

Shell Form Variation of a Freshwater Mussel *Velesunio ambiguus* Philippi from the Ross River, Australia

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Based on mussels collected from the Ross River, Australia, within 13 months, I studied the variation of their shell forms since the Ross River has changed from a flowing-water to a relatively still-water. At least four different shell forms were found including shells with characters of flowing-water species. Young mussels had distinctive “wings” at dorso-posterior part of the shells and in most cases, as the shells grew bigger, the wing development was less obvious. No significant differences were observed in obesity and relative height among mussels living in three different microhabitats (i.e. solid mud and plant litter, soft silt, soft silt and sand). The shells from Mt. Margaret Dam (a temporary dam) were thinner and their growth lines were easier to discriminate than those from the Ross River. Comparing with those living in temperate regions of Australia, the obesity and the relative height of mussels from the Ross River were smaller. Only few abnormal shells were found which usually appeared only as external deformations, such as: a light deflection on ventral margin and scars on the surface of shells. Seven age classes were found ranging between 6 and 12 years and it was estimated that the lifespan of the mussel in the Ross River was about 15 years.

Key words: *Velesunio ambiguus*, variation, mussel, tropical water, obesity, relative height

INTRODUCTION

The superfamily Unionacea consists of more than 150 genera and hundreds of species of freshwater mussels. They are found worldwide in various freshwater habitats (Haas 1969; Walker 1981a) and show great variation in inter- and intra-specific shell form (Pennak 1978; Kat 1983b). These variations are due to genetic and environmental factors.

There are only a few reports on the water depth-shell form relationship. Harman and Berg (1970) reported that the obesity (shell width/shell length ratio) of *Elliptio complanata* decreased from shallow to deeper waters. Conversely, Humphrey (1984) recorded that *Velesunio angasi* tended to be less obese in shallow waters than in deeper water. However, Humphrey pointed out that the reason for this discrepancy was ontogenetic: older mussels that tended to be more obese were living in deeper billabongs.

Water flow rate is also considered to play an important role in the variation of shell shapes or forms. Slow flowing waters or quiet waters, generally, are preferred by mussels with more obese and higher shells. Many records show that the correlation between stream velocity and shell forms is very strong. According to Ortman (1920), as quoted in many literatures, within a single stream shells of a particular mussel species tend to increase in obesity downstream, where the velocity is usually slower. These observations were confirmed by other researchers (e.g., Eagar 1977, 1978; Cvancara *et al.* 1978). However, this general rule does not always apply in different habitats and for different species (Cvancara 1970, 1972; Green 1972; Clarke 1973; Ghent *et al.* 1978). The authors also found that head waters or small streams, which usually

had a strong current, were generally appropriate environments for mussels with less obese or more compressed shells, with lower relative height, curved dorsal margin, and straight or reflected ventral margin.

Depending on the substrates in which the mussels live, there are two types of lake form. The lake-form mussels display more similarity to the down-stream form than to the head-stream form, although they are usually more obese than the river form (Eagar 1978). Mussels living in mud or soft-silt substrate develop more obese and lightweight shells with a wide ventral angle and lightweight shells. For those mussels living in hard-sand substrates, such as *E. complanata*, compressed shells with narrow ventral angle and heavier shells are more suitable (Ghent *et al.* 1978).

The general relationship between shell morphology, especially shell obesity and lateral outline, and habitat has been formulated by Eagar (1948). These generalisations were then developed in further studies (Eagar 1977, 1978) to provide an explanation of the functional morphology of mussel shells. Regarding the variations in obesity, Eagar proposed that the lake variety is more obese than the river variety of a given species. For the river variety, a positive correlation is usually found between obesity and stream size: while the correlation is negative with water velocity. Following Ortman's Law (1920) of stream distribution, obesity tends to increase as the distance downstream increases. Tevesz and Carter (1980), however, suggested that, because of the considerable variations in unionacean shell features, these generalisations should be applied with care, especially when such variations are used as an indicator of environmental changes.

Velesunio ambiguus, the most widely distributed Australian freshwater mussel (Walker 1981a). It is found in freshwater bodies from temperate (the southern part of Australia) to tropical waters (the northern part of Australia). The mussel usually lives in floodplain, habitats, including billabongs, lakes, and creeks where flows are gentle. This mussel is abundant in the Ross River, a tropical river in north Queensland, Australia. This river has been changed in 1912 when the first weir was built, followed by two more weirs and one dam several years later causing the ecology of the river has changed considerably ever since.

With its wide distribution and the changes of its habitat in the Ross River, the main aim of this study was to examine the variations of its shells. In addition, this study is also aimed to look at the relationship between the variations and its microhabitats. The latitudinal variations were also analysed by comparing the shells of this study with those of the previous studies conducted in temperate waters.

MATERIALS AND METHODS

Study Sites and Specimen Sampling. The Ross River is only a small river, but an important part of the tropical twin cities, Townsville and Thuringowa, in north Queensland, Australia served as the water supply for the residents.

A significant reduction of flood flows due to the construction three of weirs since 1912 and the Ross River dam in 1978 resulted in both channel siltation and consolidation of vegetation mass in several areas.

The main study sites were located between Aplin and Gleasons weirs. Sampling commenced in January 1992 and finished in January 1993. At least 50 mussels were collected monthly and only mussels inhabiting a depth of approximately 1.5 m were collected. Additional collections were later carried out to obtain data on the distribution of mussels from the riverbank to the middle part of the river. The mussels were collected from four different depths: 1, 2, 3, and 4 m. The collections were replicated at three different sites. Two quadrates (80 x 80 cm) were placed at each depth and all mussels within each quadrate were collected. To examine the effect of substrate type on the variation of shell morphology, collections were made at three different sites where mussels occur. The types of substrate were: solid mud with plant litter, soft silt, and a combination of soft silt and sand. In these three habitats, silt contributed to the formation of the substrate, although only in the second, silt was the main component.

For comparison, mussels were also collected from the Mt. Margaret Dam, a farm dam used for stock watering, about 12 km north of Townsville. Shells of dead mussels were collected on 13 June 1993 when the dam was drying up. Only two live mussels were found in mud of the dam. Samples were identified based on the description in a monograph by McMichael and Hiscock (1958).

Each specimen was measured along its greatest length, width, and height to the nearest 0.2 mm according to the method of McMichael and Hiscock (1958) with slight modifications (Figure 1). Observations were also carried out

to discern the variations in shape and form of shells. Analysis of covariance was used to test the differences between slopes and between intercepts.

Obesity and relative height ratios were used to measure the variation in shell forms in relation to the type of substrates on which each mussel was found.

Shell Aging. To determine the age of collected shells, a 2 cm wide section of one valve was cut through the beak using a diamond saw. This was attached to a microscope slide, ground down, and polished until a thin section of approximately 260 μm was obtained. The shells of 35 mussels with least erosion of the umbo, and representing the widest size range, were selected. A length-growth regression line was constructed with growth as the dependant variable to provide a means of age determination.

Collection of Limnological Samples. Limnological features of water were measured at monthly intervals on the same day as the mussel collection. Features recorded were bottom dissolved oxygen concentration, turbidity, pH, conductivity, and water temperature. Except for water turbidity and conductivity, the limnological features were measured directly in the field. These measurements and the water collection were undertaken in the morning, between 07.30 and 09.00, at the same location where mussels were sampled. A portable oxygen meter was used to measure the dissolved oxygen content of the water. Bottom water temperature was measured by placing a maximum-minimum thermometer on the riverbed and leaving the thermometer overnight. The pH was measured with a portable pH-meter, while turbidity was measured using a turbidimeter. The conductivity and calcium content of water samples were measured in the laboratory of the Australian Centre for Tropical Freshwater Research, James Cook University.

RESULTS

Physical and Limnological Features of the Study Sites.

Bottom water temperatures are high throughout the year and the seasonal change is considerable, from 20 °C in winter to 34.7 °C in summer. The seasonal changes follow changes in air temperature: high during summer and low during winter.

The dissolved oxygen concentration (DOC) recorded from the bottom water is low during the late wet season to the early dry season (February-August). However, DOC saturation is above 60% in all months.

In general, the conductivity of the study sites increased as the dry season progressed, although it was relatively stable

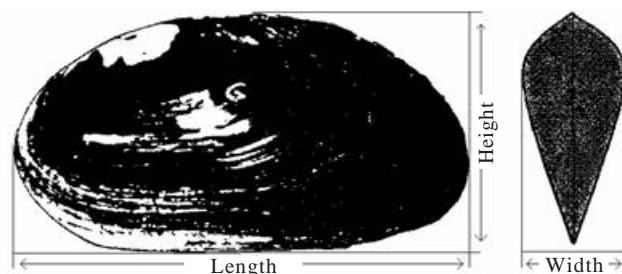


Figure 1. Measurement used in this study was based on McMichael and Hiscock (1958).

for the whole year. The conductivity ranged between 315 and 395 $\mu\text{S}/\text{cm}$. This maybe mainly accounted for by the calcium concentrations. Other ion concentrations in the water are presented in Table 1.

The pH ranged between 7 and 8.1 that showed the water was relatively alkaline. Since the Ross River was relatively still, the turbidity was only noticeably high during the wet season when the river is in flood. Turbidity would be contributed by erosion from banks or by eutrophication of the water. However, monthly records show that the turbidity of the study sites was quite low.

The aquatic macrophytes live in the river were *Azolla pinnata*, *Eichornia crassipes*, *Pistia stratiotes*, *Salvinia molesta*, *Marsilea mutica*, *Nymphaoides indica*, *Nymphaea capensis*, *Ceratophyllum demersum*, *Egeria densa*, *Potamogeton* spp., *Brachiaria mutica*, *Cyperus diformis*, *Cyperus eragrostis*, *Echinochloa colona*, *Paspalum distichum*. Their density recorded from the sites during the study period was very high, especially the floating plants.

Description of Variation in Shell Form. A selection of shells from the Ross River and the Mt. Margaret dam were shown in Figure 2a. Based on lateral outline, at least four different forms were distinguished from those found in the

Ross River. The differentiation was based on the posterior lateral outline of the shells (Figure 2b). The commonest form had an irregular curve. This shell form constituted about 43% of the collected Ross River specimens. The second form resembled the first with a flattening of the curve after initial curvature. About 27% of the shells were of this form. The third form consisted of shells with a relatively more regular curvature than the first, with the posterior end being smoothly rounded. These shells were 25% of the specimens. The last form was the least common, being only 5% of all specimens. In contrast, to the previous forms, the shells had a noticeably pointed outline at the posterior end.

For those four forms described, distinctive “wings” were found only among young mussels. In most cases, as the shells grew larger, the wing development was less obvious. This trend was accompanied by a decline in relative height (Figure 2a), so that the dorsal margin was almost straight and parallel to the ventral margin.

The shells from the Mt. Margaret Dam were thinner than those from the Ross River. In addition, their growth lines were easier to distinguish than those from the Ross River. About 56% were similar to the first Ross River form. The rest of them resembled the second form.

Variation in Obesity. For mussels from the Ross River, width/length ratios (obesity) ranged between 24.9 and 47.2% in females and between 27.6 and 42.1% in males (Table 2). For those from The Mt. Margaret Dam, samples consisted of two live mussels and 46 valves collected from the dry section of the dam. Of the valves from the dead mussels, only one valve was unbroken. Therefore, measurement could only be obtained from this single valve, in addition to the two live specimens. The shell width (i.e., two valves together) was estimated by doubling the width of one valve measured by callipers. Their obesity ranged between 23.7 and 35.0% (without considering the sexes).

Table 1. Some major ion concentrations in the Ross River recorded for seven months

Months	Alkalinity (mg/l) as CaCO_3	HCO_3^- (mg/l)	Mg (mg/l)	Hardness (mg/l) as CaCO_3
July 92	77.4	94.5	8.8	67.9
August	83.7	102.0	9.4	73.6
September	87.0	106.0	9.7	76.9
October	91.0	111.0	10.5	82.1
November	93.8	114.5	10.9	84.0
December	96.2	117.0	11.3	87.5
January 93	90.6	110.3	10.1	80.2

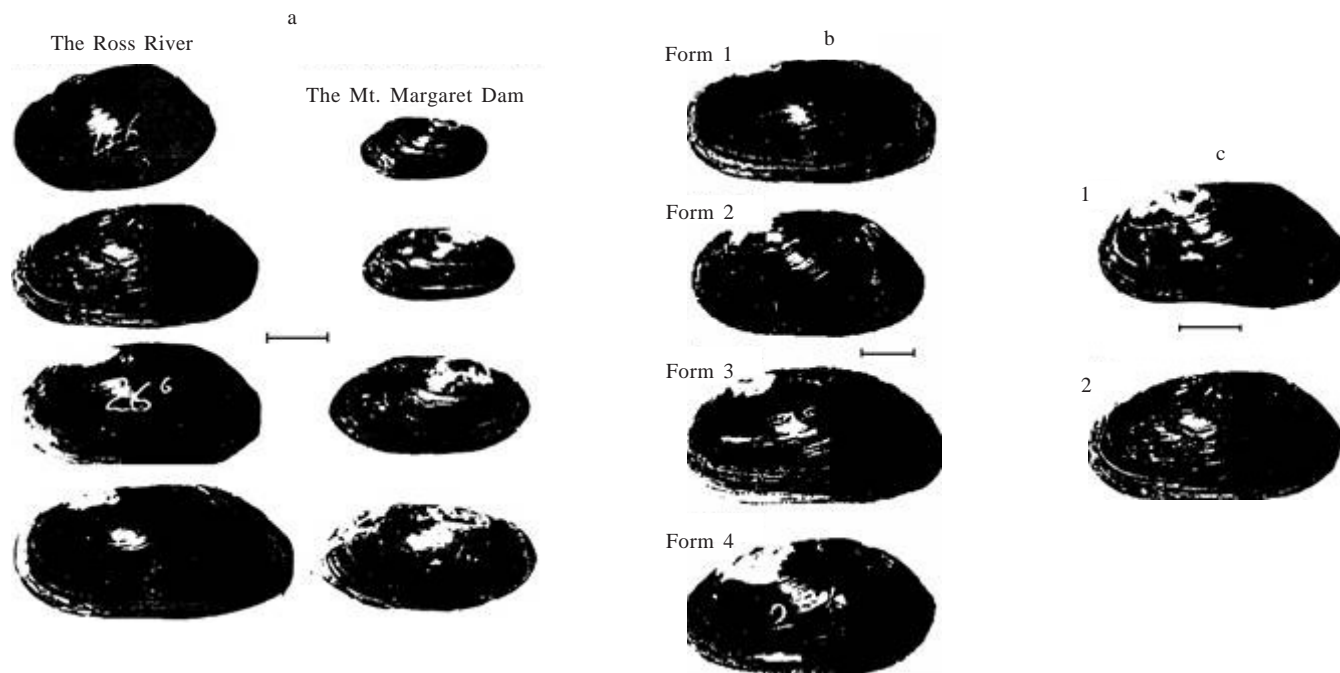


Figure 2. *Velesunio ambiguus*. (a) Some shells from the Ross River and the Mount Margaret Dam, (b) Four shell forms found in the Ross River, (c) Two types of shell abnormality found in this study: 1. ventral margin deflection, 2. scars. (Scale bars = 20 mm).

The relationship between length and width of mussels was expressed in allometric regression equations showed in Table 3. Statistical analysis showed that sexual dimorphism was displayed by *V. ambiguus* ($p = 0.047$), with females being wider than males. This was also indicated by the steeper slopes of the regression equations derived for males, as opposed to females. However, it was difficult to visually distinguish males from females. A positive correlation was found between obesity and the length of shell (Figure 3a,b). As the shell size increased, the obesity also increased.

Among three microhabitats (solid mud and plant litter, soft silt, and combination of soft silt and sand), the obesity was not significantly different (Table 4).

Variation in Relative Height. The relative height (height/length) of shells for mussels from the Ross River varied between 42.6 and 63.8% in females and between 44.2 and 61.1% in males (Table 3). For mussels inhabiting the Mt. Margaret Dam (without considering the sexes), it varied between 47.7 and 54.6%.

Allometric regression equations describing the relationship between height and length are presented in Table 4. For the mussels from the Ross River, analysis of covariance showed that the slope was not significantly different, although the shells of males tended to have a steeper slope than those of females. Unlike obesity, a negative correlation was found between relative height and shell length: relative height tended to decline as the shell length increased (Figure 4a). Thus shell height increased less in relation to shell length, while shell width increased relatively more. Mussels from the

Table 3. Regression and correlation coefficient of the allometric equations describing the relationship between shell length and height and between shell length and width of adult mussels in the Ross River from three different micro-habitats. Equation is of the forms: $\ln L = a + b \ln H$; $\ln L = a + b \ln W$; where L = shell length (mm), H = maximum shell height (mm), and W = shell width (mm)

	a	b	r ²
Obesity			
Solid Mud + Plant Litter	2.415	0.604	0.47
Soft Silt	4.407	0.615	0.83
Soft Silt + Sand	1.814	0.790	0.95
Relative Height			
Solid Mud + Plant Litter	1.044	0.901	0.76
Soft Silt	1.100	0.887	0.81
Soft Silt + Sand	1.465	0.783	0.70

Table 4. Regression and correlation coefficient of the allometric equations describing the relationship between shell length and height and between shell length and width of adult mussels in the Ross River and in the Mt. Margaret Dam. Equation is of the forms: $\ln L = a + b \ln W$; $\ln L = a + b \ln H$; where L = shell length (mm) H = maximum shell height (mm) and W = shell width (mm)

		a	b	r ²
The Ross River				
Width	Male (n=322)	-2.525	1.322	0.7516
	Female (n=375)	-2.129	1.232	0.7336
Height	Male (n=322)	-0.510	0.739	0.6887
	Female (n=375)	-0.309	0.785	0.7479
	Combined	0.390	0.767	0.7230
The Mt. Margareth Dam (n= 48)				
Width		-2.881	1.397	0.8985
Height		-0.714	1.008	0.9398

Table 2. Morphometric data of *V. ambiguus* from the Ross River and Mt. Margaret Dam (this study)

	Length		Width		Height		Obesity		RH	
	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	
The Ross River										
Mean	89.2/90.6		30.4/30.8		46.1/46.9		34.0/33.9		51.8/51.9	
SD	7.84/8.29		4.13/4.12		3.72/4.03		2.63/2.59		2.67/2.52	
Minimum	63.4/61.7		19.0/19.1		35.0/32.8		27.6/24.9		44.2/42.6	
Maximum	107/111.4		40.4/42.0		58.4/62.0		42.1/47.2		61.1/63.8	
The Margareth Dam										
Mean	60.00		17.30		30.40		28.50		50.60	
SD	8.44		3.63		4.49		2.61		1.89	
Minimum	42.20		10.00		21.00		23.70		47.70	
Maximum	77.00		24.30		38.80		35.00		54.60	

M: male, F: female, RH: relative height

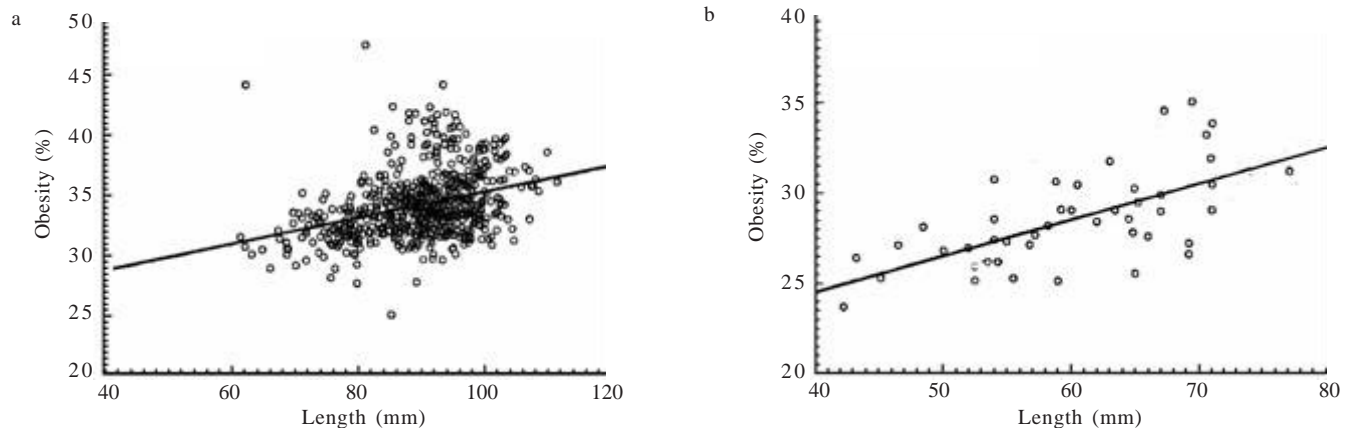


Figure 3. Relationship between obesity and shell length of mussels from: a. the Ross River; b. the Mt. Margaret Dam.

Mt. Margaret Dam showed that there was no correlation between the relative height and shell length (Figure 4b).

Among the three microhabitats (solid mud and plant litter, soft silt, and combination of soft silt and sand), relative height was not statistically significantly different (Table 3).

Latitudinal Variation in Shell Morphology. A comparison was made between *V. ambiguus* found at different latitudes (temperate regions) as recorded by McMichael and Hiscock (1958) and Walker (1981b) (Table 5). This shows that the relative height and obesity of mussels from the temperate parts of Australia were higher than those from the tropical region.

Abnormality in Shell Form. Few abnormal shells of *V. ambiguus* were found. Abnormalities usually appeared only as external deformations (Figure 2c), such as: (i) a light

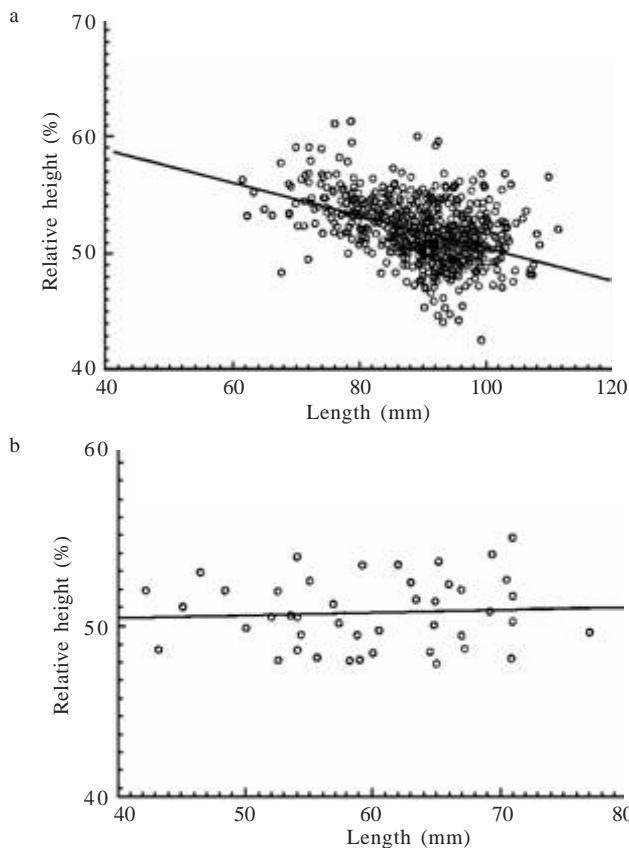


Figure 4. Relationship between relative height and shell length of mussels from a. the Ross River b. the Mt. Margaret Dam.

Table 5. Morphometric of *V. ambiguus* recorded from tropical (this study) and from temperate regions (previous studies)

	Length (mm)	Height (mm)	Width (mm)	Relative height (%)	Obesity (%)
Ross River ^T (n=702)	89.96	46.56	30.58	51.85	33.91
Aramac River ^M (n=50)	77.00	41.00	25.00	53.00	32.50
Condomine River Warwick ^M (n=126)	76.00	48.00	35.00	63.00	46.00
Murray River ^M (n=74)	73.00	46.00	30.00	64.00	41.10
Murray River ^W (n=904)	-	-	32.84	65.68	-

^T: from this study, ^M: from McMichael and Hiscock (1958), ^W: from Walker (1981b)

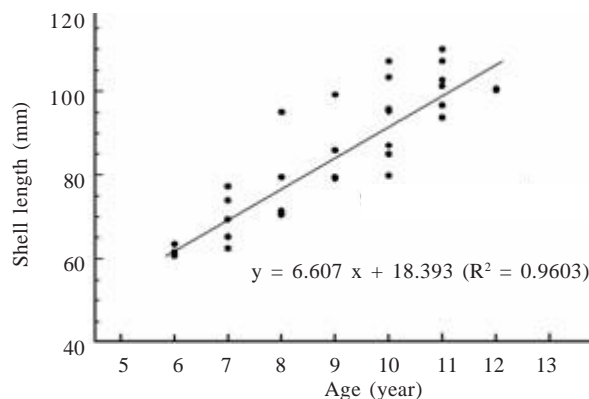


Figure 5. Age distribution among 35 selected mussels based on thin section of their shells.

deflection on the ventral margin, (ii) scars on the surface of the shells. Small irregular abscesses occasionally were found in the nacre layer.

The Age of the Mussels. Examination of the outer growth line showed that, usually, the first three lines were easily recognised. Afterward, the lines were very difficult to discern since the line increment was so small and the valves become darker and thicker with increasing age of the mussel. Based on thin sections, seven age classes were found ranging between 6 and 12 years. Figure 5 shows the plot between age and shell length ($Y = 6.607X + 18.393$; $R^2 = 0.96$). From this figure it is estimated that the lifespan of the mussel in the Ross River is about 15 years.

DISCUSSION

The weirs along the Ross River have changed the river system from a flowing river to a relatively calm river. However, it is notable that four types of shell form of *V. ambiguus* were recognisable in the Ross River during this study. These forms are different to those of *V. ambiguus* studied by Walker (1981b) in the Murray River in southeastern Australia. Walker only found the third form that he called the ‘billabong form’. This form is typical of mussels inhabiting shallow and swampy environments, and is scarcely found in the river channel or in billabongs prone to frequent flushing. The billabong form is also found in another Australian tropical species of hyriid, *Velesunio angasi*, from Magela Creek, Northern Territory (Humphrey 1984).

Humphrey (1984) recognised two different forms *V. angasi* based on the posterior outline of the shell. The first form of was called the ‘billabong form’ that is similar to the first form in this study. The second form the so-called ‘creek form’, matches the second form in this study. Humphrey (1984) found this form in the rooted mats of aquatic or bank side vegetation, or amongst the roots of *Pandanus*. In fact, some mussels of the Ross River inhabit a similar microhabitat, i.e., rooted and sandy creek bed.

Walker (1981b) and Humphrey (1984) found that both *Alathyria jacksoni* and *V. angasi* extended a blade or ‘wing’ backwards. According to Eagar (1978), such characteristics give a functional advantage in providing active movement

over the surface of the substrate. Unlike those two species, *V. ambiguus* does not have the non-winged form, which is the arcuate form with a curved dorsal margin and reflected ventral margin. This form is characteristic of mussels living in unstable environments, such as shifting sediments caused by flowing waters during wet months. Eagar (1977, 1978) proposed that such a form allows stronger anchorage and resistance to displacement by strong water currents in unstable substrates. Since *V. ambiguus* lives in environments that are relatively stable, it is therefore easy to understand why there is no non-winged form found among this species.

Some mussels from Ross River-form display the characters of a flowing-water species, although without the arcuate form of the curved dorsal margin (Figure 3a). As a still-water species, the existence of this form, but with wing development, raises an interesting question. How can this form occur in relatively still water? The Ross River has been a still water for about sixty years since the construction of the weirs, and the age of the mussel population in that study area is not older than 12 years. These facts rule out the possibility that the form is the reflection of more turbulent past. Examination of thin sections of the shell showed that the answer might be in the topography of the land next to the collection site. During the wet season, the run-off water flows into the river from the riverbank that has a slope of approximately 30 degrees. Presumably, the reflection of the ventral margin is a response of mussels to prevent them from being swept away to deeper water.

Variation in unionacean shells is also influenced by ontogeny. With age, their morphological features change, including obesity and relative height. Obesity and relative height may either increase or decrease, as mussels grow older (e.g., Eagar 1948; Humphrey 1984). From this study, the relationship between shell length and width, and between shell length and height were very obvious. As the shell length increased with age, the obesity increased and the relative height decreased. Humphrey (1984) found the same results for *V. angasi*. For stream-forms, such as *A. jacksoni*, McMichael and Hiscock (1958) and Walker (1981b) reported that as the mussels get older, relative shell height usually decreases progressively because of the development of dorsal arching of the shell. In terms of obesity, the finding of the present study confirmed the observations of Ortman (1920) and Ball (1922) who reported that younger mussels were usually less obese than the older mussels, but they are contrary to the findings of Crowley (1957).

One factor that determines shell morphology is the substrate type where the mussels live. Mussels inhabiting sandy habitats are generally more compressed than those in muddy habitats. In addition, the former, usually have thicker and bigger shells than the latter (Hinch *et al.* 1986; Bailey & Green 1988). The benefit of having big, thick and compressed shells in sandy habitats which are usually unstable and shifted easily by strong currents is to presumably enable the mussels to orientate themselves and to bury deeper and form more supportive furrow paths, by-which they can withstand dislodgment by water currents (Clarke 1973, 1979; Ghent *et al.* 1978; Stern 1983; Hinch *et al.* 1986). By having thinner, small and obese shells, mussels living in a softer and muddier

substrate may obtain an advantage, because this will increase their buoyancy and, eventually, will prevent them from sinking and asphyxiating (Tevesz & McCall 1979; Hinch *et al.* 1986). In addition, Tevesz and McCall (1979) suggested that inflated shells enable the mussels to retain enough water between the valves that, in turn, will be used to flush away silt from covering the siphon area. Results from this study, however, showed no significant differences among the shell forms from three different habitats. This may be due to silt forming part of all habitats considered in this study.

Regarding sexual dimorphism in the shell shape of *V. ambiguus*, statistical analysis showed that the differences between sexes were significant. McMichael and Hiscock (1958) and Walker (1981b) recorded no differences between males and females in *V. ambiguus* inhabiting the Murray River. Likewise, Humphrey (1984) found the same results as this study for *V. angasi*; and similar results were found by Heard (1975). According to Humphrey (1984) ecophenotypic variations in shell form tend to conceal sexual dimorphism among unionaceans. Nevertheless, among lamsiline unionids (such as *Lampsilis*), differences between males and females are conspicuous visually and statistically (Ball 1922; Kat 1983a). Invariably, females are more obese, higher and have thicker shells, with the thickness being most pronounced in their marsupial regions. This must be an adaptation that allows the mussels to bear large numbers of larvae in their outer marsupial gills and it may also provide protection from wave and/or stream currents.

It has been noted that *V. ambiguus* is the most widespread species of Australian freshwater mussels. Therefore, it is interesting to examine their variation along latitudinal lines. McMichael and Hiscock (1958), Cvancara (1963), Clarke (1973) detected that the latitudinal variations among unionaceans were apparent. McMichael and Hiscock (1958) found that the ratio between beak length (the anterior end to beak) and total length of *V. ambiguus* tends to decrease in higher latitudes. Cvancara (1963) observed that obesity and relative height of *Lampsilis* in North America increased toward lower latitudes. Clarke (1973) observed that unionids in northern Canada were often more compressed than their counterparts in southern regions. This study shows also that obesity and relative height change with increasing latitude (Table 4). They tend to have higher obesity and relative height in the southern than in the northern parts of Australia. However, this may be because the increase in shell length of the mussels from the southern parts is relatively slower than those from the north. It is possible that the temperature differences are the main cause of this cline. Harman (1970) found that within the same general habitats, unionids living in warm waters often grow faster and attain larger sizes than those living in cold waters.

Abnormalities among velesunionids are very rare, as found by Walker (1981b). However, presumably because of different habitats, abnormalities (expressed as deformations) in the shells of mussels found in the Ross River were different to those found by Walker in the Murray River. Walker, quoting Coker *et al.* (1921) suggested several possible causes including turbulent water, parasites and mechanical injury at the outer edge of the mantle.

Shells from the Mt. Margaret Dam were thinner than those from the Ross River. McMichael (1952) and Clarke (1973) suggested that the calcium or lime content in the water is correlated with shell thickness. They found that mussels inhabiting water with a low level of calcium content developed thinner and lighter shells. In addition, the shell of mussels from the Mt. Margaret Dam had more conspicuous (thicker) cessation growth lines than their counterparts from the Ross River that making it easier to determine their age. It is important to bear in mind that the Mt. Margaret Dam is a temporary dam that is empty during the dry season and full of water during the wet season. McMichael (1952), dealing with river and creek mussels, suggested that during severe drought, mussels might become dormant and bury deeply into the mud. During this period, the mussels reduce or totally stop growth of the shell altogether, resulting in edge thickening. When the wet season comes, the dormant mussels emerge from the mud and grow quickly. This makes the lines that mark the dormant period very obvious. The same scenario may happen with mussels living in the Mt. Margaret Dam.

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