 - 8.23.

As expected (Waters, 1977), the turnover ratio (P/B) of V. angasi in the Magela Creek, decreases with increasing age of mussels (Tables 8.20 - 8.23), as a result of decreasing growth rates with age. P/B ratios calculated for all age classes, are relatively constant between populations, ranging from 0.07 to 0.13. The population from Leichhardt observes the highest ratio (0.13). This population is one of the youngest in the Magela Creek (Figs 6.29 - 6.30), and as growth is continuous over the entire life span (Fig. 6.12) even the oldest

mussels are nevertheless contributing to production (Table 8.22). Proportionately more older mussels comprise the mussel populations from Georgetown, Mudginberri and Nankeen billabongs, however (Figs 6.29 - 6.30). As growth is insignificant in the oldest age classes (Figs 6.11 - 6.12), these mussels contribute little if any to the total annual production (Tables 8.20, 8.21 and 8.23 respectively). P/B ratios therefore are relatively low (0.071 - 0.088) and variations can be attributed to the relative contributions of the oldest age classes to the biomass of the respective populations. Thus in accordance with the predictions of Waters (1977), P/B ratios of $\underline{V}$. $\underline{angasi}$ in the Magela Creek are generally a function of longevity and the relative contribution of the oldest mussels to production.

D. DISCUSSION

Food ingestion

The absence of animal remains (notably zooplankters) amongst the ingested stomach contents of mussels from the Magela Creek billabongs, was taken as evidence that $\underline{V}$. $\underline{angasi}$ is a phytophagous and detritivorous filter feeder. Thus, these observations are in accord with those of other workers that the food of freshwater mussels is chiefly of plant origin (Evermann and Clark, 1917; Coker et al., 1921; Hendelberg, 1960; Clarke, 1973). Others, however, have recorded zooplankters amongst the ingested gut contents of mussels (Allen, 1921; Churchill and Lewis, 1924), and both Pennak (1953) and Fuller (1974) concluded that these forms were important as food value for freshwater mussels. Zooplankters are generally absent from the diet

of other freshwater bivalve forms and marine bivalves (section A5.1).

Based on reports that much of the phytoplankton ingested by freshwater mussels passed through the digestive tract intact and unchanged by the digestive processes, Fuller (1974) concluded that algae were overestimated as food value. Thus, the observation of only partial digestion of algae is a widespread one amongst dietary studies of bivalves (section A5.1), and it is well known that some diatoms and flagellates bear tests or cellulose cell walls resistant to digestive enzymes. Coker et al. (1921) recorded moreover, that generally less than 5% of the ingested stomach contents of mussels examined, comprised diatoms and unicellular green algae. They concluded that detritus formed the main fraction of the food of freshwater mussels.

Similarly, in the stomachs of V. angasi examined, the algal fractions were generally low ranging from 1 to 27% of the ingested materials. Moreover, the dominant genera of algae present in the stomachs, notably Trachelomonas, Peridinium and Cosmarium, are all forms with resistant cell walls - which in other studies have been shown to pass through the digestive tract undigested (e.g. Allen, 1921; Coker et al., 1921; Ten Winkel and Davids, 1982). These forms in V. angasi were also noted beyond the stomach, present in an undigested condition. The very presence of dominant, digestion-resistant algae in the stomachs, however, is taken as evidence that algae overall were underrepresented amongst the ingested material; that is, more sensitive forms presumably ingested along with the more resistant algae (assuming that ingestion is unselective), must undergo rapid breakdown and digestion. This is almost certainly the case

considering the comparatively high water temperatures sustained over the year in the Magela Creek (> 20°C), that would accelerate the digestive processes. Allen (1921) and Coker et al. (1921), also recorded dominant and resistant algae amongst the ingested contents of the gut. Unfortunately, no data were presented in either study to allow assessment of the extent to which both individual algal forms and the bulk proportion of phytoplankton present in the gut contents of the unionids were underrepresented as well.

Intestinal fullness of ingested material was argued to be the best integrated measure of feeding activity and ingestion rates of V. angasi. A positive correlation was found between the ingestion rate and phytoplanktonic biomass of the environment when the influence of periods of sustained oxygen depletion was excluded from analysis. (During periods of relative anoxia, there was no evidence of feeding regardless of the levels of algae in the plankton.) A strong correspondence was also noted between the proportion of algae in the stomach and the biomass of phytoplankton present in the surrounding waters. More studies would be needed to discern whether feeding intensity is dependent only upon the living algal component of the organic material in suspension. In this instance the appetite of mussels would be solely dependent upon algae even if ingestion was unselective. This would indicate that algae was the main utilisable food item. Both algal and detrital abundance in the suspension of the waters of the Magela Creek, however, may be simultaneous, especially if much of the detritus is of phytoplanktonic origin. A correlation between ingestion rate in bivalves and food concentration in the environment, is generally interpreted as meaning that food is at

submaximal levels (Jorgensen, 1975; Winter, 1978).

Nevertheless, while the cycles of living and dead algae could be assumed to be the same in water suspensions, the abundances of phytoplankton and total organic carbon averaged over the seasons in the Magela Creek billabongs do not correlate (see Table 2.7). This would suggest that the chief component of the organic detritus in suspension in the billabongs, is not of phytoplanktonic origin. Almost certainly the material is of a macrophytic or allochthonous nature considering that the levels of total organic carbon are highest in billabongs lying off the mainstream channel of flow of the Magela Creek (backflow billabongs and JaJa) where macrophytes are prolific and where deposition during the Wet season is relatively high.

Jorgensen (1975) and Winter (1978) state that growth in bivalves is dependent upon the amount of food ingested. In V. angasi periods of maximal uptake of food averaged over the billabongs was correlated with the abundance of phytoplankton in suspension. Importantly, both shell (section 6.4.3.2) and somatic growth (section 8.7.1) of mussels between the billabongs are correlated with algal abundance averaged over the seasons. No correlations were found between growth and mean, total organic carbon (as a measure of suspended organic detritus). These relationships strongly suggest that phytoplankton is the chief utilisable food and energy source of V. angasi. (No correlations between algal abundance i.e. trophic status, and growth rates of freshwater mussels have been clearly demonstrated within a drainage system in the literature. Green (1972, 1980) found evidence that calcium is a limiting factor to shell growth of some North American

unionid populations. However, between European lakes, higher trophic environments realise bigger and heavier _Dreissena polymorpha_, according to Stanczykowska (1978).)

That algae may be underrepresented in the stomach contents of freshwater mussels, and nevertheless pass through the digestive system in large proportions undigested, would not appear to be justification, on the results of the present study, for assuming that algae are overestimated as food value (Coker et al., 1921; Fuller, 1974). That algae were underrepresented in the guts of V. angasi, was almost certainly an artifact caused by the differential digestibilities of the various algal types. In relation to digestibility moreover, Allen (1914, 1921) showed that digestion was dependent upon the demand for nutrition; starved mussels were capable of digesting normally resistant diatoms. As further evidence, Moore (1975) and Jorgensen (1975) state that living phytoplankton is superior to both bacteria and detritus in terms of utilisable energy in the diets of deposit and filter-feeders respectively. According to Wallace et al. (1977), even diatoms potentially have a high food value in the nutrition of filter-feeders.

Species composition of the phytoplankton ingested by V. angasi was highest during the Wet season. Motile flagellates (Dinophyceae and Euglenophyceae) dominated the ingested phytoplankton during the Dry, while over the same period desmids (Zygnematales) and Chlorococcales were generally absent in material collected from turbid waters. The latter forms, however, dominated in all of the material collected during the Wet. These seasonal shifts in the abundance of major taxa

of phytoplankton have not previously been detected in the plankton of the Magela Creek waters (Pancontinental Mining Limited, 1981; Kessell and Tyler, 1983).

Various interpretations have been advanced as to whether freshwater mussels exercise selectivity over ingested materials. Allen (1914, 1921) concluded that selection is exercised - mussels avoiding particles of no food value such as silt, and rigidly excluding injurious substances. Coker et al. (1921) and Churchill and Lewis (1924), however, reported that mussels fed unselectively, noting the presence of inorganic debris amongst the ingested food. Coker et al. (1921) added that the ingested stomach contents were similar to those found in the environment in type and proportion. Both studies indicated that rejection of unwanted substances was accomplished by mussels ceasing to feed whenever these were present. The results of feeding experiments conducted by Brönmark and Malmqvist (1982) suggested that unionids have a sorting and selection capability.

Because digestion is apparently rapid in the stomach of V. angasi, the algal forms present were underrepresented. The ingested phytoplankton is a poor representation of that present in the water and selection therefore could not be determined by direct comparison between the content of the stomach and the phytoplankton suspended in the environment. Controlled feeding experiments would be required to resolve the question of whether or not V. angasi shows preference among the types of food available for ingestion. Certainly, relative to green algae, diatoms are underrepresented in the stomach contents. Finding no other indication of selection in Sphaerium transversum,

Gale and Lowe (1971) also found comparatively fewer diatoms in the guts than in water samples. Broadly speaking nevertheless, given that a significant inorganic fraction is included in the diet (not all of which could possibly have comprised the inorganic constitutent of phytoplanton and organic detritus), V. angasi is unselective in its feeding. On the same grounds both freshwater (Churchill and Lewis, 1924) and marine (Nasr, 1984) bivalves have been termed unselective feeders. It is unlikely that selection amongst algal forms (other than diatoms) occurs, moreover, given that at one time or another most of the taxa are represented in the stomach contents.

Among other lamellibranchs, corbiculaceans apparently exhibit very little selection over potential food items; the freshwater bivalve Dreissena polymorpha may be selective; and opinion is as equally divided, as it is amongst studies of freshwater mussels, as to whether marine bivalves are selective in their feeding (section A5.1).

Other than there being an increase of ingestion rate of mussels with increasing food concentration, there were clear indications from regression analyses that ingestion was also affected by dissolved oxygen and turbidity. Mussels apparently reduced their feeding and ingestion rates in response to both low environmental levels of dissolved oxygen and to high concentrations of suspended solids. The suppressive effect of low, sustained dissolved oxygen concentrations upon ingestion appears to be of overriding influence to any other environmental factor. While the reaction of freshwater mussels to anoxia can be assumed to be a cessation of water filtration (noted in laboratory experiments with V. angasi), energy might also be conserved

in turbid waters by reducing or ceasing filtering activities (as discussed below). Suppression of feeding has been observed during periods of low dissolved oxygen in both freshwater (Gale and Lowe, 1971) and marine bivalves (Riisgard and Randlov, 1981). Peddicord (1977) thought that the marine bivalve Rangia cuneata probably reduced or ceased filtering activities during periods of high turbidity to conserve energy required to sort and reject silt particles. No evidence was found to indicate that V. angasi reduced feeding activity with decreasing water temperature as other temperate bivalves including freshwater forms respond (Matteson, 1955; Gale and Lowe, 1971; Winter, 1978).

Condition

Few significant differences were found in the length/dry weight relationships of male and female mussels from the Magela Creek populations, using regression equations calculated on data averaged over the seasons. In plotted condition cycles, however, the condition of females plotted generally below that of males at any one time and place. Rarely though were these differences in condition between the sexes significant. Repetitive spawning is presumably more taxing upon female reproductive physiology of V. angasi than males, which may explain the disparities. Occasionally the condition of females exceeded that of males. These periods were mostly associated with reduced reproductive activity of females.

Very few comparative data are available on the length/weight relationship or condition of the sexes of freshwater mussels between

seasons and locations. For North American unionids nevertheless, Cameron et al. (1979) found generally no differences in the length/weight relationship between sexes while Huebner (1980) recorded only slight seasonal changes between the sexes. Huebner found that female Anodonta grandis and Lampsilis radiata exhibited higher body weights than males during the period of glochidial brooding. By contrast, in V. anqasi brooding females were mostly of lower condition than males. Female mussels in the Magela Creek, however, may be assumed to constantly channel a greater contribution of energy into reproductive effort at times of peak larval production. Few data are available on similar aspects of sexual differences in condition of marine bivalves. Apparently sexual differences at any one time are insignificant (e.g. Comely, 1978).

In waterbodies in which condition of V. anqasi was followed monthly over a two year period, a diphasic annual cycle was apparent. A major peak in the mid-Dry season and a minor peak in the eary-Wet were observed, while lulls in condition were noted at the end of the Dry and again at the end of the Wet. Food availability appeared to be the major factor determining seasonal increases and declines in condition.

From the multiple regression analyses performed on condition and environmental data from individual billabongs and from the billabongs combined, only several significant, partial regression coefficients resulted. Of these, only a few were interpretable. A negative coefficient of temperature for the Mudginberri data suggested that condition declined indirectly in response to increasing temperature, but directly in response to associated increasing reproductive

activity. Food availabiity (phytoplankton) as measured by chlorophyll was the only significant coefficient in the regression equation using the combined Magela Creek data. In 5 out of the 8 billabongs moreover, significant regressions were found between monthly chlorophyll concentrations and condition.

Thus, the two peaks in condition were generally associated with (1) increasing Dry season eutrophy and (2) major early-Wet, nutrient inputs from a drought-stricken catchment, that resulted in short-lived but significant increases in trophic conditions in the waterbodies. Declines in condition coincided with (1) periods of either increasing turbidity with resultant suppression of algal production, aestivation (Magela Creek channel) or with spawning intensity (Mudginberri), during the latter period of the Dry and (2) progressive oligotrophy of the Wet season waters.

In the few comparative studies of weight fluctuations of freshwater mussels, however, Cameron et al. (1979) and Golightly and Kosinsky (1981) found only minor seasonal variations in the length/weight regressions of unionids. Haukioja and Hakala (1978b) recorded considerable annual variation in condition of Anodonta piscinalis, but did not describe the seasonal changes, nor the factors that might influence them. Huebner (1980) in contrast, reported on seasonal body weight fluctuations of A. grandis and Lampsilis radiata. Both species peaked in condition in spring. Seasonal weight changes were attributed to whether or not females were brooding larvae, differences in food availability and quality of the environment and to possible disparities between tissue and shell growth. Seasonal weight

increases of <u>Dreissena polymorpha</u> in European lakes occur at the time of gonadal development. In marine bivalves for which cycles are well known, condition generally peaks with gonadal maturation, and falls following spawning; a correspondence is also observed between gonadal maturation and periods when food resources are abundant (section A5.2).

In contrast to both freshwater and marine bivalves from temperate regions where seasonal reproductive activity largely influences weight changes, condition in <u>V. angasi</u> is mainly influenced by food availability. Weight variations are largely independent of reproductive activity. The only apparent exception to this general rule, was the weight decline noted in mussels from Mudginberri billabong during the late Dry season. As food concentrations in this billabong are relatively meagre (by comparison with other non-turbid billabongs such as Island and Leichhardt), the intensive breeding activity observed in the late Dry was sufficient to outpace any weight increase; a net decline in weight resulted. In non-turbid billabongs that exhibited comparative eutrophy over the latter period of the Dry season, however (Island and Leichhardt), no decline in condition was noted in association with increased breeding intensity.

The effects of dissolved oxygen and temperature, upon condition of mussels amongst the billabongs were very likely underestimated from the results of the multiple regression equation averaged over the billabongs. This was because condition was estimated relative to the entire Magela Creek community and thus the magnitude of peaks and lulls in condition did not necessarily coincide between billabongs.

Nevertheless, their effects as discerned from the respective coefficients in the regression equations derived for each billabong, were either negligible or inconsistent in sign. Overall, the effect of temperature was negative but nevertheless, negligible except for the specific case of Mudginberri billabong mentioned above. Dissolved oxygen was conducive to weight increase but the effect was only noticeable in some floodplain billabongs at the Wet-Dry interchange, when condition was noticeably depressed in mussels sampled from anoxic waters.

The influence of temperature upon condition of bivalves reported in the literature is ambiguous. Increasing temperature may influence or may be associated with an increase in food availability, in which case condition may improve (Stanczykowska, 1977; various marine bivalves reported in section A5.2). Otherwise respiratory costs may increase with increasing temperature, thereby reducing energy available for somatic growth (Huebner, 1980; Dudgeon and Morton, 1983). Hickman and Illingworth (1980) observed that mean condition and latitude were negatively correlated in marine bivalves, and that broadly, temperature and condition were negatively correlated. With respect to dissolved oxygen, as mentioned above, both marine and freshwater bivalves have been reported to reduce feeding activites under conditions of oxygen depletion. Presumably body weights are affected during these periods of inactivity. V. angasi also reduces its feeding activity in oxygen-stressed environments.

Using data averaged over the seasons for each billabong, a significant linear relationship was found between mean condition and mean

chlorophyll concentration when the data from all billabongs were regressed. A feature of the plotted relationship was the observation that the condition of mussels from non-turbid environments was comparatively higher than that of mussels from turbid billabongs. This substantiated the evidence from the combined multiple regression equation of all the Magela Creek data, in which the partial regression coefficient of turbidity was negative. Of further note, was the observation that the condition of mussels inhabiting the shallow reaches of the turbid billabongs (Georgetown and Nankeen) was visibly depressed, presumably because of wave-induced resuspension of the silty sediments that may be expected to be most pronounced here. All the evidence indicates that either filtering activity is reduced in turbid waters or that extra energy is expended by mussels in feeding under the conditions. Peddicord (1977) also observed depressed condition in marine clams feeding in turbid waters. The same conclusions as drawn by Peddicord are relevant to V. angasi, namely, extra energy might be expended in cleaning the filtering apparatus of mussels feeding in dirty waters, and filtering may nevertheless be reduced under these conditions. (A reduction in feeding activity of mussels feeding in turbid waters was noted - see above.)

Very few accounts of variations in condition of freshwater bivalves between sites have been described in relation to possible factors of influence. At high densities, condition in some species is reportedly reduced, presumably as a result at least, of competition for available food resources (Tudorancea and Gruia, 1968; Stanczykowska, 1964, 1977). Stanczkowksa (1977) reported that weight variations of Dreissena polymorpha between European lakes were in proportion to

trophic conditions.

Between billabongs of the Magela Creek, flesh weights of $\underline{V}$. angasi are also dependent upon trophic conditions. As condition is largely independent of environmental factors other than chlorophyll, relative weight of $\underline{V}$. angasi may prove, regionally, to be a valuable indicator of the trophic status of billabongs. This value may be even better appreciated when applied to weight variations recorded temporally within specific waterbodies. Weight variation over time in $\underline{V}$. angasi is depicted as a smoothed and averaged response to food availability. Condition is presumably then, an integrated measure of trophic status for which productive and unproductive periods in waterbodies may be identified. This measure of trophic degree may not be so reliable in clean, oligo-mesotrophic waterbodies such as in Mudginberri (section 2.3.2.5) where spawning intensity in the warm waters of the late Dry, may affect body weight independently of food availability.

The indicator role suggested here for $\underline{V}$. angasi may be corroborative of a similar role advocated earlier (section 6.9) for which growth rates (as measured by L_∞ of the von Bertalanffy growth equation) were argued to be useful, integrated measures of trophic status of waterbodies averaged over the seasons. Condition data may be usefully employed to identify (in most cases) the trophic status of waterbodies within that timespan.

Annual production

Waters (1977) stated that production rates of organisms in tropical

regions could be expected to be several times the levels of the same groups from temperate regions. In relation to known production rates of freshwater mussels from temperate and tropical regions (Table A5.1), annual production of *V. angasi* (values ranging between 0.39 and 1.75 g shell free, dry weight) in billabongs of the Magela Creek is high, but not of the order indicated by Waters. Moreover, production of gametes in *V. angasi*, a repetitive breeder, is not included in the production estimates. Larval production especially, would amount to a very significant fraction of total annual production in some environments of the Magela Creek, given that reproductive cycles may be completed within a month (section 7.11). The production estimates calculated in this study therefore, may be grossly underestimated.

P/B or turnover ratios of *V. angasi* (0.07 - 0.13), are amongst the lowest recorded of any freshwater mussel (Table A5.1). By comparison with other mussels studied, however, *V. angasi* is one of the longest -lived freshwater mussels known (Chapter 6). Thus, while the P/B ratio is reasonably constant for a group of organisms and is generally independent of environmental influences, it is clearly a function of voltinism (life spans) (Waters, 1977). The ratio therefore may be expected to be low in long-lived populations, because of the accumulation of production with age.

The low P/B ratios observed generally in freshwater mussel communities and low production rates in comparison to the total macrobenthic production, have been variously interpreted (section A5.2), as indicating that freshwater mussels contribute very little in terms of biomass and energy to predators of the trophic level above.

Short-lived corbiculaceans, and marine bivalves by comparison may be important food sources to animals in higher trophic levels. Negus (1966) noted, however, that juvenile freshwater mussels may be significantly preyed upon. Negus added that in populations where recruitment was regular, mussel flesh of individuals that died each year, would contribute an amount of food approximately equal to annual production to scavenging fish and invertebrates, and decomposers. (Mussel flesh for animals that are consumed, has a very high caloric content - Tudorancea and Florescu, 1968).

It must be reiterated that production (and therefore the P/B ratios) of V. angasi in the Magela Creek may be severely underestimated because of the omission of the contribution by gametic and larval production. Thus, apart from providing food for predators in the juvenile stages, or for scavengers and decomposers when death occurs by natural causes, the same trophic levels may utilise the considerable production of wasted reproductive products.

Although probably utilised to only a minor degree as food for other trophic levels, mussels may contribute to the functioning of ecosystems in other important ways. At high densities, the filtration ability of mussels has been estimated (or argued) to be significantly important to the nutrient cycles of aquatic environments and to their general circulation of materials (section A5.3). Using filtration rates estimated for European unionids (Lewandowski and Stanczykowska, 1975), the entire mussel population in Mudginberri billabong (680,000 - Table 5.10) is estimated to filter almost 5 Ml of water daily. At a Dry season volume of 177 Ml of water in the billabong, this represents

an exceedingly rapid turnover equivalent to the entire volume by filtering mussels, every 36 days. During the filtration process, large amounts of seston are filtered out to return to the sediments in the form of faeces and pseudofaeces. This process results in acceleration of the breakdown of nitrogenous wastes, thereby providing nutrients at rapid disposal for plankton, and bacteria-enriched seston as food for other benthic fauna. Thus at high densities the large biomass of _V. angasi_ must play a significant role in the nutrient cycles and towards organic enrichment of the bottom sediments of billabongs. Lewandowski and Stanczykowska (1975) suggested that movement of mussels present at high densities may also be important in mixing the bottom sediments.

Mussels may also play an important role in the calcium cycles of particular aquatic environments, notably in soft, acid waters (Green, 1980). Preliminary calculations suggest that _V. angasi_ when present at high densities, may play a significant role in the calcium cycles of some Magela Creek billabongs. In the soft, acid waters of Mudginberri billabong for example, 3.9 Mg of calcium is present in the shells of living mussels. This is approximately 19 times the amount of calcium dissolved in the water. Assuming a dissolution rate of one year for empty shells in the warm acid waters, and an annual mortality rate of mussels of 10% (from the data of Table 6.44), an amount of calcium almost twice that present in the water is freed annually, to be either flushed from the billabong during the Wet, accumulate in the sediments, used for shell growth of mussels or importantly, taken up in other biological pathways.

Thus in summary, although direct predation upon V. angasi is probably minimal in the adult life, dead material and significant (but undetermined) annual production of reproductive products and newly recruited young would be provided to organisms of other trophic levels for consumption. Considering the enormous biomass of mussels in some billabongs, their filtration ability may be assumed to contribute most significantly to the ecological functioning of the environments. The mussel must almost certainly play an important role in the nutrient cycles and general circulation of materials in the Magela Creek billabongs. The extent of the importance of V. angasi in the calcium cycles of the billabongs remains to be determined. Early estimates, however, suggest that empty mussel shells may provide a significant potential source of calcium to various biological pathways.

CHAPTER 9

GENERAL DISCUSSION

The study of Velesunio angasi in the Magela Creek, has contributed a significant fund of knowledge to the biology and ecology of freshwater mussels in general, particularly to the southern hyriid unionaceans and tropical mussels for which little information is presently available. While specific findings have been brought to attention in the relevant sections, some general aspects of the study of V. angasi with respect to adaptations and life strategies, merit some final discussion in comparative relation to the freshwater mussels from Australasia, tropical regions and worldwide. Finally, some specific aspects of the biology and ecology of V. angasi are re-presented as deemed worthy of consideration in future studies of the mussel or indeed for studies of freshwater mussels generally.

McMichael and Iredale (1959) recognised in the Australian hyriids, a complete gamut of physiological and ecological adaptation, from species incapable of withstanding desiccation to any degree, to those fully adapted to drought conditions. As typical forms, McMichael and Iredale mentioned (a) the genera Hyridella and Cucumerunio, occurring in the relatively well watered, perennial east coast streams of Australia - as intolerant of desiccation, and (b) the velesunionines, V. ambiguus and V. wilsonii, which can survive for months or even years without water. The most primitive members of the Australian hyriids are the velesunionines, comprising the genera Velesunio, Alathyria and Westralunio (McMichael and Hiscock, 1958). Representative species of this subfamily occur in all principal

drainage divisions of Australia. Three species of the genus _Velesunio_ - _V. ambiguus_, _V. wilsonii_ and _V. angasi_, are the most widely distributed of the Australian fauna, and collectively their ranges almost completely superimpose the ranges of all other species.

While only the velesunionine hyriids occur in inland Australia, members of only the genus _Velesunio_ appear to be specificially adapted to the vicissitudes and aridity that are features of this vast expanse of the continent. The inland species, _Alathyria jacksoni_ for example, is intolerant of still-water environments (Walker, 1981b). At the extreme, _V. wilsonii_ which is found in drier parts of Australia than any other hyriid, reportedly aestivates during droughts in the bottom sediments of semi-permanent waterholes; it has been recorded as surviving for 3 years in a box in the laboratory without water (McMichael and Iredale, 1959). _V. ambiguus_ has preferences for still or slow flowing waters throughout its range, and is in fact intolerant of fast flowing riverine environments; in company with these habitat preferences, the mussel is markedly resistant to desiccation and has demonstrated ability to survive at least short-term anoxia (Walker, 1981b).

V. angasi does not occur in inland Australia, but nevertheless shares physiological and ecological attributes in common with _V. wilsonii_ and _V. ambiguus_ described above. Indeed, one may forward the view that _V. angasi_, by nature of its environment, will eventually prove to be amongst the most tolerant of the Australian hyriids to environmental rigours. Occurring in tropical monsoonal drainages, extreme variations are inherent in the quality of the freshwater environments

inhabited by the mussel from season to season, as the result of the annual cycle of alternating flooding and drought. As a consequence, V. angasi is adapted to a broad range of conditions from riverine, to still-water and ephemeral environments. Exemplifying these environmental extremes, constrasting ecophenotypic forms of the mussel are found, functionally adapted for life in swift-flowing waters and seasonally dry river beds. Comparable ecophenoptypes apparently are not found in V. ambiguus and V. wilsonii. (The relatively larger size attained by V. wilsonii, however, is presumably a factor contributing to burrowing powers and increased volume - behavioural and morphological attributes that would be necessary to enhance survival during periods of aestivation.) V. angasi is well adapted to life in still, Dry season waters that may be seasonally depleted of oxygen, and that may become hot and shallow. Physiological adaptations to these environmental conditions include: (1) a remarkable tolerance to anoxia (V. angasi is amongst the most tolerant species of freshwater mussel to anoxia yet reported) - adult musels may survive for months in anoxic waters; (2) tolerance to desiccation - while the Creek form aestivates over each Dry season, billabong mussels were similarly shown to survive for months out of water; and (3) a tolerance to high water temperatures - 50% of experimental mussels succumbed at water temperatures exceeding 45° C.

Thus, over vast areas of Australia occur at least a few freshwater mussel species, belonging to the genus Velesunio, that are adapted to still-water, ephemeral and drought-prone environments. V. angasi at least, however, is equally adapted to life in streams seasonally flooded by torrential Wet season rains.

Other than information related broadly to tolerances and adaptations, specific comparative information on other life-history attributes of the Australian hyriids is lacking. V. angasi in the Magela Creek, is apparently a longer-lived mussel than the two temperate velesunionines of the Murray River, V. ambiguus and Alathyria jacksoni, studied to date. While temperate hyriids are seasonal in their breeding, the effect of the northern tropical clime upon reproduction in V. angasi is reflected in much higher reproductive potentials. This potential is realised by sexual maturity reached at a very early age, repetitive breeding throughout the year, rapid larval development and ensuing development of the parasitic larvae, and long-lived populations with low adult mortality. Like other hyriids studied to date, the glochidia of V. angasi appear to be non-specific parasites of their fish hosts.

Despite warmer and less marked annual fluctuations in water temperatures in tropical than in temperate regions, the monsoonal climate of the tropics and subtropics, nevertheless confers a seasonality to many physiological processes of freshwater mussels from these regions. Because of regular, alternating wet and dry seasons, species are presumably well adapted at least to still water environments. The mutelids of tropical and subtropical Africa, according to Kenmuir (1980) are well adapted to life in disconnected pools of the dry seasons. Kenmuir reported forms resistant to desiccation and capable of aestivating, and others with demonstrated ability to withstand extremely low oxygen concentrations found in deeper pond type habitats during the dry season. This situation is

strongly paralleled in similar adaptations of V. angasi to the rigours of the tropical climate of northern Australia.

Although seasonal growth patterns have been noted in tropical mussels, the study of V. angasi in the Magela Creek is the first to provide unequivocal evidence that growth rings on the shells of tropical freshwater mussels are annular in nature and may be used to age mussels. V. angasi is longer-lived than other tropical species yet studied. Seasonal temperature fluctuations appear to be sufficiently large to preclude year round breeding in tropical unionids studied north of the equator. V. angasi in northern Australia and freshwater mussels from tropical Africa are the only reported species in which year round, repetitive breeding occurs. In most tropical species studied to date, various developmental processes are speeded up in the prevailing warm waters; mussels mature at an early age, and larval development and metamophosis during the parasitic phase are rapid.

Several investigators have observed that a close zoogeographical relationship exists between the mussel faunas of Africa, Australasia and South America; collectively they form a group clearly separable from species from the northern hemisphere (Walker, 1981a). Other than taxonomic and zoogeographic similarities, however, from the limited studies so far undertaken, it is doubtful that the Australian hyriids differ from the northern unionaceans much in the way of general living requirements. A degree of ecological similarity has been assumed for freshwater mussels as a group in such things for example as feeding ecology and microhabitat tolerances (Tevesz and McCall, 1979; Strayer, 1981; Davis et al., 1981). Nevertheless, fundamental differences in

climate and the type of environment inhabited by mussels (lotic or lentic) may impose adaptations and life strategies upon the various species shown by often profound differences in aspects of their biology and ecology. Some of these broad differences among the Australian hyriids and tropical freshwater mussels have been discussed above.

A tentative suggestion offered here, is that the Australian hyriids may be ecologically dissimilar in broad reproductive strategies and ecological tolerances, to other unionaceans from the northern hemisphere. The more temperate, drier and vicissitudinous nature of the Australian environment may yet be shown to be features that have lead to: (1) protracted and opportunistic breeding (within constraints of temperature regimes), where species have a capacity or potential to produce a number of broods per year; (2) an absence of host specificity of the glochidial larvae; and (3) broad environmental tolerances, when the fauna is viewed collectively. In view of the relatively harsh and rigorous environments of the African continent, these attributes may well extend to the mutelids; _V._ _anqasi_ is most similar in biology and ecology to tropical mussels of Africa than to other tropical unionids. Further research will reveal the truth or fallacy in these hypotheses. It should be stressed for example, that potential for multiple broods may be more prevalent in northern unionaceans than was previously thought (e.g. Heard, 1975); the glochidia of some unionid species are unspecific parasites (e.g. Kat, 1984); and that individual unionids in North America at least, are equally as tolerant of desiccation (van der Schalie, 1940) and anoxia (Fuller, 1974) as some hyriids and mutelids.

According to Kat (1984), present understanding of many basic life-history attributes of unionaceans in general, is poor. Thus, specific findings on V. angasi in the Magela Creek have contributed to a better understanding of unionacean biology and ecology. The studies have provided some information on areas of conflict or contention in the literature, and further, have exposed some salient features that may be worthy of attention in future studies of freshwater mussels generally. In the sequence that they appear in the text, these features of interest are:

1) Shell form and environment - Obesity and relative height were correlated broadly among the waterbodies with environment (depth and eutrophy respectively). Neither correlation, however, could be explained in terms of a functional morphology and both obesity and relative height were found to be more closely associated with ontogeny; obesity increased with increasing age and relative height declined with increasing growth rate of mussels. Thus future studies of shell form in unionaceans must carefully consider the effect of ontogenetic variability before interpretations of functional morphologies are offered. Ecoclines in shell form both within and among habitats may be nothing more than gradients of ontogeny.

2) Microhabitat preferences - A diversity of findings have been forwarded in the literature in relation specifically to whether or not bottom type is important or not in determining mussel distribution and abundance (section A2.1.2, Hydrology). While

bottom type is more closely correlated with relative water movement, particle size of the sediment _per se_ was found to have no effect upon distribution and abundance (and for that matter, growth rate) of _V. angasi_ in the Magela Creek. Providing sediments are firm yet yielding, bottom type whether muddy or gravelly is unimportant in regulating mussel distribution. More attention needs to be paid to the degree of associated water movement in studies of microhabitat preference, itself perhaps a reflection of the tolerances of various species to local oxygen conditions and maintenance in strong currents. Further, the degree of consolidation of the sediment needs to be reported in future studies; fewer mussels were found in the Magela Creek on muddy sediments that were unsupportive, loose and silty in nature.

3) Dissolved oxygen - A strength of the present study was an elucidation of environmental factors (in quantitative terms) that influence and govern aspects of the biology and ecology of _V. angasi_. The analyses revealed that dissolved oxygen was by far the most influential environmental factor to the development and well being of mussel populations in the Magela Creek. Dissolved oxygen concentration was a highly significant correlate of larval production, subsequent recruitment and abundance of mussels within and among billabongs, life-spans of mussels (especially females), and feeding activity of mussels in the billabongs. Future studies, particularly of still-water species, must direct more attention to the influence of dissolved oxygen in all aspects of biology and ecology.

4) Juvenile mussels - Invariably, the youngest age class is reported to be absent in most population studies of freshwater mussels. Juveniles were relatively common amongst the populations in the Magela Creek. If the youngest age class was absent from any population, it was not because their habitat was remote from that of adults, nor because of a specialised substrate requirement. Rather, the absence of young was attributed to inadquate sampling or poor conditions for survival of newly recruited mussels. Other studies of freshwater mussels have attributed the scarcity of juvenile mussels in part to their cryptic appearance and specialised habitat requirement. Future studies would do better to use sampling methods designed to retain the juvenile mussels, and adopt a methodology whereby all possible habitats are quantatively sampled.

5) Longevity - Criticism has been levelled at the diversity of reports of the extreme ages attained by _Margaritifera margaritifera_ throughout its holarctic range (see Apendix 3). A wide range of longevities was found in _V. angasi_ in populations of the Magela Creek (11-35 years). Life spans were found to be positively correlated to mean dissolved oxygen concentration. Thus a species as widely distributed as _M. margaritifera_ should vary even more greatly with respect to the maximum ages attained across its range. Therefore criticism of the reports of the longevities attained by this species may be unjustified because environmental (and phylogenetic) influences have not been considered.

6) Breeding activity - Reproductive investigation of _V. angasi_ in the Magela Creek demonstrated that two other environmental variables apart from water temperature were influential to breeding activity - namely dissolved oxygen and turbidity. The effect of environment other than temperature, has essentially been ignored in terms of its influence upon reproduction in freshwater mussels. There is obviously much potential for further study of this matter in other species of freshwater mussels. For example, _V. ambiguus_ and _Alathyria jacksoni_ in the Murray River in southeastern Australia, were observed by Walker (1981b) to peak in larval production in spring and late summer/early autumn. Do both species have the potential to breed over the entire summer, and is the potential curtailed in mid summer by some seasonal, adverse physicochemical factor such as suppressed dissolved oxygen concentration or high turbidity?

7) Glochidial attachment - With the limited data at hand, glochidial infections of _V. angasi_ appear to be higher on the gills than the fins of the host fishes. This is contrary to the general observation, that hooked or toothed glochidia tend to parasitise the external surfaces of their hosts (section A4.3). As more species are studied, host fish activities (as in the present study) will probably assume more important in explaining discrepancies in the site of glochidial attachment. The glochidia of the Australian hyriids are of the toothed variety. The glochidia of one other hyriid (_H. drapeta_ - Atkins, 1979) attaches exclusively to the gills of the host fishes.

8) Food of mussels - Unlike some reports for North American unionids that zooplankters feature in the diets (section A5.1), *V. angasi* in the Magela Creek is strictly phytophagous and detritivorous. Fuller (1974) concluded that algae were overestimated as food value for freshwater mussels, on the basis that much phytoplankton ingested by mussels passed through the digestive tract undigested. While the algal fractions were found to be low in the stomachs of *V. angasi*, the presence of mostly digestion-resistant forms in the stomachs strongly indicated that algae overall, were underestimated amongst the ingested material; much of the algae was assumed to undergo rapid breakdown and digestion. The evidence strongly indicated that phytoplankton is the chief utilisable food and energy source of *V. angasi*. Strong correlations were found between shell and somatic growth of mussels, and algal abundance averaged over the seasons among the populations. No correlations were found between growth and the measure of suspended organic detritus. With further investigation, Fuller's conclusion above, may be found to be invalid for freshwater mussels generally.

Ingestion rates in *V. angasi* were correlated with phytoplankton concentrations in the surrounding waters. To what extent, however, food intake is solely dependent upon algal concentration in the waters, independent of the levels of organic detritus would require further study. In such an event, the appetite of mussels would be solely algal-dependent even if ingestion was unselective, and would provide more evidence that algae is the main utilisable food item. To the best of knowledge, this type of feeding

behaviour has not been demonstrated in bivalves.

9) Selectivity of ingested particulates - There is debate as to whether freshwater mussels exercise selectivity over ingested materials (see section A5.1). Because of differential and rapid digestion of algae in the guts of V. angasi, controlled feeding experiments are needed to resolve the issue of whether or not the mussel shows preference among the types of food available for ingestion. However, because a significant inorganic fraction is included in the diet, V. angasi can be regarded as unselective in its feeding; this finding is in accord with most comparable studies of feeding in freshwater bivalves.

In relation specifically to the biology and ecology of V. angasi in the Magela Creek, or indeed throughout the geographical range of the mussel, the present study has exposed some features of interest that are worthy of further attention. In brief point form, these features are:

- Shell morphology of juvenile mussels in northern Australia may hold promise for species determinations in regions of doubtful species composition. Is the shell morphology of juvenile V. angasi and V. wilsonii (unaffected by environment) sufficiently distinguishable that the two species may be recognised by relative height alone?

- Does a latitudinal cline exist (as suggested) in the relative height of V. angasi across the geographical range of the species?

- Regular seasonal fluctuations were observed in the sex ratios of mussels from Georgetown billabong and the Magela Creek channel. Was this the result of a sampling bias, or are the mussels from these

populations alternatively sexual?

- The seasonal recruitment pattern of V. angasi in the Magela Creek, did not correlate with the seasonal intensity of larval production. Thus breeding was aseasonal and year round, while recruitment was seasonal, occurring in the Wet-early Dry season. With known sensitivities of juveniles to low dissolved oxygen concentrations, dissolved oxygen immediately above the bottom is presumed to be insufficient during the Dry for juvenile survival. Lack of recruitment during the Dry season is presumably the indirect result of the high macrophytic productivity of far northern Australia; decomposing plant material creates a high biochemical oxygen demand in the bottom waters of the billabongs for much of the year. What then, is the pattern of recruitment of V. angasi in other regions of its geographical range?

- While evidence suggested that V. angasi selected against diatoms in its feeding, to what extent, if any, does the mussel show preference in the size and type of green algae ingested? Further, is food intake solely dependent upon the algal concentration in the water, independent of the levels of detritus?

- High densities of mussels and estimated turnover rates of the water, suggest that V. angasi may play a significant role in the nutrient and calcium cycles of some Magela Creek billabongs. What is the extent of the contribution by mussels to these cycles? Also there is an indication that overall production is grossly underestimated because high gametic and larval production were not considered in the estimates. What contribution to overall production is gametic and larval production of V. angasi in the Magela Creek waterbodies?

Finally, attention is drawn to the contribution of the present study of the biology and ecology of *V. angasi*, to the current intensive investigations being undertaken in the Alligator Rivers Region. Research activity in the region is aimed primarily, at acquiring a general knowledge and understanding of the aquatic ecosystems, and at assessing various biological means of monitoring potential pollutants in the waterways.

In most billabongs of the Magela Creek, *V. angasi* is by far the most dominant member (in terms of biomass) of the second trophic level benthic fauna. At high densities, annual production, with the addition of larval and gametic production, is likely to be quite high. More importantly, however, it is probable that mussels contribute significantly to the nutrient and calcium cycles of many of the billabongs. The extent of this contribution has been suggested above, as worthy of further study.

The study of *V. angasi* has provided essential biological and ecological information that may be used to evaluate the potential of the mussel as a biological monitor of pollution in the Alligator Rivers Region. Importantly moreover, the studies themselves have demonstrated repeatedly the potential value that the mussel may have as an indicator organism. This potential may be realised in pollutional, but also in paleoenvironmental and present day environmental contexts as well, by studies of distribution and abundance, shell form and size, and population structure and dynamics of mussels.

The sensitivity of juvenile V. angasi to low dissolved oxygen, may make the mussel a particularly valuable indicator of the types of pollution in which oxygen concentrations are severely affected. Excessive organic enrichment is one such type, and because densities of mussels were correlated with mean dissolved oxygen concentrations, knowledge of long-term changes in abundance of mussels may usefully indicate the aerobic status (and thus polluted nature) of waterbodies. A correlation was also found between both growth rate and relative condition, and algal productivity, and thus long-term studies of growth of mussels might also be employed to identify forms of mild organic pollution. Because of the sensitivity of juveniles to low concentrations of dissolved oxygen – and presumably other toxicants, mussels in the Region may have value as indicators of nonpolluted waters, and might be used to mark the downstream areas of full biological recovery in polluted streams. With baseline data pertaining to environmental correlates of recruitment, mortality and growth rates, V. angasi has considerable potential as an indicator of environmental impact in the Alligator Rivers Region.

Densities of mussels reflect local and regional Wet season flow patterns in the mainstream channel of the Magela Creek, as a result of the reliance upon adequate dissolved oxygen sustained throughout the Wet for successful recruitment. For the complex flow patterns on the floodplains of drainage systems in the Alligator Rivers Region therefore, (and presumably in other locations under monsoonal influence), study of the distributional patterns of V. angasi may assist in unravelling the pathways of water movement. In present day environments as yet unstudied by man, distributional data, and growth

rate and condition data may usefully and rapidly indicate to the investigator some measure of the overall aerobic and trophic status of the environment in question. Further, condition data in most environments of the Magela Creek at least, was an integrated measure of seasonal trophic status. Thus, estimations of condition may usefully identify productive and unproductive periods in a particular environment.

Shell size and form of *V. angasi* on a regional scale at least, may be useful indicators of paleoenvironments. While shell size and relative height may indicate 'paleotrophic' conditions, an arcuate shell form and distinctive, swollen Creek form may respectively indicate (a) environments of relatively unstable, shifting sediments where waters are swiftly flowing for some part of the year at least; and (b) seasonally ephemeral, stream environments.

Overall, the present study of *V. angasi* in the Magela Creek, has shown how a valuable store of limnological and hydrological information, may be gleaned from ecological studies of freshwater mussels.